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The translocation of white rhino (Ceratotherium simum) to the Okavango Delta, Botswana

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The translocation of white rhino (*Ceratotherium simum*) to the Okavango Delta, Botswana

Caroline Rees

A dissertation submitted to the University of Bristol in accordance with the
requirements of the degree of Doctor of Philosophy in the Faculty of Science
School of Biological Sciences

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30,722 words

Abstract

Poaching and the illegal wildlife trade results in conservation managers considering alternative approaches to preserve wildlife populations. Translocation could be used as a mitigation strategy when protected areas struggle to maintain large animal populations. My research was instigated by the ‘Rhinos without Borders’ organisation which translocated six white rhino (*Ceratotherium simum*) from a high-risk poaching reserve in southern Africa to the relative safety of the Okavango Delta in Botswana. Data were collected over a 29 month period. The aim of rhino conservation in Botswana is to establish a gene depositary for the future survival of the species.

For successful translocations it is important to examine the behaviour of animals, so the main aim of this thesis was to investigate how the rhino adapted to translocation. Most translocations involving large herbivores involve small numbers of individuals. Generally short-term translocation success rates are poor and are affected by mortality during the translocation process or after release, large dispersal distances - sometimes leaving the release area entirely, or rejection of resources at the release site.

Acclimating wild rhino established stable hierarchy, but the results highlighted the requirement for a better understanding of captive rhino social groups, and social pressure within a contained environment. Rhino formed paired companionships during the acclimation period in the boma, and cohorts were sustained after initial release into the Okavango Delta. Rhino had extensive ranges compared to reserves with high populations, and despite acclimation they dispersed over large distances. Forcibly moving rhino from certain areas did not stop them from returning, and was therefore an ineffective method of control. Rhino employed a varied mixed movement strategy at the landscape scale. Grassland was a key habitat for rhino and was related to availability. Rhino made selections based on high intake rate to maximise energy. Annual diet mainly comprised tufted caespitose and stoloniferous high and average quality swards.

My results illustrate the importance of understanding how the translocation process affects wild animals, and how they adapt to new environments.

Dedication

For my parents

Thank you for your love and support in helping me follow my dreams.

Diolch am popeth.

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Lastly, I would like to thank my family: mum and dad, Mike and Jemma for supporting me on this epic journey.

Author’s declaration

I declare that the work in this dissertation was carried out in accordance with the requirements of the University's *Regulations and Code of Practice for Research Degree Programmes* and that it has not been submitted for any other academic award. Except where indicated by specific reference in the text, the work is the candidate's own work. Work done in collaboration with, or with the assistance of, others, is indicated as such. Any views expressed in the dissertation are those of the author.

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Chapter 1. General Introduction

1.1 Foreword

Preserving wildlife benefits human society, increases the intrinsic value of the species, and improves ecosystems functions (Wei *et al.*, 2018). However, the increasing human impact upon wildlife populations has led to declining numbers and extinctions (Dirzo *et al.*, 2014). Protected areas that are needed to support wildlife are small and spatially discontinuous (Saunders *et al.*, 1991). Fragmented populations may suffer with severe losses in genetic variation (Goossens *et al.*, 2016; Moodley *et al.*, 2017; Leroy *et al.*, 2018), but extirpations and habitat biodiversity losses also have cascading effects on ecosystem functions and services (Saunders *et al.*, 1991; Lindenmayer & Fischer, 2008; Dirzo *et al.*, 2014).

The relocation of wildlife can be used to restore ecological processes (Fritts *et al.*, 1997; Krausman, 2000; Tuberville *et al.*, 2005), to supplement existing populations, or to reintroduce organisms within or outside their indigenous ranges, primarily to avoid extinction (Seddon, 2010; Corlett, 2016; Towns *et al.*, 2016). In the current poaching climate (Emslie, 2013), and in the absence of adequate law enforcement and poor governance (Maisels *et al.*, 2013), it is likely that an increased number of wildlife will be moved to safer locations. However, there are also risks associated with interventions (Corlett, 2016). Risks in the target ecosystem include the alteration of ecosystem functions and processes, the disruption of ecological interactions, and the spread of parasites and diseases (Ricciardi & Simberloff, 2009). Activities associated with the deliberate movement of animals such as capture, handling, captivity, transportation, and release into a novel site all increase the risk of mortality (Dickens *et al.*, 2010).

Translocation has limited success rates, at around 23% (Griffith *et al.*, 1989; Fischer & Lindenmayer, 2000; Seddon *et al.*, 2014; Houde *et al.*, 2015).

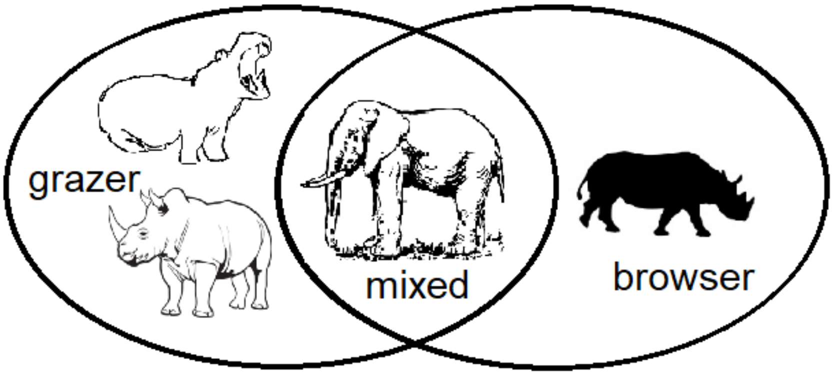
Translocation generally failed where animals were moved due to human-wildlife conflict issues (Fischer & Lindenmayer, 2000). Translocation for conservation success rates may be improved by selecting a large number of founder individuals (Fischer & Lindenmayer, 2000) before the population is in decline or has a low population density (Griffith *et al.*, 1989), along with applying an optimal population selection strategy by choosing individuals with high fitness, and high genetic variation, so that individuals may respond to selection pressures (Houde *et al.*, 2015). However, habitat quality at the release site was found to be a key determinant of translocation success (Griffith *et al.*, 1989; Fischer & Lindenmayer, 2000; Seddon *et al.*, 2014). Post-release monitoring and research is therefore essential, so that release location factors limiting reintroduction success are identified and the risks associated with reintroductions are reduced (Armstrong & Perrott, 2000; Bar-David *et al.*, 2005; Varley & Boyce, 2006; Seddon *et al.*, 2007; Taylor *et al.*, 2017; Drummond *et al.*, 2018).

1.2 Megafauna

Some mammals have evolved to be very large (megafauna) when compared to members of other vertebrate classes (Sinclair, 2003; Malhi *et al.*, 2016). For example, large carnivores include the lion (*Panthera leo*), leopard (*Panthera pardus*) and grey wolf (*Canis lupus*) (Ripple *et al.*, 2014), and large herbivores are represented by the elephants (*Loxodonta africana* and *Elephas maximus*), and hippopotamus (*Hippopotamus amphibious*) (Ripple *et al.*, 2015). Megaherbivore populations (in this research terrestrial herbivores ≥ 1000 kg) (Owen-Smith, 1987) are generally resource-limited (Hairston *et al.*, 1960; Hopcraft *et al.*, 2010; Malhi *et al.*, 2016). Megaherbivores have a disproportionately large impact upon the structure of habitats relative to their abundance (Paine, 1969; Power *et al.*, 1996; Gill, 2014; Malhi *et al.*, 2016), affecting ecosystem processes and the diversity of communities (Sinclair, 2003). These taxa are therefore known as keystone species (Gill, 2014).

The digestive physiology and nutritional ecology of megaherbivores differs to smaller herbivores because megaherbivores have longer gut retention times and can therefore tolerate lower quality food. Compared to small herbivores large herbivores have lower energetic needs (Demment & Van Soest, 1985; Arsenault & Owen-Smith, 2002; Clauss *et al.*, 2003). Megaherbivore mouth morphology also influences forage efficiency (Pretorius *et al.*, 2016). Leaves generally contain less fibrous material and are therefore of higher nutritional quality compared to plant stems (Demment & Van Soest, 1985). Large herbivores may then be subjected to lower bite quality and digestibility since the fraction of good quality leaf biomass is offset by lower quality fibrous material (Shipley & Spalinger, 1995; Niklas, 2004; Pretorius *et al.*, 2016). To conteract this some large herbivores are able to utilise their enlarged soft mouthparts to select soft plant parts, however this is not the case for megaherbivores where there is a negative relationship between volume of digestible material consumed to body mass (Pretorius *et al.*, 2016). Megaherbivores counteract this by bulk feeding (Shrader *et al.,* 2006a). Futhermore, to offset periods of nutrient deficiency (Owen-Smith *et al.*, 2010), megaherbivores modify their diet, migrate to more profitable sites, consume larger quantities, increase intake-rates (Beekman & Prins, 1989), or mobilise fat reserves (Demment & Van Soest, 1985; Gerhart *et al.*, 1996).

Figure 1.1. African species of megaherbivores with body mass ≥1000 kg. The hippopotamus (Hippopotamus amphibious*) and white rhino* (Ceratotherium simum) *are grazers, the black rhino* (Diceros bicornis) *is a browser and the African elephant* (Loxodonta africana*) is a mixed feeder* (Owen-smith, 1992; Van Soest, 1994; Bonyongo & Harris, 2007).



The digestive system between herbivore species differs; they can be ruminant (multi-chambered stomach) or non-ruminant (single compartment stomach) (Clauss *et al.*, 2003). African megaherbivores are non-ruminants that differ in their diet selection. The hippopotamus and white rhino (*Ceratotherium simum*) are both classified as grazers, the black rhino (*Diceros bicornis*) utilises its prehensile lip to browse and the African elephant is a mixed feeder (Owen-Smith, 1992; Van Soest, 1994) (Figure 1.1).

Being larger animals, megaherbivores travel further than smaller herbivores and thereby distribute nutrients and seeds over larger scales (Guimarães *et al.*, 2008; Doughty *et al.*, 2013; Gill, 2014). Large bodied herbivores trample on plants and open up areas that benefit smaller animals (Malhi *et al.*, 2016). However, trends in global declines show that megaherbivores are more at risk of extinction than large carnivores (Di Marco *et al.*, 2014).

1.3 Body size and extinction risk

The intrinsic drivers of megafaunal extinctions are linked to biological life history traits associated with body size (McKinney, 1997; Fritz & Purvis, 2010), such as low fecundity rates, slow growth rates (Wallach *et al.*, 2015; Ripple *et al.*, 2016) and the need for large home ranges (Galetti & Dirzo, 2013; Ripple *et al.*, 2016). Extrinsic direct drivers include persecution through hunting, poaching (Galetti & Dirzo, 2013; Darimont *et al.*, 2015) as a result of the economic value of body parts (Ripple *et al.*, 2015), and threats from invasive species, with extrinsic indirect drivers of extinction comprising habitat loss and fragmentation (Galetti & Dirzo, 2013). A combination of extrinsic factors and intrinsic traits results in a larger extinction risk for bigger species compared to smaller ones (Cardillo *et al.*, 2005; Galetti & Dirzo, 2013). The loss of these large species, otherwise known as ‘defaunation’ (Dirzo *et al.*, 2014), occurs at different spatial scales, across different timescales, and affects behavioural, physiological, ecological, and evolutionary processes (Galetti & Dirzo, 2013).

1.4 Drivers and consequences of Quaternary mass extinctions

It is difficult to evaluate the ecological repercussions of the removal of present-day apex consumers (trophic downgrading), because consequences may not become apparent until after the fact. However, previous extirpations of megafauna in the late Quaternary period may provide some answers (Estes *et al.*, 2011). Late Quaternary extinctions occurred on a global scale (Hansen & Galetti, 2009; Gill, 2014), but were concentrated in the Americas and Australia (Doughty *et al.*, 2013).

There has been much deliberation of the cause of Quaternary mass extinctions: possible causes include extra terrestrial impact (Firestone *et al.*, 2007), human effects (Gill *et al.*, 2009; Johnson, 2009; McGlone, 2012; Sandom *et al.*, 2014), and climate change (Owen-Smith, 1987; Barnosky, 2008; Nogués-Bravo *et al.*, 2010; Prescott *et al.*, 2012), with the combined effect of humans and climate altering vegetation (Villavicencio *et al.*, 2015). However, the global extinction pattern was found to correlate with the geography of human population spread and growth (Sandom *et al.*, 2014).

After the Quaternary mass extinctions, there was a succession of changes to the vegetation structure over a few thousand years (Rule *et al.*, 2012). Fossil and dung fungi records from the late Quaternary period provided evidence of the cascading effects caused by megafaunal extinctions (Gill *et al.*, 2013; Gill, 2014; Johnson *et al.*, 2015). Nutrients were widely dispersed before the mass extinctions, but after the loss of megafauna the lateral transfer of nutrients became localised (Doughty *et al.*, 2013). Likewise, seed dispersal distances were reduced and more clumped, probably causing a reduction in long distance gene flow (Jordano *et al.*, 2007; Guimarães *et al.*, 2008; Hansen & Galetti, 2009). Plant communities were affected by the loss of species and habitat diversity. The demise of mosaic woody habitats and open spaces (Johnson, 2009) led to a rise in vegetation biomass and an increase in major fires (Gill *et al.*, 2009; Johnson, 2009; McGlone, 2012). Defaunation altered ecosystem processes and functions, causing a knock-on effect for sympatric species and leading to cascades of extinction (Johnson, 2009; Rule *et al.*, 2012; Malhi *et al.*, 2016).

1.5 Extant megafauna at risk

Table 1.1. Extant herbivore species at risk with body mass ≥1000 kg. Species assessed as Critically Endangered (CR) face an extremely high risk of extinction in the wild, Endangered (EN) face a very high risk of extinction in the wild and Vulnerable (VU) face a high risk of extinction in the wild. Collectively they are referred to as "threatened" species: Near Threatened (NT) describes a species close to qualifying for, or is likely to qualify for, a threatened category in the near future (IUCN, 2018).

Family and Common name	Species name	IUCN Status	Estimated population	Population trend
Elephantidae				
African elephant	Loxodonta africana	VU		
Asian elephant	Elephas maximus	EN		
Hippopotamidae				
Hippopotamus	Hippopotamus amphibious	VU		
Rhinocerotidae				
Southern white rhinoceros	Ceratotherium simum spp. simum	NT	19,666-21,085	↑
Northern white rhinoceros	Ceratotherium simum spp. cottoni	CR	2	↓
Indian rhinoceros	Rhinoceros unicornis	VU	2575	↑
Javan rhinoceros	Rhinoceros sondaicus	CR	46-66	Unknown
Sumatran rhinoceros	Dicerorhinus sumatrensis	CR	220-275	↓
Black rhinoceros	Diceros bicornis	CR	5,040-5,458	↑

Many of the megafauna currently at risk are flagship species that are mostly found in the developing countries of southeast Asia and sub-Saharan Africa (Ripple *et al.*, 2016). However, Africa has lost half of its large-mammal population over the last 40 years (Craigie *et al.*, 2010). Current megaherbivores at risk include Elephantidae, Hippopotamidae and Rhinocerotidae (Table 1.1), all of which are classified as threatened or likely to be classified as threatened in the near future (IUCN, 2018).

1.5.1 Rhinocerotidae

The family Rhinocerotidae consist of five extant species the white (*Ceratotherium simum*) and black rhino (*Diceros bicornis*) located in Africa and the Indian (*Rhinoceros unicornis*), Javan (*Rhinoceros sondaicus*), and Sumatran rhino (*Dicerorhinus sumatrensis*) located in Asia (Table 1.1). Black rhino occur in a range of habitats including deserts, savannahs, forests and shrubland habitats.

As browsers, black rhino use their hooked lips to select small *Acacia* as well as palatable herbs and succulents (IUCN, 2018). The Indian rhino resides in riverine grasslands (Foose *et al.,* 1997) and has a diet consisting mainly grasses, with some fruit, leaves, shrub and tree branches, and cultivated crops (Nowak & Walker, 1999). Javan rhino occupy lowland tropical rainforests close to water but it is likely that they utilise other habitats as well. There are limited data available since the population is so small (Schenkel & Schenkel-Hulliger, 1969). The Sumatran rhino is a reclusive species mainly being found in tropical rainforests and montane moss forests. They are dependent upon salt licks and are usually located in hilly areas near to water sources (Nowak & Walker, 1999)

Two subspecies of white rhino, the northern (*Ceratotherium simum cottoni*) and southern (*Ceratotherium simum simum*) white rhinos are distributed discontinuously across Africa. As well as populating different areas of Africa (Cave, 1962; IUCN, 2018) white rhino subspecies differ anatomically and physiologically (Groves *et al.*, 2010). For example, southern whites are larger, have different shaped skulls and have more body hair compared to the smaller northern white rhino. The northern white rhino dorsal profile is straighter, but southern white rhino have a more concave shape behind the shoulder (Cave, 1962; Groves *et al.*, 2010). The southern white rhino, which I will refer to as white rhino hereafter, is the more abundant of the two subspecies (Table 1.1) (Emslie, 2012). Males tend to be heavier than females at around 2300kg compared to 1600kg. As the largest of its species, the white rhino uses its wide lips and low slung head to crop swards that form patches of short grasses known as grazing lawns (Owen-Smith, 1992) (Figure 1.2). White rhino select tropical and subtropical grasslands, shrublands and savannah habitats (IUCN, 2018). Females reproduce every two to three years, reaching sexual maturity at around seven years of age. Males reach maturity at between 10 and 12 years of age (Shrader & Owen-Smith, 2002). Mature males are solitary with mature females and other social classes being generally more social (Van Gyseghem, 1984).

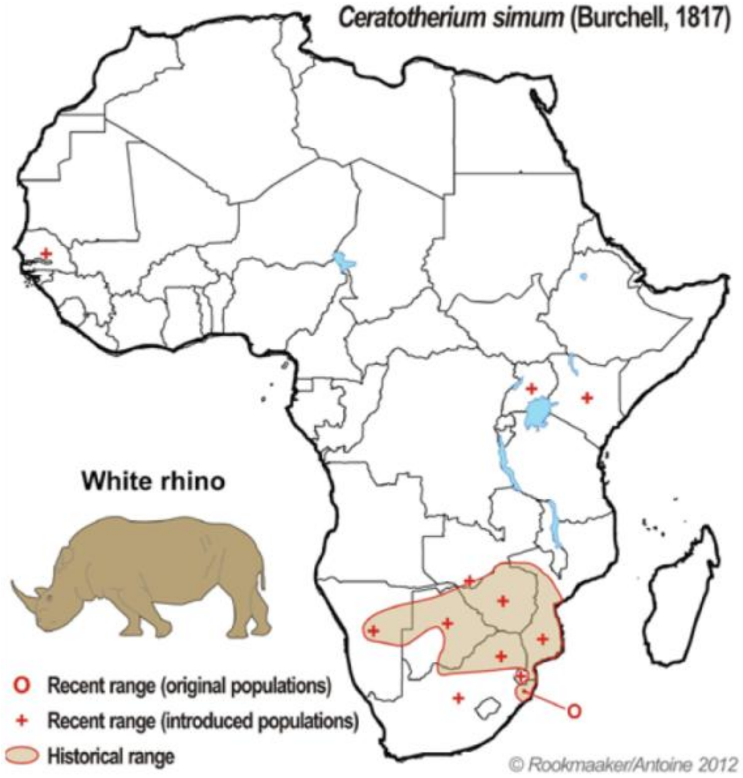
*Figure 1.2 Southern white rhino (*Ceratotherium simum*) photographed grazing in the Okavango Delta, Botswana. The rhino facing the camera is a female and the larger rhino facing left is a male.*

Scent marking and dung scraping is carried out by territorial males, although all rhino contribute to dung heaps (middens) scattered throughout ranges (Owen-Smith 1974; Rachlow *et al.*, 1999). Calves may be predated by lions but it is likely that larger individuals and fully grown adults are able to defend against such attacks (Shrader & Owen-Smith, 2002).

1.5.2 Rhino crisis

Rhino populations are in crisis globally because their horn is viewed as a lucrative commodity. Rhino horn has been harvested for two main reasons: for ornamental use and for it has been used in Chinese traditional medicine as a supposed cure for a variety of illnesses (Nowell, 2010; Emslie, 2012; Biggs *et al.*, 2013). However, rapid economic growth in east and southeast Asia is thought to have fuelled recent demand for rhino horn boosting the black market price and leading to a rise in poaching activities (Biggs *et al.*, 2013; Emslie, 2012; Emslie, 2013). Poaching in southern Africa in the last decade (Emslie, 2013; Hübschle, 2017) has increased the urgency of mitigation strategies because population estimates showed that rhino numbers were declining (Milliken *et al.,* 2009; Ferreira *et al.*, 2015), and this has been a key motivation for relocating animals to safer regions (Støen *et al.*, 2009).

*Figure 1.3. Current and historic ranges of the southern white rhino (*Ceratotherium simum simum*). The KwaZulu-Natal region of South Africa provided remaining refuge for populations in the early 20th century from which animals selected for conservation translocation were derived (Rookmaaker & Antoine, 2012).*



White rhino previously occupied Botswana, Namibia, South Africa, Swaziland, Zambia and Zimbabwe, but by the late 19th century due to relentless hunting, poaching and loss of habitat these ranges had contracted until they were localised in the KwaZulu-Natal coastal region of South Africa (Figure 1.3) (Amin, 2006; Rookmaaker & Antoine, 2012; Hübschle, 2017). Development of translocation procedures in the 1960s (Player, 1967) enabled individuals from this last remaining stronghold of *c.* 20 to 50 animals to be reintroduced to historic ranges, while others were introduced to areas outside of former ranges (Emslie & Brooks, 1999; Amin, 2006; Emslie, 2011, 2012). With the aid of formal protection rhino numbers recovered (Amin, 2006). However, in the 21st century the rhino is again under threat as a result of its highly prized horn.

1.6 Rhino in Botswana

My research was instigated by the 'Rhinos without Borders' organisation in 2013. The project was set up to relocate rhino from densely populated high-risk poaching reserves in southern Africa to the relative safety of the Okavango Delta in Botswana, a country that in recent years has invested a lot of resources towards the conservation of megafauna (Lindsey *et al.*, 2017). The aims of the project were: (1) to reduce the risk of poaching by relocating individuals to a vast protected landscape, (2) to increase the genetic diversity of the local population, and (3) to improve the population growth rate. Rhino in Botswana were extirpated by poaching in the 19th century (Emslie & Brooks, 1999), but now have full protection under the Wildlife Conservation and National Parks Act, 1992 (Department of Environmental Affairs, 2008). Along with a commitment to wildlife security, the Okavango Delta was designated as a wetland of international importance, demonstrating a commitment to preserve the habitat (https://www.ramsar.org/wetland/botswana, Wolski *et al.*, 2005). However, gaps in herbivore assemblage have been identified in the Okavango Delta, in particular of those over 1000kg. In fact the explosion of the elephant population in Botswana and across Africa may be due to the lack of competition from other large herbivores, so bringing rhino back to the delta may help rebalance the ecosystem (Bonyongo & Harris, 2007).

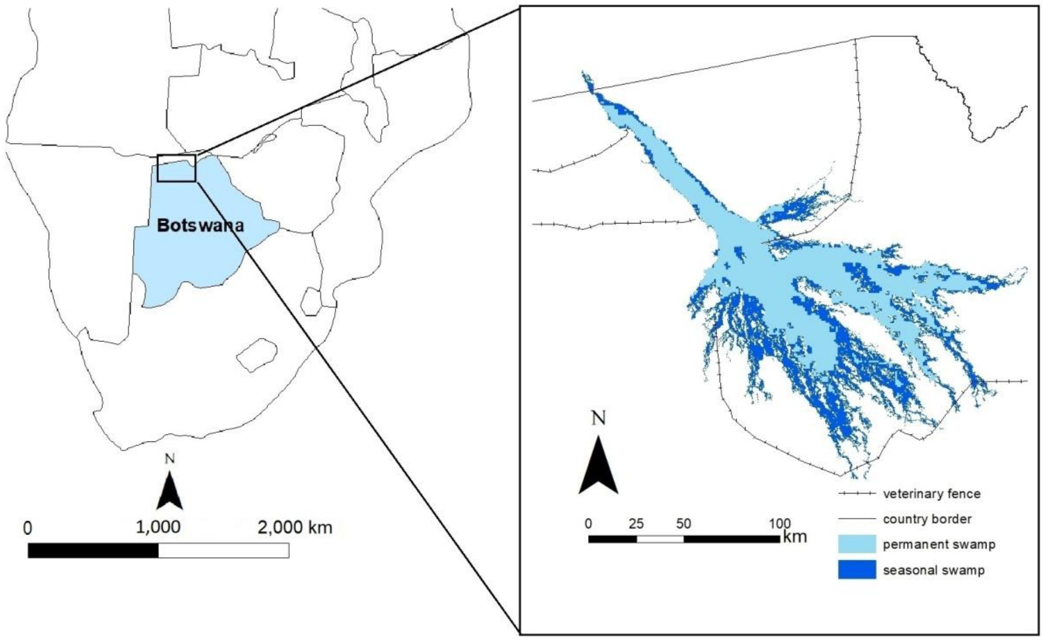
Africa is the only continent with most lateral nutrient dispersal systems still operating (Doughty *et al.*, 2013), where large herbivores make a disproportionately large contribution to nutrient transfer in dung or flesh (Doughty *et al.*, 2013; Wolf *et al.*, 2013). Large herbivores affect consumers through food webs (Estes *et al.*, 2011) and manage plant communities (Johnson, 2009). For example, the African elephant changes woodland to shrubland, improving spatial heterogeneity and enhancing browsing opportunities for impala (*Aepyceros melampus*) and other mixed feeders (Johnson, 2009; Haynes, 2012; Ripple *et al.*, 2015). The open vegetation improves the opportunity of predation success by mammalian carnivores attracted to the area due to the increased number of prey (Ripple *et al.*, 2015). Large carnivores in turn have top-down trophic cascade effects upon other species including richness and abundance, e.g. by providing carcasses for scavengers (Ripple *et al.*, 2014), increased carbon sequestration in plants by restricting numbers of herbivorous prey (Estes *et al.*, 2011; Tanentzap & Coomes, 2012; Ripple *et al.*, 2014), and controlling the spread of disease (Estes *et al.*, 2011; Ripple *et al.*, 2014). So it is likely that reintroducing rhino will help to restore ecological services and functions that other herbivore species and carnivores rely upon (Ripple *et al.*, 2015; Mauro *et al.*, 2018).

1.7 The study area

The Okavango Delta is located in semi-arid northern Botswana (Milzow *et al.*, 2010) between E 22.0° – E 24.0° and S 18.5° – S 20. 5° (Heinl *et al.*, 2006) and covers an area of roughly 40,000 km² (McCarthy *et al.*, 2012). This wetland ecosystem is fed by the Okavango River (Milzow *et al.*, 2010), which originates in the Angola highlands (Ramberg *et al.*, 2006). Rain falling in this catchment area is transported though Namibia and ends in the Okavango Delta, arriving between February and May (McCarthy *et al.*, 2003; Ramberg *et al.*, 2006). These waters spread into an alluvial fan because water is slowed by topographical fault lines (Hutchin *et al.*, 1976) and a shallow gradient (Ramberg *et al.*, 2006). The flood waters take some three to four months to travel from the Delta channel in the north-west to the lower (south-eastern) parts of the Delta (McCarthy *et al.*, 2003).

The Delta includes 2500 km² of permanent wetland and up to 8000 km² of seasonal floodplains (McCarthy, 2006) created by the influx of water from the Okavango River (Figure 1.4). Some of the most common large herbivore species found in the Okavango Delta in order of abundance are impala, buffalo (*Syncerus caffer*), red lechwe (*Kobus leche*), African elephant, zebra (*Equus quagga*), wildebeest (*Connochaetes taurinus*), giraffe (*Giraffa camelopardalis*), tsessebe (*Damaliscus lunatus*) and hippopotamus (*Hippopotamus amphibious*), along with carnivores such as African lion (*Panthera leo*), leopard (*Panthera* *pardus*), cheetah (*Acinonyx jubatus*), spotted hyaena (*Crocuta crocuta*) and African wild dog (*Lycaon pictus*) (Bonyongo, 2004; Ramberg *et al.*, 2006).

Figure 1.4. Location of the Okavango Delta, Botswana, including the boundaries of the two study areas, 1) in the peripheral region and 2) an area within the Moremi game reserve.



The majority of the study took place in the southern Okavango Delta in the peripheral region (Figure 1.4), which consisted of dry and seasonally flooded swamp areas with a small number of main river channels. Some data for grazing selectivity were collected in the central delta region of the Moremi game reserve. The size of the study area varied with the flood regime, and covered approximately 3000 to 5000 km². The southern parts of the Okavango were surrounded by a veterinary fence erected to manage the spread of disease, and protect Botswana's beef export market (Darkoh & Mbaiwa, 2009). There were access roads to tourist lodges and remote villages within the study area.

1.7.1 Seasons

Seasonal comparisons of data were carried out according to the following definitions:

i. The rainy season was generally limited to the hot months between November and February (Bartlam-Brooks *et al.*, 2013).
ii. The flood season occurred between March and June when floodwater was delivered from the upper Okavango basin and flowed into the lower regions. This timescale corresponded with colder temperatures and the absence of rain (Ramberg *et al.*, 2006; Bartlam-Brooks *et al.*, 2013).
iii. The hot dry season occurred when receding floodwaters coincided with higher temperatures between the dry months of July and August (Bartlam-Brooks *et al.*, 2013).

1.7.2 Habitat description

A LANDSAT image by S. Ringrose and T. Meyer at the Harry Oppenheimer Okavango Research Centre (HOORC) was used as a vegetation base map (Jellema *et al.*, 2002; Ringrose *et al.*, 2003) (Figure 1.5 and Table 1.2). Seven habitats were identified in the study area. These were dry floodplains, shrubbed grassland on a former floodplain, grassland with wild sage, swamp vegetation, riparian woodland, mopane woodland and *Acacia* woodland. Information on sward species found in each habitat class can be located in supplementary information Table S5.1.

Figure 1.5. Habitat classes for the study areas.

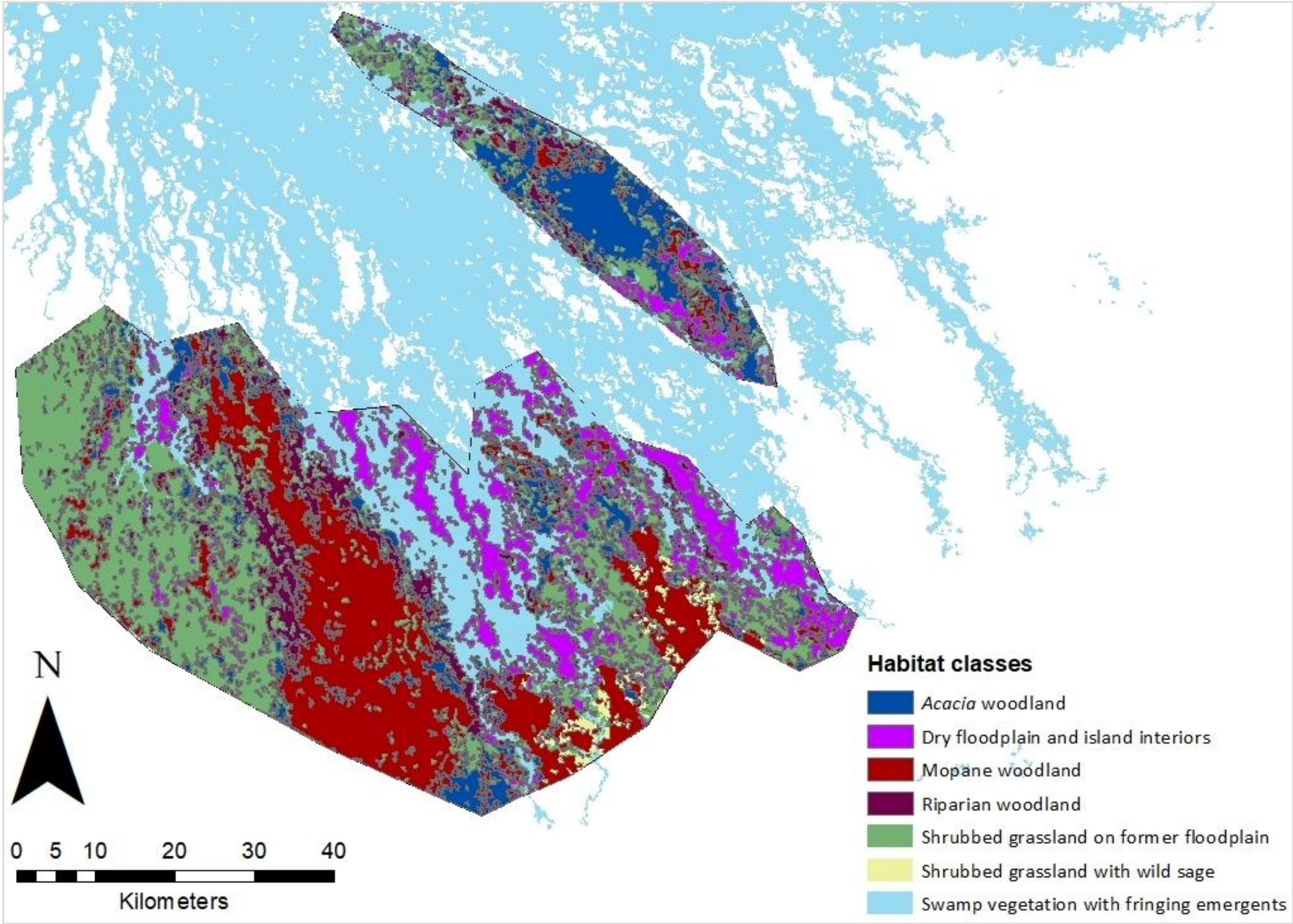


Table 1.2. Habitat classes from a georeferenced LANDSAT image by S. Ringrose and T. Meyer (HOORC). Photographs by author unless otherwise stated.

Habitat classes	**Description**
Dry floodplains 	Seasonally flooded grassland
Shrubbed grassland on former floodplain 	Predominantly *Cynodon dactylon* grasses with sporadic shrubs and trees
Grassland with wild sage 	Predominantly *Cynodon dactylon* grasses with sporadic *Pechuel-Loeschea leubnitziae* bushes
Swamp vegetation 	Permanently flooded vegetation
Riparian woodland 	Mixed tall woodland near watercourse or historical watercourse
Mopane woodland 	*Colophospermum mopane* with light undergrowth
Acacia woodland  (Bartlam-Brooks *et al.*, 2013)	Mixed *Acacia* woodland

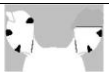
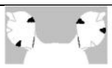
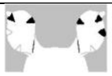
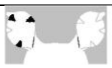
1.8 Project individuals

Figure 1.6. The pre-translocation process showing a) a partly sedated rhino being walked towards a transportation crate in the boma in KwaZulu-Natal, South Africa, and b) rhino loaded into individual crates and placed onto a flatbed truck for transportation by road to Botswana.


a) b)

In March 2013 the ‘Rhinos without Borders’ organisation translocated six white rhino to the study area from KwaZulu-Natal, South Africa (Figure 1.6). Three male subadults, two female subadults, and one pregnant adult, were transported approximately 1500 km by road to historical ranges in the Okavango Delta, Botswana (Emslie, 2011, 2012). F1 the female pregnant adult lost her horn during transportation when it broke off inside her crate (Figure 1.6b).

Table 1.3. Composition of rhino studied in Botswana between 07/04/2013 and 15/10/2015.

Rhino ID	Name	Sex	Estimated age (yrs) on arrival	Status	Ear notch identification
M1	Bruce	Male	Subadult - 6		
M2	Bertie	Male	Subadult - 5.5		
M3	Mikey	Male	Subadult - 5		
F1	Stumpy	Female	Adult - 6	Pregnant	
F2	Helen	Female	Subadult - 5.5		
F3	Jemma	Female	Subadult - 4		

At the age of between two and three years old rhino calves are chased away by their mothers in preparation for the birth of new offspring. From this period until rhino reach sexual maturity they are described as subadults. For females this is usually at around seven years of age, and for males between ten and twelve years when they settle within a territory as a subordinate or dominant adult (Shrader & Owen-Smith, 2002). All six rhino were identified via unique ear notches (Table 1.3).

1.9 Thesis rationale

Literature of the study of white rhino in-situ in relation to this thesis can be divided into two main categories: reintroduction (Boeer *et al.*, 1999; Pitlagano, 2007; Pedersen, 2009; Støen *et al.*, 2009; Patton *et al.,* 2016) and established population analysis (Pienaar, 1970; Owen-Smith, 1971, 1973, 1974, 1975; Rachlow *et al.*, 1999; Shrader & Owen-Smith, 2002; Shrader *et al.*, 2006a; White *et al.*, 2007; Waldram *et al.*, 2008; Cromsigt *et al.*, 2014; Jordaan, 2015). Of the reintroduction studies Boeer *et al.* (1999) observed pre-release behaviour and post-release short term movement behaviour of captive bred animals, Pitlagano (2007) described maximal distances travelled from the release site, range size and mortality rates, Pedersen (2009) detailed range analysis, landscape and dietary preferences, Støen *et al.* (2009) also analysed maximal distances travelled from the release site and range sizes while the focus of Patton *et al.* (2016) study was the development of social associations. Existing studies of established rhino populations are more varied and include analyses of dispersal, home ranges and territoriality, sociality, grazing, habitat and landscape selection, rhino effects on ecosystem functions.

There are various studies on social behaviour of zoo kept rhino (Schmidt & Sachser, 1997; Metrione *et al.*, 2007; Cinková & Bičík, 2013) and the associated reproduction issues (Schmidt & Sachser, 1997; Kuneš & Bičík, 2002; Carlstead & Brown, 2005; Hermes *et al.*, 2005; Swaisgood *et al.*, 2006; Tubbs *et al.*, 2016).

Translocated rhino are often kept individually in enclosures for acclimation before release and these are most commonly of solid pole construction (Emslie *et al.*, 2009). Therefore not much is known about how a small group of wild caught captive held rhino are affected by living collectively in close proximity in an electrified 'bonnox' boma (enclosure) (Reilly, 2005). Current data of wild rhino behaviour following translocation and reintroduction are limited. There therefore appears to be a requirement for a more rounded assessment.

I joined the Rhinos without Borders project during the acclimation period, so I was able to monitor the rhino in their boma in the Okavango Delta. Direct observation during acclimation, and GPS-enabled anklets enabled me to analyse rhino sociality before and after release. I also observed interaction behaviour so that I could compare this with captive-born and wild-caught rhino held in captivity, and after the release I investigated movements and resource selection across a range of spatial scales. Owing to unexpected dispersal patterns, the anti-poaching teams needed to move rhino to reduce the risk of them coming into contact with humans. They did this by herding the animals using vehicles or on foot. I used this as an opportunity to assess how successful herding was as a means to control dispersal. My research differs to previous analyses because it encompasses a wider range of topics, and uses methods of data analysis previously unexploited for analysing white rhino behaviour.

1.10 Thesis plan

In chapter two I examine the behaviour of captive held wild rhino, their sociality and responses to herding as a viable security method. Keeping rhino in zoo environments leads to increased competition for food and agonistic behaviour. The demographics of these small herds tend to be weighted towards females since adult male rhino compete for territories and mates (Schmidt & Sachser, 1997; Metrione *et al.*, 2007; Cinková & Bičík, 2013). Therefore not much is known about the behaviour of a small mixed herd, in particular of wild caught animals. Subadult wild rhino often assemble in pairs or small groups (Owen-Smith, 1974; Waldram *et al.*, 2007), so companionships formed within the acclimation period may influence cohort choices after release. After their release, for their protection, the project animals needed to be herded from unsafe locations. Continued human induced disturbance may lead to a decline in the degree of perceived threat (Frid & Dill, 2002). Conversely, animals may repeatedly flee from the perceived risk (Frid & Dill, 2002) and so this may affect companionships between rhino. In particular I hypothesise that (1) wild rhino adopt similar behaviours to their captive counterparts while held during a short period for acclimation to their new environment, (2) companionship selection during captivity is a predictor of post-release companionship selection, (3) herding successfully stops rhino from revisiting unsafe locations, and (4) human disturbance has a negative impact on rhino sociality.

In chapter three I examine the post-release spatial responses of translocated animals in a novel environment. Within familiar surroundings adult female home ranges often overlap and are larger compared to males, whereas males fight to gain distinct smaller territories. Subadults may be semi-nomadic, remaining in one area for several months before dispersing and settling (Owen-Smith, 1974). These movement bouts may be as a result of seasonal resource availability (Schoener, 1971; Pyke *et al.*, 1977). Previously translocated rhino have dispersed over large distances from their release site (Pienaar, 1970; Herbert & Austen, 1972). Although there is an apparent species specific distance after which animals are no longer able to navigate to their capture site, some individuals of those species are still able to 'home' (Rogers, 1984). I hypothesise that (1) rhino would replicate the movement behaviour of typical subadults within a year, (2) range sizes would be smaller in the flood season and largest in the resource abundant rainy season, but that ranges would be larger than typical due to being released in an unoccupied area, (3) range size, and overlap of ranges between individuals, would be affected by season and sex, with adult females having larger overlapping ranges compared to male rhino territories: in particular, I tested the hypotheses that subadult female rhino shared more space than subadult male rhino and that range sizes and the sharing of ranges would differ as a result of the variation in seasonal resources, and (4) rhino translocated 1,500km from the capture site do not possess the ability to navigate ‘home’.

In chapter four I investigate rhino habitat selection at the landscape scale using data from resource extraction sites. Dispersal and the restriction of movement are affected by the scattered spatial distribution of resources (Bennitt *et al.*, 2014), overgrazing, seasonal changes (Mueller & Fagan, 2008), or an animal’s internal state (Fryxell *et al.*, 2008). In my study the animals were relocated to an unknown environment, therefore home ranges and territories had not been established. I used movement patterns to establish encamped behaviour (Fryxell *et al.*, 2008; Morales *et al.*, 2010; Bunnefeld *et al.*, 2011; Papworth *et al.*, 2012; Benhamou, 2014) and used restricted movements within profitable sites to identify preferred landscape characteristics (Benhamou & Cornélis, 2010; Papworth *et al.*, 2012). In particular I hypothesise that (1) characteristics for each resource extraction site are likely to be different, so I aimed to establish which factors influence space use, (2) the relative importance of each habitat class would be the same across resource extraction sites and the relative use of habitats is related to the proportional availability of each habitat, and (3) rhino shared core areas within resource extraction sites.

In chapter five I look at grazing site selection criteria. There are both conflicting, and a lack of information as to what drives rhino grazing selection (Owen-Smith, 1992; Shrader & Perrin, 2006). As monogastric bulk grazers, rhino either compensate for reduced quality graze by selecting taller low quality grasses, and in so doing increase intake rate (Owen-Smith, 1973), or mobilise fat reserves (Shrader & Perrin, 2006; Shrader *et al.,* 2006a). Additionally results suggest rhino are both grass species selective (Kiefer, 2002) and species unselective (Melton, 1987; Perrin & Brereton-Stiles, 1999), or only select for particular sward characteristics i.e. short grasses (Owen-Smith, 1973, 1992; Perrin & Brereton-Stiles, 1999; Shrader *et al.,* 2006a). I test the hypotheses that (1) specific habitat types would be selected in periods of food abundance, but would change to random choices in periods of food shortage, (2) at the feeding site seasonal adjustments would be made by switching from high quality plentiful short grasses in the rainy season, to taller lower quality swards in the hot dry season, and (3) as bulk grazers, once within a preferred feeding site, rhino would not be selective.

In Chapter 6 I will discuss the results from each chapter and how they can be used to improve the translocation conservation of large herbivores. I also summarise the limitations of my study and propose future research topics.

Chapter 2. The social organisation and spatial relationships of relocated white rhino, and implications for security

2.1 Introduction

Large long-lived mammalian herbivores sometimes live in complex societies (Jarman, 1974; Brashares *et al.*, 2000; Couzin, 2006). Group living may offer advantages in fitness such as reduced predation risk, foraging and resource gains through acquired knowledge from conspecifics (Krause *et al.*, 2007; Fortin & Fortin, 2009; Croft *et al.*, 2011), cooperative vigilance and anti-predator tactics (Caro *et al.*, 2004; Pays *et al.*, 2007; Sih *et al.*, 2009), and access to sexual partners (Croft *et al.*, 2011). However, there is a trade-off to these advantages given that aggregation can also contribute to the spread of disease (Krause *et al.*, 2007; Cross *et al.*, 2009; Griffin & Nunn, 2012), increased density-dependent forage competition, and intensify rivalry for access to mates (Hay *et al.*, 2008).

The assemblages of ungulate societies are highly flexible (VanderWaal *et al.*, 2014). For example, ‘fusion’ occurs when ungulate groups join together to form larger herds (Rubenstein & Wrangham, 1986; Couzin, 2006; VanderWaal *et al.*, 2014), such as in buffalo (Bennitt *et al.*, 2018), elephant (Archie *et al.*, 2006b), giraffe (*Giraffa camelopardalis*) (Bercovitch & Berry, 2013) and bighorn sheep (*Ovis canadensis*) (Vander Wal *et al.*, 2015). The splitting of these herds is known as ‘fission’ (Couzin, 2006). Associations may also occur within a multitiered society (Wittemyer *et al.*, 2005; Couzin, 2006; VanderWaal *et al.*, 2014) or between individuals rather than groups (Evans & Harris, 2008). The variation of behaviour of individuals within networks (Pinter-Wollman *et al.*, 2013) may relate to the individuals characteristics, the animal’s internal state (Moreno & Acevedo-Gutiérrez, 2016; Muller *et al.*, 2018) or the spatial distribution of resources (Naud *et al.*, 2016; Bennitt *et al.*, 2018). These non-random repeated associations form the basis of social relationships (Hinde, 1976; Muller *et al.*, 2018).

In megaherbivores, gregariousness is evident within large herds of the African elephant (*L. africana*) (Wittemyer *et al.*, 2005; Archie *et al.*, 2006; Couzin, 2006), but sociality between rhino differs between species and demographically (Swaisgood *et al.*, 2006). Black rhino are mainly solitary animals. Exceptions to this include adult males that follow females in oestrus during the consort period (Hitchins & Anderson, 1983; Berger, 1995), subadults and young adults sometimes form loose associations with older individuals of both sexes (Tatman *et al.*, 2000) with the only sustained strong bond being between a cow and her youngest calf (Tatman *et al.*, 2000). By comparison, white rhino usually congregate in small numbers, usually in pairs but sometimes in groups of up to six individuals (Owen-Smith, 1974; Waldram *et al.*, 2007). It is likely that companionships lessen the risk of predation or attack from territorial bulls (Owen-Smith, 1975; Shrader & Owen-Smith, 2002). The dynamics of these assemblages comprise adult cow-calf pairs, adult cow-cow pairs that are sometimes joined by subadults, solitary adults bulls that may temporarily associate with a female in oestrus during the consort period, and adolescents of mixed but more often same-sex groups (Owen-Smith, 1974). To explore novel areas, individuals often 'buddy up' with a knowledgeable partner for the duration of the excursion (Shrader & Owen-Smith, 2002). Wild rhino sociality has mainly been studied in relation to group composition and associations between individuals (Owen-Smith, 1974, 1975; Van Gyseghem, 1984; White *et al.*, 2007). A social hierarchy in wild rhino has been widely accepted as only occurring in 'dominant' territorial adult bulls from comparatively few studies (Owen-Smith, 1974, 1975; Van Gyseghem, 1984).

Data on wild rhino social behaviour is largely observational, and most were obtained over 40 years ago (Owen-Smith, 1971, 1974, 1975). GPS tracking devices, providing continuous spatiotemporal data, have been used to measure home ranges and overlapping range areas (Pienaar *et al.*, 1993b; Pienaar, 1994; Rachlow *et al.*, 1999; White *et al.*, 2007). Shrader & Owen-Smith (2002) assessed temporary associations between 'buddies' by computing excursions beyond the defined home range, but no one has measured social relationships using social network analysis (Wey *et al.*, 2008; Krause *et al.*, 2011; Pinter-Wollman *et al.*, 2013). Social network analysis offers much greater insight into relationship dynamics than using overlapping home ranges (Farine & Whitehead, 2015), which does not quantify time and proximity of associations, only the static representation of shared space (Benhamou & Riotte-Lambert, 2012).

Owen-Smith (1973) suggested that evaluating dominance relationships in captive white rhino has little significance because they would not compete for the same resources in nature (Metrione *et al.*, 2007). Dominance typically occurs between wild rhino bulls contesting territories, or subordinates yielding to more dominant individuals, but dominance hierarchies have not been recorded in wild females (Owen-Smith, 1974, 1975; Van Gyseghem, 1984; Cinková & Bičík, 2013). Territorial alpha males have exclusive territories, whereas female ranges tend to overlap with no rivalry between individuals (Owen-Smith, 1975). Captive rhino display an increase in agonistic behaviour and space-maintenance vocalisations, mostly when defending their food, compared to their free-roaming counterparts (Metrione *et al.*, 2007).

Confinement forces a change in natural behaviour, and competition for food is intensified by an increase in proximity that would not occur in the wild (Metrione *et al.*, 2007). An increase in stress hormones in white rhino coincides with an increase in agonistic behaviour (Schmidt & Sachser, 1997; Cinková & Bičík, 2013). In particular female wild-caught captive rhino have higher corticosterone concentrations than captive-born females (Metrione & Harder, 2011), and poor reproduction in captivity has been linked to raised stress hormones (Schmidt & Sachser, 1997; Kuneš & Bičík, 2002; Carlstead & Brown, 2005; Hermes *et al.*, 2005; Swaisgood *et al.*, 2006; Tubbs *et al.*, 2016).

With the current decimation of rhino through poaching (Biggs *et al.*, 2013), captive mixed sex herds may enable the conservation of some genetic differentiation and/or behaviours of a small population. In the future wild caught small populations of wild rhino may need to be housed in safer captive facilities. Information on how wild caught rhino live collectively in smaller spaces could be invaluable, and analysing the behaviour of mixed sex captive-held wild rhino may help contribute to welfare and breeding success and improved captive management for zoo animals. For example, northern white rhino captured in the 1970s are now the last of their species, since the remaining wild individuals were killed in Garamba National Park, DR Congo (Hermes *et al.*, 2006; Hillman-Smith *et al.*, 2009). The captured rhino were held in captivity but did not breed well. In 2009 this prompted their release at Ol Pejeta Conservancy in Kenya in an attempt to encourage reproduction, supported by a highly publicised *in vitro* fertilisation (IVF) project (Callaway, 2016). A southern white rhino was successfully impregnated using IVF, but the oocyte was developed from the same subspecies rather than from a northern white rhino (http://zoonooz.sandiegozoo.org/zoonooz/to-the-rhino-rescue/). Breeding viable captive reserve populations has been successful for species such as the Arabian oryx (*Oryx leucoryx*) (Ochoa *et al.*, 2016) and Przewalski's horse (*Equus ferus przewalskii*) (Xia *et al.*, 2014). Therefore it may be possibly to improve the long term outlook for captive bred and wild-caught captive rhino by learning how wild rhino behave in captivity.

There is still much to be discovered about how animals avoid or minimise anthropogenic disturbance (Francis & Barber, 2013). The presence of humans may be perceived as a threat (predation risk hypothesis) where animals are less tolerant to disturbance (Benhamou, 1997; Frid & Dill, 2002; Gonzalez-Gomez & Vasquez, 2006; Fagan *et al.*, 2013; Avgar *et al.*, 2015), or continued exposure to humans may lead to a decline in the degree of perceived threat (refuge hypothesis) (Frid & Dill, 2002), whereby individuals may be more relaxed and decrease their vigilance (Samia *et al.*, 2015; Lesmerises *et al.*, 2017).

Large herbivores avoid roads with high traffic density (Leblond *et al.*, 2013), but these choices sometimes come at a cost to fitness because animals select lower quality habitat to avoid disturbance (MacNearney *et al.*, 2016). Ungulates may run from a perceived risk, the distance from the cause being called the 'fleeing distance'. The fleeing distance may be greater depending upon the degree of the perceived threat as well as the availability of a suitable refuge (Stankowich, 2008; McGowan *et al.*, 2014). During my research, the released rhino visited certain areas which exposed them to the threat of poaching. It was necessary, therefore, for anti-poaching teams to herd reintroduced rhino away from potentially dangerous or exposed areas using game vehicles and/or on foot.

I hypothesised that:-

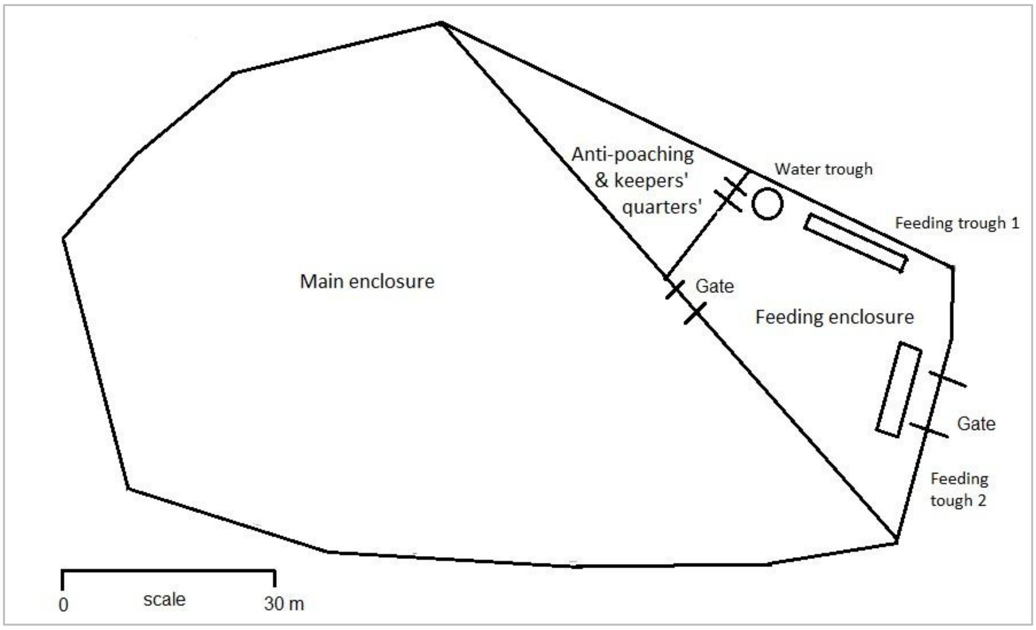
1) Wild rhino adopt similar behaviours to their captive counterparts while held during a short period for acclimation.
2) Pre-release companionships can be used to predict post-release companionship selection.
3) Herding is a successful method of stopping rhino from revisiting dangerous locations, and an appropriate long-term security strategy.
4) Anthropogenic disturbance has a negative impact on rhino sociality.

2.2 Methods

The six southern white rhino translocated to Botswana were placed on a remote island in the Okavango Delta and acclimated for two months in a holding pen (boma) prior to release (Figure 2.1).

The relatively short period of captivity allowed me to investigate whether the wild caught project rhino developed behavioural traits resembling those displayed by captive rhino. Idiosyncratic behaviours observed in captive rhino that are not classed as normal behaviour in free-ranging wild rhino include agonistic interactions during feeding, the establishment of a social hierarchy (Mikulica, 1991; Kuneš & Bičík, 2002; Metrione *et al.*, 2007; Cinková & Bičík, 2013), females displaying male dominance behaviour such as urine squirting and scraping (Metrione *et al.*, 2007), and poor breeding rates (Schmidt & Sachser, 1997; Kuneš & Bičík, 2002; Seror *et al.*, 2002; Carlstead & Brown, 2005; Hermes *et al.*, 2005; Hermes *et al.*, 2006; Swaisgood *et al.*, 2006; Tubbs *et al.*, 2016). I could not consider effects on reproduction due to the time scale of my study.

Figure 2.1. Diagram showing the boma design. It was constructed of wooden poles and a hard-wired electric fence. The rhino boma was mapped using a hand-held Garmin Montana 600 GPS.



For security reasons, throughout the acclimation period, anti-poaching teams guarded the rhino 24-hours a day. Each day keepers placed tef (*Eragrostis tef*), lucerne (*Medicago sativa*) and pellet compound feed on a rubber-bottomed feeding trough at approximately 08:00 h and 17:00 h CAT (Central Africa Time). Water was available *ad libitum*. Tourists also visited and were usually restricted to viewing the animals adjacent to the feeding area (Figure 2.1). The rhino were exposed to noise, visual contact, and close physical proximity to humans during confinement, which heightens stress levels (Carlstead & Brown, 2005; Tarlow & Blumstein, 2007). However, chronic stress levels may depend upon the familiarity of the visitor to the animal: a known caretaker or anti-poaching officer may yield different stress levels to an unknown tourist visitor (Hutchins &

Kreger, 2006). The rhino were sourced from a fenced reserve with a relatively high tourist visitor pressure. However, game vehicles were familiar and animals had the opportunity to retreat to refuges.

Acclimation procedures for white rhino recommend individual holding pens made of a pole construction for each animal (Emslie *et al.*, 2009), but the rhino in this study were held collectively, emulating some of the conditions of captive rhino. This provided the opportunity to determine whether wild rhino held for a short period replicated the behaviours of captive rhino.

2.2.1 Observational data collection

Table 2.1. Shaded areas indicate 58 h of observational data collected while rhino were held in the boma. Each line represents one observation day between 07/04/13 and the day of release, 16/05/13.

Time Date	07:00	07:30	08:00	08:30	09:00	09:30	10:00	10:30	11:00	11:30	12:00	12:30	13:00	13:30	14:00	14:30	15:00	15:30	16:00	16:30	17:00	17:30	18:00
07/04/13																	🟦	🟦	🟦	🟦	🟦	🟦	🟦
08/04/13														🟦	🟦	🟦	🟦	🟦	🟦				
09/04/13																	🟦	🟦	🟦	🟦	🟦		
10/04/13				🟦	🟦	🟦	🟦	🟦	🟦	🟦													
11/04/13					🟦	🟦	🟦	🟦	🟦	🟦													
12/04/13																	🟦	🟦	🟦	🟦	🟦		
13/04/13							🟦	🟦	🟦	🟦	🟦												
15/04/13							🟦	🟦	🟦	🟦	🟦	🟦	🟦										
16/04/13																🟦	🟦	🟦	🟦	🟦	🟦		
19/04/13																			🟦	🟦	🟦	🟦	🟦
20/04/13					🟦	🟦	🟦	🟦	🟦	🟦													
21/04/13																		🟦	🟦	🟦	🟦		
22/04/13					🟦	🟦	🟦	🟦	🟦	🟦	🟦												
28/04/13					🟦	🟦	🟦	🟦	🟦	🟦	🟦												
29/04/13																		🟦	🟦	🟦	🟦	🟦	
30/04/13																🟦	🟦	🟦	🟦	🟦			
01/05/13					🟦	🟦	🟦																
02/05/13																	🟦	🟦	🟦	🟦			
05/05/13																	🟦	🟦	🟦	🟦			
11/05/13									🟦	🟦	🟦	🟦											
14/05/13	🟦	🟦	🟦	🟦	🟦																		
16/05/13						🟦	🟦																

The boma was only accessible by a boat owned by the local safari operator. I was permitted to use the boat if it was not needed by guides hosting guests staying at the safari lodge; consequently, there was some restriction on the time and frequency of my visits to the rhino. I was unable to observe the rhino after 19:00 h due to the danger posed by hippopotamus in the water channels. I observed the rhino for 58 h while they were in the boma (Table 2.1). I mostly avoided observational periods between 11:00 h and 15:00 h when the rhino were inactive.

2.2.2 Social and spatial data

I observed all animals simultaneously and recorded data for each individual i.e. for M1, M2, M3, F1, F2 and F3 in sequence at 10-min intervals. I recorded each rhino's nearest neighbour and the dyadic distance, along with the behaviour of the individual to estimate behavioural time budgets (Altmann, 1974). Behaviours were classified as either resting, feeding or mobile. I plotted a frequency histogram of the total observed dyadic distances for all individuals (n=1074) to identify the fission-fusion drop-off between individuals while in the boma (Figure S2.1). I identified this as being around 6 m and so chose a conservative estimate of 5 m for use in analyses, approximately two body lengths.

2.2.3 Competitive interactions

Table 2.2. Recorded behaviours (n=447) of rhino (n=6) held in the boma during the observation period. See Table S2.1 for details.

	Vocal	Physical
Winning dominant behaviours	Snarl – gruff roar with mouth open and ears laid back, used as a distance-increasing tool	Horn/head clash Chase/charge Body blow - horn attack to body Push - using body weight to push opponent
Losing submissive behaviours	Shriek – high pitched attack inhibiting call Squeak – distress signal usually used by calves, abrupt and high pitched	Moving away Yielding food/ground
Additional recorded behaviours	Snort – nasal inhalation or exhalation, a mild keep away warning	

I used the behavioural ethogram by Metrione *et al.* (2007), compiled from observations made by Owen-Smith (1973), to classify dominant and subordinate behaviours that occurred during interactions between individuals (Table S2.1). Agonistic encounters were identified as being either a dominant winning behaviour, or a submissive losing behaviour (Table 2.2) (Owen-Smith, 1975; Swaisgood *et al.*, 2006). These data were recorded concurrently with the social and spatial data as and when interactions occurred. Only dyadic encounters were recorded: polyadic interactions excluded to avoid confounding factors (Deag, 1977; Stevens *et al.*, 2007). Vocalisation data were merged into 30 min intervals for ease of plotting in R (R Core Team 2016) using the *ggplot2* package (Wickham, 2009).

2.2.4 Static dominance tests

I determined whether a hierarchy was present to assess the presence of dominance i.e. agonistic behaviour not suppressed by another individual (Deag, 1977). I generated a dominance matrix (*dm*) from raw data (Table 2.6) (n=382) as described below, using the package *igraph* (Csardi & Nepusz, 2006) in R (R Core Team, 2016), and plotted this using *qgraph* (Epskamp *et al.*, 2012).

The hierarchy of assemblages are generally transitive, where animal A dominates B, B dominates C and C dominates D (Shizuka & McDonald, 2012). The linearity of dominance is a conventional method for establishing orderly transitive relationships between dyads (Landau, 1951; de Vries, 1995, 1998; Shizuka & McDonald, 2012; Shizuka & McDonald, 2015). The steepness of the linear slope can be used to assess whether the dominance hierarchy is significant. In primates, steep gradients may represent despotic societies, whereas in egalitarian societies dominance gradients are shallower (Henazi & Barrett, 1999; Stevens *et al.*, 2007).

Using a randomisation test I compared the null hypothesis of random wins between each dyad to the observed steepness. That is, the number of times that randomly generated steepness was greater than or equal to the observed steepness (de Vries *et al.*, 2006). The steepness package (Leiva & de Vries, 2014) in R (R Core Team, 2016) was used for all linearity and steepness calculations, with R code adapted from www.shizukalab.com/toolkits. I generated a matrix of proportional wins (Pij) for each dyad (David, 1988). These data were available from matrix *dm.* For each dyad I calculated the proportion of wins (Pij) between individuals i and j as:

$$Pij = Sij/nij \tag{2.1}$$

where Sij was the number of wins i had over j and nij was the total number of interactions between dyads. Pij was corrected for chance by calculating the Dyadic Dominance Indices (Dij) (de Vries, 1998). Dij takes into account the asymmetry of wins and losses, and differing interaction frequencies between dyads (de Vries, 1998; Gammell *et al.*, 2003; de Vries *et al.*, 2006) and was calculated using the formula:

$$Dij = Pij - \{(Pij - 0.5) \times Prob[Pij]\} \tag{2.2}$$

where $Prob[Pij]$ was the probability that the observed proportion occurred by chance.

I established the cardinal rank of each animal using David's Scores (DS) (equation 2.3) that uses a weighting method to calculate an animal's overall success, whereby defeating a higher ranking animal was given a heavier weighing than defeating a lower ranking individual (David, 1987; Gammell *et al.*, 2003; de Vries *et al.*, 2006):

$$DS = w + w_2 - \ l - l_2 \tag{2.3}$$

where w signified the sum of i's Pij values, w_2 signified the weighted sum of i's Pij values, l signified the sum of i's Pij values, and l^2 signified the weighted sum of i's Pij values. DS was computed for both Pij and Dij. However, the fitted line for DS varies between 0 and N, so the David Score was corrected for chance, known as the Normalised David's Score ($NormDS$) (equation 2.4), which generated a steepness between 0 and 1 (de Vries *et al.*, 2006). The $NormDS$ was plotted against the animal's dominance rank order, and the regression line represented the linearity and steepness of the dominance relationship between individuals (David, 1988; de Vries *et al.*, 2006):

$$NormDS = (DS + N(N-1)/2)/N \tag{2.4}$$

where *N* represented the group size and DS represented the David's Score.

To perform the steepness test I generated 1000 repeated randomisation simulations of matrices based on both the Pij and Dij dominance matrix measures and compared it to the sample distribution (David, 1988; de Vries *et al.*, 2006).

To assess the significance of transitive linear relationships, I calculated Landau's Linearity Index (*h*) (Landau, 1951), and corresponding improved test (*h'*) (de Vries, 1995). The matrix was transformed into a binary matrix, where 1 was allocated to dominant relationships and 0 to subordinates. Since I knew all the relationships between dyads, the *p*-value was the probability that 'the degree of linearity in the original dominance matrix (*dm*) as expressed by the value *h'* results from random processes' (de Vries, 1995). This was based on a series of 10,000 randomisations (de Vries, 1995; Shizuka & McDonald, 2012).

2.2.5 Dynamic dominance test

Elo (1978) developed a method known as 'Elo-rating' for ranking chess players, and was utilized by Albers & de Vries (2001) and Neumann *et al.* (2011) as a method of analysing how the dominance of individuals may change over time. I used the package EloRating (Neumann & Kulik, 2014) in R (R Core Team, 2016) to analyse the sequence of interactions between dyads and plotted dominance trajectories. Typically each individual is given the same starting Elo-rating value of 1000 (y axis), with each sequential win or loss leading to an addition or subtraction in Elo-rating (McDonald & Shizuka, 2013). I calculated the Stability Index, representing the overall stability of the dominance hierarchy over the observed period, where 0 denotes an unstable hierarchy and 1 a stable hierarchy with no rank order changes (Neumann *et al.*, 2011; McDonald & Shizuka, 2013).

2.2.6 Pre-release companionship selection

Analyses of network structure, notably the existence of 'communities' (subgroups of densely connected nodes), were carried out in the package *igraph* (Csardi & Nepusz, 2006) in R (R Core Team (2016)). I transformed nearest neighbour data into matrices for each category of behaviour (mobile, resting, and feeding), as well as a matrix combining all of these behaviours. I also split the data into distinct periods based on observation dates (Table 2.3) to determine if bonds changed over time. The dates for periods 3 to 5 were partitioned due to the random availability of transport to the boma, so I used these dates as sample periods. I was able to observe rhino on consecutive days between 07/04/2013 and 16/04/2013, but I divided these into periods 1 and 2 so that the number of days across each sampling period was more uniform. I identified bonds between individuals for each behaviour type, and identified any social divisions in the community.

Table 2.3. Sampling periods defined for nearest neighbour analysis on white rhino while held in a boma for acclimation. Observations took place between 07/04/2013 and 16/05/2013.

Period	1	2	3	4	5
Dates	07/04/2013 to 11/04/2013	12/04/2013 to 16/04/2013	19/04/2013 to 22/04/2013	28/04/2013 to 05/05/2013	11/05/2013 to 16/05/2013
Observations	534	390	360	516	174

I used the 'leading eigenvector' algorithm to calculate network community structure. This acquires the highest 'modularity index' (Q) after comparing it to all potential partitions in the network (Newman, 2006a, b). Q represented the quality of the division of the social network that lies between 0 for a random community network, and 1 for a strong community structure. In practice values between 0.3 and 0.7 normally represent the latter (Newman & Girvan, 2004). The modularity index was calculated using the equation:

$$Q = A - P \tag{2.5}$$

where A is the observed proportion of associations between individuals in the nearest neighbour matrix, and P represents the probability of a relationship between individuals being present in a random network matrix.

2.2.7 Post release companionship selection

To compare post-release spatiotemporal associations of dyads with pre-release companionship bonds, I used the package *wildlifeDI* (Long, 2014; Long *et al.*, 2014) in R (R Core Team, 2016) that analyses animal trajectories using GPS fixes. I used one GPS fix per 24 h period for each individual, as close to midday as possible, for analysis with a horizontal dilution of precision HDOP<10 to ensure accuracy (D'Eon & Delparte, 2005) and an adequate sample size. This was because comparable GPS data beyond midday ±3 h between dyads were too irregular. GPS data needed to be transformed from decimal degrees into UTM coordinate format, thereby giving an output in meters. I separated GPS fixes into six seasons for comparison before calculating distinct bursts for each individual (Table 2.4), using the *adehabitatLT* R package (Calenge, 2006). The package *adehabitatHR* (Calenge, 2006) in R (R Core Team (2016)) was used to calculate 95% kernel density estimations (KDE) from utilization distributions (UD) (Lichti & Swihart, 2011) and overlap zones (OZ) between dyads within these KDE ranges (Cantor *et al.*, 2012).

Table 2.4. The number of GPS fix locations used to calculate temporal and spatial proximity for social network analyses using wildlifeDI *R package and* AdehabitatLT.

I.D. / Season	F1	F2	F3	M1	M2	M3
Flood* 2013	42	45	42	46	46	42
Hot dry 2013	118	78	117	122	121	118
Rainy 2013/14	38	73	105	112	117	112
Flood 2014	0	24	116	96	73	111
Hot dry 2014	0	0	111	116	0	117
Rainy 2014/15	0	0	84	95	0	93
* Rhino were released mid-way though the flood season 2013 on 16/05/2013						

Differences between pre and post release associations could be made in relation to visual comparisons between pre and post release sociograms. However, the two sets of data comprised of different variables therefore sociograms had to be produced using differing methods so directly comparable models could not be produced.

2.2.7.1 *Time and distance thresholds*

Rhino are typically inactive during the hottest part of the day, so I selected a time threshold of midday $\pm$3 h to calculate *wildlifeDI* dynamic interactions. To calculate a suitable distance threshold and Benhamou's critical distance(Δ) (Benhamou *et al.*, 2014), I took a random sample of 500 fusion events of <1 km and plotted a histogram of Euclidean distances (Figure S2.2). I identified the break-point in the frequency of observations as a distance of 200m and used this for calculations in section 2.2.8. (Cross *et al.*, 2005; Bennitt *et al.*, 2018).

2.2.7.2 *Association calculations*

I used the following Indices to measure dynamic associations:-

- Coefficient of association (Ca) is an indicator of attraction, with Ca < 0.5 representing no association and Ca > 0.5 indicating an association (Cole, 1949; Bauman, 1998; Long *et al.*, 2014). The coefficient of association was calculated as:

$$Ca = \frac{2\alpha\beta}{\alpha+\beta} \tag{2.6}$$

  where individuals of a dyad were α and β, and $\alpha\beta$ was the number of times the individuals were observed together.

- Half-weight Association Index (HAI) was used to determine whether individuals avoided each other ($HAI \cong 0$) or were attracted ($HAI \cong 1$) within overlap zones of shared home ranges (Atwood & Weeks, 2003; Long *et al.*, 2014):

$$HAI = \frac{ST\alpha\beta}{ST\alpha\beta + \frac{x+y}{2}} \tag{2.7}$$

  where $ST\alpha\beta$ was the number of simultaneous spatially and temporally proximal fixes of dyads based on time and distance thresholds, and x and y were the number of solitary fixes for each individual.

- Benhamou's IAB index (IAB) was used to determine if individuals moved independently of each other by analysing the distance between individuals at a given time (t) (Benhamou *et al.*, 2014; Long *et al.*, 2014). The index was calculated using the equation:

$$IAB(t) = \exp\left[-0.5\left(\frac{DAB(t)}{\Delta}\right)^2\right] \quad (2.8)$$

where D_{AB} was the distance between two $T\alpha\beta$ GPS fixes, and Δ represented the maximum distance at which social cohesion was calculated, i.e. 200m.

- Proximity analysis ($Prox$) was used to calculate the proportion of fixes in trajectories that were proximal based on time and distance thresholds (Bertrand *et al.*, 1996; Long *et al.*, 2014) using the formula:

$$Prox = \frac{T\alpha\beta}{ST\alpha\beta} \quad (2.9)$$

where $T\alpha\beta$ represented the proportion of simultaneous GPS fixes for dyads defined within a temporal threshold that are proximal ($ST\alpha\beta$) based on a spatial threshold.

2.2.8 Post-release sociograms

Splitting data into seasons, I transformed the proximity analysis results (Tables S2.2 to S2.7) into matrices. I plotted community structure and identified companionship selection choices (Section 2.2.6).

2.2.9 Measuring the effects of anthropogenic contact

Net squared displacement (NSD) has conventionally been used to analyse coarse scale animal movements (Fryxell *et al.*, 2008; Bunnefeld *et al.*, 2011; Borger & Fryxell, 2012). I use NSD to analyse small scale movements (Papworth *et al.*, 2012) since it was sometimes necessary for the anti-poaching teams to herd rhino away from potentially dangerous or exposed areas. Herding was carried out on foot and/or using game vehicles. NSD plots were used to assess whether anthropogenic contact affected companionship selection, and stopped rhino from returning to the same location.

GPS anklets also needed to be replaced before the battery life expired, so I also used these game capture events to assess how rhino behaved following this type of contact. For this, the rhino were chased by helicopter and game vehicles. I did not participate in the game capture process so I do not have any data relating to the sedation and immobilisation of the animals.

To allow for the timescale involved in capture, I allocated the latest possible GPS point for the day of capture, or the first GPS point of the following day as the starting point where I set NSD to be zero, and used the package *adehabitatLT* (Calenge, 2006) in R (R Core Team, 2016) to calculate NSD from UTM transformed GPS data. I used all GPS points with HDOP<10 so that I could capture small and large movements (D'Eon & Delparte, 2005).

To analyse how anthropogenic contact affected the distance travelled, I used ANOVA with repeated measures design to account for pseudoreplication to compare the mean distances moved over a 5-day period after a herding or capturing event (Table 2.5) to a random 5-day period without contact. I used a random number generator to select the day and month of the random period which was chosen within the same season to control for seasonal variation in movement. Euclidean distances were calculated between concurrent time periods using the Spherical Law of cosines formula (Gellert *et al.*, 2012), but not all GPS fixes registered at specific time intervals within each 5-day period. To account for these missing data I generated predicted values from Euclidean distances corresponding to each time interval (Figures S2.3 and S2.4). These data were then used to sum total daily movements. A paired samples t-test was used to evaluate whether there was a difference in movement between re-collaring attempts compared to herding events.

Table 2.5. Herding and game re-collaring of rhino events used to analyse the effect of anthropogenic contact on animal movements and social relationships.

Date	10/10/13	18/10/13	21/10/13	28/10/13	06/02/14	27/03/14
Event	Herding	Herding	Herding	Herding	Herding	Re-collaring
Animal	F3, M3	F3, M3	F2, M1, M2	F2, M1, M2	F2, M2	M1, M2, F3, M3

2.3 Results

2.3.1 Interaction behaviour

The frequency of rhino vocalisations i.e., mild keep away warning (snort), and agonistic distance increasing tool (snarl), along with physical altercations were recorded during the acclimation period. There was a correlation between the frequency of vocalisations and when rhino fed from troughs (Figures 2.2 and 2.3).

Figure 2.2. Proportion of each behaviour for estimated daily time budgets for rhino while held in a boma. The rhino were fed at approximately 08:00 and 17:00 each day.

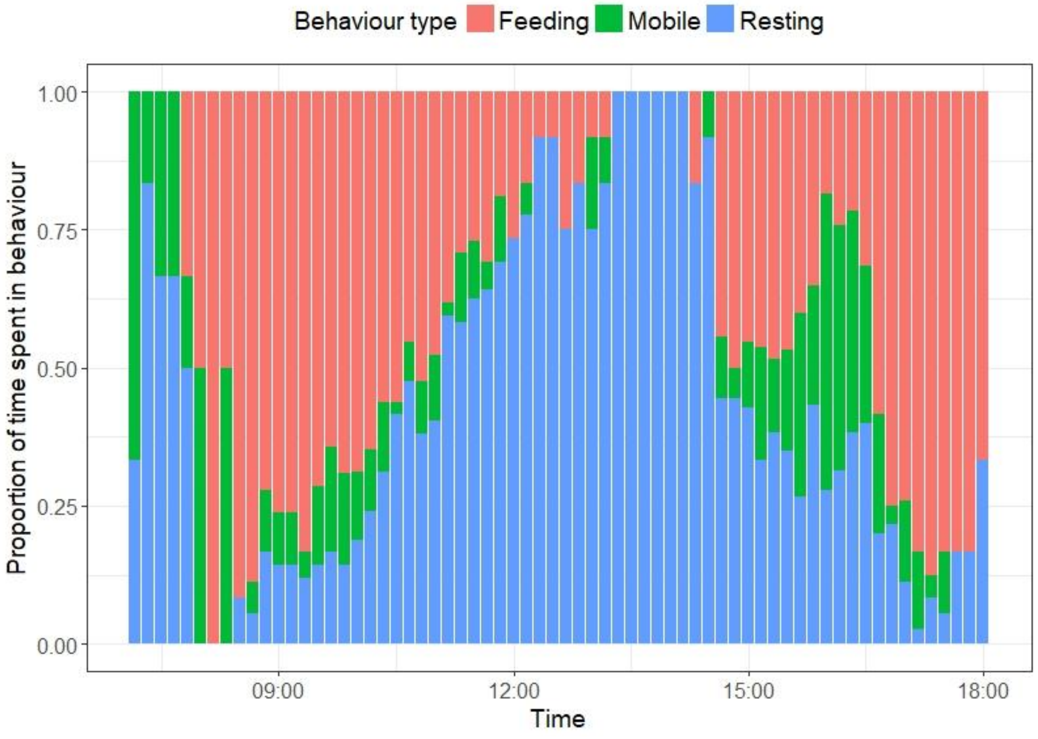
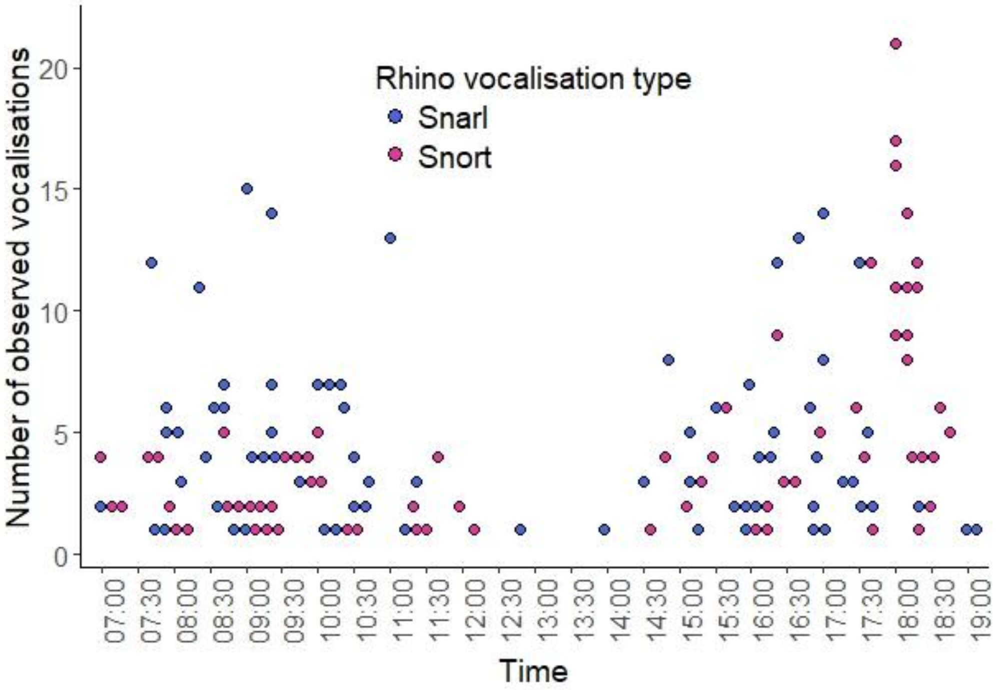
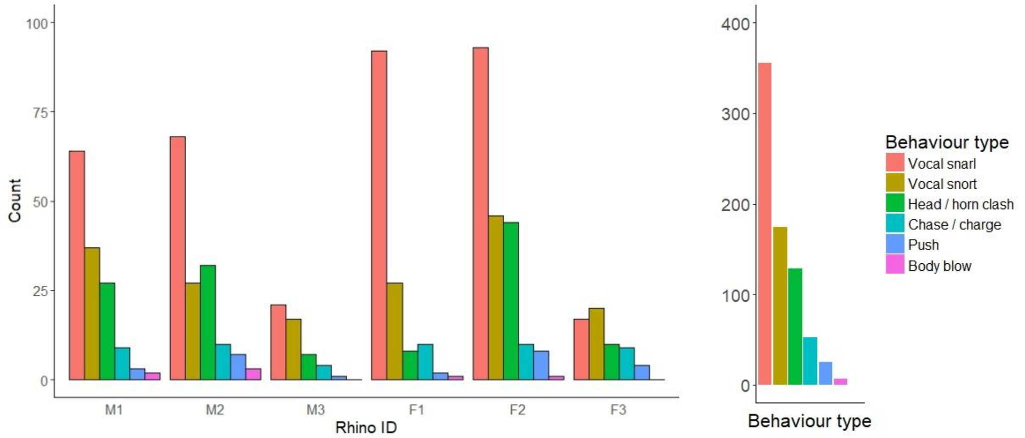


Figure 2.3. Snarl and snort daily vocalisations made by rhino while held in the boma during acclimation. Vocalisation peaks corresponded with feeding times at approximately 08:00 hours and 17:00 hours.



Of all the behaviours recorded, 71% were vocalisations and 29% were physical interactions (Figure 2.4). Those behaviours classified as agonistic, i.e. all behaviours excluding the mild keep-away warning (snort) included 63% vocalisations and 37% physical altercations. Snarl vocalisations were the most successful method of winning interactions. This is probably because physical battles could potentially be more costly than vocalisations (Owen-Smith, 1974). A head-on 'clash of horns' was the most widely used method of winning physical altercations (23%).

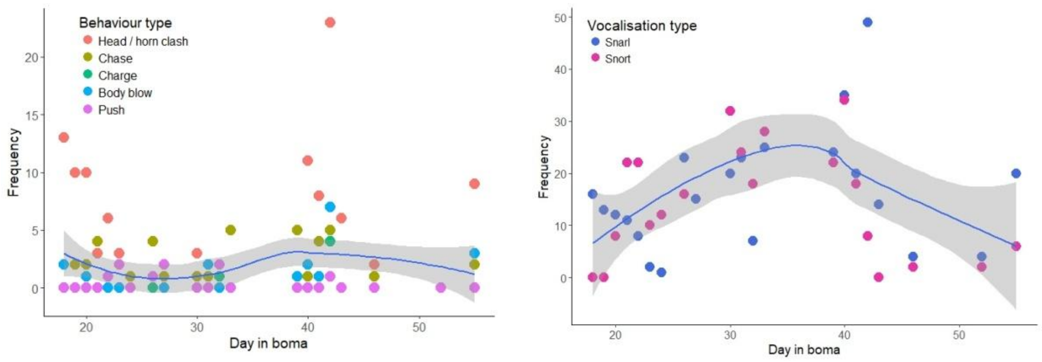
Figure 2.4. Frequency of behaviours observed in the boma by individual and overall. Vocalisations accounted for 71% and physical interactions 29% of recorded behaviours.



A Loess (non-parametric polynomial regression smoothing) curve was used to describe the pattern in the data, therefore no goodness of fit measure (e.g. R^2) is provided. It is not a statistical statement about the form of the relationship that you would expect to find in other similar datasets (i.e. the population). The Loess line indicated that the frequency of daily physical altercations between dyads remained below 5 throughout the observation period, whereas vocalisations continued to increase to around 25 per day until 35 days of capture, when they began to decline to original levels of <10 vocalisations per day (Figures 2.5a, b).

Figure 2.5. Interaction frequency plots between dyads with fitted Loess curve and 95% confidence intervals to describe the pattern in the data, from day 18 (07/04/13) to release day (16/05/13), for a) physical interactions and b) vocalisations.

a) b)



2.3.2 Hierarchy establishment

Hierarchy and dominance tests were carried out on a total of 382 agonistic interactions between rhino dyads (Table 2.6). The four older rhino F1, F2, M1 and M2 won the majority of their altercations against younger rhino M3 and F3 (Figure 2.6).

Table 2.6. Matrix with number of wins verses losses (n=382) between 6 wild white rhino during the acclimation period in the boma.

	M1	M2	M3	F1	F2	F3	Total wins
M1	*	28	17	2	8	18	73
M2	8	*	31	1	6	31	77
M3	3	2	*	0	0	16	21
F1	14	16	25	*	20	14	89
F2	25	22	19	2	*	30	98
F3	2	6	13	0	3	*	24
Total losses	52	74	105	5	37	109	**382**

Figure 2.6. Qgraph displaying percentage wins of competitive interactions between dyads during acclimation. Thick darker edges indicate supremacy and thin faded edges indicate weaker performances, with numerical values indicated on each line. F1-3 are females, M1-3 males; F3 and M3 are younger individuals.

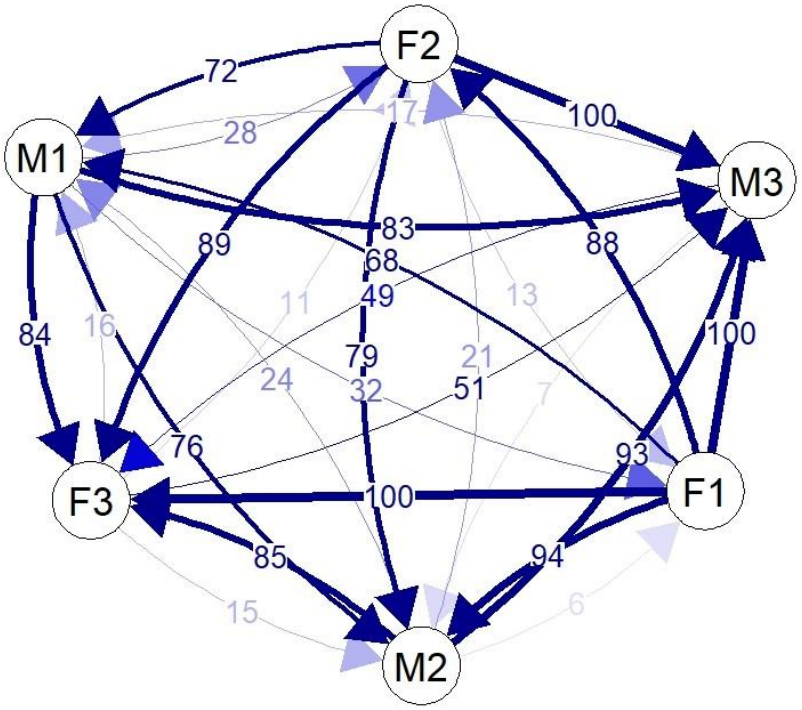


Table 2.7. Matrix in order of hierarchy, illustrating proportional (Pij) wins (in rows) verses losses (in columns) and dyadic dominance indices (Dij) in the boma, with w, w2, l, l2, David's score (DS) and normalised DS(NormDS).

	F1	F2	M1	M2	F3	M3	*w*	*w2*	DS	NormDS
Win proportions P*ij*										
F1	*	0.91	0.88	0.94	1.00	1.00	4.73	9.5	13.35	4.73
F2	0.09	*	0.76	0.79	0.91	1.00	3.54	5.9	6.26	3.54
M1	0.13	0.24	*	0.78	0.90	0.85	2.90	4.6	2.37	2.90
M2	0.06	0.21	0.22	*	0.84	0.94	2.27	3.1	-1.36	2.27
F3	0.00	0.09	0.10	0.16	*	0.45	0.80	1.3	-10.19	0.80
M3	0.00	0.00	0.15	0.06	0.55	*	0.76	1.0	-10.43	0.76
l	0.27	1.46	2.10	2.73	4.20	4.24				
l2	0.56	1.73	3.01	3.98	8.12	7.96				
Dyadic dominance indices D*ij*										
F1	*	0.89	0.85	0.92	0.97	0.98	4.61	9.35	12.65	4.61
F2	0.11	*	0.75	0.78	0.90	0.97	3.51	6.04	6.04	3.51
M1	0.15	0.25	*	0.77	0.88	0.83	2.88	4.79	2.29	2.88
M2	0.08	0.22	0.23	*	0.83	0.93	2.29	3.33	-1.24	2.29
F3	0.03	0.10	0.12	0.17	*	0.45	0.88	1.63	-9.74	0.88
M3	0.02	0.03	0.17	0.07	0.55	*	0.83	1.31	-9.99	0.83
l	0.39	1.49	2.12	2.71	4.12	4.17				
l2	0.92	2.01	3.26	4.16	8.12	7.97				

Landau's dominance tests ($h=1.571$ and $h'=1$) were carried out on data in Table 2.7. There was a significant linear hierarchy ($p<0.05$), and the steepness test of both P*ij* ($p=0.001$) and D*ij* ($p=0.001$) were significant (Figures 2.7 and 2.8). This indicated a more despotic (dominance) than egalitarian society (Henazi & Barrett, 1999; Leinfelder *et al.*, 2001). The differences in rank (NormDS) were large enough to maintain dominance stability within the hierarchy.

Figure 2.7. Landau's dominance plot, where arrows indicate direction of dominance, Landau's h=1.571, modified Landau's h' index=1, p-value from simulations=0.022.

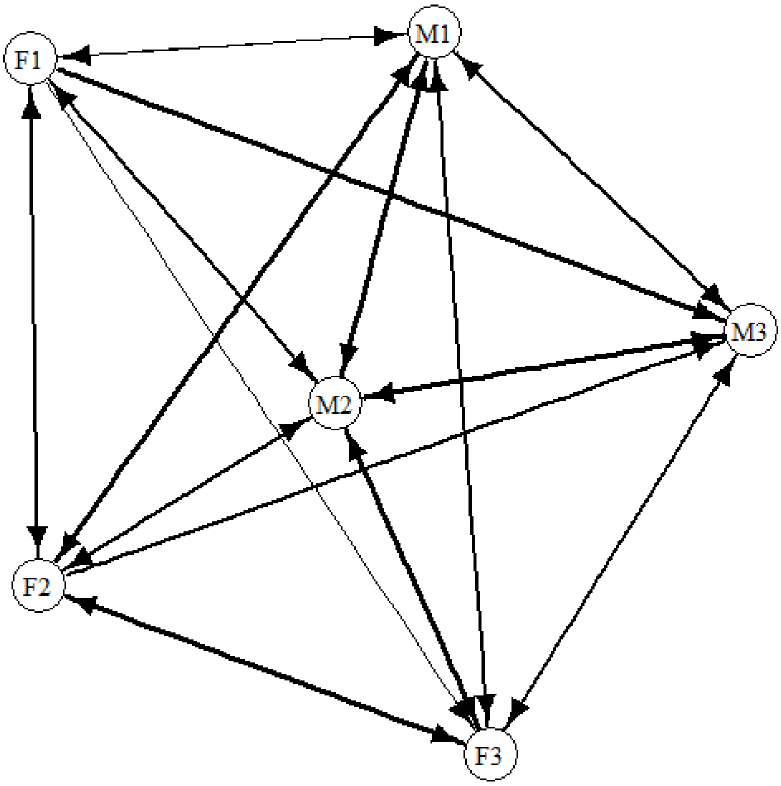
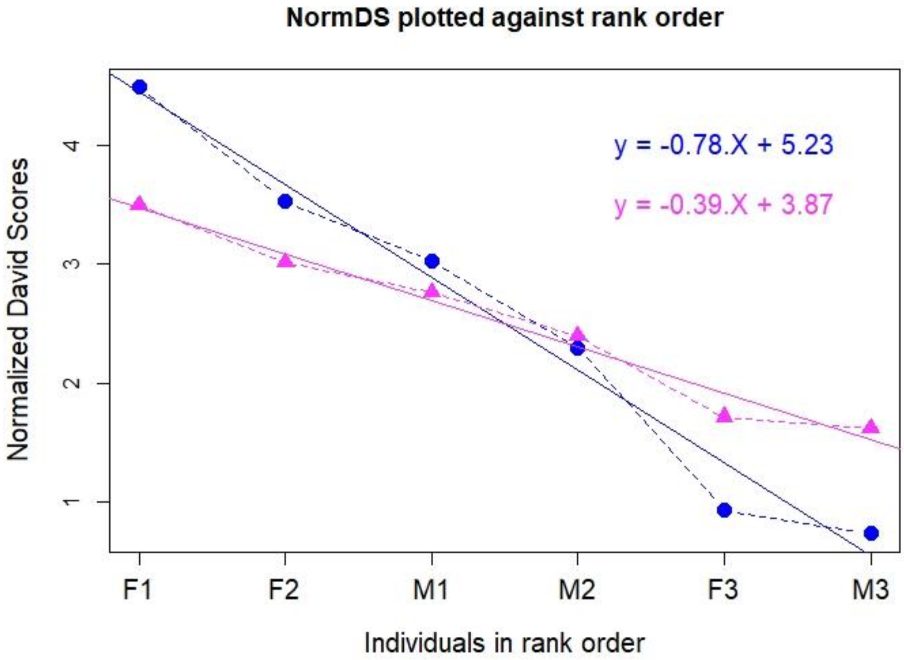
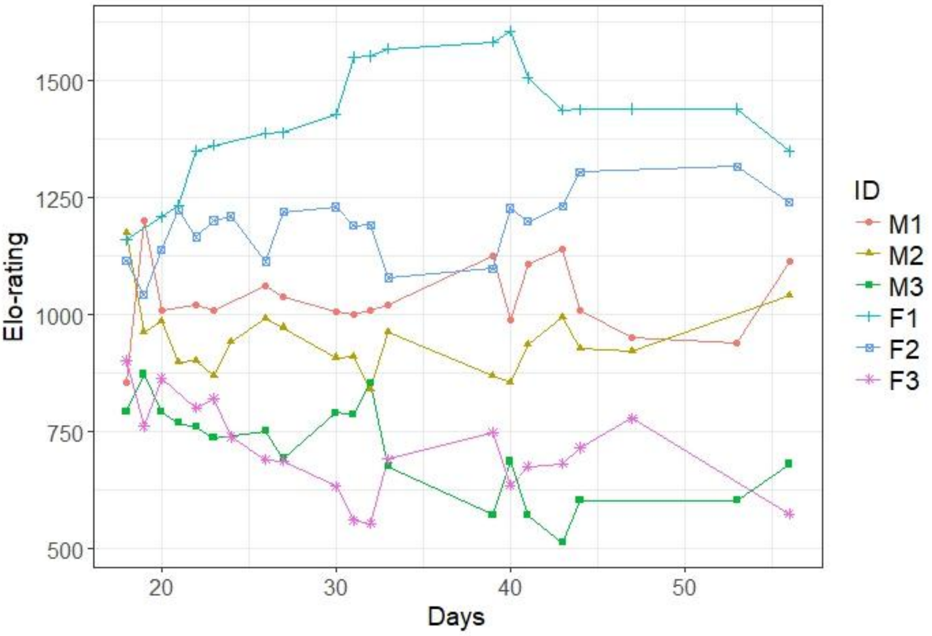


Figure 2.8.Normalised David's scores (NormDS) plotted against rhino in rank order, with straight line fitted through NormDS based on both proportion of wins (Pij) in blue and dyadic dominance indices (Dij) in pink.



I calculated Landau's *h′* using data from previous studies by Metrione *et al.* (2007) and Kuneš & Bičík (2002) (Table S2.8 and Figure S2.5). Six of the seven dominance matrices I analysed had values of Landau's $h' \geq 0.7$, indicating smaller differences between ranked individuals than my data, and none was significantly linear, with p>0.05 for all analyses. The Elo-rating test confirmed linearity in my dataset, with a hierarchical stability index of 0.965; i.e. there were only eleven changes in the hierarchy throughout the entire acclimation period. The highest ranked individual was F1, the pregnant adult female, and second ranked was F2, followed by M1 then M2 (Figure 2.9). The lower ranking animals, F3 and M3, were the youngest of the group.

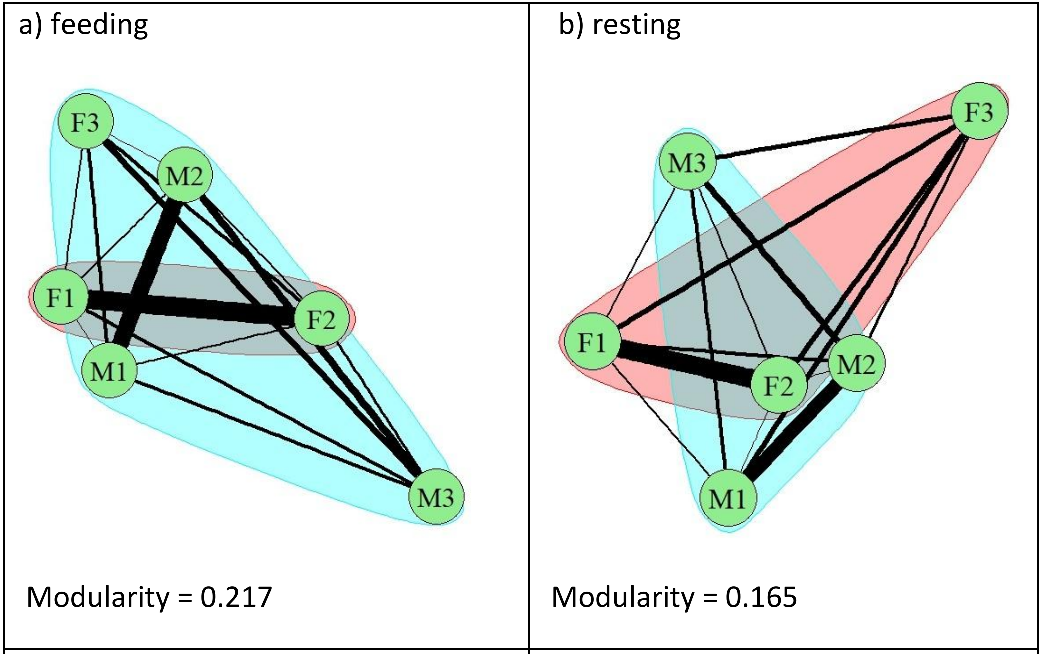
Figure 2.9. Elo-rating plot (n=382 interactions) shows dynamic changes in dominance while the rhino were held in the boma. The hierarchical stability index was 0.965, where a value of 1 represents a stable hierarchy.



2.3.3 Pre-release companionship selection

The modularity index (the test of the strength of division of individuals into groups) revealed that the rhino groups identified by behaviour type while in the boma were statistically insubstantial (Q<0.3) (Figure 2.10). However, the final period in the boma produced a significant, but slight, division (Q=0.33) between male and female rhino (Figure 2.11).

Figure 2.10. Sociograms for each behaviour type, a) feeding, b) resting, c) when mobile, d) combined behaviours, for rhino during the acclimation period in the boma. Green circles represent each rhino by ID, thickness of the node lines denotes relationship strength, blue and red clusters indicate separate communities of the network identified using the leading eigenvector algorithm.

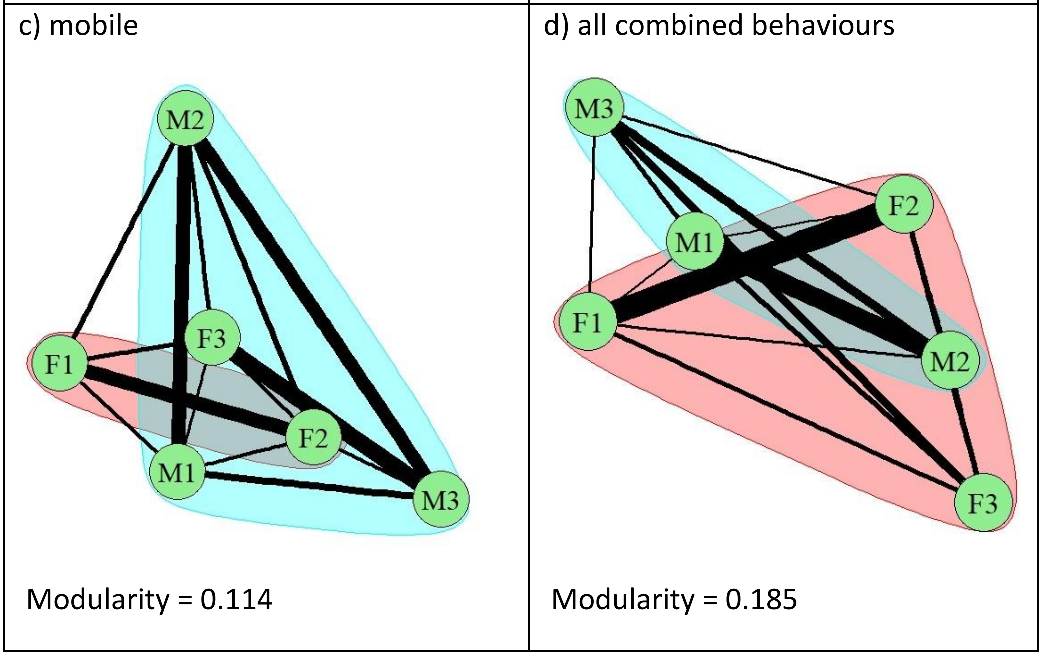


a) feeding

b) resting

Modularity = 0.217

Modularity = 0.165



c) mobile

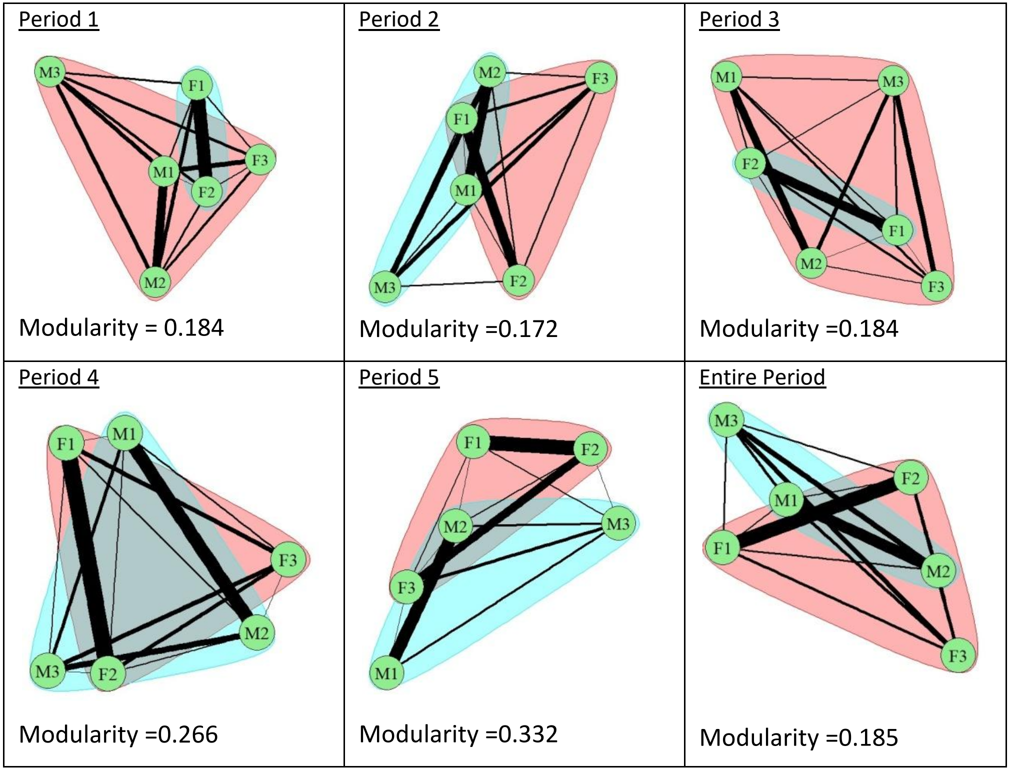
d) all combined behaviours

Modularity = 0.114

Modularity = 0.185

There was a ‘mutual preference’ between same sex pairs F1 and F2, and M1 and M2 during the acclimation period, with the remaining younger mixed sex pair F3 and M3 on the fringes (Kuneš & Bičík, 2002). Choice of cohort corresponded with findings by Owen-Smith (1974), where companions were of a similar age, and the Elo-rating test showed that companions were of a similar hierarchical ranking.

Figure 2.11. Sociograms for rhino divided into time periods (defined in Table 2.3) for the duration of acclimation in the boma. Green circles represent each rhino by ID, thickness of the node lines denotes relationship strength, blue and red indicates separate communities of the network identified using the leading eigenvector algorithm.



Period 1
Modularity = 0.184

Period 2
Modularity =0.172

Period 3
Modularity =0.184

Period 4
Modularity =0.266

Period 5
Modularity =0.332

Entire Period
Modularity =0.185

Mean inter-individual distance (IID) for both resting (n=722) and feeding (n=949) was 3 metres, and when mobile (n=303) mean IID was 6 m. Cohesive pairs were often observed in very close proximity, almost touching or in actual bodily contact (Figure 2.12).

Figure 2.12. Photographs displaying inter-individual distances between wild rhino when resting and feeding while in the boma.

I aimed to predict the companionship choices of rhino after they were released based upon sociograms created from pre-release data (Figure 2.10). The choice of companion for the top two dominance pairs did not change during the period of confinement. My estimates of post-release companionship choices are summarised in Table 2.8.

Table 2.8. Rhino cohesive pairs in order of dominance observed in the boma based upon sociogram plots; the data represent predicted selection of post-release companions.

Pair 1	F1 & F2
Pair 2	M1 & M2
Pair 3	F3 & M3

2.3.4 Post-release companionship selection

The association between paired companions in the boma was a good predictor of companionship choice after release, because cohorts selected the same companion for the part flood season 2013 (modularity index=0.67) (Figure 2.13) that I had predicted (Table 2.8). Companionship selection remained unchanged in the hot dry season 2013, but showed some interaction with individuals from the other cohesive pairings (Table 2.8) (modularity = 0.5). F3 and M3 stayed together for a total of 29 months (Figure 2.13 and Table 2.9), excluding periods of anthropogenic disturbance.

During the rainy season 2013 F1 calved, and this probably affected the entire dynamics of each companionship pair. The F1 and F2 pairing split days before the onset of parturition, with F2 joining M1 and M2. F1 probably selected isolation because cows may no longer accept companions after giving birth (Shrader & Owen-Smith, 2002).

Social division occurred when M1 left M2 and F2 (who dispersed from the area) and established a loose association with F3 and M3 (modularity index (Q) = 0.5). This was initially brought about by spatiotemporal overlap of ranges formed in the rainy season 2013/14. The strength of M1's relationship with F3 and M3 became firmer in the flood season 2014 and was sustained until the end of the study period (rainy season 2014/15).

Table 2.9. Summary of the dynamic association indices for each rhino dyad for the first 12 months after release. Half-weight Association Indices (HWAI) >0.5 represent preferred association within shared areas: HWAI<0.5 equates to avoidance within a shared area, Coefficient of association (Ca) >0.5 signifies attraction, Ca<0.5 relates to avoidance, Benhamou's IAB Index where p-Avoid represents the probability of significant avoidance, p-Attract represents the significance of attraction, the Proximity Index (Prox) indicates the proportion of fixes within time and distance thresholds.

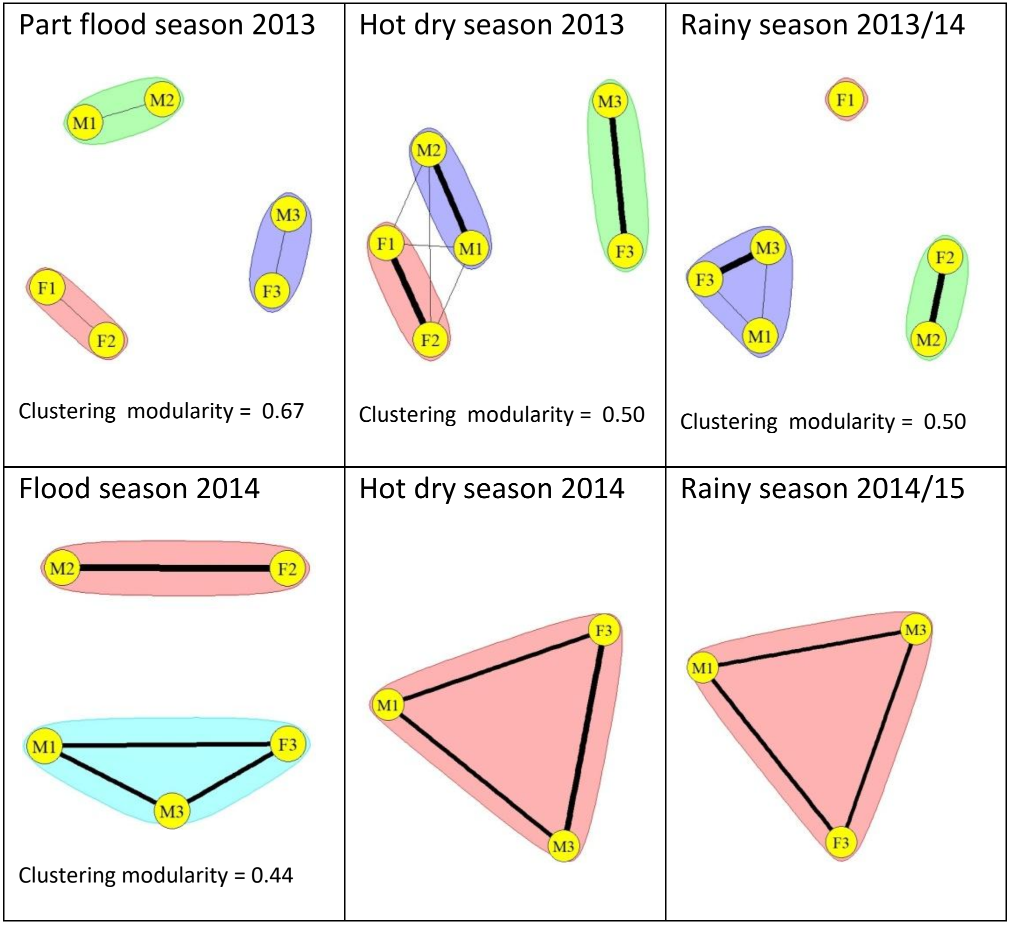
Dyad		HWAI	Ca	IAB		Prox
				p-Avoid	p-Attract	
F1	F2	0.918	0.459	1	0.010*	0.980
F1	F3	0.000	0.000	0.500	0.508	0.000
F1	M1	0.000	0.004	0.885	0.123	0.008
F1	M2	0.000	0.004	0.866	0.142	0.008
F1	M3	0.000	0.000	0.532	0.476	0.000
F2	F3	0.000	0.000	0.578	0.430	0.000
F2	M1	0.000	0.004	0.970	0.037	0.006
F2	M2	0.147	0.339	1	0.005*	0.488
F2	M3	0.000	0.000	0.580	0.426	0.000
F3	M1	0.008	0.050	1	0.005*	0.074
F3	M2	0.000	0.000	0.697	0.307	0.000
F3	M3	0.753	0.869	1	0.003*	0.937
M1	M2	0.711	0.457	1	0.004*	0.601
M1	M3	0.000	0.053	1	0.004*	0.074
M2	M3	0.000	0.000	0.726	0.278	0.000

*F1's collar dropped off in December 2013; all other rhino were sampled from 16/05/13 to 15/05/2014, * indicates significant results.*

Benhamou's IAB index registered statistically significant avoidance behaviour between animals belonging to different groups that shared overlap zones in their home ranges (Tables S2.2 to S2.7). F3 and M3 avoided other groups during the rainy season 2013/14, which coincided with social group changes that were probably instigated by the birth of F1's calf.

The GPS anklet on F1 failed during the flood season 2014, with anklets on F2 and M2 failing in the hot dry season 2014. I was therefore not able to analyse companionship data for those rhino after those time periods.

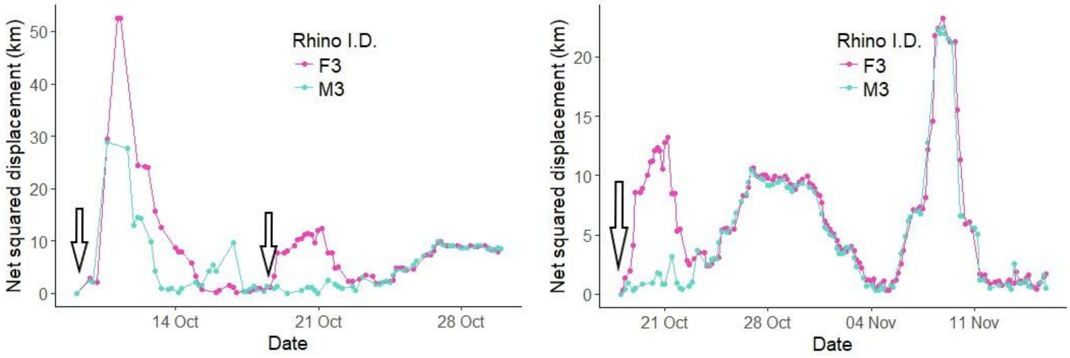
Figure 2.13. Post-release sociograms calculated using proximity index (Bertrand et al.*, 1996) and separated by season. Season definitions: Part Flood season -16th May 2013 to end of June 2013, when rhino were released, Hot dry season -July to October, Rainy season - November to February, Flood season – March to June. Yellow circles represent each rhino by ID, thickness of the node lines denotes relationship strength, and blue, purple, red, and green clusters indicate separate communities of the network identified using the leading eigenvector algorithm.*



2.3.5 Anthropogenic contact and the effect on social relationships and movement

Anthropogenic disturbances divided cohort companions in 67% of cases. In all 3 occasions when F3 and M3 came into contact with humans it caused a split in their association from 6 to 10 days (Figure 2.14). In the first herding event, F3 dispersed >50 km, and M3 dispersed >30 km, both within 2 days. The second herding event was less effective for M3, whereas F3 moved >13 km in 3 days. After their re-association F3 and M3 dispersed, but then returned to the location from where they were herded on two further occasions within a 10 day period.

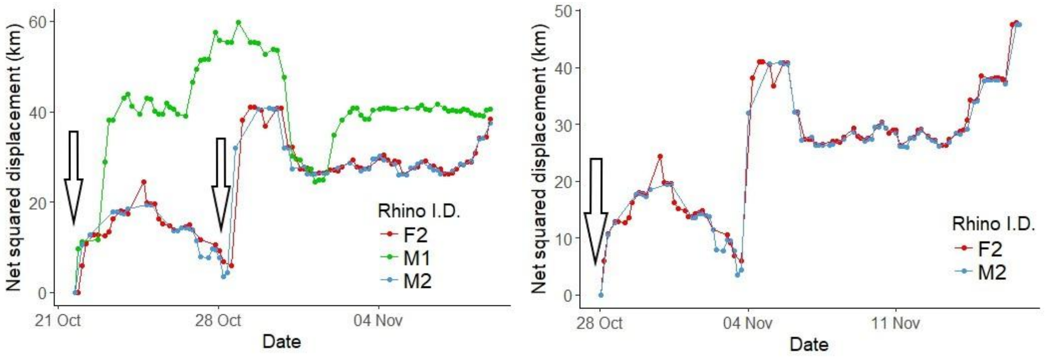
Figure 2.14. Net squared displacement showing the effect of herding rhino on their movements. Arrows denote the start point of herding events for F3 and M3 that took place on the a) 9th and b) 18th October 2013. The herding event on the 18th October is plotted separately because the geographical position where herding took place is different to that of the 9th October.



a) b)

M1, F2 and M2 were herded together on the first occasion, causing the separation of M1 from the group (Figure 2.15). M1 dispersed 38 km within 2 days of the herding, and F2 and M2 returned to within <6 km of the location of the herding within 7 days, when they were herded again and came to within <4 km of the second herding location after 5 days. In the third herding of F2 and M2 they dispersed >117 km in 18 days and did not return while the GPS collar anklets were transmitting (Figure 2.16).

Figure 2.15. Net squared displacement showing the effect of herding rhino on their movements. Arrows denote start point of herding events on a) 21st October 2013 for F2, M1 and M2, and b) 28th October 2013 for F2 and M2. The herding event of the 28th October is plotted separately because the geographical position where herding took place is different to that of the 21st October.



a) b)

Figure 2.16. Net squared displacement to measure the effectiveness of herding rhino from the fence line. The arrow denotes the herding event for F2 and M2 on 6th February 2014.

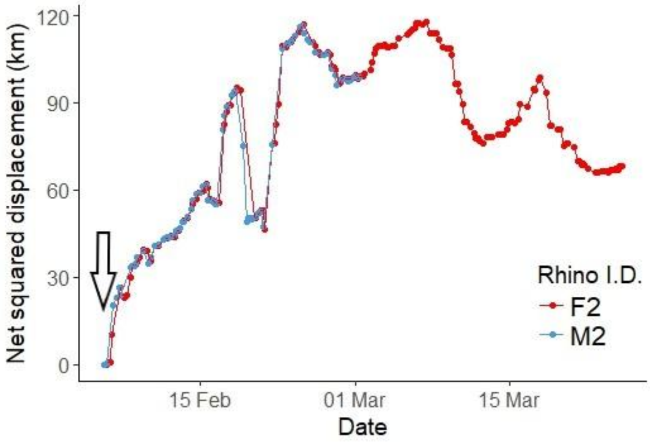
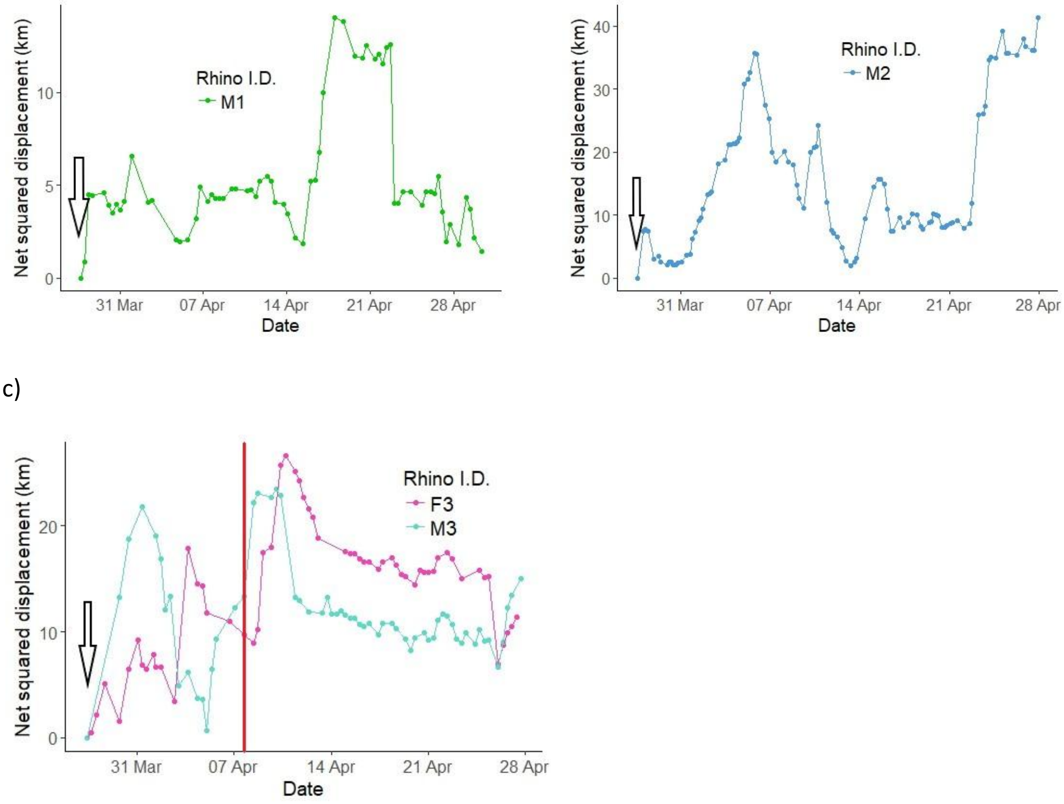


Figure 2.17. Net squared displacement to measure rhino movements after re-collaring on 27th March 2014. Arrows indicate start point a) for M1, b) for M2, c) for F3 and M3, and red line indicates the re-association of F3 and M3.


a)

b)

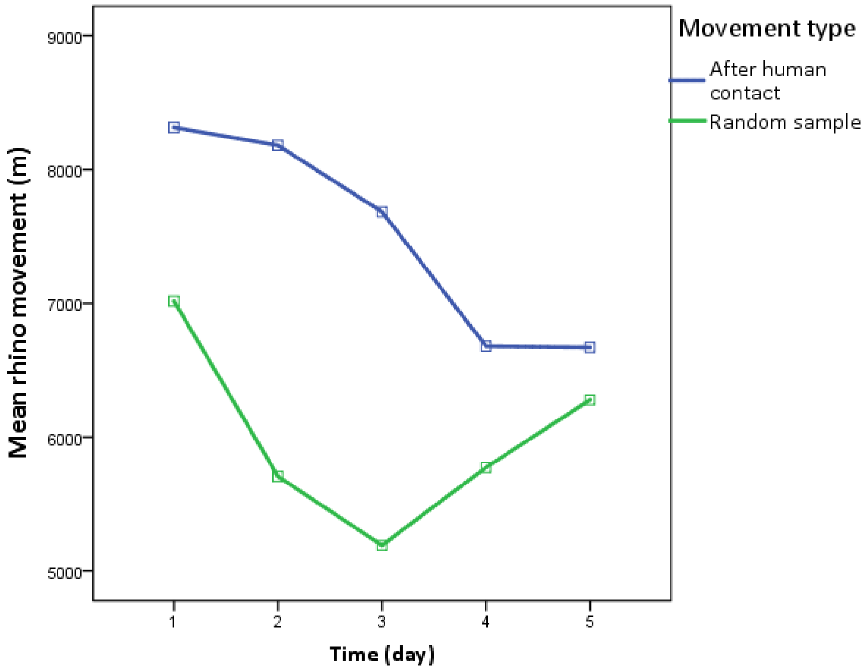
c)

M1 displayed mainly sedentary behaviour after being re-collared (Figure 2.17a), mostly staying within 5 km of the re-collaring site, whereas M2 (Figure 2.17b) left but returned to ≈2 km of the re-collaring site around 2 weeks later. F3 and M3 were split during the re-collaring (Figure 2.17c); M3 returned to the re-collaring site 8 days later but F3 did not.

2.3.5.1 *Daily movement effects*

Using a repeated measures design to account for pseudoreplication I found a significant difference when comparing random movement behaviour with movements after human contact (Figure 2.18) (ANOVA, $F_{1,4}$=12.268, p=0.025), but there was no significant difference in movement over time between these factors ($F_{4,16}$=0.930, p=0.471). I compared herding and re-collaring events to determine whether they had an equal effect on rhino mobility, irrespective of the type of disturbance. There was no difference in movement between rhino being chased for re-collaring (mean=5462.52, S.D.= 3207.32) and being herding for security (mean=8328.52, S.D.= 3962.85); t(3)=0.883, p=0.442).

Figure 2.18. Results of ANOVA, showing mean movements for the 5 day period after human contact compared to a 5 day random sample.



2.4 Discussion

2.4.1 Acclimation behaviour

My research highlights the importance of rhino sociality and management, before capture and relocation (the selection of individuals to be transported), during acclimation (exposure to stressors) and release (monitoring and security) into novel environments. Stress is a predictable consequence of the translocation process because animals go through the process of capture, handling, captivity, transportation and release into a novel environment (Millspaugh *et al.*, 2007; Dickens *et al.*, 2010; Snyder *et al.*, 2012). Captivity imposes environmental depravation, reduced inter-individual distance (IID) and less opportunity for avoidance (Deag, 1977). In the wild, free ranging territorial white rhino bulls sometimes clash at the territory border (Owen-Smith, 1974). However, cows are unconcerned with the company of other cows and subadults (Patton *et al.*, 2016), whereas subadults are generally curious and may form small groups (Patton *et al.*, 2016; Owen-Smith, 1974, 1975).

With little refuge available within the boma, the rhino established a hierarchy which was most probably induced by environmental stressors (Metrione *et al.*, 2007; Price & Stoinski, 2007). In primates, stressful situations and intragroup competition for resources force hierarchical social structures (Rowell, 1974; Price & Stoinski, 2007; Stevens *et al.*, 2007). Unlike Meister (1998), I found a statistically significant linear hierarchy within the group. Although some caution should be applied since the size of the sample group was just 6 individuals. Previous research also showed that captive adult rhino females established a hierarchical social system (Mikulica, 1991; Kuneš & Bičík, 2002; Metrione *et al.*, 2007; Cinková & Bičík, 2013).

Wild giraffe behaviour resembles rhino since it is only males that exhibit dominance interactions (Coe, 1967; Horová *et al.*, 2015). Using the same method as in this study (Landau's index of linearity) hierarchical social structures were found in captive giraffe and these were stronger in herds of 8 –

14 individuals, compared to smaller ones of 6 – 8 individuals. In contrast to my study however, one adult male was present in each herd, and in all but one case the male was highest ranked (Horová *et al.*, 2015). However, observed in their natural habitat a family group of guanacos (*Lama guanicoe*) demonstrated a highly linear female hierarchy with males placed at the bottom (Correa *et al.*, 2013). Female family groups of the African elephant display asymmetric dyadic relationships between older and younger females, with older individuals dominating younger individuals (Archie *et al.*, 2006).

Swaisgood *et al.* (2006) suggested that limited evidence for asymmetric dominance in rhino females may have been due to a lack of sufficient data, and Metrione *et al.* (2007) found evidence of both linear and intransitive (circular) relationships in certain groups. I re-examined these data plotting NormDS scores, calculating Landau's dominance tests (Landau, 1951), and tested for statistical significance. I found statistically non-significant linear hierarchies for each of the datasets (Figure S2.5) but on some occasions the order of dominance was different from that which was reported (Kuneš & Bičík, 2002; Metrione *et al.*, 2007). Swaisgood *et al.* (2006) argued that reproductive suppression in female subordinates by dominant females would only occur in a highly social species with a structured dominance hierarchy, and that this is improbable in rhino since sociality between wild rhino is not obligatory (Owen-Smith, 1975). A female dominance hierarchy in Cuvier's gazelle (*Gazella cuvieri*) triggered lower fecundity, decreased offspring survival and an increase in the age of the animal at its first birth in lower ranked individuals (Escós, 1992). However, social integration between unrelated female feral horses increased birth and survival rates irrespective of dominance rank (Cameron *et al.*, 2009). Although the timescale of my study did not extend to analysing the reproductive impacts of captivity, the wild rhino I studied developed a hierarchy within a relatively short period of captivity probably because they were kept in a smaller enclosure.

A linear hierarchy structure could indicate to lower ranking individuals that they would expect to lose an altercation with a higher ranking individual (de Vries *et al.,* 2006). Elo-rating tests revealed some dominance switching between selected cohorts, but not between pairs, perhaps indicating that the animals were operating in set pairs. Forming a stable hierarchy could lead to lower aggressiveness and competition, but the advantages and disadvantages associated with stability are not necessarily equal between individuals of differing ranks (de Vries *et al.*, 2003). Rowell (1974) and Archie *et al*. (2006) hypothesised that altercations reduced over time when individuals had learned their position in the social order. My results supported this theory, as demonstrated by the decline of agonistic interactions half-way (35 days) through the captivity period.

The adult-subadult female companions F1 and F2 (around 6 years old) won more altercations and were higher ranked than similarly aged subadult male companions M1 and M2. My results corresponded with findings that aggressive behaviour between companion females was rare, using vocal rather than physical interactions (Swaisgood *et al.*, 2006). However, in this mixed sex group vocalisations were used by all individuals more frequently than aggressive interactions.

Abnormal animal behaviour in captivity has been linked to suboptimal group size (Price & Stoinski, 2007). Snarls were more commonly used as a demonstration of supremacy than physical altercations and, as with previous research of captive rhino interactions, the majority of vocalisations took place during feeding when competition was highest (Kuneš & Bičík, 2002; Metrione *et al.*, 2007; Cinková & Bičík, 2013). In agreement with previous findings, interactions could be managed by spreading food piles more widely within the boma, and increasing enclosure size could contibute to increasing proximal distance and reducing competition for food (Hutchins & Kreger, 2006; Metrione *et al.*, 2007). Results were determined using a small number of animals over a relatively short period, so caution should be applied in examining these results.

My results supported the hypothesis that wild rhino held in temporary captivity engaged in similar behaviour as their captive counterparts. Perhaps this is not surprising since stereotyped behaviours such as licking and pacing have been observed in two species of ungulates, giraffes and okapi (*Okapi johnstoni*) (Bashaw *et al.*, 2001). However, the group composition differed from other studies because it comprised mixed sex subadults, compared to others that consisted of adult cows and juvenile rhino, which were sometimes joined with an adult bull (Kuneš & Bičík, 2002; Swaisgood *et al.*, 2006; Metrione *et al.*, 2007). In future research affiliative behaviour should be included to give an overall representation of all interaction behaviour, but more research is needed to determine optimal composition and group size in captivity.

2.4.2 Companionship selection predictions

Companionships between social animals can contribute to greater reproductive success, longer lifespan, and better fitness (Wittig *et al.*, 2016). In relation to translocation, the social integration of introduced bighorn sheep to resident population was analysed (Poirier & Festa-Bianchet, 2018), as well as the sociality between individuals within a small population of translocated giraffe (*Giraffa camelopardalis giraffe*) (Malyjurkova *et al.*, 2014). However, neither study compared pre-release to post-release cohort relationships. Social behaviour studies of animals tend to incorporate either captive populations (Schulte, 2000; Metrione *et al.*, 2007; Stevens *et al.*, 2007; Price & Stoinski, 2007), of which some may be released into free ranging environments (Evans *et al.*, 2013) or of resident free-ranging animals (Robbins, 1996; Evans & Harris, 2008). Therefore, a comparable analysis of the behaviour of wild animals in both a captive and free ranging environment is rare.

Metrione *et al.* (2007) reported companionships between captive white rhino, although it is uncertain as to how these companionship bonds were analysed.

However, companionships between captive rhino do not compensate for the stress of captivity since reproduction is notoriously poor (Schmidt & Sachser, 1997; Kuneš & Bičík, 2002; Carlstead & Brown, 2005; Hermes *et al.*, 2005; Hermes *et al.*, 2006; Swaisgood *et al.*, 2006; Tubbs *et al.*, 2016).

I used social network analysis to identify social bonds between wild captured rhino that were being acclimated before release into the Okavango Delta. I established that the group divided into companionship pairs, with companions being adjacent in hierarchical rank. However, it is unclear whether hierarchical rank influenced companionship choice, or whether choice of cohort influenced hierarchical status. Companions were also of a similar age (Owen-Smith, 1974) and the choice of cohort did not appear to change throughout the acclimation period.

Overall for the first 2 years after their release in the Okavango, the rhino generally preferred to be associated with a companion rather than be alone. Persistent associations (29 months) were recorded between these subadults (Patton *et al.*, 2016). However, since there were only 6 rhino involved in the translocation, this provided limited companionship choices.

Pre-release companionship selection may assist in identifying rhino dispersal ‘buddies’ (Shrader & Owen-Smith, 2002), since the bonds detected before release continued after the animals dispersed, as hypothesised. This information could help conservation managers to identify how to distribute anti-poaching teams, but further research is necessary to establish whether hierarchy, age or gender have any significant influence on companionship choice. Conversely long distance dispersal may be a result of unsuitable or limited companionship choices in small population releases, as was the case here. For successful post-release adjustment, suitable friends or mates are necessary (Linklater *et al.*, 2012).

2.4.3 Herding and anthropogenic disturbance effects

After re-collaring and herding events, individuals increased their daily movement patterns, potentially contributing to physiological stress (Wilson & McMahon, 2006; Tarlow & Blumstein, 2007). However, there were relatively few disturbance events from which to collate data. Nevertheless, conservation managers need to be aware of the animal's physical condition, reproductive state, group composition, time of day, season, and type of disturbance, and take these into account when considering the fitness costs to the animal if it is herded or re-collared (Wilson & McMahon, 2006; Tarlow & Blumstein, 2007; Stankowich, 2008).

The rhino were chased with a helicopter and vehicles for re-collaring and with vehicles and on foot for herding events. These induced avoidance behaviour in the form of flight responses in all animals (McGowan *et al.*, 2014). When approached by recreational game vehicles several weeks and months later, rhino displayed the same response and therefore possibly the same perceived predatory threat (McGowan *et al.*, 2014; Samia *et al.*, 2015). This is contrary to anecdotal evidence of their relaxed behaviour towards game vehicles before being relocated from South Africa. From a security perspective, flight responses in rhino are more favourable than the adaptation of tolerance to people, vehicles or helicopters.

I cannot substantiate the hypothesis that herding rhino from areas perceived as dangerous is an effective method of control, since some animals returned to herding sites (<5 km). The same was true of re-collaring exercises. In cases where rhino met boundary fences they became exposed and needed to be moved. Use of an additional fence line as an additional 'biosecurity barrier' (Bode & Wintle, 2010) would create buffer zones (Blumstein *et al.*, 2003; Koch & Paton, 2014) to help prevent animals from locating to potentially dangerous areas.

Rhino may have encountered social stress by being temporarily, and in one case permanently, separated from their chosen cohort or group (Kikusui *et al.*, 2006), but this may depend upon the type of association (Hennessy *et al.*, 2009). Since 'social buffering' (Cohen & Wills, 1985) assists in recovery from stressful encounters (Kikusui *et al.*, 2006; Young *et al.*, 2014), stress levels in rhino would need to be measured under each circumstance to determine if stress was raised (Moberg, 2000; Creel *et al.*, 2002; Laws *et al.*, 2007; Viljoen *et al.*, 2008; Linklater *et al.*, 2010) as a consequence of disturbance or due to being separated from a companion. A stress response results in the secretion of glucocorticoid hormones, and these can be measured via a non-invasive approach of assaying fecal glucocorticoid metabolites. Metabolites are usually elevated in animals exposed to human activity (Sapolsky *et al.*, 2000; Dickens *et al.,* 2010). In time dyads reassembled, or individuals formed with other groups, and so I cannot support the hypothesis that herding has a negative long-term effect on rhino social groups.

2.5 Conclusions

Captured wild rhino held in temporary captivity displayed similar behaviour as a captive held zoo rhino, and possibly as a result of intragroup competition. Snarling took place mostly during feeding times. Rhino established a stable linear hierarchy compared to statistically non-significant linear hierarchies in previous research. Furthermore, using the same techniques to re-examine previous studies provided differing results, highlighting the requirement for a better understanding of rhino social groups. The optimal captive group size and composition still needs to be determined.

Rhino formed paired companionship selection during the acclimation period in the boma, and cohorts were sustained after initial release into the Okavango Delta. Generally subadult rhino preferred the company of other conspecifics than being alone. This is the first social network analysis of a captured wild rhino social group carried out before, and after their subsequent re-release.

Anthropogenic disturbance caused an increase in usual daily movement activities. Therefore there was an energetic cost associated with herding. Herding rhino for security had little success, with some animals returning to the area from where they were herded or re-collared. Associations between individuals were mostly temporary, but sometimes permanently disrupted as a result of disturbance.

2.6 Link to next chapter

In this chapter I established that wild caught mixed sex subadult rhino group held collectively for a short period established a dominance hierarchy, and that their behaviour was similar to captive held rhino. I determined that some rhino selected long-term companions, but were temporarily affected by anthropogenic disturbance. Herding rhino was not effective for all rhino as a security management tool.

In the next chapter I analyse the post-release movement behaviour of rhino in greater detail at different spatial scales. I use GPS data to assess the movement strategies between individuals.

Chapter 3. Post-release movements of a translocated ‘sedentary’ megaherbivore

3.1 Introduction

The deliberate movement or ‘translocation’ of animals can be used to re-establish lost ranges, manage populations under threat of persecution (IUCN, 1998; Linklater & Swaisgood, 2008), and resolve human-wildlife conflict (Fischer & Lindenmayer, 2000; Read *et al.*, 2007; Fernando *et al.*, 2012; Swan *et al.*, 2017). The impact of translocation on the target animals can be measured by comparing body condition, physiological stress measures and behavioural time budgets to those of the resident population (Molony *et al.*, 2006; Armstrong & Seddon, 2008; Pinter-Wollman *et al.*, 2009). The rate of mortality, reproduction, dispersal movements, and territory establishment are also indicators of translocation success or failure (Armstrong & Seddon, 2008; Flanagan *et al.*, 2016).

Given the time scale of this study, animal movement behaviour was used to assess the short-term success or failure of the translocation (Fernando *et al.*, 2012; Flanagan *et al.*, 2016). Fernando *et al.* (2012) showed that elephants displayed different responses to translocation: ‘homers’ attempted to return to the capture site, ‘wonderers’ ranged widely and ‘settlers’ established home ranges or territories. I aimed to use homing, settlement and dispersal/wondering behaviour to assess translocation success. After introduction into new environments animals usually disperse (Stamps & Swaisgood, 2007; Yiu *et al.*, 2015). Following a period of exploration and familiarisation of the new environment, introduced animals should modify their behaviour from large dispersal movements, to small movements within a familiar range (Berger-Tal & Saltz, 2014).

As an example of where translocation was negatively affected by dispersal, the reintroduction of caribou (*Rangifer tarandus*) in Newfoundland, eastern North

America failed because the resident animals emigrated and joined introduced herds, thereby creating a vacuum effect (Bergerud & Mercer, 1989; Mihoub *et al.*, 2011). As a founding population in an unfamiliar area, displaced animals may disperse over large distances and have larger home range sizes than natural populations (Burns, 2005; Mihoub *et al.*, 2011).

Burt (1943) first described a home range as the area 'traversed by the individual in its normal activities of food gathering, mating, and caring for young'. While the standard definition for some time, the concept has evolved to include the analysis of resources used for survival and reproduction, as well as population and community dynamics (Brown, 1975; Schoener, 1981). Most recently home range has been used to describe the updated cognitive map of an individual's environment (Powell & Mitchell, 2012). However, translocated animals are not acquainted with their surroundings or resource availability (Borger *et al.*, 2008), so it is difficult to apply this concept to translocated animals. I therefore use the term range rather than home range in this chapter.

Table 3.1. White rhino range statistics for parks and reserves in South Africa.

Reserve	**Available area (km²)**	**Density per km²**	**Male territory size (km²)**	**Female home range size (km²)**	**Method of calculation**	**Reference**
South-west Kruger national park	-	0.5 to 1.4	6.2 to 13.8	7.2 to 45.2	MCP	Pienaar *et al.* (1993b)
Ndumu Game reserve	100	0.6 to 1.8	2.5 to 13.9	4.7 to 22.9	MCP	Conway & Goodman (1989)
Hluhluwe-Umfolozi	960	3.0 to 5.7	0.8 to 2.6	8.9 to 20.5	MCP	Owen-Smith (1973) and White *et al.* (2007)
Hluhluwe-Umfolozi	960	>3.0	2.6 to 9.0	≈ 30.0 ≈ 19.0 (KDE)	MCP KDE	White *et al.* (2007)
Welgevonden Game Reserve	<400	0.2	1.0 to 22.0	Mean 17.5	KDE	Thompson *et al.* (2016)
MCP: minimum convex polygon, KDE: kernel density estimator, ≈ indicates approximation.						

Adult territorial male rhino and adult female rhino have distinct ranges (Table 3.1). Sometimes subordinate males, territorial males, and female adult rhino temporarily leave their ranges to access water resources (Owen-Smith, 1974; Shrader & Owen-Smith, 2002). Subadult rhino may be semi-nomadic, remaining in one area for several months before dispersing and settling elsewhere (Owen-Smith, 1974). So a successful translocation should also be represented by typical rhino movement behaviour.

Large migratory herbivores such as elephants can orientate towards specific goals (Duffy *et al.*, 2011; Leo Polansky *et al.*, 2015), or use pathways that direct them towards resources (Blake & Inkamba-Nkulu, 2004). Conversely, sedentary (non-migratory) animals tend to restrict their movements to selected areas (Benhamou, 1989). Information about mammal navigation is largely based on animals translocated due to human wildlife conflict (Fritts *et al.*, 1984; Linnell *et al.*, 1997; Bradley *et al.*, 2005; Fernando *et al.*, 2012; Priatna *et al.*, 2012). True navigation (‘homing’) is apparent when translocated animals are able to orientate towards their capture site without the aid of cues (Miller & Ballard, 1982; Fritts *et al.*, 1984; Boles & Lohmann, 2003; Read *et al.*, 2007; Tsoar *et al.*, 2011; Fernando *et al.*, 2012). Research into homing abilities in animals has largely focussed on marine life (Boles & Lohmann, 2003; Read *et al.*, 2007; Lohmann *et al.*, 2008; Putman *et al.*, 2013; Brothers & Lohmann, 2015), birds (Kramer, 1961; Wiltschko & Wiltschko, 2003; Thorup *et al.*, 2007) and insects (Collett, 1996; Tsoar *et al.*, 2011; Wolf, 2011; Collett *et al.*, 2013). Although there is a species specific distance whereby animals are no longer able to navigate home, some individuals of those species are still able to ‘home’ (Rogers, 1984). Large unidirectional dispersal movements have been recorded for translocated rhino (Pienaar, 1970; Herbert & Austen, 1972; (Armstrong & Seddon, 2008), therefore perhaps rhino are able to navigate towards particular goals. I determined whether individuals in a small group of translocated rhino sought to return to the capture location, and so perhaps possessed homing ability (Fernando *et al.*, 2012). Rhino had limited local cues since they were placed into crates at the capture site for transportation to the release site 1,500km away (Boles & Lohmann, 2003). Therefore, dispersal from the release site with orientation towards the capture site may mean rhino are able to utilise global cues (Gould, 2015).

Remote monitoring of animal movements has been made easier with the advent of Global Positioning System (GPS) technology, allowing analysis of continuous data at different spatial scales (Fryxell *et al.*, 2008). For example, GPS data have been used to analyse the turn angles of elk (*Cervus elaphus*) during foraging and non-foraging movements (Fryxell *et al.*, 2008) and the relocation behaviour of female Cape buffalo using random walk models (Benhamou, 2014). At the landscape level, GPS has been used to determine animal movements (Brooks & Harris, 2008; Bartlam-Brooks *et al.*, 2011) and estimate home range size for various mammal species (Borger *et al.*, 2008; Bartlam-Brooks *et al.*, 2013; Bennitt *et al.*, 2014; Owen-Smith & Martin, 2015; Aronsson *et al.*, 2016). At larger scales, GPS facilitated the recent discovery of long-distance migration of Burchell's zebra (*E. quagga*) in Botswana (Bartlam-Brooks *et al.*, 2011), and has been used to map wildebeest (*C. taurinus*) migrations across the Serengeti-Mara ecosystem (Thirgood *et al.*, 2004; Harris *et al.*, 2009). VHF (very high-frequency) technology relies on receivers to be close enough to be able to triangulate the animal's position, with the additional drawback of researchers' presence possibily affecting the animal's behaviour (Cagnacci *et al.*, 2010). GPS has the advantage of remotely determining animal movement behavioural patterns e.g., migratory, mixed migratory, home ranging (resident), dispersive or nomadic (Bunnefeld *et al.*, 2011; Borger & Fryxell, 2012; Papworth *et al.*, 2012; Singh *et al.*, 2016), or whether relocated animals display navigation abilities by means of orienting towards their capture or natal site (Read *et al.*, 2007; Miller *et al.*, 2011; Fernando *et al.*, 2012; Odden *et al.*, 2014). However, the weight ratio of tracking devices to body mass may cause a disruption in natural behaviour (Berteaux *et al.*, 1996; Murray & Fuller, 2000; Kumpula *et al.*, 2001). Brooks *et al.* (2008) found that small changes in GPS collar weights and fit altered natural behaviour. Zebra fitted with heavier collars (0.6% of total body mass) travelled at less than half the speed within foraging patches compared to zebra fitted with lighter ones (0.4% of total body mass), thereby potentially increasing the cost of foraging.

In this chapter I investigated the movement behaviour of six translocated subadult rhino. The animals were released into an unoccupied area of the Okavango Delta. GPS anklets were used to collect movement data at larger scales, and a hand held GPS device was used to collect fine scale turn angle data along the movement pathways of rhino. These movement data were used to test the following hypotheses:-

1) After their release, rhino would initially disperse to investigate their new environment. I hypothesised that this would be followed by typical subadult behaviour of semi-nomadic settlement followed by short periods of movement, and would happen within a year from the date of release.

2) Range sizes would be smaller in flood season and largest in the resource abundant rainy season and, because the area of release was unpopulated by other rhinos, ‘ranges’ would be larger than previously recorded ‘home ranges’.

3) Range size, and overlap of ranges between individuals, would be affected by season and sex. Adult females typically have larger ranges that overlap more compared to male rhino territories, so I tested the hypotheses that subadult female rhino shared more space than subadult male rhino and that range sizes and the sharing of ranges would differ as a result of the variation in seasonal resources.

4) Rhino translocated 1,500 km from the capture site are not able to navigate ‘home’.

5) Rhino orientation along relocation pathways does not vary between seasons since they orientate towards particular goals, but I hypothesise that rhino take a more direct route through open grasslands compared to closed vegetation

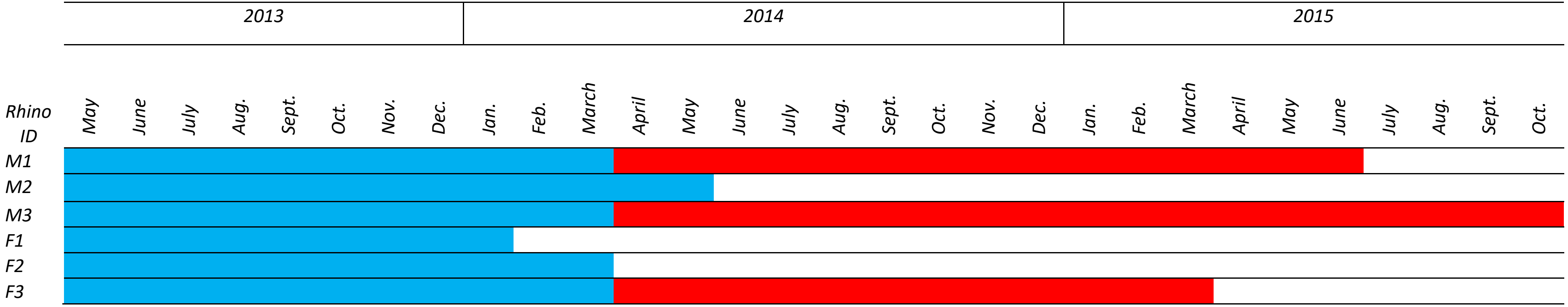
woodland habitats, and so the degree of orientation will vary between habitat types.

3.2 Methods

3.2.1 GPS

GPS anklets were fitted to six white rhino before they were released in the Okavango Delta on 16th May 2013. For approximately the first 10 months the position of each animal was recorded at 4h intervals. In March 2014 an effort was made to replace all anklets, but this was only possible on three rhino. Due to sample size issues only data from the first 10 months was used. Replacement anklets recorded the individuals' position at 8h intervals (Table 3.2). To reduce positional error of measurements, 3D fixes with horizontal dilution of precision (HDOP) of <10 were used in the analyses (D'Eon & Delparte, 2005).

Table 3.2. GPS data collection period from devices deployed on six rhino. Blue represents the original set of GPS anklets with location fix intervals every 4 hours, and red indicates deployment of replacement anklets with location fix intervals every 8 hours. There were limited data collected from February 2014 onwards due to anklet failures.



	2013								*2014*												*2015*									
Rhino ID	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*March*	*April*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Feb.*	*March*	*April*	*May*	*June*	*July*	*Aug.*	*Sept.*	*Oct.*
M1	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥				
M2	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦																	
M3	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥
F1	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦																					
F2	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦																			
F3	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟦	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥	🟥							

*Table 3.3. Recorded location information gathered from GPS anklet deployed on rhino (n=6). Fixes with horizontal dilution of precision HDOP<10 (10,139 fixes from a total of 17,805) were used. Data includes a combination of original (fix interval every 4 hours) and replacement anklets (fix interval every 8 hours), *indicates faulty anklet.*

Rhino ID	Anklet transmission dates		GPS fixes HDOP<10 4h interval	% fixes HDOP<10	Replacement anklet transmission dates		GPS fixes HDOP<10 8h interval	% fixes HDOP<10	Total number of fixes
	From	To			From	To			
M1	16/05/2013	22/03/2014	1323	97	27/03/14	24/06/2015	831	96	2154
M2	16/05/2013	17/05/2014	1511	96	-	-	-	-	1511
M3	16/05/2013	24/03/2014	1145	94	27/03/14	18/10/2015	1032	96	2177
F1	16/05/2013	13/12/2013	1181	97	-	-	-	-	1181
F2	16/05/2013	24/03/2014	1248	95	25/03/14	30/03/2014	21 *	96	1269
F3	16/05/2013	17/03/2014	1258	96	26/03/14	19/03/2015	589	94	1847

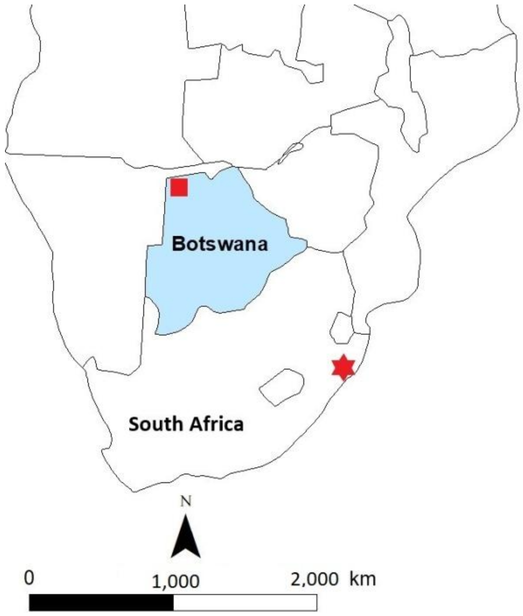
3.2.2 Homing Behaviour

The bearing angle (equation 3.1) between the release site and capture site (Figure 3.1) was calculated using the formula:

$$\theta = atan2(\sin \Delta\lambda \cdot \cos \varphi 2, \cos \varphi 1 \cdot \sin \varphi 2 - \sin \varphi 1 \cdot \cos \varphi 2 \cdot \cos \Delta\lambda) \tag{3.1}$$

where ϕ1, λ1 signified the release site, and ϕ2, λ2 signified the capture site, and Δλ was the difference in longitude .

Figure 3.1. Translocation map. The star indicates the capture site in South Africa and square indicates release site in the Okavango Delta, Botswana. The distance between the capture and release site was approximately 1500km.



Location data for each rhino were collected from the time of release until the individuals were impeded by a boundary fence (Table 3.4). I examined the data and identified data points when it was likely that rhino were inactive during the hottest part of the day. Therefore, to avoid spatiotemporal autocorrelation for this time period distances ≤ 4h within 200m were excluded (Turchin, 1998). The relative angles for each rhino were calculated from UTM transformed GPS data by using the package *adehabitatLT* version 0.3.20 (Calenge, 2006) in R (R Core Team, 2016). For each animal the *Circstat* package (Berens, 2009) was used in *MATLAB* 2016a (The Mathworks Inc., Natick, MA 01760-2098, USA) to map the distribution of turning angles, the mean turning angle (α) and the standard deviation around the mean. I also calculated the length of the mean resultant vector (r). The value of r between 0 and 1 represented the degree of scatter of the distribution of angles around the mean turning angle (α). The closer r was to 1, the more concentrated the angles were around the mean (α), thereby displaying a more straight line movement strategy in a particular direction (Batschelet, 1981; Benhamou, 2004; Åkesson *et al.*, 2016).

Table 3.4. GPS data used to analyse homing behaviour of six translocated rhino moved approximately 1500km from the capture site. To avoid spatiotemporal autocorrelation GPS fixes within 200m in ≤ 4 hours were removed.

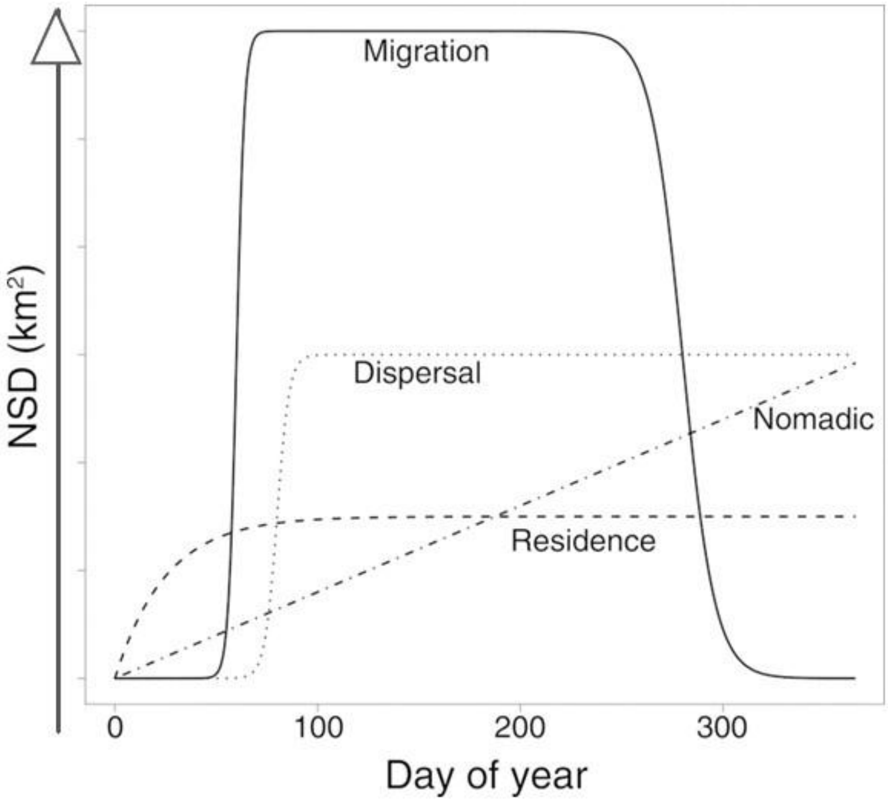
Rhino ID	Dates included	% of fixes HDOP <10	Number of fixes removed to avoid autocorrelation	Number of GPS fixes with HDOP <10 included in calculations
M1	16/05/2013 – 21/05/2013	100	2	16
M2	16/05/2013 – 21/05/2013	96	6	15
M3	16/05/2013 – 19/05/2013	100	1	8
F1	16/05/2013 – 22/05/2013	100	2	21
F2	16/05/2013 – 22/05/2013	100	2	17
F3	16/05/2013 – 18/05/2013	100	2	7

An adaptation of Rayleigh’s test, known as the V test, was used to measure the circular uniformity around the angle of the capture site (Batschelet, 1981; Zar, 1999; Berens, 2009; Åkesson *et al.*, 2016). Significant results indicate directional movement towards the capture site.

3.2.3 Post-release movement behaviour

To determine whether rhino became settled within the first year after release, I analysed movement behaviour strategies using net squared displacement (NSD) (Fryxell *et al.*, 2008; Bunnefeld *et al.*, 2011; Papworth *et al.*, 2012; Singh *et al.*, 2016). NSD was calculated as the squared straight line Euclidian distance between the start location and subsequent locations (Kareiva & Shigesada, 1983; Gaudry *et al.*, 2015) (Figure 3.2).

Figure 3.2. Movement behaviour categories defined by the shape of the change in net squared displacement (NSD) over time. Reprinted from Singh et al. *(2012).*



One GPS location per day, per rhino, was used as close to midday (Central Africa Time - CAT) as possible, with GPS locations >4h deviation from midday excluded (Table 3.5). More than one location per day would clutter the NSD plot, so as advocated by Bunnefeld *et al.*(2011) one location per day was used. The package *adehabitatLT* was used to compute NSD from GPS coordinates (Bunnefeld *et al.*, 2011; Papworth *et al.*, 2012).

Table 3.5. GPS fixes for rhino movement analysis using net squared displacement (NSD).

Rhino ID	Dates		Usable daily GPS fixes
	From	To	
M1	16/05/2013	24/03/2014	333
M2	16/05/2013	17/05/2014	358
M3	16/05/2013	24/03/2014	342
F1	16/05/2013	13/12/2013	198
F2	16/05/2013	24/03/2014	220
F3	16/05/2013	18/03/2014	312

A generalised additive mixed model (GAMM) using the package *mgcv* (Wood, 2011) was fitted to NSD movements with animal ID as the random effect, and included 95% confidence intervals. GAMM models enabled the smoothed relationship between NSD and time to be displayed thus enabling clearer identification of differences between individuals in movement behaviour.

3.2.4 Range estimation

Minimum Convex Polygons (MCP) has been most commonly used for rhino range analysis (Owen-Smith, 1973; Conway & Goodman, 1989; Harris *et al.*, 1990; White & Garrott, 1990; Pienaar *et al.*, 1993b; White *et al.*, 2007). However, MCP calculations can include large areas of non-utilised habitat. Alternatively kernel density estimators (kde) may fragment data into clusters that exclude movement corridors (Fieberg & Börger, 2012). A Brownian bridge approach would include the area traversed by investigating animals and exclude unused areas (Bullard, 1999; Horne *et al.*, 2007), but this method was not previously used to detect rhino ranges. I used MCP as an estimator of range size so that I could compare range sizes to those in other studies.

ArcMap 10.3.1 (ESRI, 2015) was used to calculate 100% MCPs to cover the entire series of movements (Mohr, 1947; Kernohan *et al.*, 2001; Fernando *et al.*, 2012). One outlier was removed from the MCP analysis because human disturbance caused individual F3 to relocate a distance of 40km within a 24h period. Up to six fixes per 24h period were used to estimate the exploratory movement of the rhino, with analyses starting from the day of release (16/05/2013) for a period of 365 days, or until collar failure.

Ranges were calculated by individual, by season (Section 1.7.1), as well as the proportion of inter-seasonal range overlap between rhinos (Tables S3.1 to S3.4) using equation 3.2 (Fieberg & Kochanny, 2005):

$$\mathrm{HR}_{i,j} = \frac{\mathrm{A}_{i,j}}{\mathrm{A}_{i}} \tag{3.2}$$

where $\mathrm{HR}_{i,j}$ represents the proportion of home range that animal i is overlapped by animal j. A_{i} is the area range of animal i, and $\mathrm{A}_{i,j}$ is the overlapping area between the ranges of the two animals i and j.

3.2.5 Range modelling

The *nlme* package (Pinheiro *et al.*, 2016) in R was used to fit general linear mixed models to examine the effects of the fixed factors ‘season’ (with 4 levels: flood 2013, hot dry 2013, rainy 2013/14, flood 2014) and ‘sex’ (male or female), on the dependent variables range and range overlap. Both dependent variables were log-transformed to produce Gaussian residuals. Rhino ID was entered as a random effect to account for pseudoreplication (Hurlbert, 1984; Bunnefeld *et al.*, 2011; Gaudry *et al.*, 2015). Three candidate models were produced alongside the null model. Models were ranked by second-order Akaike Information Criterion (AICc) to account for small sample bias adjustment (Burnham & Anderson, 2004), using the *MuMIn* package (Barton, 2016). Model residuals were plotted using the *DHARMa* package (Hartig, 2017) and checked visually for normality and homoscedasticity.

3.2.6 Tortuosity of rhino relocation pathways

Short fix intervals in GPS technology allow fine scale analysis of animal movement turn angles (Franke *et al.*, 2004). Rhino tracks were recorded on foot using a hand-held GPS device (Garmin Montana 600). As a result, the speed of travel of the animal was not recorded (Bailey *et al.*, 1996; Fryxell *et al.*, 2008). The aim was to identify differences in tortuosity of rhino pathways between seasons and habitats (Nams, 1996, 2006; Gumbricht *et al.*, 2004; Bradley, 2012). Paths were recorded for any rhino in the Okavango: this included the 6 project rhino located in the peripheral Delta and existing rhino in the central Delta. In both locations it was difficult to identify individuals. This was largely because not all tracks gave unique clues and not all the individual rhinos tracks were known to conservation teams. These were therefore sampled as a collective. Data were usually gathered within 2 days, or were otherwise spoiled by other animals or weather conditions. There was some bias because it was easier to map tracks where the ground was soft.

Tracks were separated into seasons and edited into usable sections using Garmin BaseCamp 4.6.2. These were imported into R and each coordinate transformed from decimal degrees to UTM format (in meters) to be used in the program Fractal 5 version 5.26 (Nams, 1996). I discretised each track into 100m segments (Table 3.6) and estimated the tortuosity index known as the Fractal Mean (D), giving a value between 1 and 2. An index (D) of 1 corresponded to a straight line path, and a value of 2 characterised a movement with random turns (Nams, 2005). I used a Kruskal-Wallis test to determine whether there was a difference in D between seasons.

Table 3.6. Movement of rhino along relocation pathways were collected on foot using a hand held GPS device. Tracks were edited using Garmin BaseCamp 4.6.2, and split into seasons for analysis.

Season	Dates: From – To	No. of Tracks*	No. angles #	Mean track length (m)
Hot dry	15/12/14 – 07/02/15	13	506	234
Flood	29/03/15 – 02/05/15	6	152	300
Rainy	23/07/15 – 24/09/15	15	429	363

* No. of tracks is the number of independent relocation pathways recorded for unidentified rhino, # No. of angles used after being discretised into 100m segments

3.2.7 Turn angles along rhino pathways

Tracks were discretised into 100m segments using the R package *adehabitatLT* (Calenge, 2006), allocated a relative turn angle, and a GPS coordinate. Rayleigh's Uniformity test was carried out using the Circstat package (Berens, 2009) in MATLAB 2016a to compare relative turning angles between seasons. The null hypothesis of moving in a uniform direction was tested against the alternative hypothesis that movement was not uniformly distributed, and therefore unimodal (Fisher, 1995; Berens, 2009).

To test if rhino moved differently in alternate habitat classes, every turning point was assigned a habitat class. Coordinates corresponding to turns at 100m intervals were imported into Arcmap 10.4.1 (ESRI, 2015) and assigned a habitat class (Section 1.7.2). A circular ANOVA was carried out using the R package *circular* (Agostinelli & Lund, 2013) to test for differences in turning angles between habitats.

3.3 Results

3.3.1 Homing Behaviour

The time-scale of homing behaviour was varied between two and five days, this was because there was some difference in movement patterns between individuals (Table 3.4). The distance between the release site and when rhino met the boundary fence was approximately 40 km and distance to capture site was approximately 1500 km. Data points could not be pooled to analyse movements for the rhino as a population since they did not disperse as a group. Even with a relatively small number of data points the results show that all individuals dispersed in a similar direction until they meet the boundary fence (Figure 3.3 and Figure 3.4). The mean resultant vector demonstrated that F1 and F2 displayed significant variation from a uniform circular distribution (Table 3.7). V test results for M2, F1, and F2 implied a significant unimodal direction towards the capture site (Figure 3.3 and Figure 3.4). Mean turning angles for 5 rhino were within 40° of the bearing angle, with an average of 29.08° $\pm$ 7.40.

*Table 3.7. Circular descriptive statistics including mean resultant vector with 0<r<1, where a value closer to 1 indicates concentration of angles around the mean ($\overline{\alpha}$°) and V test measuring the significance of directional uniformity towards the capture site; *indicates significant values at p<0.05.*

Rhino ID	Mean relative turning angle ($\overline{\alpha}$°)	Angle of variance (degrees^{o})	Circular standard deviation	Mean resultant vector		Distance from mean angle ($\overline{\alpha}$°) to bearing angle (b°)	V test	
				length *r*	P-value		V statistic	*p*-value
M1	16.156	34.033	1.090	0.406	0.070	60.846	0.198	0.133
M2	-16.639	34.143	1.092	0.404	0.085	28.051	0.357	0.025*
M3	-21.687	32.075	1.058	0.440	0.217	23.003	0.405	0.053
F1	-12.149	34.563	62.9333	0.397	0.035*	32.540	0.335	0.015*
F2	-19.996	26.227	54.8218	0.542	0.005*	24.694	0.493	0.002*
F3	-39.348	46.930	73.3334	0.181	0.806	5.342	0.180	0.255

Figure 3.3. Rhino movement after release from the boma during the 2013 flood season until rhino met a boundary fence approximately 40km from the release site. GPS location information was taken from data in Table 3.4. The blue triangle indicates the release site and the red square signifies the point at which rhino met the boundary fence.

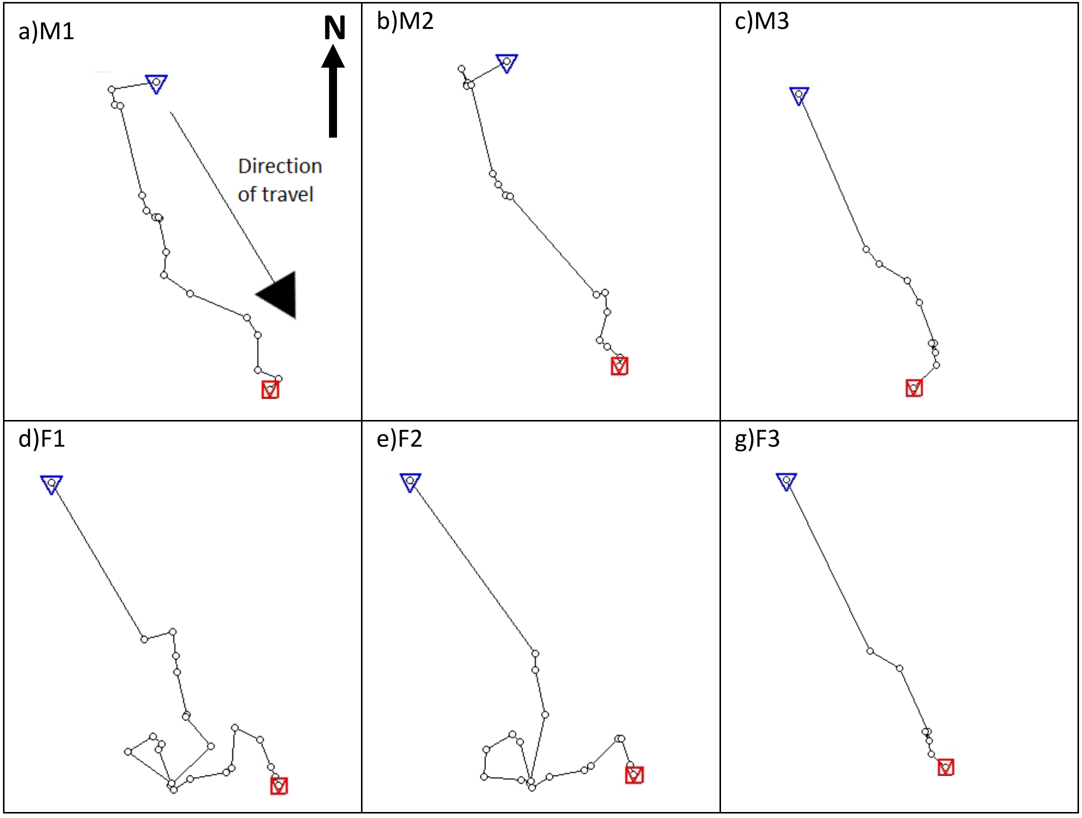
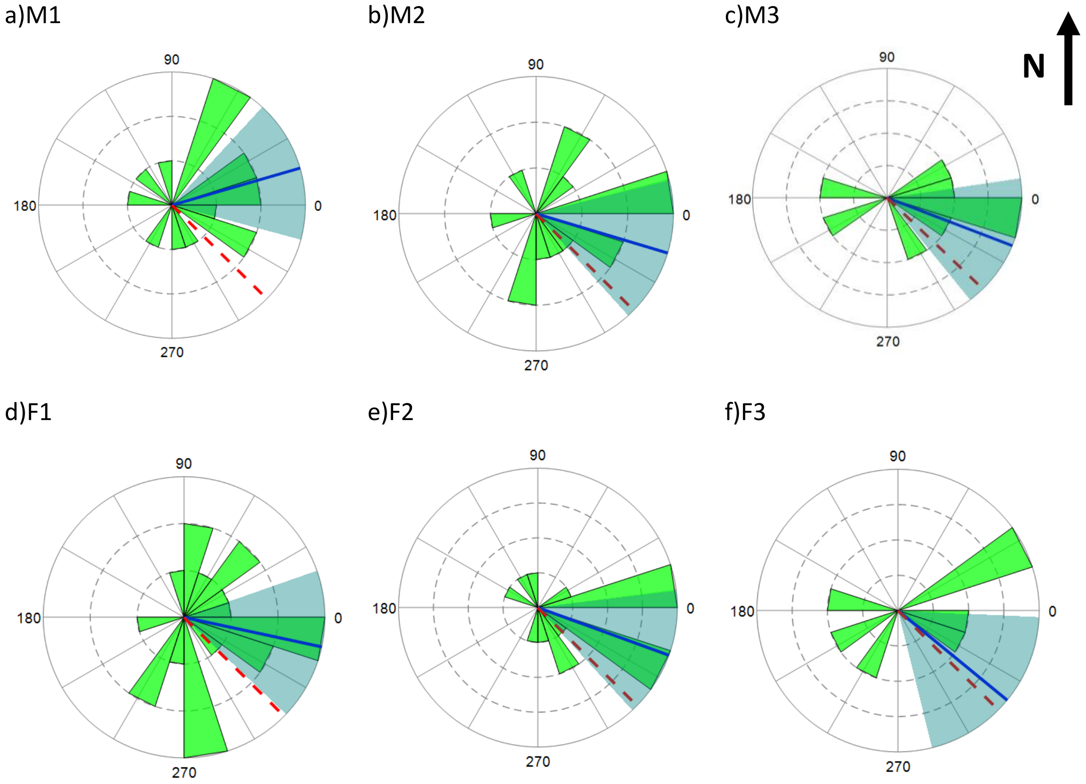


Figure 3.4. Rose histograms showing the spatial orientation of rhino after release during the 2013 flood season, until they met a boundary fence. The histograms' origins represent the site of release, which was the same for all animals. The green wedge within each diagram refers to the number of orientations towards each 20-degree segment. The mean direction is a solid blue line with standard deviation areas around the mean shaded blue. The bearing to the capture site is represented by the dotted red line.


a)M1 b)M2 c)M3

d)F1 e)F2 f)F3

3.3.2 Movement behaviour of rhino after relocation

A GAMM was applied to the NSD of each animal (Figure 3.5) to quantify the rhino's movement behaviour with respect to time. The peaks in the curve of each smoothed GAMM (Figure 3.6) represented the furthest displacement distance from the release site. Conversely, the troughs represented movement back towards the release site. I plotted the GPS coordinates for each peak and trough to ensure they correspond to different areas of exploration. This was to ensure that data were not misinterpreted and that rhino were not revisiting the same areas. The average peak dispersal distance of the GAMM models ranged between 31km and 105km (Table 3.8). Movement behaviour varied between individuals during the first year, with M1 displaying the shortest time from dispersal behaviour towards settlement behaviour. M2 alternated between short dispersal bouts and settlement for the first 200 days, after which M2 and

F2 dispersed together (travelling approximately 30km over 24h, and 50km over 48h). This pairing travelled the furthest distance from the release site (Table 3.8) during the 265 days after release. F1, F3 and M3 carried out semi-nomadic behaviour of repeated short distance dispersal bouts with brief settlement periods. They also dispersed shorter distances from the release site compared to the other rhino.

Table 3.8. Dispersal movement parameters of six translocated rhino. Data were produced by modelling the net squared displacement (NSD) of each individual with a GAMM (generalised additive mixed model).

	Rhino ID					
Parameter	F1	F2	F3	M1	M2	M3
NSD asymptotic height ($^{\delta}$)km^2	1035	10992	944	3445	6674	944
Peak distance travelled (km) $\sqrt{\delta}$	32	105	31	59	82	31
Time for peak dispersal (days)	101	265	195	10	266	195

Figure 3.5. Displacement distance (km) of six white rhino released into the Okavango Delta, Botswana in relation to time (days since release). Rhino IDs: M1, M2, M3, F1, F2, F3.

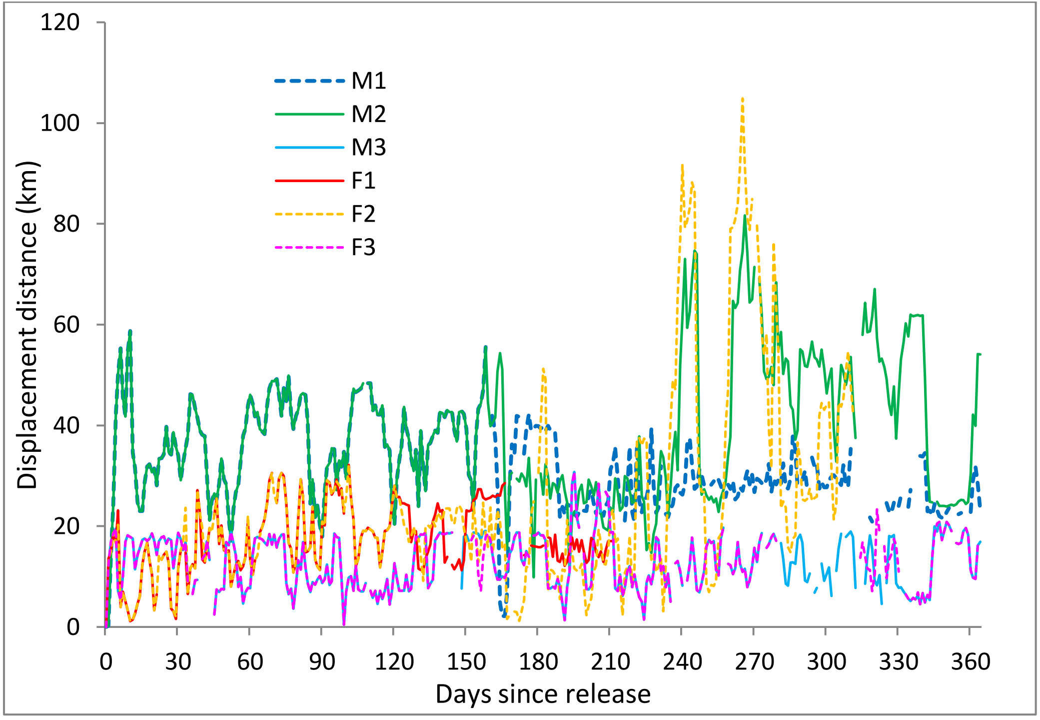
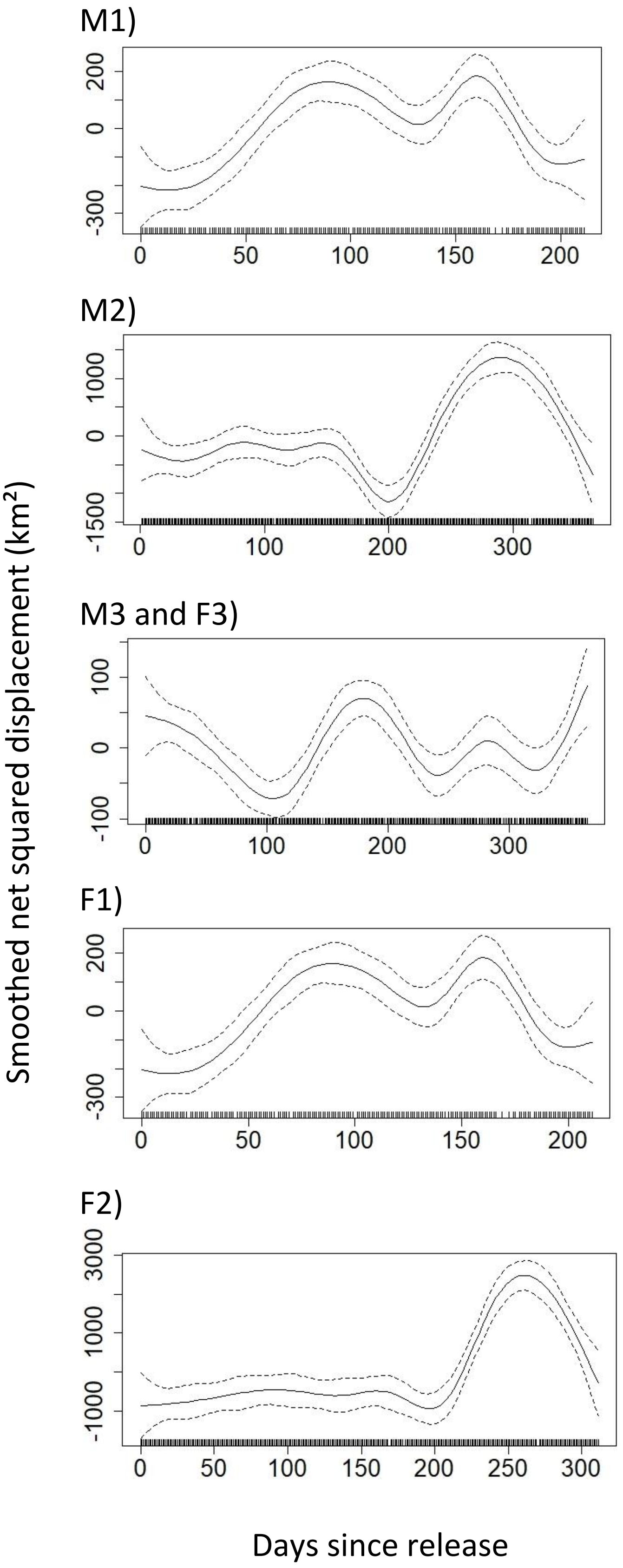


Figure 3.6. Generalised additive mixed models (GAMM) showing smoothed plots of net squared displacement (km²) against time (days since release) for six rhino (M1, M2, M3&F3, F1 and F2). The continuous line represents the fitted model and dashed lines represent 95% confidence intervals. Tick marks signify periods of data collection: *plotted concurrently because both rhino moved together in time and space.*



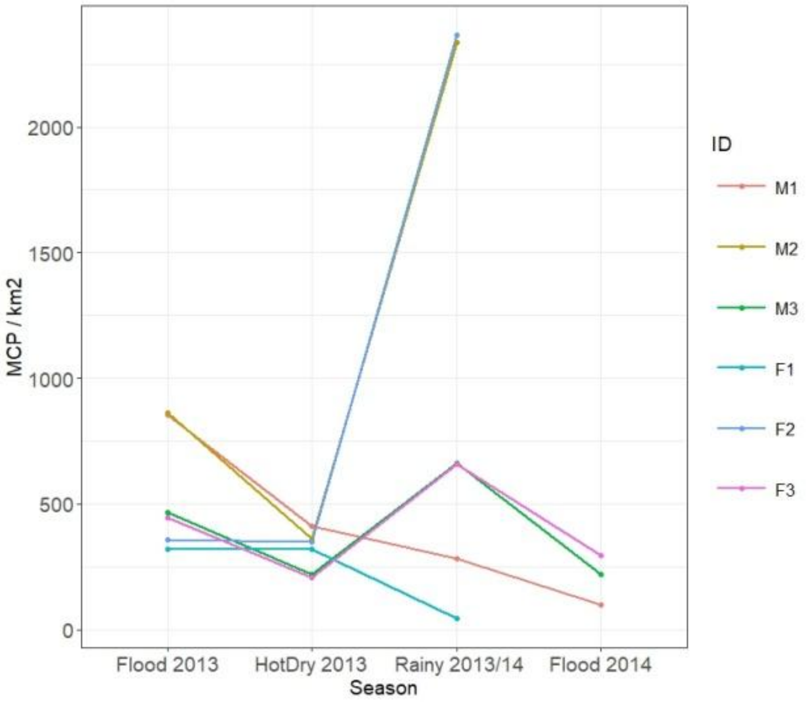
3.3.3 Range size and overlap

Table 3.9. Rhino seasonal ranges and mean percentage overlap between rhino within seasons (Table S3.1 to Table S3.4).

				Range analysis (MCP)	
Rhino ID	GPS fixes	Season	Year	Range size (km²)	Mean overlap (%)
M1	127	flood	2013	853	50.4
	406	hot dry	2013	412	46.4
	373	rainy	2013/14	283	14.3
	181	flood	2014	101	30.8
M2	142	flood	2013	861	49.7
	389	hot dry	2013	364	48.3
	319	rainy	2013/14	2337	23
	181	flood	2014	-	-
M3	114	flood	2013	468	63.9
	334	hot dry	2013	219	18
	329	rainy	2013/14	662	26.7
	186	flood	2014	221	50.4
F1	130	flood	2013	320	56.9
	410	hot dry	2013	321	46.9
	128*	rainy	2013/14	43*	6.3*
	-	flood	2014	-	-
F2	128	flood	2013	356	60.9
	395	hot dry	2013	350	48
	336	rainy	2013/14	2367	22.2
	-	flood	2014	-	-
F3	132	flood	2013	446	65.3
	391	hot dry	2013	208	18
	368	rainy	2013/14	657	26.9
	160	flood	2014	294	49.9

*anklet dropped off 13/12/13

Figure 3.7. Seasonal range size differences between rhino



3.3.4 Range modelling

Table 3.10 Results of GLMM analysis of exploratory range (a) and range overlap (b), of relocated rhino (n=6). Rhino IDs were incorporated as a random factor. Models are ranked by second-order small-sample-adjusted Akaike Information Criterion (AICc). Ki is the number of parameters, ∆ AICc the change in AICc compared to the most parsimonious model, wi the Akaike weight and LogLik the log likelihood.

a) Log transformed range size

Model	*ki*	AICc	logLik (β)	∆ AICc	wi
Null model	0	63.0	-27.81	0.00	0.73
Range ~sex	1	65.5	-27.49	2.46	0.21
Range ~season	1	68.2	-25.12	5.21	0.05
Range ~season+sex	2	72.1	-24.73	9.04	0.01
Range ~season:sex (global model)	3	84.7	-21.36	21.69	0.00

b) Log transformed range overlap

Model	*ki*	Aic c	logLik (β)	∆ Aic c	wi
Range overlap ~season	1	43.5	-12.77	0.00	0.81
Null model	0	47.1	-19.87	3.61	0.13
Range overlap ~season + sex	2	49.6	-13.51	6.10	0.04
Range overlap ~ sex	1	51.0	-20.25	7.47	0.02
Range overlap ~season:sex (global model)	3	66.6	-12.29	23.04	0.00

Table 3.11. β estimates and S.E. for most parsimonious model

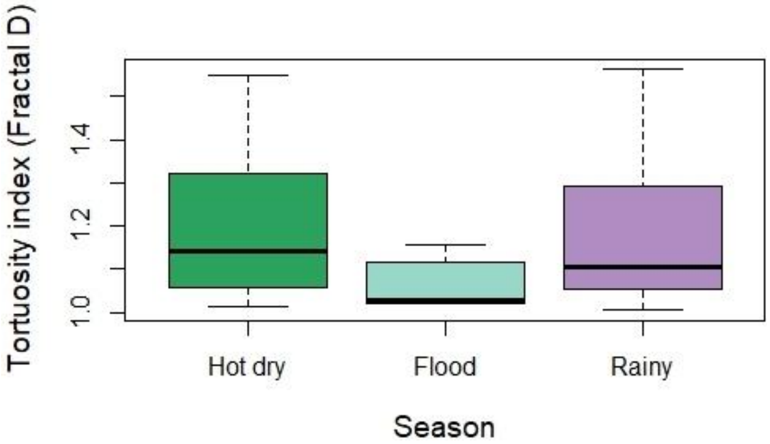
			95% CI	
Fixed Factor	β	S.E	Lower	Upper
Intercept (Flood 2013)	4.052	0.173	3.671	4.548
Hot Dry 2013	-0.516	0.245	-1.194	0.047*
Rainy 2013/14	-1.667	0.245	-1.986	-0.745
Flood 2014	-0.297	0.298	-1.077	0.678*

General linear mixed models with rhino ID as a random factor analysed the effects of fixed factors (season and sex) on range, and range overlap. Models were evaluated based on AICc scores adjusting for small sample sizes (Burnham & Anderson, 1998). The most parsimonious model for range size was the null model, and so there was no evidence of an effect of season and sex on range (Table 3.10a). However, season as an independent variable was the most parsimonious model for range overlap (Nagelkerke R^2=73%) (Table 3.10b). Examining ß estimates for the best fit model (Table 3.11), with the flood season 2013 as the intercept, showed that all other seasons had a negative effect on range overlap.

3.3.5 Track analysis

There was no significant difference in the tortuosity index of tracks (D) between seasons (Kruskal-Wallis x^2=3.588, d.f.=2, Monte Carlo p=0.169 (Figure 3.8) or turn angles ($F_{2,1016}$=2.148 p=0.1173). Therefore either rhino had a clear preferred direction that did not differ between seasons, or rhino moved randomly in all seasons.

Figure 3.8. Variation of rhino seasonal track tortuosity. Tracks were compiled by mapping rhino pathways on foot using a hand held GPs device (Hot dry n=13, Flood n=6, Rainy n=15).



The Rayleigh test results showed a significant departure from uniformity (Table 3.12). Rhino therefore moved non-randomly in all seasons. Contrary to my hypothesis there was no significant difference in turn angles between habitat classes ($F_{2,1014}$=0.73812, p=0.566), and the Rayleigh test indicated unimodal direction (Table 3.13).

Table 3.12. Orientation data for rhino seasonal movements, with 0° being towards a particular resource. Rayleigh tests indicated non-random movement across all seasons.

Parameters in radians	**Hot dry**	**Flood**	**Rainy**
Mean direction	-0.0326	0.0825	-0.0160
Circular variance	0.1567	0.1069	0.1682
Circular SD	0.5756	0.4624	0.5800
Median direction (degrees)	-0.0475	0.0692	-0.0117
Rayleigh test p-value	<0.0001	<0.0001	<0.0001

Table 3.13. Orientation tests for rhino moving through different habitat classes, with 0° being towards a particular resource. Rayleigh tests indicated non-random movement across all habitats.

Parameters in radians	***Acacia* woodland**	**Dry floodplain**	**Mopane woodland**	**Riparian woodland**	**Swamp vegetation**
No. of angles *	6	279	16	85	633
Mean direction	-0.0224	0.0289	0.0949	-0.0719	-0.0216
Circular variance	0.0806	0.1448	0.1382	0.1804	0.1632
Circular SD	0.4014	0.5381	0.5257	0.6007	0.5713
Median direction (degrees)	0.0627	0.0052	0.1044	-0.1111	-0.0108
Rayleigh test p-value	0.0022	<0.0001	<0.0001	<0.0001	<0.0001

*Generated from discretised 100m track segments

3.4 Discussion

3.4.1 Homing behaviour

Homing occurs when an animal attempts to return to some focal point (e.g. a capture site) after it has been relocated to an unfamiliar area (Rogers, 1984; Boshoff, 1988; Linnell *et al.*, 1997; Boles & Lohmann, 2003; Bradley *et al.*, 2005; Read *et al.*, 2007; Landriault *et al.*, 2009; Fernando *et al.*, 2012; Priatna *et al.*, 2012). If dead reckoning is not possible, which is likely if the journey to the new site is tortuous, displaced animals need a familiar landmark detectable from the new site, or a map sense, to ascertain their position (Gould, 2011, 2014). They achieve this by utilising a variety of cues such as the stars, sun (Lohmann *et al.*, 2004), olfactory cues (Lohmann *et al.*, 2004; Lohmann *et al.*, 2008; Brothers & Lohmann, 2015; Safi *et al.*, 2016) and/or geomagnetic imprinting (Lohmann *et* *al.*, 2004; Lohmann *et al.*, 2008; Brothers & Lohmann, 2015; Gould, 2015). True navigation takes place over large distances without the aid of landmarks (Gould & Gould, 2012; Gould, 2014).

The rhino were placed into crates at the capture site and transported approximately 1,500 km to the release site, so visual information assimilated during the outward journey was limited (Boles & Lohmann, 2003). There is a species-specific critical distance at which animals are no longer able to 'home' (Rogers, 1973; Rogers, 1988), so rhino should move randomly and not show unidirectional movement. However, some individuals of these species have been found to navigate homewards from novel areas but the mechanisms for these animals remain unknown (Rogers, 1984).

Rhino dispersed in pairs; this may have had some social context, and/or be because teamwork reduced navigational error (Bergman & Donner, 1964; Wallraff, 1978; Shrader & Owen-Smith, 2002; Simons, 2004; Codling *et al.*, 2007). For example, flock-flying enhanced the homing ability of pigeons compared to lone individuals (Dell'Ariccia *et al.*, 2008). Grouped dispersal occurs in relation to a perceived danger (Shrader & Owen-Smith, 2002; Bélisle, 2005; Bonte *et al.*, 2012; Visscher *et al.*, 2017), or if environmental factors limit the use of compass cues (Simons, 2004).

The rhino did appear to navigate towards the capture site. However, there are factors that may explain this behaviour. Dispersal north would have been difficult due to a barrier of flood water, but the animals did cross several deep channels. Sometimes homing is a result of being released without any acclimation period (hard release), or not being acclimated for long enough (Bradley *et al.*, 2005; Berger-Tal & Saltz, 2014). In mammals, the greater the translocation distance, the more the individuals lose their ability to navigate home, although this is species and age specific (Rogers, 1988; Linnell *et al.*, 1997). Black bears (*Ursus americanus*) have been found to home up to 271km, but after being translocated over 1400 km they lost this ability and moved large random distances. Rhino on the other hand did not move randomly but in a directed movement away from the release site towards the capture site. Additional explanation could be stress avoidance behaviour (i.e. dispersal away from the release site), where the introduction to an unfamiliar environment instigated stress control behaviour by searching for a memorable range (Drugan *et al.*, 1997; Dickens *et al.*, 2010). An increase in physiological state can lead to short-term escape behaviour (Jachowski *et al.*, 2012) linked to unidirectional large-scale movement away from disturbances (Jachowski *et al.*, 2013). The possibilities to explain this movement in rhino are three fold; rhino may have been homing, moving away from disturbance, or the initial dispersal was affected by the topography of the release site.

3.4.2 Dispersal and settlement behaviour

A consequence of translocation is dispersal (Mihoub *et al.*, 2011; Yiu *et al.*, 2015), where the assimilation of resource information and breeding possibilities are offset against the risk associated with dispersal (Bonte *et al.*, 2012). Rapid dispersal in an unfamiliar environment can affect fitness and increase mortality risk (Stamps & Swaisgood, 2007; Berger-Tal & Saltz, 2014; Yiu *et al.*, 2015). Large dispersal distances of translocated animals may occur in response to stress avoidance after a short captivity period (Drugan *et al.*, 1997; Dickens *et al.*, 2010; Mihoub *et al.*, 2011; Merrick & Koprowski, 2017) or because the animal perceives the habitat at the release site as unsuitable (Stamps & Swaisgood, 2007). However, as animals learn about their environment they may develop site-fidelity (Van Moorter *et al.*, 2009; Spencer, 2012; Bracis *et al.*, 2015).

There were varied post-release movement patterns between rhino. Some appeared more settled, moving short distances between patches, whilst others dispersed over considerable distances. Short distance relocation behaviour is synonymous of large herbivores moving in accordance with forage availability and quality (Owen-Smith & Martin, 2015; Flanagan *et al*., 2016), whereas long distance movements may be facilitated by resource availability and landscape functional connectivity (Taylor *et al.*, 1993; Bélisle, 2005; Yiu *et al.*, 2015). The excursion of F2 and M2 took place during the rainy season when resources were plentiful (Pienaar *et al.*, 1993b). Long-distance dispersal by translocated rhino is not a new phenomenon. Movements between 150km and 200km were recorded following releases in Kruger National Park, South Africa (Pienaar, 1970) and Botswana (Herbert & Austen, 1972), respectively. However, in the Botswana study a female and calf perished through dehydration, so high dispersal rates can sometimes lead to reintroduction failure (Armstrong & Seddon, 2008).

Of all the individuals, male M1 displayed more typical settlement behaviour within the first 12 months, but after 2 years dispersed over 70km before returning to the settlement area. Therefore, perhaps rhino in low density areas do not display as much sedentary behaviour as rhino in higher density areas. Another study recorded individuals roaming up to 30km overnight, with rhino of both sexes taking an estimated 15 months to settle (Booth & Coetzee, 1988). I also found no sex-biased dispersal (Van Coeverden de Groot *et al.*, 2011).

Survival and physiological changes are often used to evaluate translocation success (Molony *et al.*, 2006; Pinter-Wollman *et al.*, 2009) and applying animal movement characteristics to evaluate the success of this translocation was complex (Pinter-Wollman *et al.*, 2009; Flanagan *et al.*, 2016). Temperament controls behaviour, including the propensity to disperse and response to new environments (Berger-Tal & Saltz, 2014). Rhino displayed inter-individual behavioural heterogeneity (Merrick & Koprowski, 2017) within an unoccupied landscape, so their behaviour could not be compared to a resident population (Pinter-Wollman *et al.*, 2009).

In the short-term the translocation was only partly successful. Some of the rhino displayed typical subadult short distance relocation behaviour or settlement behaviour synonymous with range establishment. However, others continued with exploratory behaviour dispersing over large distances. None of the animals settled near the release site and so was not successful for ecotourism.

3.4.3 Range size and overlap

Home range size in established white rhino populations varies temporally and spatially according to the number of individuals in the population, sex, age, the size of the reserve, and the availability and quality of resources (Owen-Smith, 1971; Conway & Goodman, 1989; Pienaar *et al.*, 1993b; White *et al.*, 2007; Thompson *et al.*, 2016). Previous analyses (Table 3.1) showed low densities of adult rhino generally correlated with larger home ranges. In this study ranges were large, and it was likely that this was because the area was unpopulated by other rhino.

In the Okavango Delta newly released subadult rhino had complete freedom to roam, only being spatially restricted by a boundary fence, or water channels that were too deep to cross. Subadult ranges in the Okavango were vast compared to other studies (Owen-Smith, 1974), supporting my hypothesis that ranges would be larger than previously recorded 'home ranges'. My results corresponded with previous studies that at low densities rhino have large ranges (Owen-Smith, 1971; Conway & Goodman, 1989; Pienaar *et al.*, 1993b; White *et al.*, 2007).

In the short-term, overlapping ranges are used to assess the sharing of space and resources (Fieberg & Kochanny, 2005) but, in the long-term, overlapping ranges between individuals can be used as a measure of settlement behaviour (Janmaat *et al.*, 2009).

Results were determined using a small sample size, so caution should be applied in examining these results. Contrary to my hypothesis that subadult female rhino shared more space than subadult male rhino, I detected no difference in range sizes or overlapping range sizes between subadult males and subadult females (Owen-Smith, 1973; Pienaar *et al.*, 1993b; Thompson *et al.*, 2016). This was probably because the sample size was small and because rhino formed mixed-sex paired companionships. It has been suggested that where subadults move in pairs, the older individual determines the range size (Pienaar *et al.*, 1993b). I was unable to corroborate this since the companionships I observed were between rhinos of a similar age.

The extent of overlap was affected by season, so this supported my hypothesis that range sizes and the sharing of ranges would differ as a result of the variation in seasonal resources. The hot dry 2013, flood 2014, and rainy 2013/14 seasons had a negative effect on range overlap compared to the flood season 2013 (intercept). The rainy season had the largest negative effect upon overlapping ranges. Rhino displayed different ranging strategies between individuals and seasons. Ranges in the hot dry and flood seasons were more restrictive than the rainy season, which supported my hypothesis that range sizes would be smaller in flood season and largest in the resource abundant rainy season.

It is likely that the differences between flood season overlapping ranges are affected by processes such as localised rainfall, rainfall within the upper Okavango River catchment basin, as well as the changes made to water channels by hippopotamus which facilitate flooding (Ramberg *et al.*, 2006). Floodwaters create deep seasonal channels that may limit dispersal, while seasonal swamps reduce habitat availability (McCarthy & Ellery, 1994). Incoming floodwaters also bring nutrient deposits (Cronberg *et al.*, 1995). Nutrients are then released following the retreat of floodwaters, producing productive grasslands during dry seasons (McCarthy & Ellery, 1998; Ramberg *et al.*, 2006). The assimilation of nutrients from these patches may lead to smaller range sizes (Bartlam-Brooks *et al.*, 2013). Animal movements may be greater during the rainy season owing to the increased availability of water (Redfern *et al.*, 2006), and fresh green leaved vegetation (Pienaar *et al.*, 1993b).

Generally, graze quality decreases during dry seasons (Waite, 1963). However, rhinos are non ruminants and are able to tolerate lower quality graze (Cromsigt *et al.*, 2009). Restricted ranges could also be influenced by the availability of high sward biomass that rhino bulk graze to mitigate against reduced quality

(Shrader *et al.,* 2006a), or the use of spatial memory to facilitate the return to profitable grazing sites (Bailey *et al.*, 1996; Gautestad & Mysterud, 2010; Fagan *et al.*, 2013). Additionally, spatial memory processes and expanding resource knowledge through random walks may also explain why ranges became smaller over time (Van Moorter *et al.*, 2009). Larger ranges for M2 and F2 during the rainy season were attributable to an extensive excursion, when fresh growth (Pienaar *et al.*, 1993b) and water (Redfern *et al.*, 2006) were available. Parturition in late September by F1 may account for her smaller ranges during and after gestation, since access to resources is linked with offspring survival (McLoughlin *et al.*, 2007).

The spatiotemporal shifts in ranges and the sharing of ranges between individuals may be attributable to factors other than seasonal changes in resource abundance or rhino sociality. For example, there is evidence that black rhino are negatively affected by the presence of elephants through interspecies competition, habitat modification via the availability of biomass (de Boer *et al.*, 2015) and interspecies avoidance (Berger & Cunningham, 1998). Elephants may compete with, or facilitate grazing and foraging and this may impact the presence and density of other herbivore species (Okita-Ouma *et al.*, 2008; de Boer *et al.*, 2015). The presence of elephants may initially increase browse availability by improving access via elephant pathways, but in the long-term the available biomass decreases negatively impacting resource availability for other browsers (Landman & Kerley, 2014). However, elephants may facilitate grazers by pushing over or breaking trees thereby decreasing tree cover and increasing grass availability (de Boer *et al.*, 2015).

Some herbivores shift temporal resource use to avoid temporally overlapping with elephants (Valeix *et al.*, 2007). Aggressive encounters between black rhinos and elephants revealed that female elephants dominated both sexes of rhino, and only male black rhino displaced elephant bulls (Berger & Cunningham, 1998). Therefore elephants may also trigger the spatial and temporal displacement of subadult rhino in the Okavango Delta (Slotow & van Dyk, 2001).

3.4.4 Relocation pathways

Rhino pathways have been classified as movements between grazing areas, resting places, drinking points, middens, and potentially the patrolling of ranges (Owen-Smith, 1971). I was not able to analyse movements within grazing patches because the tracks were too difficult to interpret. I hypothesised that rhino turning angles (directed movements) would not vary between seasons, but would vary between habitat classes. I predicted that turn angles would be more tortuous through wooded habitats, but in fact there was no difference in turn angles during travel between seasons or habitats. This suggested familiarity with resource availability throughout the year (Bailey *et al.*, 1996; Brooks & Harris, 2008), so it is likely that rhino were revisiting profitable areas (Fryxell *et al.*, 2008; Wolf *et al.*, 2009). A unimodal direction between habitats suggested that rhino were orientating towards a particular goal. Rhino therefore minimise travel time and distance by using directional movement (Polansky *et al.*, 2015) in all habitat types. It would have been useful to determine the time spent in each habitat type at a fine scale, but the time intervals of the GPS collars did not make this possible.

3.5 Conclusion

Animals have a greater propensity to explore (Berger-Tal & Saltz, 2014) in a competitor-free environment (Yiu *et al.*, 2015). Differences in personality can account for differences in inter-individual movement behaviour (Merrick & Koprowski, 2017), as well as capacity to assimilate resource knowledge (Benhamou, 1997).

Rhino had expansive ranges compared to high population density areas (Table 3.1). Range sizes were not sex-biased, and were large on account of vast dispersal distances. As reported by Shrader and Owen-Smith (2002), rhino reduced risk by dispersing in pairs or groups. Despite a period of acclimation, upon release into a novel environment all six individuals dispersed over large directed distances. This correlated with the findings of previous dispersal movements of rhino in the Okavango Delta (Pitlagano, 2007). The angles of direct movement between resource patches were equally distributed across all seasons and between habitats. This indicated that the rhino had developed spatial and temporal resource awareness.

Although none of the rhino settled at the release site, a decline in the exploratory range area of rhino during the first year initially suggested a certain amount of site fidelity. However, some individuals continued to disperse vast distances after this time period. This initial research was limited by the number of animals, and the time period of available GPS data. Despite the small sample size, conservation mangers should therefore be aware of the long-term long-distance movement potential in rhino for monitoring and security purposes.

3.6 Link to next chapter

In this chapter I have shown how the movements of translocated rhino differ between individuals. At large scales these can be hugely varied. Rhino have the ability to navigate efficiently towards spatial and temporal goals.

It is essential to evaluate the habitat suitability of the release site for translocated animals. In the next chapter I will discuss how rhino movements are influenced by habitat at the landscape level.

Chapter 4. Using animal movement strategies to identify landscape scale resource selection of a translocated megaherbivore

4.1 Introduction

It is important to assess how translocated animals react to vacant habitats since relocation projects are likely to become common practice as a result of climate change, habitat loss (Bowler & Benton, 2005), persecution (Miller *et al.*, 2011; Risdianto *et al.*, 2016) and human-animal conflict (Fernando *et al.*, 2012). Habitat suitability modelling can delineate ecological niches from landscape variables (Hirzel & Le Lay, 2008; Moorcroft & Barnett, 2008), but we do not know how habitat selection is defined for animals translocated and released into unfamiliar landscapes with no predefined home range.

Landscapes vary ecologically, spatially and temporally (Zhang *et al.*, 2014) and are selected by grazing herbivores to enhance acquisition of resources (Owen-Smith, 2002; Mitchell & Powell, 2004; Fryxell *et al.*, 2008), described as physical and biological factors that comprise an organism's principal requirements (Kertson & Marzluff, 2010). The structure of heterogeneous landscapes may consist of fine-scale dense mosaic patches sitting within a broader hierarchical scale with lower density patches (Kotliar & Wiens, 1990; Fauchald & Tveraa, 2006). It is likely that habitat features influence scale-dependent space and resource use (Borger *et al.*, 2008; Kertson & Marzluff, 2010). The scattered spatial distribution of resources (Bennitt *et al.*, 2014), overgrazing, seasonal changes (Mueller & Fagan, 2008), or an animal's internal state (Fryxell *et al.*, 2008) can all induce unrestricted movements (Borger *et al.*, 2008). Conversely, movements are restricted when resources are clustered (Mitchell & Powell, 2004). Once we start to understand how an animal responds to the spatial distribution of the resources upon which it depends, we can start to predict its response to translocation. Population distributions (Patterson *et al.*, 2008), and the effect on communities and ecosystems (Nathan *et al.*, 2008), can be simulated from intra- and inter-species movement data (Polansky *et al.*, 2010).

What is currently understood about rhino habitat selection varies between studies, but it is generally thought that grasslands are an important habitat type. In one study of northern rhino, Van Gyseghem (1984) found that rhino were reliant upon open grassland habitats, while White *et al.* (2007) found that southern white rhino readily used the most common habitat (open woodland), as was also found by Melton (1987). Rhino disproportionately utilised grassland habitats, but selected grasslands to a lesser amount during the dry season (White *et al.,* 2007). In a separate study, grasslands were classified as being of higher importance than woodland grasslands (Shrader *et al.,* 2006b), but this study did not take proportional availability into account. Other studies concluded that rhino avoided mopane woodland in favour of more open habitats, and this may be due to the increased availability of grass biomass in more open areas (Pedersen, 2009). Similarly Owen-Smith (1992) concluded that rhino switched between short and tall grassland habitats depending upon seasonal availability.

The advancement of GPS collar capabilities has facilitated the investigation of space use and habitat selection (Calenge, 2006; Patterson *et al.*, 2008; Cagnacci *et al.*, 2010; Calenge, 2015; ESRI, 2015; Rodgers *et al.*, 2015). Using GPS data, modelling techniques can identify changes in animal movement phases across different spatial scales (Nams, 2005; Fauchald & Tveraa, 2006; Borger *et al.*, 2008; Patterson *et al.*, 2008), and distinguish between different transient movement states, such as dispersal, migratory, and nomadic (Fryxell *et al.*, 2008; Morales *et al.*, 2010; Bunnefeld *et al.*, 2011; Papworth *et al.*, 2012; Benhamou, 2014). A plateau in net squared displacement (NSD) corresponds to the low dispersal of individuals over large scales, and is designated a period of settlement (Owen-Smith *et al.*, 2010), sometimes described as profitable ‘resource extraction’ (RE) sites (Benhamou & Cornélis, 2010; Papworth *et al.*, 2012).

Within these relatively defined areas, the availability of habitats can be determined and compared to an animal's ranked relative use of habitats (Aebischer *et al.*, 1993; Kertson & Marzluff, 2010). This is achieved by identifying areas of concentrated use by means of a probabilistic utilisation distribution (UD) (Van Winkle, 1975) and then delineating favoured habitat characteristics (Barraquand & Benhamou, 2008; Horne *et al.*, 2008) through the application of modelling techniques such as resource utilisation functions (RUFs) (Kertson & Marzluff, 2010).

Previous methods of calculating white rhino resource selection at large scales used observational data (Pienaar *et al.*, 1993b, 1993a; White *et al.*, 2007; Thompson *et al.*, 2016). However, results can be biased if habitats where animals are thought not to be found are excluded (Pedersen, 2009), similarly they are biased because data can only be gathered if animals are observed. GPS enables data collection across inaccessible landscapes (Weimerskirch *et al.*, 2002; Brooks *et al.*, 2008), however there is bias if signal reception differs between habitats (Jiang *et al.*, 2007). White *et al.* (2007) quantified habitat selection by calculating the proportion of habitat classes within a polygon. Such methods are simple to implement but may misrepresent true habitat selectivity. I define these published results as 'habitat availability within a range', and equate resource selection to the landscape characteristics that correlate to areas of concentrated use.

Using GPS data from 6 rhino, I applied a framework consisting of net squared displacement (NSD) to demarcate breaks in movement (the resource extraction site), kernel density estimators (KDE) to delineate utilisation distributions, and resource utilisations functions (RUFs) along with Generalised Linear Mixed Models (GLMMs) to identify landscape characteristics and habitat classes linked to areas of concentrated use.

I hypothesised that:

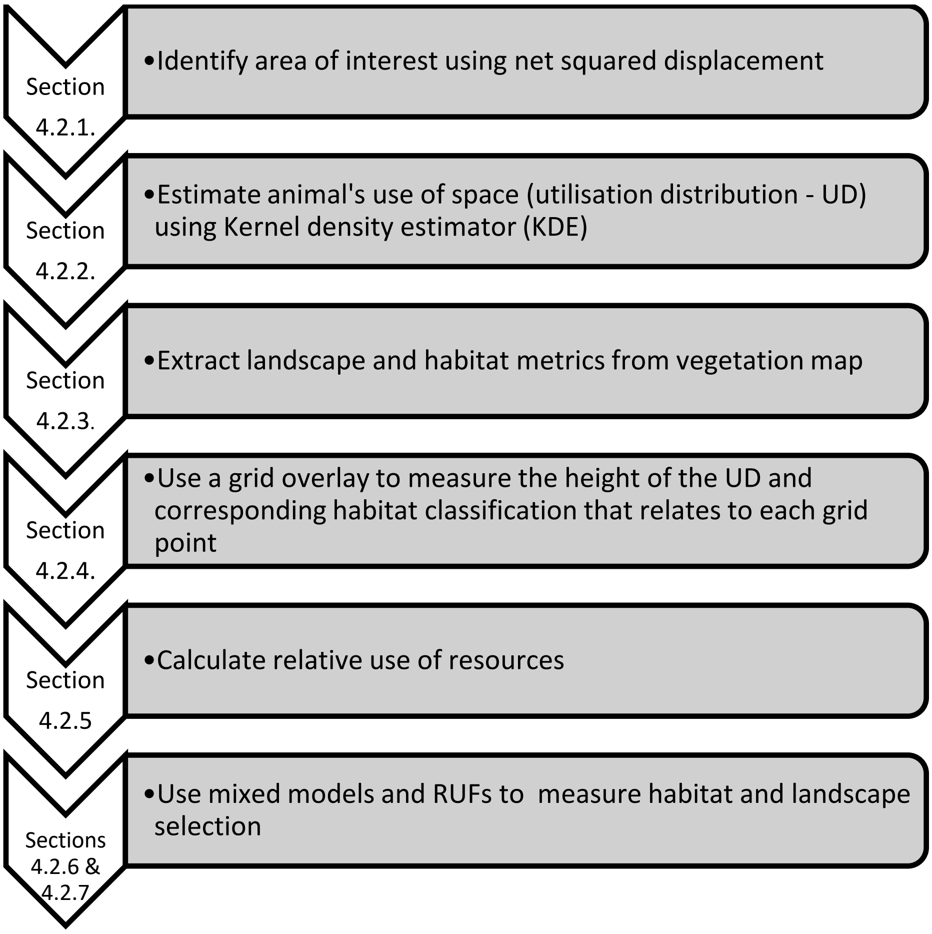
1) Animal movement is affected by the spatial and temporal distribution of resources. Within a vast dynamic landscape, features such as habitat characteristics and landscape metrics are highly heterogeneous. Therefore, features contained in resource extraction sites are likely to be different. I aimed to establish which features influence space use.
2) The relative importance of each habitat class would be the same across resource extraction sites and the relative use of habitats is related to the proportional availability of each habitat.
3) Highly utilised areas include resources of high importance such as water and feeding stations, and as such may be revisited by rhino. Therefore key resources known as 'core areas' within resource extraction sites are likely to be shared.

4.2 Methods

4.2.1 Movement metrics

To analyse rhino habitat selection (Hall *et al.*, 1997), I first had to define the area of interest (Figure 4.1). Traditionally this has been described as the animal's home range during a set time period (Harris *et al.*, 1990) from which resource use can be measured (Aebischer *et al.*, 1993; Gustine *et al.*, 2006; Reyna-Hurtado *et al.*, 2009; Thurfjell *et al.*, 2009; Zweifel-Schielly *et al.*, 2009; Bartlam-Brooks *et al.*, 2013; Bennitt *et al.*, 2014). However, within a patchy habitat network such as the Okavango Delta (Ramberg *et al.*, 2006; van der Valk & Warner, 2008), it was likely that range estimates would include large patches that would be of no relevance to a rhino but would affect resource selection calculations (Mitchell & Powell, 2008). In addition, since the rhino in my study had been released into an unfamiliar habitat, they did not have an established home range.

Figure 4.1. Flow diagram summarising steps of data extraction and analysis for habitat and landscape selection of white rhino in the Okavango Delta.



Using GPS data (Section 3.2.1 and Table 3.3), NSD (net squared displacement) was used to model daily animal movements (Section 3.2.3) for the entire range of GPS transmission dates displayed in Section 3.2.1 and Table 3.3. Rhino were displaying settlement behaviour when NSD was relatively constant, and so I used this to identify areas of interest where it was likely that resource extraction (RE) took place (Papworth *et al.,* 2012). Conversely when rhino were travelling, NSD would increase or decrease in relation to the starting point.

REs were identified from NSD and GAM (Generalised Additive Model) plots for each individual (Figures S4.1 - S4.10). Breaks in movements were found by visual inspection of the NSD of animal trajectories that were calculated using *adehabitatLT* (Calenge, 2006), where the closer the NSD was to zero the less distance the animal moved. GAMs were also fitted using the *mgcv* package

(Wood, 2011) to help identify REs. The dependent variable NSD was plotted against the smoothed continuous variable (Days). After visual inspection of the graphs, I examined the raw data and identified the precise dates of large daily shifts in movement patterns that corresponded with changes in NSD movement behaviour. A summary of identified REs are displayed in Table 4.1.

Table 4.1. Resource extraction areas (REs) based on examining GAM models and NSD plots to establish breaks in movements. AdehabitatLT *in R was used to inspect Euclidean squared distances for each individual (Figures S4.1 – S4.10).*

RE	Rhino ID	Dates tested		Number of days	No. GPS fixes	% GPS fixes
		From	To			
1	M1	27/12/2013	01/04/2014	96	84	88
2		06/04/2014	19/08/2014	136	121	89
3		27/11/2014	23/06/2015	209	187	90
4	M2	29/10/2013	06/01/2014	70	67	96
5	M3&F3	01/12/2014	19/03/2015	109	88	81
6	F1	07/11/2013	14/12/2013	38	36	95
7	F2	16/05/2013	23/12/2013	222	219	99

4.2.2 Measuring space use

Given that an RE site represented an area of resource extraction within a particular time span (Table 4.1), I determined which resources were being selected by the rhino by calculating areas of concentrated space use within each RE site.

As described by Marzluff *et al.* (2004), an animal’s use of geographic space is assumed to equate to resource use (Aebischer *et al.*, 1993; Kernohan, 2001). The kernel density estimator (KDE), a non-parametric probability density function, which I used to identify areas of concentrated space use (Millspaugh *et al.*, 2006; Fury *et al.*, 2013) to produce a utilisation distribution (UD) (Van Winkle, 1975; Silverman, 1986). The fixed KDE is considered the best method for estimating habitat use (Silverman, 1986; Worton, 1989; Borger *et al.*, 2006; Fury *et al.*, 2013) and uses probability contours (isopleths) which equate to the relative frequency of space use within each RE (Van Winkle, 1975; Worton, 1989). I calculated probability contours using 95% KDE.

Benhamou & Cornélis (2010) recommended the use of movement-based kernel methods for a highly mobile species with short GPS fix intervals. I used the fixed KDE method since GPS fix intervals used for estimation were at 24-hour intervals for a sedentary species, and most had fewer than 200 fixes per RE site (Papworth *et al.*, 2012).

KDEs with least squared cross validation (LSCV) were calculated using a cell size of 100m for each RE site using the Home Range Tools 2.0 extension package (Rodgers *et al.*, 2015) for ArcMap 10.4.1 (ESRI, 2015). I chose LSCV as the smoothing parameter because it selects the band width with the lowest estimated error (Powell, 2000) and it is also the most frequently used method for calculating KDE (Worton, 1989; Fury *et al.*, 2013).

KDEs per RE site (i.e. treated as per individual) were used to test habitat selection (White & Garrott, 1990). This method avoids the pseudo-replication issues that can occur when location estimates are taken as the sampling unit (Hurlbert, 1984; Aebischer *et al.*, 1993; Otis & White, 1999).

4.2.3 Vegetation map preparation and computation of metrics

Patch Analyst extension version 5.2.0.16 (Rempel *et al.*, 2012) for Arcmap 10.4.1 (ESRI, 2015) was used to quantify the landscape metrics of each RE site. In this section a patch is defined as the habitat class area that is bordered by different habitat types. Adjacent boundaries between habitats of the same classification (Section 1.7.2, and Table 4.2) were dissolved so that landscape fragmentation was not exaggerated and therefore habitat patch size was not underestimated (Rempel *et al.*, 2012). Metrics were categorised under the following subheadings: area, (habitat) patch density and size, (habitat) patch shape, and landscape diversity (Table 4.2). I used Spearman’s rank correlation to test if there was any correlation between the landscape composition of RE sites.

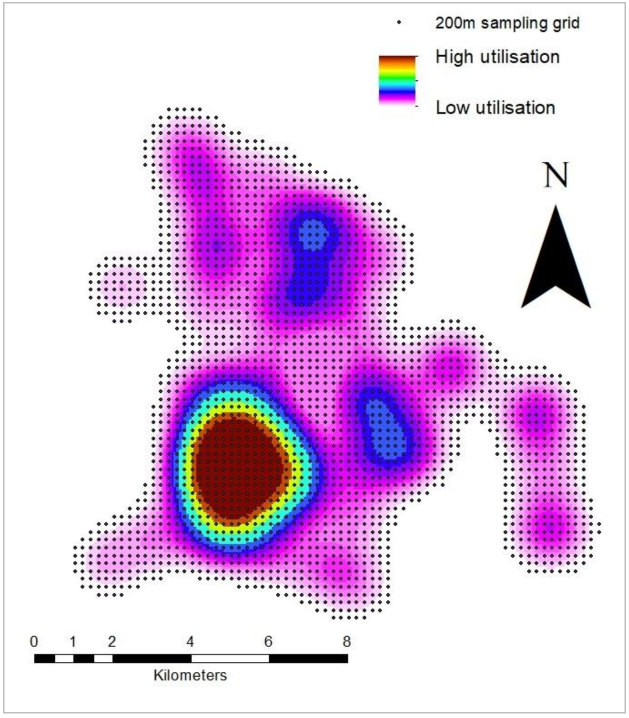
Table 4.2. Abiotic covariates (landscape metrics modified from Patch Analyst extension version 5.2.0.16 (Rempel et al.*, 2012)) used to capture large scale rhino resource selection variables.*

	Landscape metrics and acronyms	Description
Area	Total landscape area (TLA)	Measure of the total area in km² within the specified contour boundary
	Class area (CA)	Sum of the area in km² of all patches belonging to a habitat class within the TLA
Patch density & size	Number of habitat patches (NP)	Number of patches for each habitat class within the TLA
	Patch Richness (PR)	Number of different habitat class types within the TLA
	Mean patch size (MPS)	Average patch size per class and by landscape
Shape	Mean shape index (MSI)	Refers to shape intricacy and measured at class and landscape levels. MSI=1 when patches are circular, and MSI increases as their shape increases in complexity
	Area-weighted mean shape index (AWMSI)	Same as MSI but weighted by patch area i.e. larger patches score higher
Landscape diversity	Shannon’s diversity index (SDI)	Measure of relative patch diversity. Index=0 when there is only one patch; this increases with more patches or higher proportional distribution
	Shannon’s evenness index (SEI)	Measure of patch distribution and abundance. Index between 0<1, where 0 low distribution and 1 equals even distribution
	Distance to nearest patch edge (PE)	Distance from a sample point within a habitat to the adjacent boundary of a habitat with a different classification

4.2.4 Capturing habitat resource use

To estimate resource use within each RE site, a sampling point mesh was draped at 200m intervals (Kertson & Marzluff, 2010; Kertson *et al.*, 2011) over the utilisation distribution (UD) (Figure 4.2) and the vegetation map with defined habitat classes (Section 1.7.2, Table 1.2). The classes were identified as dry floodplains, shrubbed grasslands on former floodplains, grasslands with wild sage, swamp vegetation, riparian woodland, mopane woodland and *Acacia* woodland. Each point was allocated a UD value, habitat classification, landscape metrics (Table 4.2) and a co-ordinate (Marzluff *et al.*, 2004; Millspaugh *et al.*, 2006; Kertson & Marzluff, 2010; Handcock, 2015). Data were exported as a table for statistical analysis in R (R Core Team, 2016) and SPSS v23.0.0 (SPSS, 2015). Unless specified, all packages referred to below are R packages.

Figure 4.2. Example of combining sampling point mesh with kernel density estimation to extract landscape resource selection covariates that relate to the co-ordinate for each point.



4.2.5 Calculating proportional and relative use of resources

To calculate the ‘relative use’ of habitats (UDrel), UD values for each habitat class was divided by the total UD for all classes within the RE site (determined in section 4.2.4). UDrel was generated from continuous data and as such was analysed using generalised linear mixed models as opposed to binomial GLM.

To calculate the ‘proportional use’ of each habitat class within each RE site, CA (the sum of the area in km² of the same habitat class within the resource extraction site) was divided by the TLA (total landscape area) of the RE site.

Regression analysis was used to investigate the significance of any relationship between habitat class proportional availability and UDrel for each RE site. I checked the normality of residuals by eye.

4.2.6 Mixed models

I used linear mixed models to investigate the effect of landscape metrics (Table 4.2) (e.g. MPS, MSI, and NP) and habitat classes (defined in Table 1.2) on UDrel.

Candidate models were produced alongside the null model. Models were ranked by second-order Akaike Information Criterion (AICc) using the *MuMIn* package (Barton, 2016) to account for small sample bias adjustment (Burnham & Anderson, 2004). I plotted model residuals using the *DHARMa* package (Hartig, 2017) and checked them visually for normality and homoscedasticity. Since UDrel was generated from continuous data it was arcsine square-root transformed to meet model assumptions.

4.2.7 RUF analysis

I used the utilisation distribution (UD) data collated from section 4.2.4. The *ruf.fit* package (Handcock, 2015) was used to estimate resource utilisation functions (RUFs) using each RE as the sampling unit for a Type III study design, i.e. individual REs were identified with resource use and availability measured for each RE (Marzluff *et al.*, 2004; Manly *et al.*, 2007; Sheppard *et al.*, 2010; Zhang *et al.*, 2014). I log-transformed UD data to create normally distributed residuals (Kertson & Marzluff, 2010; Papworth *et al.*, 2012).

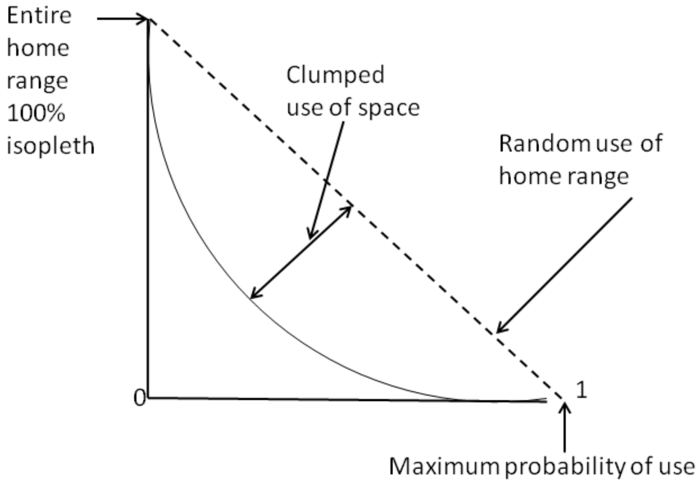
I used estimates of standardised RUF $\hat{\beta}_j$ coefficients to rank the importance of covariates on log(UD), where *j* corresponded to covariates at each animal's UD sampling point (Equation (1) in Marzluff *et al.,* 2004), and because standardised RUFs accounted for scale difference between samples, thereby allowing relative use comparisons (Zar, 1999). Coefficients >0 represented covariates (habitat classes) that were utilised more relative to availability, whereas coefficients <0 represented covariates that were used less relative to availability.

The RUF calculations used a maximum likelihood estimator with the Matérn correlation function to account for spatial autocorrelation (Marzluff *et al.*, 2004; Koper & Manseau, 2009). Two parameters are used for the Matérn correlation functions, the range for spatial dependence, and the smoothness of the UD surface. As advocated by Marzluff *et al.* (2004), the bandwidth for estimating kernels for each RE were used as the range for spatial dependence, and the smoothness of each UD was set to 1.5 (Raynor *et al.*, 2017).

4.2.8 Core area calculations

To analyse how intensively used space overlapped between REs, I first defined the core area, i.e. the area with highly concentrated use. Powell (2000) defined the core area of an animal's range as being clumped as opposed to randomly used, and said that the estimation can be biased by selecting an arbitrary percentage contour value (White *et al.*, 2007). To calculate an objective value for the core area, I used a similar method to that advocated by Harris *et al.* (1990) and Powell (2000) for each RE site. I calculated the proportion of area (km²) at 5% intervals between 100% and 0% isopleths (Section 4.2.2) and plotted these against relative use.

Figure 4.3. Core area calculations for each RE site. The dotted diagonal line denoted the random use of space. The curved line was the relative use of space plotted against the proportion of area (km²) for isopleths at 5% intervals (from 0 to 100%) within each RE. The clumped use of space (core area) was represented by the maximal distance between the random use diagonal and the curve.



A descending diagonal line was also plotted that represented random use. The maximal distance between the random use diagonal to the point in the curve closest to the origin represented core area usage. To find this point I used equation 4.1 to calculate the largest distance between the curve and the random use diagonal. Maximal distances were obtained for each RE site (Table 4.3) by reading from the maximal distance point on the curve to the y-axis; this produced the isopleths that represented the core area.

$$\text{Distance} = \frac{ax^1 + by^1 + c}{\sqrt{(a^2 + b^2)}} \quad (4.1)$$

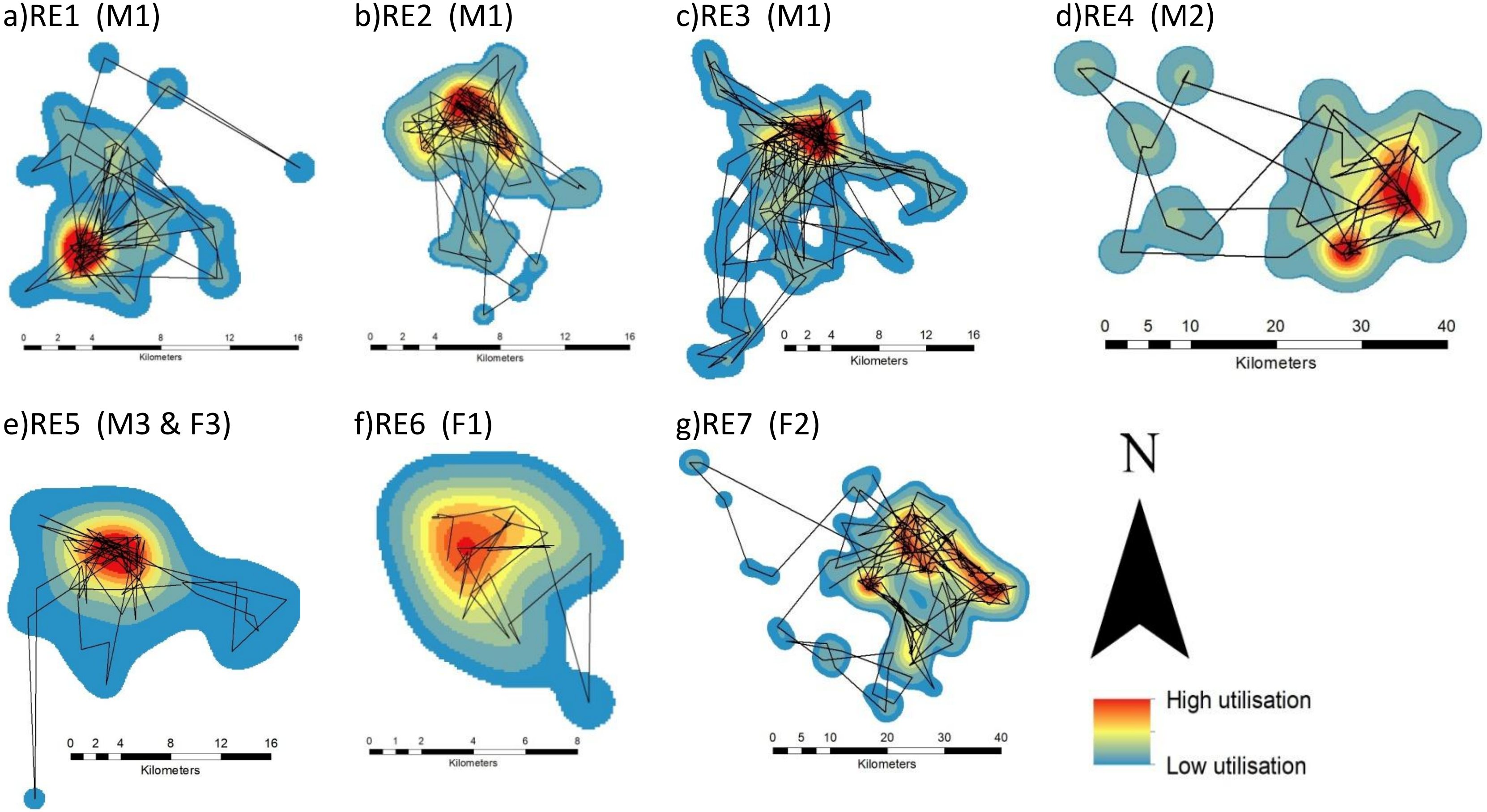
Table 4.3. Isopleths representing core areas for each RE site area (km²) derived from plotting isopleths at 5% intervals against random use to establish the region of clumped use.

RE	1	2	3	4	5	6	7
Isopleth	45	45	50	50	60	50	55

4.3 Results

Movement behaviour between individuals varied, with breaks in dispersal behaviour allowing the identification of areas of concentrated use (Figure 4.4). Landscape characteristics were extracted and resource selection between RE sites examined. The difference in the number of data points generated by the draped mesh varied between RE sites from 1669 to 23,224 (Table 4.5). This was probably related to the area that the RE site covered. Smaller RE sites had fewer GPS location data points and RE sites with a larger geographical spread contained more GPS location data points. Some exploratory behaviour occurred mainly within REs 1, 4 and 7. Exploratory behaviour in RE1 spanned 4 days. In RE4 excursions away from the core area occurred twice, both for 6 day periods and journeys crossed paths. In RE7 excursions occurred 4 times and spanned 3, 5, 3 and 7 days, with some areas being traversed several times or revisited.

Figure 4.4. Examples of rhino movements for each RE site calculated (with rhino ID in brackets) using one GPS point per 24-hour period because these gave a high proportion of comparable data points. Ranges were calculated using 95% kernel density estimation (KDE) utilisation distributions.



4.3.1 Landscape characteristics and the factors influencing space use

There was a highly significant correlation between SDI and SEI with Area (km²) and NP respectively (all r_s=0.964, N=7, p<0.001 (Table 4.4 and Figure 4.5a) across RE sites. MPS and MSI were significantly correlated (r_s=0.991, N=7 p<0.001) (Table 4.4 and Figure 4.5b). There were many other significant results, indicating a strong correlation between RE sites (Table 4.4). Characteristics that were not correlated included Area verses PR, NP verses PR.

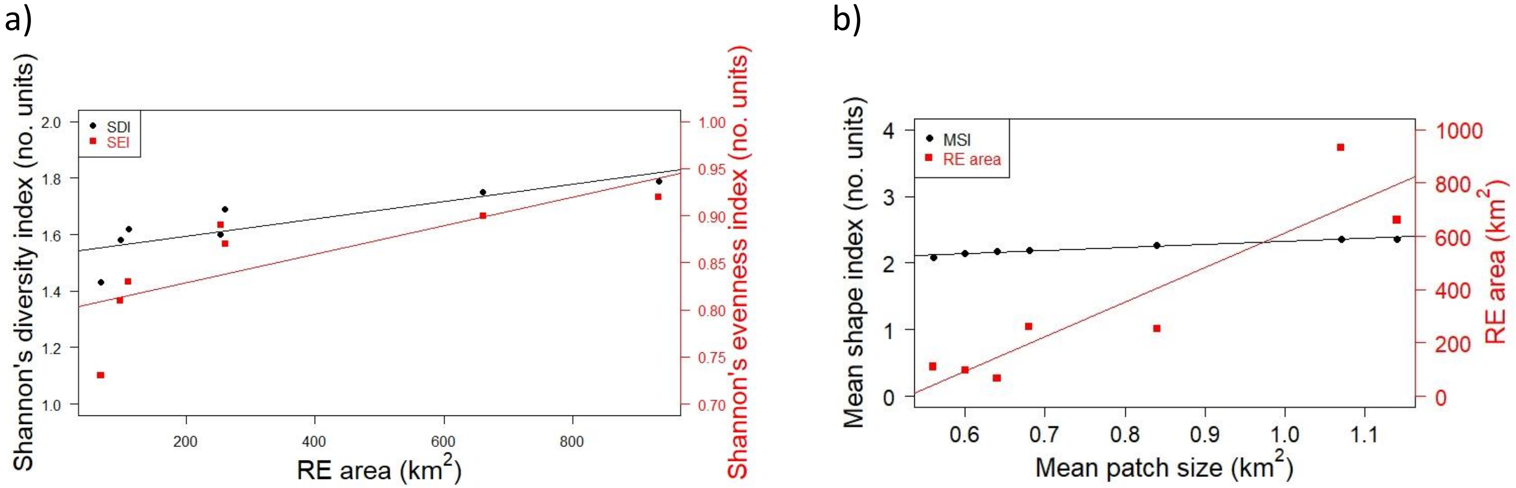
Table 4.4. Results from Spearman's rank correlation tests carried out on landscape metrics; Area (km²), PR (patch richness), MSI (mean shape index), AWMSI (area weighted mean shape index), MPS (mean patch size), NP (number of habitat patches), SDI (Shannon's diversity index), and SEI (Shannon's evenness index) between resource extraction sites.

		Area	**PR**	**MSI**	**AW MSI**	**MPS**	**NP**	**SDI**	**SEI**
Area	Correlation Coefficient	*	.000	.811	.901	.786	1.000	.964	.964
	Significance		1.000	**p<0.05**	**p<0.05**	**p<0.05**	.	**p<0.05**	**p<0.05**
	N		7	7	7	7	7	7	7
PR	Correlation Coefficient		*	-.206	-.206	-.204	.000	.204	-.204
	Significance			.658	.658	.661	1.000	.661	.661
	N			7	7	7	7	7	7
MSI	Correlation Coefficient			*	.836	.991	.811	.667	.847
	Significance				**p<0.05**	**p<0.05**	**p<0.05**	.102	**p<0.05**
	N				7	7	7	7	7
AW MSI	Correlation Coefficient				*	.811	.901	.847	.955
	Significance					**p<0.05**	**p<0.05**	**p<0.05**	**p<0.05**
	N					7	7	7	7
MPS	Correlation Coefficient					*	.786	.643	.821
	Significance						**p<0.05**	.119	**p<0.05**
	N						7	7	7
NP	Correlation Coefficient						*	.964	.964
	Significance							**p<0.05**	**p<0.05**
	N							7	7
SDI	Correlation Coefficient							*	.893
	Significance								**p<0.05**
	N								7

Table 4.5. Data generated using Patch Analyst extension in ArcGIS used to quantify the landscape metrics of 95% KDE from GPS coordinates identified as sites of resource extraction.

Resource extraction no.	Number of UDrel data points	RE area (km²)	Patch Richness	Mean shape index	Area weighted mean shaped index	Mean patch size (km²)	Total no. of patches in landscape	Shannon's diversity index	Shannon's evenness index
1	2,727	110	7	2.08	4.74	0.56	195	1.62	0.83
2	2,391	97	7	2.14	3.95	0.60	162	1.58	0.81
3	6,399	260	7	2.19	4.74	0.68	381	1.69	0.87
4	16,458	661	7	2.36	6.09	1.14	581	1.75	0.90
5	6,307	253	6	2.27	5.64	0.84	300	1.60	0.89
6	1,699	67	7	2.18	4.50	0.64	105	1.43	0.73
7	23,224	934	7	2.36	6.83	1.07	876	1.79	0.92

Figure 4.5. a) Variation in RE site area (km²) with Shannon's diversity and evenness indices, and b) variation in mean patch size (km²) with mean shape index and RE area (km²).



Generalised linear mixed models were used with arcsine square root transformed *UDrel* as the dependent variable, with habitat classes (Section 1.8.2 and 4.2.4) and landscape metrics (as defined in Table 4.2) as the independent variables applied to the results in Table 4.5. RE site was treated as a random factor. I used AICc to determine the most parsimonious model (Burnham & Anderson, 2004) which was composed of habitat class and MPS (Table 4.6), with $R^2 = 0.74$. Results in Table 4.6 support the findings from the Spearman's rank tests in Table 4.4. The number of UDrel values per RE site used in the model are displayed in Table 4.5.

Table 4.6. Generalised linear mixed models were used to analyse how landscape metrics and habitat class influenced relative resource utilisation by white rhino in the Okavango Delta, Botswana. Individual REs (n=7) were incorporated as a random factor. Models were ranked by second-order Akaike Information Criterion (AICc) to account for small sample bias adjustment (Burnham & Anderson, 2004). Ki was number of parameters in the model. Δ AICc was the change in AICc compared to the most parsimonious model. Wi was the Akaike weight and LogLik the log likelihood. UDrel = the relative utilisation distribution; see Table 4.2 for further acronym definitions.

Model	*ki*	AICc	logLik (β)	Δ AICc	wi
UDrel~Habitat class +MPS	2	-31.4	28.693	0	0.626
UDrel~ Habitat class +MPS+MPS:MSI	3	-30.4	29.850	1.07	0.366
UDrel~ Habitat class +MSI	2	-22.4	24.192	9.00	0.007
UDrel~null model	0	-15.0	10.766	16.45	0.000

Table 4.7. ß estimates, SE and 95% confidence intervals for most parsimonious model UDrel~HC+MPS for REs.

Fixed Factor	ß	SE	95% CI	
			Lower	Upper
Acacia woodland (intercept)	0.382	0.038	0.313	0.451
Dry floodplain	0.098	0.051	0.005	0.191
Mophane woodland	-0.132	0.052	-0.227	-0.037
Riperian woodland	-0.200	0.051	-0.294	-0.106
Grassland with wild sage	-0.331	0.054	-0.429	-0.233
Shrubbed grassland former floodplain	0.019	0.051	-0.074	0.113*
Swamp vegetation	-0.280	0.056	-0.384	-0.178
MPS	0.074	0.016	0.044	0.104

Examining ß estimates for the best fit model (Table 4.7), with *Acacia* woodland as the intercept, showed that floodplain and shrubbed grassland habitat classes and MPS had a positive effect on resource utilisation across all RE sites. Within the Okavango's fragmented landscape, the number of different habitat classes increased with area (km²) (McCarthy & Ellery, 1998; Ramberg *et al.*, 2006). Intricacy of patch shape increased with mean patch size, but patch richness (the number of different habitat classes within each RE) was the same for six of seven RE sites.

4.3.2 Habitat selection

I used regression analysis to test for a significant relationship between proportional habitat class availability and relative use (Figures 4.6a, b). The results were significant ($F_{1,46}$=185.2, p<0.001). RUF analysis showed a variation of the relative importance of habitat classes between RE sites (Table 4.8).

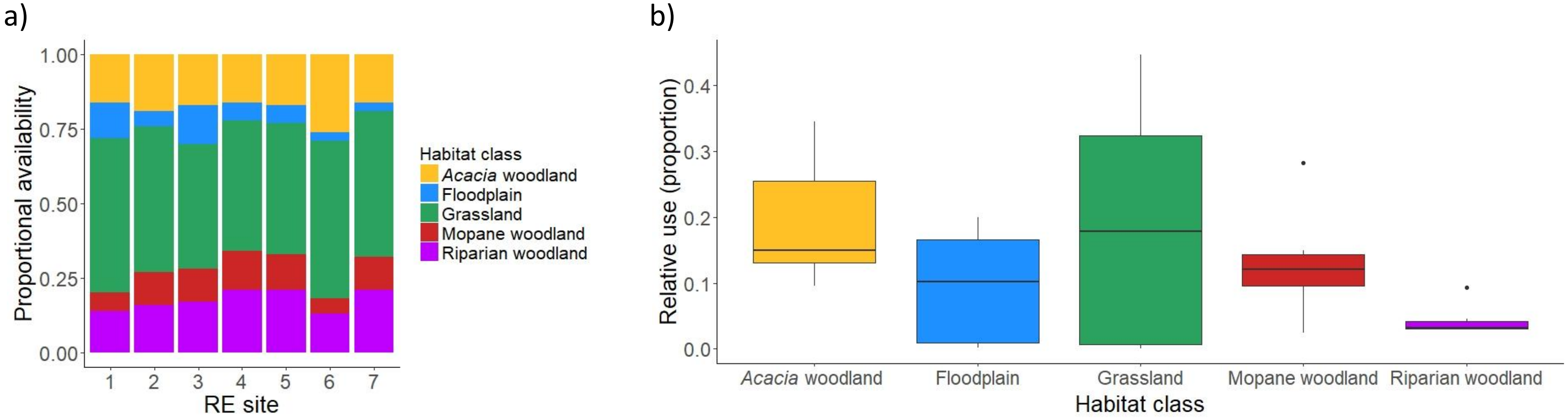
Table 4.8. Ranked relative importance of habitat classes using RUF coefficients for each RE site. (Actual ß values are available in Table S4.1).

Habitat Class	RE site						
	1	2	3	4	5	6	7
Acacia woodland (Intercept)	5	7	7	7	6	7	7
Dry floodplain	4	1	1	2	2	2	3
Shrubbed grassland former floodplain	1	3	3	1	4	3	1
Grassland with wild sage	7	6	6	5	N/A	1	2
Riparian woodland	6	2	5	3	5	4	6
Mopane woodland	3	4	2	6	1	5	4
Swamp vegetation	2	5	4	4	3	6	5

I carried out a Spearman's rank test on RUF results (Table S4.1) between RE sites to determine whether any were correlated. RE3 and RE5 (r=0.886, N=7, p=0.019), RE2 and RE4 (r=0.857, N=7, p=0.014) and RE6 with RE7 (r=0.786, N=7, p=0.036) were significantly correlated. In the next section (4.3.3) I examined shared areas between RE sites and identified the percentage of overlap. I found that RE3 overlapped RE5 by 85%, and RE5 overlapped RE3 by 57%. RE2 overlapped RE4 by 53%, and there was 100% overlap between RE6 and RE7. Therefore it is likely that the sharing of space resulted in the sharing of resources.

The most important habitats were grasslands (dry floodplains, shrubbed grassland on former floodplain, and grassland with wild sage) in all but one case, irrespective of spatiotemporal differences. These results supported the conclusions in section 4.3.1.

Figure 4.6. a) The proportion of available habitat classes was calculated by dividing CA by TLA for each RE, and b) Relative use (UDrel) was calculated by dividing the sum of UD heights for each habitat class by the total UD heights for all classes. Bold horizontal lines represent median values, boxes represent interquartile ranges, and vertical lines standard error ranges. Dry floodplains, shrubbed grasslands and grasslands with wild sage bush were combined as 'grasslands' for illustration.



4.3.3 Shared core areas of resource extraction sites

Figure 4.7. a) Overlapping core RE areas (% UD), RE1=green, RE2=purple, RE3=yellow/brown, RE4=pink, RE5=blue, RE6=multi, RE7=black/grey, and b) Proportion of overlapping core RE areas. Core area ranges, RE1=14km², RE2=15km², RE3=36km², RE4=122km², RE5=53km², RE6=15km², RE7=223km². Bold numbers indicate spatiotemporal overlap.

a)

b)

RE	1	2	3	4	5	6	7
1	*	0	0	**0.86**	0	0	1
2	0	*	0.13	0.53	0	0.13	0.73
3	0	0.06	*	0.08	**0.83**	0.03	0.06
4	**0.10**	0.07	0.02	*	0	**0.12**	**0.69**
5	0	0	**0.57**	0	*	0	0
6	0	0.02	0.07	**1**	0	*	**1**
7	0.06	0.05	0.01	**0.38**	0	**0.07**	*

The proportion of overlap between core REs was calculated using the formula Hij=Aij/Ai, where Hij=proportion of REi's range that is overlapped by REj, Aij=overlap between 2 REs, Ai=area of focal RE range (Fieberg & Kochanny, 2005).

Total core areas equated to 308km^2, with a variation between REs from 15km^2 to 223km^2 (Figures 4.7 a, b). This indicated different energetic costs and behavioural movement strategies, which was likely to have been affected by resource availability within the range (Pyke *et al.*, 1977; Bailey *et al.*, 1996). Despite being the only white rhino in the area, there is strong evidence that the landscape was being utilised as a shared resource. In Chapter 2 I found that rhino sometimes moved in pairs and groups, and this explained some of the overlap in resource selection. However, there was complete spatial overlap between RE1 and RE7, but no temporal overlap. Time spent at each RE site varied with 5 out of 7 REs spanning across more than one season.

4.4 Discussion

Resources are spread heterogeneously across the landscape, so animals must modify their movements to access them (Fryxell *et al.*, 2008). Random movements occur when animals are unfamiliar with their environment (Papastamatiou *et al.*, 2011) but, after a period of familiarisation, may reduce movements to graze in selected profitable areas (Brooks & Harris, 2008; Owen-Smith *et al.*, 2010; Fagan *et al.*, 2013). Movement strategies may also be influenced by other factors. For example, there is a trade off between energetic gains and predation in profitable but risky foraging patches (Houston *et al.*, 1993). The life history of the animals is also a factor, female elephants and weaned calves are known to limit movements when forage quality is lower in order to store energy (Birkett *et al.*, 2012), whereas mature solitary bull elephants roam large distances looking for mates (Pinter-Wollman *et al.*, 2009). Additionally, older matriarch and male elephants are considered to be spatial information repositories that govern movements via prior knowledge (Evans & Harris, 2008; Pinter-Wollman *et al.*, 2009). Dispersal distances are also affected by personality. For instance, larger dispersal distances were recorded in bold and least co-operative compared to shy individuals in both birds and fishes (Fraser *et al.*, 2001; Dingemanse *et al.*, 2003; Bonte *et al.*, 2012).

Long-distance movements by rhino (Chapter 3) may suggest that they utilise resources along dispersal routes and therefore adopt a flexible mixed movement strategy at the landscape scale, as opposed to being locally restricted (Owen-Smith & Martin, 2015). Herbivores may take advantage of temporary water supplies during rainy and flood seasons to enable them to disperse greater distances (Pienaar *et al.*, 1993b). Volatile movement behaviour, by switching between large dispersal movements and sedentary behaviour, has been observed in subadult rhino (Owen-Smith, 1971). Elephants tend to travel less when resources are available locally but are affected by water source availability, travelling further if the distance between profitable feeding sites and water increases (Harris *et al.*, 2008).

Keystone species such as elephant and rhino (Paine 1995) have a disproportionately large impact on the environment (Cromsigt *et al.*, 2014). Feeding and defaecation behaviours of herbivores influence nutrient cycling (Stock *et al.*, 2010). Large aggregations of mixed grazing herbivores may also increase nutrient cycling by grazing and then spreading dung over large areas. However, rhino differ because they consume large amount of nutrients and their bodies act as a pump, producing nitrogen-rich dung that is dispersed in small areas, thereby creating nutrient rich hot-spots (Stock *et al.*, 2010). As ecosystem engineers, megaherbivores are able to alter landscape heterogeneity and increase habitat and sward diversity (McNaughton *et al.*, 1988; Adler *et al.*, 2001; Waldram *et al.*, 2007), with the potential of benefitting other grazers. Grazing lawns are often located near dung piles (Coetsee *et al.*, 2011; Cromsigt *et al.*, 2014), and influence the behaviour, movement, and density of other grazing species beyond the boundaries of lawns (Hempson *et al.*, 2014). Cromsigt *et al.* (2014) found that the density of buffalo, wildebeest and zebra did not influence the occurrence of lawns, but are able to benefit from them (Hempson *et al.*, 2014).

The nutritional value of swards varies temporarily, so some animals move away to find better grazing. Megaherbivores are limited by graze quantity, not quality (Fritz *et al.*, 2002). Bulk grazers are capable of surviving on lower quality taller grasses (Owen-Smith, 1992; Shrader & Owen-Smith, 2002; Waldram *et al.*, 2007). This is because they are hindgut fermenters and have longer digestive retention times (Owen-Smith, 1992). Their ability to utilise large volumes of low quality graze enables them to maintain body condition in periods with lower than average rainfall (Grant & Scholes, 2006), but when necessary some megaherbivores mobilise fat reserves in order to survive (Shrader *et al.,* 2006a).

I used rhino movement patterns to identify highly utilised sites, and these uncovered some of the ecological components required to sustain populations of white rhino in the peripheral Okavango Delta. Contrary to my hypothesis, there was a high correlation between many of the landscape metrics across RE sites, indicating that sites shared certain properties. However, it may be that the spatial area overlap between several of the RE sites influenced these results. My analysis did not take preferential resource use areas into account, and so only gives an indication of what landscape metrics lay within the 95% utilisation distribution for each RE site.

The utilisation of space was influenced by habitat class and habitat patch size. Utilisation distributions were used to analyse habitat use between RE sites and produced results that conflicted with my hypothesis. The importance of habitat varied across RE sites, with only 14% of all possible paired combinations having significantly correlated results. However, the habitats ‘dry floodplain’ and ‘shrubbed grasslands on former floodplain’ were ranked most highly in RUF analysis and were also both positive covariates in GLMM tests. This suggests that habitats with high grass quantity were preferred (Bartlam-Brooks *et al.*, 2013). However, this was only what was proportionally available. By including landscape metrics, I found that mean habitat patch size was related to relative use, and was probably connected to rainfall and the flooding regime of the Okavango Delta. In a study on the relationship between home range sizes and landscape metrics of elephants, ranges did not decrease with the increase in Shannon's diversity index (patch richness) as was found in my study (de Beer & van Aarde 2008). However, de Beer & van Aarde (2008) could not draw firm conclusions relating to landscape metrics and their effect on range sizes, so it is likely that results are affected by individual differences (Harris *et al.*, 2008). Additionally habitat class was not included in the study as was the case in this study.

In addition, my results showed that profitable sites temporally stretched across more than one season, usually the rainy and flood seasons, but also into the early part of the hot dry season, and on one occasion throughout the hot dry season (Arsenault & Owen-Smith, 2011). This may be because large herbivores spend more time at abundant productive patches (Pyke *et al.*, 1977; Bailey *et al.*, 1996), or because the animals returned to known profitable sites (Owen-Smith *et al.*, 2010). Rhino have been observed grazing on high nutritional quality grasses left after the retreating floodwaters (Krah *et al.*, 2006; Ramberg *et al.*, 2006; Pitlagano, 2007). In dry seasons non-migratory elephants have been found to select lower quality habitats close to water (de Beer & van Aarde 2008), so perhaps rhino switched from quality to quantity of swards.

In the Okavango Delta, Levels of nitrogen increase on floodplains as a result of the incoming seasonal flood waters, which also bring about the release of phosphorous (Mubyana *et al.*, 2003). The retreating floodwater leaves highly biologically productive grasslands (Krah *et al.*, 2006; Ramberg *et al.*, 2006). Rainfall also enables herbivores to profit from fresh leaf growth (Coe *et al.*, 1976; East, 1984; Bonnet *et al.*, 2010). These favourable nutritional transformations mainly occur in grasslands (O'Connor & Bredenkamp, 1997) and savannahs (Rutherford, 1965; Balfour & Howison, 2002). During rainy seasons it is likely that, after a period of regeneration, and using spatial memory, herbivores re-use grazing lawns (Ford, 1983; Hobbs *et al.*, 1991; Bailey *et al.*, 1996; Van Moorter *et al.*, 2009; Bonnet *et al.*, 2010; Seidel & Boyce, 2015). Defoliation stimulates the increase of nitrogen in grass through a positive feedback loop that would improve the quality of swards in all seasons (McNaughton *et al.*, 1988; Voeten *et al.*, 2010).

Previous estimates of resource selection used animal home ranges to allocate the area to be analysed. However, these estimates were largely subjective and individual movement behavioural ecology was ignored. I was able to calculate areas of concentrated use for animals with no 'home range' (Powell & Mitchell, 2012), while also taking individual behavioural ecology into account (Hebblewhite & Haydon, 2010; Merrick & Koprowski, 2017). I found that there was an overlap in core areas which was in agreement with my hypothesis. This was probably as a result of companionships between individuals, but could also be related to animals visiting areas by utilising olfactory cues (Owen-Smith, 1974). However, the sharing of space could also indicate that rhino shared resources. For example, subordinate rhino males sometimes travel into the territory of dominant bulls in order to drink (Owen-Smith, 1975). Furthermore, White *et al*. (2007) found that females mated with the most familiar males, so the sharing of space may also contribute to mating strategy.

4.4.1 Conclusion

Tracking rhino movement enabled me to quantify spatiotemporal resource extraction sites and corresponding landscape features. Rhino employed a plastic mixed movement strategy at the landscape scale by switching between large dispersal movements and sedentary behaviour. The overlap of core ranges were consistent with findings of Pedersen (2009), who found that rhino focused movements in one particular area, and that range areas varied largely in size. The long-distance movements suggest that rhino utilise resources along dispersal routes. Megaherbivores movements may be affected by water availability, displaying encamped behaviour when water is abundant and dispersing over sometimes great distances between feeding sites and water sources when it is not (Harris *et al.*, 2008). Despite differences in movement behaviour between individuals, rhino all selected the same key habitats.

Grassland areas were favoured more than woodland habitats, and were related to availability. These results differ to those found by Pedersen (2009), where rhino showed no habitat preference but suggested that resources were distributed in every habitat type. However, more research is needed into behaviour-related habitat selection at the landscape scale, since observation of the animals was difficult due to the challenging environment and problems with technology. Additionally, no other research has applied resource use functions to quantify selected landscape characteristics for white rhino, so these results cannot be easily compared with earlier studies.

4.4.2 Link to next chapter

In this chapter I have shown that is it possible to use the movement strategies of animals introduced into new environments to identify intensely-used areas and corresponding landscape characteristics.

In the next chapter I move from identifying resource selection at the landscape scale to habitat scale, and also analyse sward selection at the feeding site. I will use rhino movement pathways to compare the habitat features of selected grazing patches to a random sample of non-chosen sites along the path. I also assess any differences in sward characteristics between selected patches and across compare then across seasons.

Chapter 5. Habitat and grazing site sward selection by white rhino in the Okavango Delta

5.1 Introduction

The biomass of large herbivores is highly dependent upon the production of plant material which, in turn, is influenced by climate (Coe *et al.*, 1976; Prins & Loth, 1988). Fire (Bond & Keeley, 2005) and past grazing (McNaughton, 1983) also contribute to the quality and quantity of available forage, as does the nutrient status of the soil (East, 1984). Large herbivore resources are distributed widely across the landscape, leading to foraging decisions across different spatial scales. For example, selection takes place within feeding stations, plant community, landscape and regional levels along an ecological hierarchy. The challenge for large herbivores is acquiring the best quality and greatest quantity of graze (Senft *et al.*, 1987). Foraging strategies are variable and herbivores may change selection in order to maximise energetic yield (Schoener, 1971). For example, in dry seasons when resources are scarce, large grazers may reduce selectivity and instead increase quantity consumed (Bell, 1971).

African savannahs consist of guilds of primary consumers. For example, grazers and browsers at risk of predation by carnivores, megaherbivores and predators. Smaller herbivores tend to utilise areas of high quality forage with good visibility of potential predators, whereas larger herbivores utilise the entire landscape (Anderson *et al.*, 2016). Foraging strategies also vary according to environmental constraints (Schoener, 1971; Pyke *et al.*, 1977), as well as the internal state of the animal (Johnson *et al.*, 2001; Houston & McNamara, 1999; McNamara & Houston, 1992, 1996). To optimise energy intake rates, and thus fitness, animals must make the right decisions about (i) where to search for food, (ii) when to feed, (iii) what to consume, (iv) and when to stop feeding (Schoener, 1971; Pyke *et al.*, 1977; Stephens & Krebs, 1986; Owen-Smith *et al.*, 2010). Small herbivore populations are regulated by top-down processes, whereas megaherbivore populations are regulated by bottom-up processes, and so are more strongly affected by periods of food shortage (Phillipson, 1975; Sinclair, 1975; Coe *et al.*, 1976). To counteract any decline in nutritional quality (Owen-Smith *et al.*, 2010), large herbivores may increase time feeding, increase their intake-rate, alter their diet, migrate to a more profitable site (Beekman & Prins, 1989), or mobilise fat reserves (Demment & Van Soest, 1985; Gerhart *et al.*, 1996).

Two differences types of digestive physiology have evolved in herbivores, pre-gastric and post-gastric fermentation also known as ruminant and non ruminant, or hindgut fermenters (Dehority, 2002). Ruminants are the more abundant of the two (Dehority, 2002), and are generally medium-sized animals, whereas non-ruminants are either small or very large (Demment & Van Soest, 1985).Differences in digestive physiology and energetic requirements, as affected by surface area to volume relationships, between the two non-ruminant groups has a major influence on their nutritional regime (Cromsigt *et al.*, 2009). Large herbivores have low energy requirements for their body size and long gastrointestinal passage rates. This allows them to utilise high biomass, lower quality, forage (Demment & Van Soest, 1985; Arsenault & Owen-Smith, 2002; Clauss *et al.*, 2003). Conversely small animals usually select higher quality but smaller biomass because of their lower absolute requirements. As well as gut morphology, the size of an animal’s mouthparts influences selection (Arsenault & Owen-Smith, 2002), so larger animals tend to be less selective at the feeding site (Van Soest, 1994).

The white rhino is a mega-grazer capable of enduring lower quality graze (Shrader *et al.,* 2006a). Rhino have an advantage over other large herbivores: their required intake rate is smaller because their longer gut retention time enables them to extract more nutrients. The energy requirement for rhino has been measured at 63g/kg $BM^{0.75}$/day of organic matter (BM-body mass, with allometric scaling) with a mean retention time (MRT) of 64.0h (Clauss *et al.*, 2009; Steuer *et al.*, 2010, 2011). In contrast, the African elephant requires

86g/kg $BM^{0.75}$/day of organic matter with a mean retention time of 52.3h, and the plains zebra requires 105g/kg $BM^{0.75}$/day of organic matter with a mean retention time of 46.0h (Clauss *et al.*, 2009).

Contrasting results have reported that rhino are both grass species selective (Kiefer, 2002) and species unselective (Melton, 1987; Perrin & Brereton-Stiles, 1999), or only select for particular sward characteristics i.e. short grasses (Owen-Smith, 1973, 1992; Perrin & Brereton-Stiles, 1999; Shrader *et al.,* 2006a). There are also varying reports of dietary strategies for coping with dry season shortages. One study determined that rhino swapped to taller, low quality grasses, thereby increasing intake rate (Owen-Smith, 1973), while another in a high rainfall year found that rhino did not alter their grazing behaviour between seasons but that intake rates fell below the maximum, and used fat reserves to compensate for nutritional deficits (Shrader & Perrin, 2006; Shrader *et al*., 2006a).

At larger scales white rhino were found to switch from grazing in open *Acacia* woodland in summer to a random selection of habitats during the limiting winter period (Melton, 1987). In some cases rhino have been found to avoid mopane woodlands (Pienaar *et al.*, 1993a), whereas in others they do not (Pedersen, 2009). Rhino appear to have a flexible feeding strategy but it is likely that this affected by its digestive anatomy, coupled with the capacity to utilise subcutaneous fat reserves (Shrader & Perrin, 2006). Rhino employ different strategies depending upon the conditions and the system which they inhabit, so there is a lack of information as to what drives selection (Owen-Smith, 1992; Shrader & Perrin, 2006).

The Okavango Delta is a low nutrient wetland ecosystem (McCarthy & Ellery, 1998), but the mobilisation of nutrients through seasonal flooding leads to high plant productivity and attracts high numbers of grazing herbivores (Ramberg *et al.,* 2006). Hydrogeological processes influence soil nutrient status through variation in surface water, groundwater and soil chemistry (McCarthy, 2006;

Milzow *et al.*, 2009; McCarthy *et al.*, 2012). Grazing herbivores in this system must adapt to large spatiotemporal deviations in habitat and sward features, with rain typically falling annually between December and March (Ramberg *et al.*, 2006).

In response to the lack of clarity on rhino foraging strategies, I examined rhino grazing selection at the habitat scale and at the feeding site in the Okavango Delta. My original aim was to analyse the chemical composition of swards, since these may influence selection (Georgiadis & McNaughton, 1990; McNaughton, 1990); however, this was not possible due to budgetary constraints. I also experienced problems locating rhino for direct observation, so I was unable to assess changes in body condition.

I hypothesised that:-

1) Site selection at the habitat scale would vary across seasons. Since rhino build fat reserves in periods of food abundance they should select productive grassland habitats. In periods of food shortage rhino do not expend energy searching for productive food patches that may not be found, but graze on lower quality swards in a variety of habitats.
2) Rhino make seasonal dietary adjustments at the feeding site by switching from high quality plentiful short grasses in the rainy season, to taller lower quality swards in the hot dry season.
3) As bulk grazers, once within a preferred feeding site, rhino would not be selective.

5.2 Methods

5.2.1 Field problems and change of methods

To assess grazing selection by rhino, my first plan was to locate rhino using VHF radio transmitters and GPS technology, and observe them grazing at sites across five habitat categories (open mopane woodland, closed mopane woodland, *Acacia* woodland, riparian woodland and grassland). The site would then be sampled (Section 5.2.3) and the sward characteristics compared to reference sites, with at least 6 samples for each habitat category (to obtain a habitat average) by season.

However, the battery life on all of the VHF radio transmitters failed a year earlier than anticipated, and GPS coordinate information was infrequent (Section 3.2.1). This made obtaining a location to start searching for the animals very difficult. Trials between 15th June and 15th September 2014 showed that the success of locating any rhino was limited and continuing this method of data collection would have resulted in inadequate sample sizes.

The next season I received the most recent GPS coordinate information around 08:00 daily. However, due to technological problems the coordinates were sometimes from the previous day, or no up-to-date information was available. After driving to the coordinate location I utilised the skills of my tracker to find rhino tracks. The rhino pathway was followed and, if a grazing site was found, it was sampled. However, sample sizes were still limited.

5.2.2 Route marking and site ID

As described in section 3.2.6, the pathways followed by rhino were recorded using a hand-held GPS device (Garmin Montana 600). Grazed sites along the path were identified using the expertise of my tracker and assigned a GPS coordinate. These were categorised as being ‘selected’ by rhino. Sites that had been spoiled by trampling, or that had been grazed by other herbivores were excluded from the analysis.

The sward characteristics rhino selected were compared to a randomly selected site along the track. The random sites represented sward characteristics that not been selected by rhino, hereafter called the ’unutilised site’. The unutilised site was chosen by randomly generating a number between 1 and 300. This represented the number of seconds to walk or slowly drive at approximately 10-

15km/hour in a vehicle (if it was unsafe to walk) away from the selected site along the track. I flipped a coin to determine whether to travel backwards or forwards along the path. However, on occasions it was only possible to travel a limited distance along the track, or in one direction. This was due to rhino crossing watercourses that I could not cross, tracks being washed away by rainfall, or hard ground and vegetation not leaving obvious prints. A GPS coordinate was taken of the unutilised site. Both the selected and unutilised sites were sampled using the methods described in section 5.2.3. I used tracks from the same sample as section 3.2.6 Table 3.6, however not all tracks provided grazing sites, and along some tracks more than one selected grazing site could be sampled. Of the 15 tracks sampled for the rainy season 20 grazing sites were sampled, for the flood season this was 6 selected grazing site from 6 tracks sampled and for the hot dry season this was 12 grazing sites from 13 tracks sampled. These gave a small sample size of 19 paired tests between selected and unutilised sites collected along these transects (Vinton *et al.*, 1993; Bakker *et al.*, 2003).

5.2.3 Grass sampling

I used the same techniques as previously used by Bennitt *et al*. (2014) to sample buffalo foraging preferences. A 0.5m x 0.5m quadrat was thrown randomly four times and the results were combined to represent a 1m² sample for each utilised and unutilised site. Grass species were identified in each quadrat (Oudtshoorn, 1999), and the area each species covered was estimated to the nearest 5%. The species with the greatest area was categorised as the dominant species for each site. I counted the number of individual species within each quadrat, and this was used as a measure of species richness (spp./m²) (Bartlam, 2010; Gotelli & Colwell, 2011 ; Bennitt, 2012). For each species, I took five measurements (cm) of leaf height from different plants. I also estimated the overall ground cover (%) within the quadrat. For each dominant species the grass was cut to 1cm and stored in an envelope.

Grass biomass (equation 5.1) was measured using a disc pasture meter (DPM) (Bransby & Tainton, 1977) that was dropped at 1m intervals along a 50m transect. The DPM was only dropped onto grass: wooded and herbaceous plants were avoided. Biomass was calculated using the formula:

$$Y = -1633 + 1791\left(\sqrt{X}\right) \tag{5.1}$$

where Y represented grass biomass (kg/hectare), and X represented the mean of 50 DPM settling height drops (cm) (Trollope *et al.*, 2006).

Sward roughness (equation 5.2) was calculated by dropping a 10cm cardboard disc down a measuring pole and reading its resting height (cm) (Drescher, 2003). This was carried out along a 4m transect at 10cm intervals, equating to 40 measurements along the plane. Sward roughness, defined as the root mean square (RMS) height, was calculated using the equation:

$$\sigma = \sqrt{\left[\frac{1}{N}\sum_{I=1}^{N}(S_x - \overline{S_x})^2\right]} \tag{5.2}$$

where σ represented the root mean square height (cm), N was the number of recorded sward heights measured, S_x was the sward height at the xth position (cm) and $\overline{S_x}$ was the mean sward height along the transect (cm). The RMS height revealed the extent that the sward heights fluctuated from the mean plane. The greater the fluctuation from the mean, the greater the RMS height (Oelze *et al.*, 2003).

Habitat density was estimated using a striped pole with alternate 10cm sections coloured white and red. The pole was placed at 5m intervals in each cardinal direction up to a distance of 25m, and the number of visible red and white stripes counted (Toledo *et al.*, 2010).

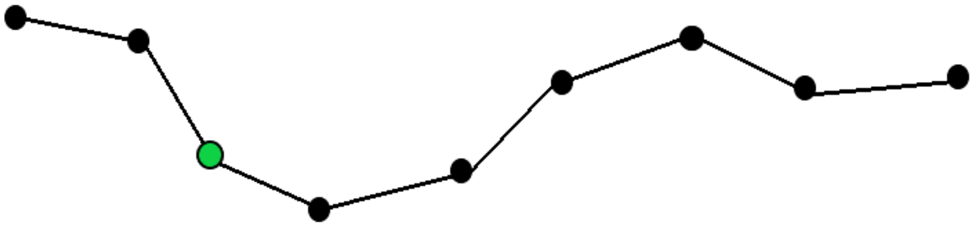
5.2.4 Analysis of sward characteristics

Field data were organised into three groups for analysis, 1) sample type (selected site by rhino compared to the unutilised site), 2) by season and 3) habitat class, to assess whether there was a significant difference in the proportion of dominant species, grass biomass, species richness, proportion of ground cover, sward roughness, leaf height and habitat density. T-tests, and Wilcoxon matched pairs signed rank tests for variables where the residual variation was not normally distributed, were used for selected and unutilised sites, and Mann-Whitney U tests with Monte Carlo-based calculation of *p*-values were used for season and habitat class comparisons. For seasonal analysis, the flood season was discounted due to insufficient data (sample size, n=3). Habitat classes were combined to create two dummy categories. Dry floodplains and island interiors, shrubbed grassland on formed floodplain and grassland with wild sage were joined to create a single category 'grasslands'. *Acacia*, riparian and mopane woodlands were merged to create the 'woodland' dummy category (Table 5.5). Tests were carried out in IBM SPSS Statistics for Windows, version 24.0.0.0 (IBM Corp., Armonk, N.Y., USA) and R (R Core Team, 2016). I used the reference book by Oudtshoorn (1999) to determine the palatability of swards. Swards were categorised as unpalatable, average palatability or highly palatable where palatability is described as the acceptability of the grass for grazers based upon digestibility and nutritional value (Oudtshoorn, 1999; Treydte *et al.*, 2013; Huruba *et al.*, 2018).

5.2.5 Data analysis of habitat characteristics

Habitat characteristics along the movement pathway were compared to those at the selected grazing sites to assess whether habitat features influenced grazing site selection. Rhino pathways (Section 5.2.2) were imported into R (R Core Team, 2016). The *adehabitatLT* package (Calenge, 2006) was used to re-compute trajectories into 100m segments (Figure 5.1). A coordinate was allocated to each point at the end of every segment. In Figure 5.1 the black dots represent random unutilised sites along the path that had not been grazed, and green dot represents a selected grazed site. I plotted each trajectory point along with the selected grazing site as a visual check that there was no overlapping data capture.

Figure 5.1. Example of a rhino pathway. Each pathway was transformed into 100m segments with a coordinate point at each end. Black dots indicate coordinates of random unutilised sites along the path and the green dot represents the coordinate of the site that had been selected.



Coordinates were transformed using *ArcCatalog* 10.4.1 (ESRI, 2015) from decimal degrees to UTM coordinates, and imported into *Arcmap* 10.4.1 (ESRI, 2015). Each point also represented independent variables, and these were assigned a habitat class (Section 1.7.2) and landscape metrics (Table 4.2). I also included the distance (m) to the nearest habitat patch edge. This was because plant species are considered to be more diverse at habitat edges, due to increased vegetation complexity and access to more than one habitat (Yahner, 1988). I included this metric so that I could determine whether rhino utilised this landscape structure for grazing, and used movement data to assess rhino responses to habitat edges (Schtickzelle & Baguette, 2003; Miranda *et al.*, 2011).

The dependent variable was assigned a value of zero if it corresponded with an unutilised site (black dot), or assigned a value of 1 if it corresponded with a selected site (green dot). These data were then analysed in R (R Core Team, 2016) using the function *glm* to fit Generalized Linear Models with binomial error. Model selection was carried out using Akaike's Information Criterion (AIC) (Burnham & Anderson, 2002) via the R package *bblme* (Bolker, 2017). The global (saturated) model contained the predictors of season interacting with habitat type, as the hypothesis was that patch selection at the habitat scale would vary across seasons, from selection of specific habitat types in periods of food abundance to random choice in periods of food shortage. Habitat was fitted as a series of dummy variables as described in Section 5.2.4. The AIC score of the global model (using the logit link function) was then compared to simplified models by a stepwise removal process. These intermediate models were derived by removing the least influential variable from the model and repeating the process until AIC scores plateaued. The final model was also judged against the null model, and the model with the lowest AIC score selected (Bolker, 2017). The relative explanatory power of the final model was checked using Nagelkerke's pseudo-R^2 from the package *rcompanion* (Mangiafico, 2018).

5.3 Results

5.3.1 Analysis of sward characteristics

The physical attributes of swards were analysed by selected versus unutilised (Figure 5.2 Figure 5.3, Figure 5.4 and Table 5.1), and by season and habitat (Figure 5.5, Figure 5.6 and Table 5.1). Species richness was significantly higher in selected compared to unutilised sites (t_{36}=2.296, *p*=0.028), but there was no difference in the distribution of any of the other sward variables (Table 5.2). Selected and unutilised sites were broken down into seasons and habitat types (Table 5.3). In selected sites, grasslands had significantly more ground cover (%) compared to woodlands (*U*= 7.0, *N1*=10, *N2*=9, Monte Carlo *p*=0.001), and sward height (cm) was significantly higher in grasslands compared to woodlands (*U*= 10.0, *N1*=10, *N2*=9, Monte Carlo *p*=0.004). Therefore it is likely that rhino selected more densely packed grassland habitats with particular sward height characteristics.

Comparing rhino selection to what was available, the proportion of ground cover (%) was significantly higher in the rainy season compared to the hot dry season (U=66.5, N_1=20, N_2=12, Monte Carlo *p*=0.035). Ground cover was also higher in grasslands compared to woodlands (U=104.0 N_1=17, N_2=21, Monte Carlo *p*=0.029) (Table 5.2). I analysed the interaction between season and habitat type for ground cover (Table 5.4). Ground cover (%) in grasslands was significantly higher in the hot dry season (U=2.5, N_1=3, N_2=9 Monte Carlo *p*=0.038) compared to the rainy season.

Figure 5.2. Species richness from selected and unutilised grazing sites. Thick horizontal lines are medians with boxes spanning the interquartile ranges, vertical reach to the first data point falling within 1.5 inter-quartile ranges from the box, and circles denote outliers (Chambers et al.*, 1983).*

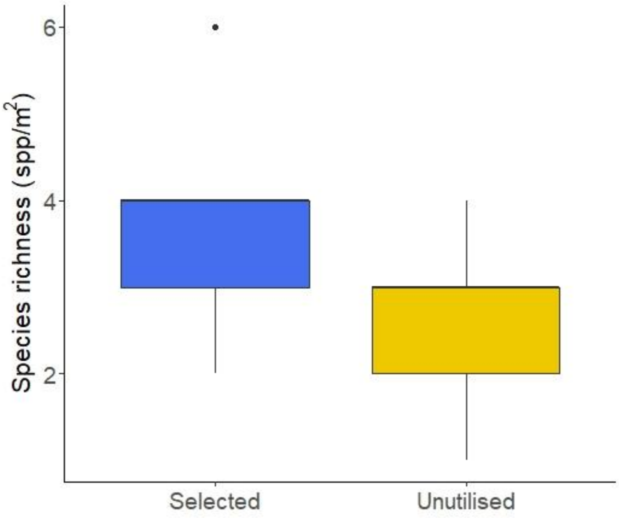


Figure 5.3. a) proportion of dominant species (%), b), sward roughness (no. of units), and c) biomass (kg/ha) from selected and unutilised grazing sites. Thick horizontal lines are medians with boxes spanning the interquartile ranges, vertical reach to the first data point falling within 1.5 inter-quartile ranges from the box, and circles denote outliers (Chambers et al.*, 1983).*

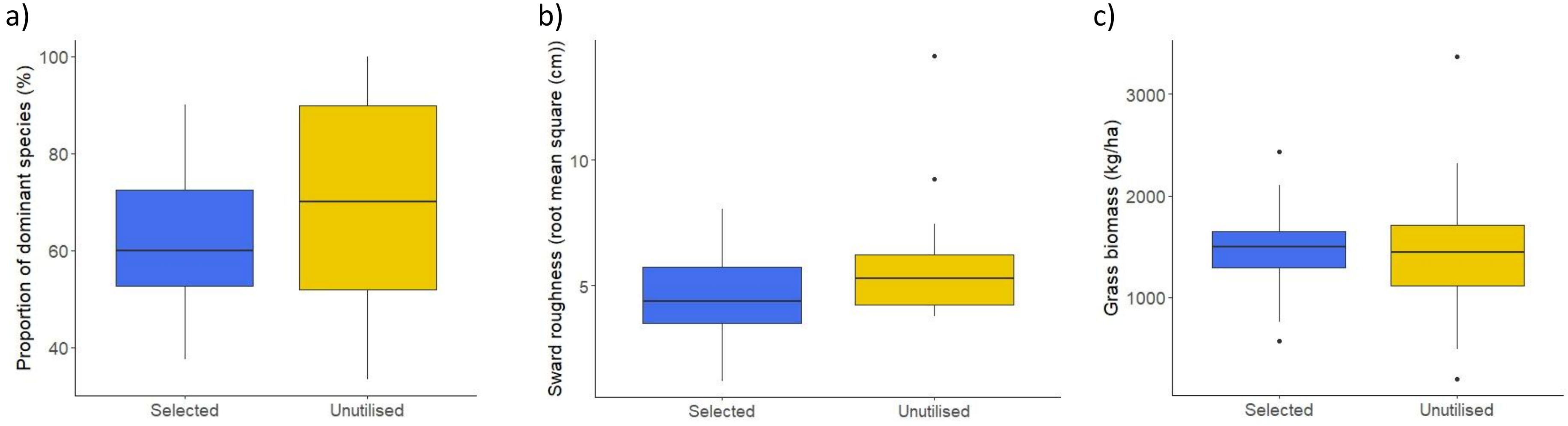


Figure 5.4. a) proportion of ground cover (%), b), sward height (cm), and c) habitat density (no. units) from selected and utilised grazing and sites. Thick horizontal lines are medians with boxes spanning the interquartile ranges, vertical reach to the first data point falling within 1.5 inter-quartile ranges from the box, and circles denote outliers (Chambers et al.*, 1983).*

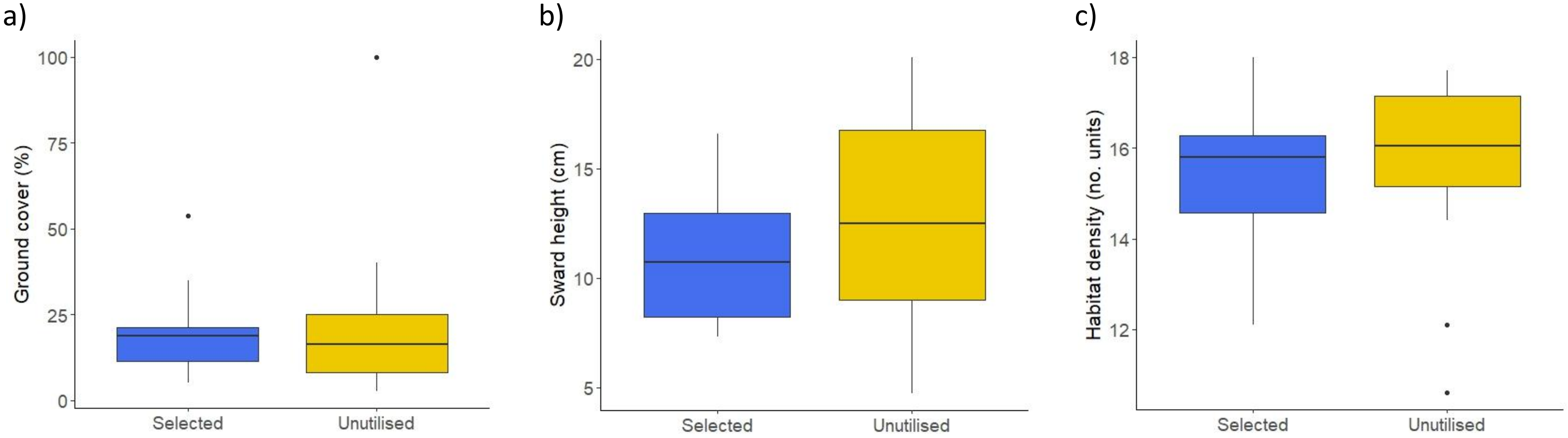


Figure 5.5. a) proportion of dominant species (%), b), sward roughness (no. of units), and c) biomass (kg/ha) in grasslands (GR) and woodlands (WD) in the hot dry and rainy seasons. Thick horizontal lines are medians with boxes spanning the interquartile ranges, vertical reach to the first data point falling within 1.5 inter-quartile ranges from the box, and circles denote outliers (Chambers et al.*, 1983).*

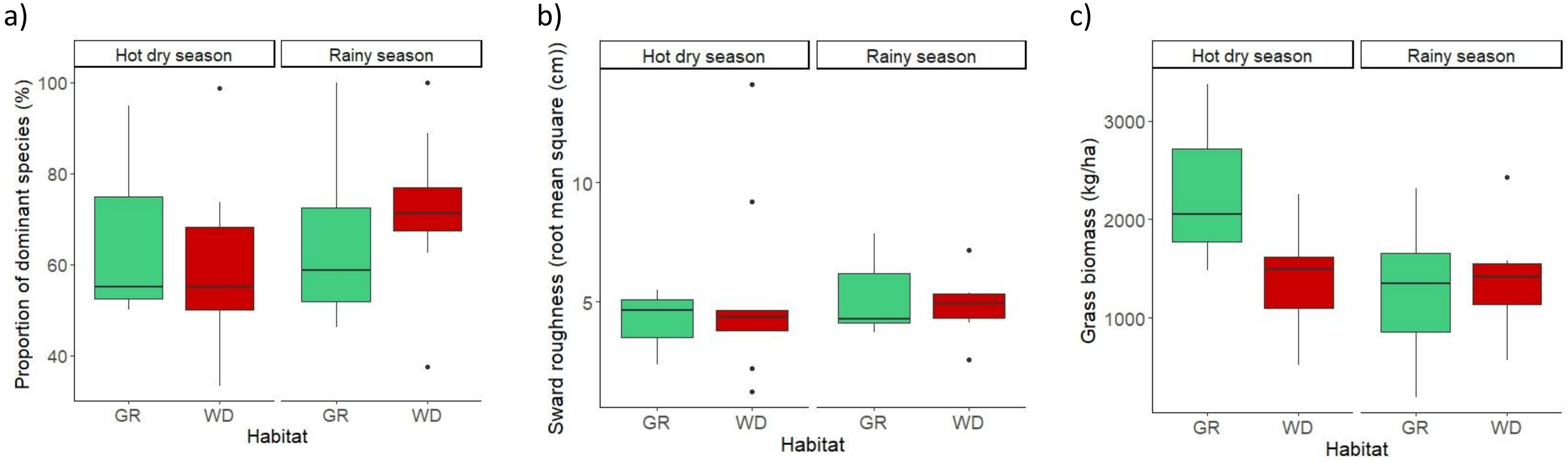


Figure 5.6 a) ground cover (%) b), sward height (cm), and c) habitat density in grasslands (GR) and woodlands (WD) in the hot dry and rainy seasons. Thick horizontal lines are medians with boxes spanning the interquartile ranges, vertical reach to the first data point falling within 1.5 inter-quartile ranges from the box, and circles denote outliers (Chambers et al.*, 1983).*

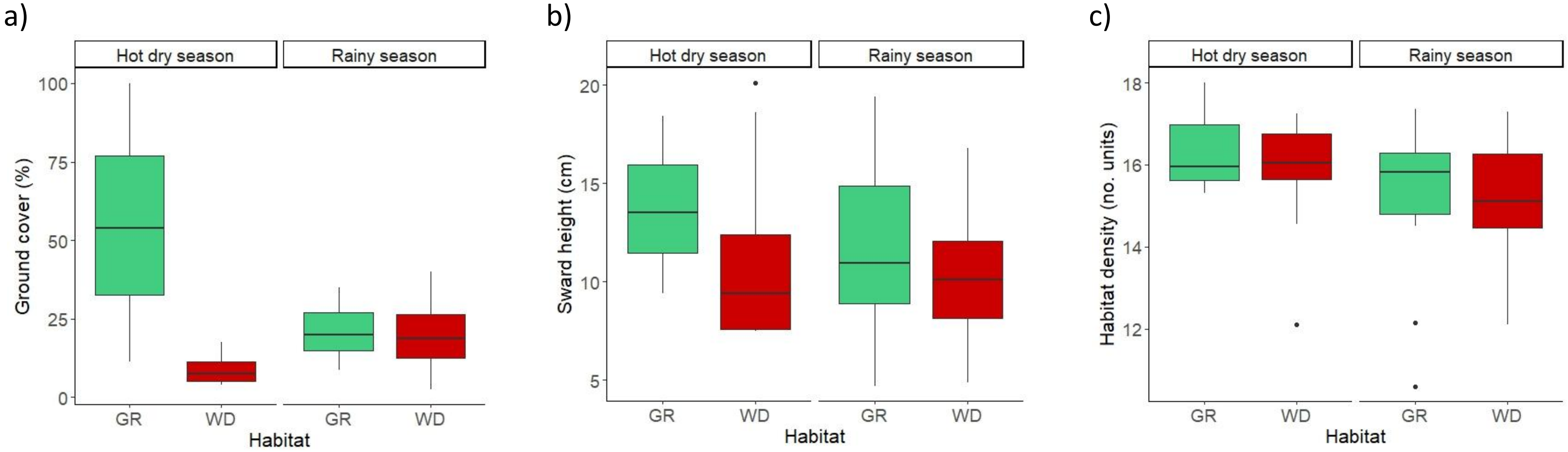


Table 5.1. Summary of sward characteristics for selected grazing and unutilised grazing sites by season and habitat, sampled along rhino tracks. Values are medians with interquartile ranges.

Sward characteristic	n	Proportion availability of dominant species (%)	Species richness (species/m²)	Biomass (kg/ha)	Habitat density (no. units)	Ground cover (%)	Sward roughness (no. units)	Sward height (cm)
Sample type								
Selected	19	60.00 (37.5-72.50)	4.00 (2.00-4.00)	1494.80 (567.80-1647.40)	15.80 (12.10-16.27)	18.75 (5.00-21.25)	4.38 (1.21-5.75)	10.70 (7.30-12.95)
Unutilised	19	70.00 (33.30-89.80)	3.00 (1.00-3.00)	1448.40 (193.50-1715.3)	16.05 (10.60-17.15)	16.30 (2.50-25.00)	5.31 (3.81-6.23)	12.50 (4.70-16.75)
Season								
Flood	6	77.50 (40.00-83.75)	3.50 (2.00-4.00)	1629.00 (1277.00-1721.00)	16.12 (12.25-16.86)	16.90 (7.50-21.88)	6.90 (3.31-7.44)	15.45 (7.30-16.45)
Hot dry	12	55.00 (33.3-69.67)	3.00 (2.00-3.26)	1545.3 (523.6-2067.8)	16.00 (12.70-16.88)	10.62 (3.80-13.75)	4.48 (1.21-4.88)	10.00 (7.50-14.73)
Rainy	20	68.75 (37.5-75.62)	3.00 (1.00-4.00)	1411.5 (193.5-1587.0)	15.47 (10.60-16.38)	19.38 (2.5-27.5)	4.51(2.59-5.35)	10.65(4.70-13.15)
Habitat								
Grassland	17	62.50 (43.80-80.00)	4.00 (1.00-4.00)	1484.60 (193.50-1722.40)	15.90 (10.60-16.85)	20.00 (7.50-27.50)	4.67 (2.38-6.75)	13.50 (4.70-15.70)
Woodland	21	67.50 (33.30-75.00)	3.00 (1.00-3.00)	1494.80 (523.60-2431.40)	15.75 (12.10-16.70)	11.25 (2.50-18.75)	4.59 (1.21-5.34)	6.90 (4.90-12.50)

*Table 5.2. One-way tests of sward characteristics between 1) selected versus unutilised grazing sites, 2) hot dry versus rainy seasons, and 3) grassland versus woodland. *and bold type indicate significant values at $p<0.05$.*

Sward characteristic	Proportion availability of dominant species (%)	Species richness (species/m²)	Biomass (kg/ha)	Habitat density (no. units)	Ground cover (%)	Sward roughness (no. units)	Sward height (cm)
Sample type: Selected versus unutilised	t_{36}=-1.438, p=0.160	t_{36}=2.296, p=**0.028***	t_{36}=0.236, p=0.794	Z= -0.624, N=19, exact p=0.548	Z= -0.040, N=19, exact p=0.977	Z= -0.885, N=19, exact p=0.395	Z= -1.389, N=19, exact p=0.172
Season: Hot dry versus rainy	U=89.0, N_1=20, N_2=12, Monte Carlo P=0.233	U=101.5, N_1=20, N_2=12, Monte Carlo P=0.456	U=90.0, N_1=20, N_2=12, Monte Carlo P=0.252	U=86.0, N_1=20, N_2=12, Monte Carlo P=0.185	U=66.5, N_1=20, N_2=12, Monte Carlo **P=0.035*** (Rainy season higher mean rank)	U=102.0, N_1=20, N_2=12, Monte Carlo P=0.490	U=118.5, N_1=20, N_2=12, Monte Carlo P=0.963
Habitat class: Grassland versus woodland	U=176.0 N_1=17, N_2=21, Monte Carlo P=0.946	U=123.0 N_1=17, N_2=21, Monte Carlo P=0.093	U=162.5 N_1=17, N_2=21 Monte Carlo P=0.653	U=160.0 N_1=17, N_2=21, Monte Carlo P=0.591	U=104.0 N_1=17, N_2=21, Monte Carlo **P=0.029*** (Grassland higher mean rank)	U=153.5 N_1=17, N_2=21 Monte Carlo P=0.468	U=117.5 N_1=17, N_2=21Monte Carlo P=0.076

Monte Carlo method based on 10,000 samples

*Table 5.3. 2-way analysis of interaction of selected and unutilised grazing sites broken down by habitat and season. *and bold type indicate significant values at $p<0.05$.*

Sward characteristic	Proportion availability of dominant species (%)	Species richness (species/m²)	Biomass (kg/ha)	Habitat density (no. units)	Ground cover (%)	Sward roughness (no. units)	Sward height (cm)
Selected							
Habitat	U= 34.5, $N1$=10, $N2$=9, Monte Carlo p=0.407	U= 24.5, $N1$=10, $N2$=9, Monte Carlo p=0.090	U= 10.5, $N1$=10, $N2$=9, Monte Carlo p=0.732	U= 44.0, $N1$=10, $N2$=9, Monte Carlo p=0.949	U= 7.0, $N1$=10, $N2$=9, Monte Carlo **p=0.001*** (Grassland higher mean rank)	U= 27.0, $N1$=10, $N2$=9, Monte Carlo p=0.157	U= 10.0, $N1$=10, $N2$=9, Monte Carlo **p=0.004*** (Grassland higher mean rank)
Season	U= 22.0, $N1$=10, $N2$=6, Monte Carlo p=0.404	U= 27.5, $N1$=10, $N2$=6, Monte Carlo p=0.830	U= 21.0, $N1$=10, $N2$=6, Monte Carlo p=0.373	U= 20.5, $N1$=10, $N2$=6, Monte Carlo p=0.322	U= 15.0, $N1$=10, $N2$=6, Monte Carlo p=0.112	U= 17.0, $N1$=10, $N2$=6, Monte Carlo p=0.185	U= 20.0, $N1$=10, $N2$=6, Monte Carlo p=0.306
Unutilised							
Habitat	U= 42.0, $N1$=7, $N2$=12, Monte Carlo p=1.000	U= 30.5, $N1$=7, $N2$=12, Monte Carlo p=0.349	U= 41.5, $N1$=7, $N2$=12, Monte Carlo p=0.945	U= 34.0, $N1$=7, $N2$=12, Monte Carlo p=0.530	U= 30.0, $N1$=7, $N2$=12, Monte Carlo p=0.330	U= 37.5, $N1$=7, $N2$=12, Monte Carlo p=0.734	U= 42.0, $N1$=7, $N2$=12, Monte Carlo p=1.000
Season	U= 30.0, $N1$=10, $N2$=6, Monte Carlo p=1.000	U= 23.5, $N1$=10, $N2$=6, Monte Carlo p=0.511	U= 22.5, $N1$=10, $N2$=6, Monte Carlo p=0.450	U= 23.0, $N1$=10, $N2$=6, Monte Carlo p=0.498	U= 24.0, $N1$=10, $N2$=6, Monte Carlo p=0.552	U= 19.0, $N1$=10, $N2$=6, Monte Carlo p=0.255	U= 26.0 $N1$=10, $N2$=6, Monte Carlo p=0.712

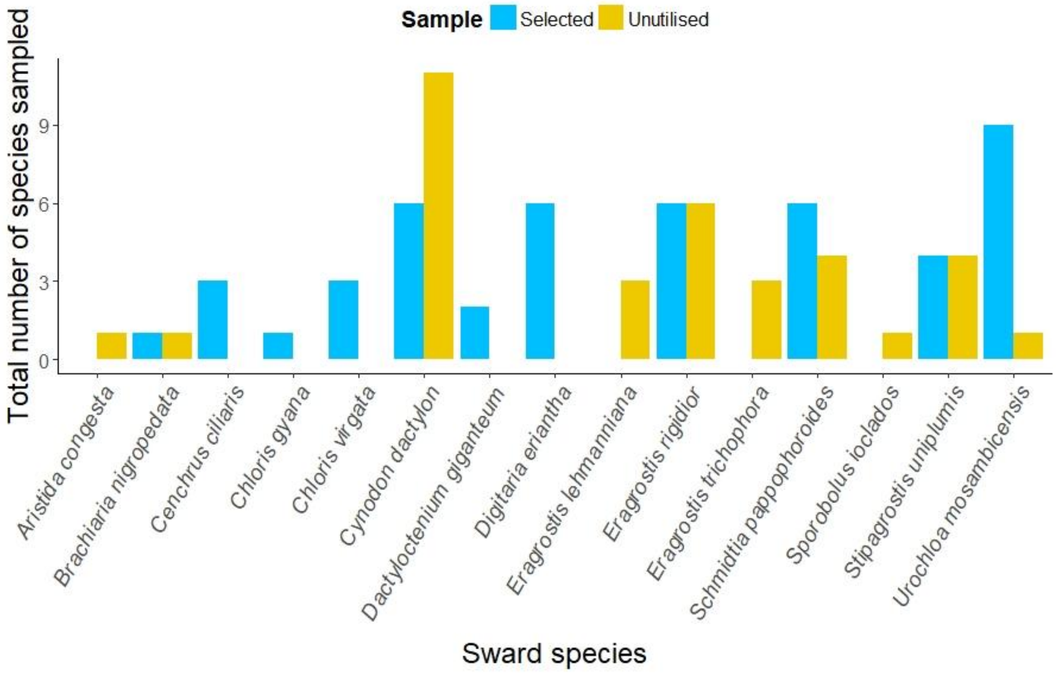
*Table 5.4. Analysis of ground cover interaction between season and habitat type. *and bold type indicate significant values at p<0.05.*

	Hot Dry season	**Rainy season**
Habitat type Grassland versus woodland	*U*= 2.5 *N1*=3, *N2*=9, Monte Carlo *p*=**0.038*** (Grassland higher mean rank)	*U*= 45.5 *N1*=10, *N2*=10, Monte Carlo *p*=0.748
	Grassland Habitat	**Woodland Habitat**
Hot dry season versus rainy season	*U*= 9.0 *N1*=10, *N2*=3, Monte Carlo *p*=0.344	*U*= 16.0 *N1*=10, *N2*=9, Monte Carlo *p*=0.016

5.3.2 Sward species

I sampled 26 sward species (Table 5.5); for details of all species see Table S5.1. Fifteen species were identified as dominant from the total number of samples. *Urochloa mosambicensis* was the most prevalent species within selected grazing sites and *Cynodon dactylon* was more common in unutilised sites (Figure 5.7).

Figure 5.7. Number of dominant grass species sampled by selected grazing and unutilised sites. Dominant grass species were defined as the species that had the largest proportion of ground cover (%) within the sample site.



Highly palatable grasses in selected sites were *Brachiaria nigropedata, Cenchrus ciliaris, Cynodon dactylon, Chloris gyana, Digiteria eriantha, Dactyloctenium giganteum* and *Schmidtia pappophroides*, and those of average palatability were *Chloris virgata, Eragrostis rigidor, Stipagrostis uniplumis* and *Urochloa mosambicensis* (Oudtshoorn, 1999). The most utilised species was *U. mosambicensis* (pers. obs.).

Table 5.5. Recorded grass species from the study area, separated by dummy categories 'grassland' and 'woodland', both of which comprised three habitat classes each (see section 5.2.4) .

Dummy category	**Habitat class**	**Grass species**
grassland	Dry floodplain and island interiors	*Cenchrus ciliaris* *Chloris gyana* *Chloris virgata* *Cynodon dactylon* *Digitaria eriantha* *Eragrostis rigidior* *Eragrostis trichophora* *Pogonarthria squarrosa* *Sporobolus ioclados* *Schmidtia pappophoroides* *Stipagrostis hirtigluma* *Stipagrostis uniplumis* *Urochloa mosambicensis*
	Shrubbed grassland former floodplain	*Cenchrus ciliaris* *Chloris virgata* *Cynodon dactylon* *Eragrostis rigidior* *Eragrostis trichophora* *Schmidtia pappophoroides* *Sporobolus ioclados* *Stipagrostis hirtigluma* *Urochloa mosambicensis*
	Grassland with wild sage	*Cynodon dactylon* *Cyperus fulgens* *Oxycaryum cubense (sedge)*

Dummy category	**Habitat class**	**Grass species**
woodland	*Acacia* woodland	*Aristida adscensionis* *Brachiaria nigropedata* *Cenchrus ciliaris* *Chloris virgata* *Cynodon dactylon* *Digitaria eriantha* *Echinochloa colona* *Eragrostis lehmanniana* *Eragrostis rigidior* *Eragrostis superba* *Eragrostis trichophora* *Eragrostis viscosa* *Panicum repens* *Stipagrostis hirtigluma* *Stipagrostis uniplumis* *Urochloa mosambicensis*
	Riparian woodland	*Aristida congesta* *Chloris virgata* *Dactyloctenium giganteum* *Eragrostis lehmanniana* *Urochloa mosambicensis*
	Mopane woodland	*Aristida congesta* *Cenchrus ciliaris* *Cynodon dactylon* *Dactyloctenium giganteum* *Digitaria eriantha* *Eragrostis lehmanniana* *Eragrostis rigidior* *Hyperthelia dissoluta* *Schmidtia pappophoroides* *Stipagrostis uniplumis* *Urochloa mosambicensis* *Urochloa trichopus*

5.3.3 Analysis of habitat-level selectivity

The null model was the best fitting model (Table 5.6), suggesting that there were no seasonal changes in habitat preferences. The grassland model was the next best fit (∆AIC = 1.7), but was not significantly better than the null model (likelihood ratio test = 0.35, p = 0.5545) and had poor explanatory power (Nagelkerke's pseudo-R^2=0.003; Mangiafico, 2018). The global model was the worst fitting model compared to the null model (likelihood ratio test = 1.38, d.f. = 6, p = 0.9668).

Table 5.6. Analysis of the effect of habitat and landscape characteristics on grazing site selection by white rhino. Models, fitted by Binomial GLM, are ranked by Akaike Information Criterion (AIC). ki is number of parameters in the model. ∆ AIC the change in AIC compared to the most parsimonious model, logLik the log-likelihood, and wi the Akaike weight.

Model	Model structure and variables	ki	AIC	logLik	∆ AIC	wi
null	Selection~ 1	1	133.9	-65.9	0.0	0.693
grassland	Selection~ grassland	2	135.5	-65.8	1.7	0.304
global	Selection~ + woodlands*season + grasslands*season + distance to habitat edge	7	144.5	-65.2	10.6	0.003

5.4 Discussion

I sampled 19 transects across three seasons: the small sample number was due to difficulty in locating rhino tracks and grazing patches. At the habitat scale no discriminant features influenced site selection, and the model did not include water availability, which is crucial for survival in this dynamic wetland system (McCarthy & Ellery, 1998). In different ecological systems rhino were found to exploit a diverse range of habitats (Cromsigt *et al.*, 2009) and utilise selected habitats (Melton, 1987). I cannot conclude whether Okavango rhino make site selection choices at the habitat scale. Given a larger sample size and the acquisition of more data, if the rhino establish ranges and become settled, selection at the habitat scale may become more detectable.

At the patch scale rhino selected sites with higher species richness, so it was unlikely that the rhino were selecting for a specific species but may have been selecting grasses with particular features. I found that rhino preferred grassland habitats with a higher proportion of ground cover and taller than average swards. My analysis showed that rhino nutritional regime consisted of highly palatable perennial grasses, most of which were tufted, or had high leaf production (*B. nigropedata, C. ciliaris, C. dactylon, C. gyana, D. eriantha, D. giganteum* and *S. pappophroides*) . Grasses sampled with average palatability were again perennial grasses *(E. rigidor, S. uniplumis* and *U. mosambicensis). C. virgata* was only present at selected sites, it provides valuable grazing in areas where few perennial grasses occur. However, in both selected and unutilised sites I did not identify any grasses that were classified as poor quality grazing (Oudtshoorn, 1999). Grazing of productive tufted swards suggests that rhino meet their metabolic requirements by selecting quantity. Conversely plants with high leaf:stem ratios have been used as a measure of nutritional quality (Buxton, 1996; Moore & Jung, 2001; Bennitt, 2012). When productive grasses are in short supply, rhino are able to tolerate lower quality swards (Shrader *et al.,* 2006a). However, in contrast to Owen-Smith (1992) and Perrin & Brereton-Stiles (1999), rhino in the Okavango Delta did not select taller lower quality swards, but maintained a preference for tufted and stoloniferous species (Owen-Smith, 1973). Therefore rhino made selection choices at the tuft scale (Hempson *et al.*, 2014).

Unlike smaller ungulate species, large bodied herbivores are not constrained by sward characteristics (Illius *et al.*, 1995; Kleynhans *et al.*, 2011); instead rhino crop grasses to ≤5cm in height (Owen-Smith, 1973; Arsenault & Owen-Smith, 2011). Re-using grazed patches (Archibald, 2008) facilitates the production of profitable grazing sites (McNaughton, 1984; Cromsigt & Olff, 2008; Bonnet *et al.*, 2010). Keeping grasses in a phonologically young state aids herbivore fertility by providing nutritionally high forage in growing seasons (Waite, 1963; Verweij *et al.*, 2006; Archibald, 2008; Bonnet *et al.*, 2010; Hempson *et al.*, 2014). Lawns provide swards with higher leaf:stem ratios (Hempson *et al.*, 2014) that are more digestible (Chaves *et al.*, 2006). Moreover, mature tufts of species such as *C. ciliaris and C. gyana* increase in nutritional quality when cropped (Tuffa *et al.*, 2017). Grazing lawns alleviate some of the grazing pressure to other herbivores in dry seasons. During these challenging times some degree of resource partitioning between divergent herbivore species takes place (Arsenault & Owen-Smith, 2002).

U. mosambicensis is a high quality creeping grass (Owen-Smith, 1973; Oudtshoorn, 1999) which was selected more than any other species, while *C. dactylon*, a matt-forming species, was mostly ignored (Oudtshoorn, 1999). Jordaan *et al.* (2015) found that *Cynodon* grasslands comprised the largest proportion of rhino grazing. However, in agreement with Shrader *et al.* (2006a) I found that along rhino pathways *Cynodon* grasslands were mostly ignored in favour of patches of perennial tufted species.

Access to quality grazing is related to rainfall, when leaf biomass and protein content are at their highest (Beekman & Prins, 1989) and leaves contain less fibrous material compared to grass stems (Prins & Loth, 1988). In the dry seasons leaf production virtually halts and the shortage of quality graze begins. Hind-gut fermenters can combat this by increasing intake rate (Beekman & Prins, 1989) and reducing handling time (Ginnett *et al.*, 1999). The increase of food intake has been correlated to the acceleration of the passage of food through the gut (MRT), thereby decreasing digestive efficiency (Clauss *et al.*, 2007). Based upon allometric comparisons with hippopotamus and African elephant, rhino diet consists of higher quality graze than expected (Kleynhans *et al.*, 2011). This improves animal nutrition, body condition and reproductive capabilities (Ungar & Noy-Meir, 1988). My results were in agreement with Shrader *et al.* (2006a) who purported that rhino do not make seasonal dietary adjustments. Instead, it is likely that rhino mobilise fat reserves. Energetic costs can be minimised by bulk grazing during dry periods (Shrader *et al.,* 2006a).

Megaherbivores respond to resource scarcity in the dry season by contracting or expanding ranges (Owen-Smith, 2008; Shannon *et al.*, 2010) or decreasing movement rates (Birkett *et al.*, 2012). Elephants which are mixed feeders (Birkett *et al.*, 2012) and black rhino which are browsers restrict ranges to productive areas, whereas a grazing species the white rhino may expands ranges (Owen-Smith, 2008). In dry seasons, elephant ranges are often concentrated close to water (de Beer & van Aarde 2008) this is because they adjust their diet for woody vegetation and are therefore constrained by water availability. Rhino on the other hand reduce grazing time as a result of the longer time required to digest mature dry grasses (Owen-Smith, 2008). However, some grazers cannot remain in semi-arid environments because surface water evaporation and lack of moisture available from graze forces them to migrate (Fryxell & Sinclair, 1988). Both the hippopotamus and rhino are able to survive by utilising fat reserves in peiords of food shortage (Owen-Smith & Cromsight, 2017), while bulk grazing on lower quality swards (Shrader *et al.,* 2006a).

However, rhino in the Okavango may not be overly disadvantaged since tufted species were selected year round. A chemical analysis of these swards would help to identify whether this was an accurate hypothesis. Rhino dietary requirements have been estimated at 5% crude protein and 36% crude fibre (Kiefer, 2002; Clauss & Hatt, 2006).

5.5 Conclusion

Rhino cropped at the tuft scale (Hempson *et al*., 2014) and made selections based on high intake rate to maximise energy. Diet mainly comprised high and average quality swards consisting of stoloniferous and caespitose grasses. Rhino did not make seasonal dietary adjustments, but probably mobilised fat reserves during the hot dry season (Shrader *et al*., 2006a). Research on seasonal body condition scores would help determine whether this assumption was correct. Elemental and fibrous analysis of swards could help establish whether the quality of swards varied across seasons, habitats, and selected grazing sites. From these data it may be possible to determine whether sward nutrient levels decline at grazing sites during dry periods, and the impact this has on rhino in the Okavango Delta.

This research was a snapshot of rhino grazing behaviour. More research is needed in order to get a better understanding of the significance of selection across patch and habitat scales.

5.6 Link to next chapter

In this chapter I have shown that rhino showed little alteration in selection of sward characteristics between seasons, but continued selection at the tuft scale. There was insufficient data to conclude whether selection was made at the habitat scale.

In the next chapter I will combine the results from all chapters and discuss proposals for the conservation management of rhino in the Okavango Delta and other areas. I also discuss limitations of my research and potential future research topics.

Chapter 6. Discussion

6.1 Foreword

The global wildlife trade is unsustainable (Nijman, 2010; Nijman & Shepherd, 2015) and is exacerbated by poaching and the illegal trade of wild animal body parts (Li & Lu, 2014; Sharma *et al.*, 2014; Ogada *et al.*, 2016; Zhang *et al.*, 2017). Animals are valuable commodities (Collard, 2014; Webb, 2016) that are traded alive, for meat, or as body parts used for decoration or medicine (McClenachan *et al.*, 2016). The legal international trade and illegal wildlife trade threaten wild populations (Williams *et al.*, 2017) through biodiversity loss, species loss, and the spread of disease and invasive species (Baker *et al.*, 2013). Current worldwide biodiversity losses may affect ecosystem functions with cascading effects (Dirzo *et al.*, 2014). The failure of security measures to deter poachers (Barichievy *et al.*, 2017) from profiting from the illegal trade in megafauna (Gray *et al.*, 2017) may drive conservation managers to consider alternative approaches to preserve wildlife populations (Molony *et al.*, 2006). Translocation could be used as a mitigation strategy (Germano *et al.*, 2015; Corlett, 2016) when protected areas struggle to maintain large animal populations (Newmark, 2008). For successful translocations it is important to examine the effects on survival rates and the behaviour of relocated animals (Molony *et al.*, 2006).

In this thesis I analysed the sociality, movement behaviour, and resource selection (at different spatial scales) of six translocated white rhino. While the sample size was small, it was only what was available for the research. The duration of comparable GPS data between the six individuals was limited to a ten month period (Table 3.2), and affected the ability to collect field data throughout most aspects of the research. Monitoring survival rates was beyond the scope of this short-term study.

I found that the group split into pairs during acclimation, and these pairings were maintained for a period after release. Wild-caught rhino displayed similar behaviours during the acclimation as rhino in captivity. Translocated animals may have the ability to navigate over longer distances than has been previously found. Additionally, after being forcibly moved from certain areas they sometimes returned. Individuals displayed different movement strategies, and large variation in range sizes. Grasslands and habitat patch size were key criteria of space-use at the landscape scale, but grazing patch selection at the habitat scale did not vary with season. At the grazing site, tufted swards with a large proportion of ground cover and with high leaf production were prominent, and these selection criteria were not modified with seasonal fluctuations.

In this chapter, I will review my results from previous chapters and discuss how my results can be utilised by conservation managers. I will also discuss the limitations of my study, and propose future research topics.

6.2 GPS

GPS was a major source of data for the project, which I used to track animals on the ground (Tomkiewicz *et al.*, 2010) and for remote behavioural analysis. I utilised GPS data to identify resource use at different scales (Chapters 4 and 5), discriminate the distribution of individuals by estimating ranges and dispersal strategies (Chapter 3), explore fine-scale movement paths (Chapter 5) and analyse animal sociality (Chapter 2).

6.2.1 Remote sensing

Animals that need to be observed are often tagged with a GPS device, but in many studies their individual behaviour is ignored (Hebblewhite & Haydon, 2010; Merrick & Koprowski, 2017). I found that analysing data on an inter-individual basis revealed very different behavioural movement strategies (Chapter 3). For example, individuals displayed periods of settlement in areas where resources were important across varying spatial and temporal scales. This is significant because large scale resource use between individuals is often measured and compared across predefined seasons, and therefore may identify areas that were not biologically important, or ignore significant areas. Resource use should not be analysed until individual movement behaviours are understood: this would enable conservation managers to identify those habitats that are important for large herbivores.

GPS data revealed direct dispersal away from the release site. However, it was difficult to determine whether this long-distance orientation towards the capture site was true homing behaviour, or as a result of other factors. Dispersal distances also tend to be larger in bolder individuals compared to shy individuals (Fraser *et al.*, 2001; Dingemanse *et al.*, 2003; Bonte *et al.*, 2012). Since it is known that rhino travel together, dispersal may be relating to associating with a familiar individual (Shrader *et al.,* 2006a), additionally younger animals tend to disperse more than older knowledgeable individuals (Evans & Harris, 2008; Pinter-Wollman *et al.*, 2009; Støen *et al.*, 2009). Large immediate dispersal movements (Chapter 3) may also be related to exploratory behaviour (Berger-Tal & Saltz, 2014), or a result of the trauma associated with the translocation process (Drugan *et al.*, 1997; Dickens *et al.*, 2010; Merrick & Koprowski, 2017). An increase in physiological state can lead to short-term escape behaviour (Jachowski *et al.*, 2012) linked to unidirectional large-scale movement away from disturbances as was the case here (Chapter 3) (Jachowski *et al.*, 2012). Nevertheless, had the rhino not been impeded by a boundary fence it is likely that they would have continued on their trajectory, which ultimately would have taken them into a human populated area, putting them at risk. I have shown that conservation managers need to be aware of the potential for large herbivores to disperse over large distances in a relatively short period of time and put intensive monitoring protection strategies in place in advance of a release as opposed to a reactive course of action, as occurred during this release.

GPS showed that there was a physiological cost associated with human disturbance (Chapter 2). This was because a flight response (Jansen *et al.*, 1995) was observed by a short period of increased daily post-disturbance movement, after which rhino movement behaviour returned to pre-disturbance daily movement distances. Although fitting tracking devices to animals is extremely important for monitoring and security purposes, conservationists largely ignore how long the animal is in a heightened physiological state after the disturbance. One such study on mule deer (*Odocoileus hemionus*) found seasonal variation in the short-term increases in movement after a disturbance (Northrup *et al.*, 2014). Repeated invasive conservation actions could lead to long-term chronic stress with a deleterious effect on animal physiology and reduced fitness (Munck *et al.*, 1984; Moberg, 2000; Millspaugh *et al.*, 2007; Merrick & Koprowski, 2017). I showed that large herbivores should be given a period of respite after human disturbances (Chapter 2). Therefore, if there is an attempt to fit a tracking device, or the animals are forcibly moved, this may have a knock on effect to being exposed to other human disturbances such as game viewing tourist vehicles. Conservation managers should therefore be aware of the affect of tourism on animals already exposed to recent disturbances. There is an awareness of the influence of ecotourism on animals (Taylor & Knight, 2003; Cressey, 2014), but the impact of researchers is less known or often not considered (Spotswood *et al.*, 2012; Todd Jones *et al.*, 2013).

6.2.2 Where do we go next with GPS?

Movement data is used to detect the sharing of space and resources between large herbivores (Thouless, 1996; White *et al.*, 2007; Thompson *et al.*, 2016), as well as fusion events of dyads within large herbivore subpopulations (Bennitt *et al.*, 2018). I used GPS and social network analysis to identify simultaneous temporal and spatial interactions between individuals (Chapter 2). Social network analysis could be further used to assess gene flow (Biosa *et al.*, 2015), the sharing of information (Shrader & Owen-Smith, 2002; Biosa *et al.*, 2015) and interactions (Morales *et al.*, 2010) between introduced and existing populations to determine the success of re-stocking (Armstrong & Seddon, 2008). Combining social network analysis location data with the use of space and resources may indicate important habitats for mating strategy ranging patterns (White *et al.*, 2007).

After translocation, animals may display long-term escape behaviour by using altered habitat preferences as refugia (Jachowski *et al.*, 2012). Movement data are used to assess how long a population acclimates to a new area (Flanagan *et al.*, 2016), because encamped behaviour (Fryxell *et al.*, 2008) (Chapter 3) coincides with the selection and availability of optimal resources (Chapters 4 and 5) (Gautestad & Mysterud, 2010; Fagan *et al.*, 2013). Identifying early landscape preferences using GPS data revealed that rhino initially sought refuge in dense mopane woodland, but were later found to occupy grasslands more than any other habitat (Chapters 4 and 5). I found that movement behaviour between individuals varied (Chapter 3), whereas the important habitats were similar (Chapter 4). Therefore, GPS could be a useful tool to assess the shift from refuge behaviour of large herbivores in atypical habitats towards encamped behaviour in typical habitats. It is difficult to determine a timescale at which the project rhino settled. There is evidence from local conservation groups that since the end of the study period, some individuals dispersed over large distances and then returned several weeks later. Therefore, even more than two years since being translocated rhino still appear to be exploring.

GIS can be used to identify suitable landscapes to which species can be translocated (Niemuth, 2003; Tash & Litvaitis, 2007). However, in this research pre-translocation landscape selection data were not available. Selection at the feeding site before and after translocation would also allow conservation managers to model species adaptation to new areas, and identify whether grazing strategies or other behaviours are altered. There is anecdotal evidence that rhino at the capture site preferentially grazed on *C. dactylon* lawns, but my data showed that *C. dactylon* was mostly avoided. However, I did not have enough data to analyse flood season selection so I could not establish whether rhino utilised *C. dactylon* grazing lawns during this season as was found in zebra (Bartlam, 2010). However, if large herbivores do alter selection strategies after translocation, this may be incorporated into release site modelling. In doing so, new areas outside of former ranges could be earmarked as suitable landscapes for endangered populations. This is important because some historical ranges no longer have suitable habitats due to anthropogenic factors such human population expansion (Vanderpost, 2007; Spear *et al.*, 2013), land-use changes (Serneels & Lambin, 2001), hunting, poaching, disease, pollution, habitat loss or fragmentation (Fol ey *et al.*, 2005; Bolger *et al.*, 2008; Davies *et al.*, 2008), and climate change (Barrett *et al.*, 2013).

6.2.3 Project limitations of GPS

The GPS location information for each animal was set to record at 4 hours intervals and replacement anklets at 8 hour intervals. Therefore, I was not able to use these data to identify changes between inter and intra-patch movement (Fauchald & Tveraa, 2003; Benhamou, 2004; Bartlam, 2010; Bradley, 2012; Gurarie *et al.*, 2016). Using first passage analysis (Fauchald & Tveraa, 2003) to identify area-restricted search behaviour as used by Bartlam (2010) would likely have made finding grazing sites much easier (Chapter 5), and would have increased the sample size of swards collected for analysis. First passage time, combined with larger scale GPS data, would indicate the length of time rhino spent grazing within a patch, the time spent searching for patches, and the lag time between revisiting grazing patches. Although shorter fix intervals provide more accurate movement details, they are only an interpretation of actual movement (Cagnacci *et al.*, 2010; Bradley, 2012). However, these types of data may be particularly useful for locating and monitoring rhino if preferred patches can be identified.

6.3 Future research

6.3.1 The consequences of alternative translocation acclimation procedures

The acclimation period before release (soft release) is important since it ensures that translocated animals have fully recovered from their journey (Emslie *et al.*, 2009). It also allows the building fat reserves before release, thereby reducing post-release stress effects (Molony *et al.*, 2006). Acclimation procedures are adaptable and vary according to species. For white rhino, Emslie *et al.* (2009) suggests that bomas should be constructed of solid poles, however see through electrified “bonnox” bomas (Reilly, 2005) are possible alternatives, but these have not been thoroughly tested.

The translocation process for the white rhino in this project was different to previous releases in the Okavango Delta, in that all animals were held collectively in an electrified bonnox boma (Chapter 2) (Reilly, 2005). Subsequent releases in the same location of the peripheral Delta were ‘hard’ releases, where animals were released without any acclimation (Bright & Morris, 1994). However, animals previously reintroduced into the Moremi Game Reserve were acclimated independently in boma’s constructed of solid poles (Galpine, 2006). Therefore, there is a rare opportunity to analyse three sets of data to determine movement behaviour patterns of rhino exposed to alternate translocation methods that were released into the same ecosystem. Comparisons may be made between ‘hard’ versus ‘soft’ releases (Richard son *et al.*, 2013; Attum & Cutshall, 2015), or solid pole construction (Emslie *et al.*, 2009) versus bonnox boma design (Reilly, 2005) and their effect on post-release movement.

In a previous rhino translocation in Botswana 5 of 27 animals died, while some of the individuals permanently dispersed away from the release site. In Zimbabwe 4 of 12 white rhino died during the translocation process; however some were in poor health and one died as a result of tranquilisation. Of the released animals, one died shortly afterwards following an illness caused by darting. The remaining animals took around 14 months to settle, but none of the females produced any calves within that timescale. In another translocation in South Africa, 6 rhino were reintroduced, but one male permanently dispersed beyond the release area and one female gave birth to her first calf. These studies related to short-term projects, but demonstrate issues relating to mortality and dispersal.

6.3.2 Long-term research in the Okavango Delta

In the short-term the translocation could be considered a mixed success. Some animals remained close to the release site and displayed typical subadult semi-nomadic movement behaviour (Owen-Smith, 1974). Another trait of subadults is the propensity to disperse, and some of the individuals travelled vast distances from the release site and had to be herded back to safer areas. More rhino have since been brought to the Okavango Delta and were released without any acclimation, the aim of Rhinos without Borders was to contribute a further 100 animals to the existing population. The current estimate of white rhino in Botswana stands at in excess of 200, with an increasing population (Emslie *et al.*, 2016).

There are not enough grazers with body mass >1000kg in the Okavango Delta, and this may have contributed to the upsurge of the elephant population. It is likely that this is linked to the disappearance of other megaherbivores during the Pleistocene extinction, such as the Giant hippo (*Hippopotamus gorgops*), giant hartebeest (*Megalotragus priscus*) and giant buffalo (*Pelorovis antiques*). The removal of these competitors may have enabled elephants to exploit vacant habitats (Bonyongo, 2004; Bonyongo & Harris, 2007). Therefore, reintroducing a competitor may rebalance the ecosystem. Rhino, a keystone species, may restore top down and/or bottom up trophic effects via ecosystem functions and services (Hopcraft *et al.*, 2010; Ripple & Beschta, 2012; Sandom *et al.*, 2013; Ripple *et al.*, 2015). ‘Rewilding’ (Soulé & Noss, 1998; Soulé & Terborgh, 1999) describes the return of species to former ranges from where they were locally extinct (Armstrong & Seddon, 2008; Corlett, 2016) either through restocking or reintroduction (Seddon, 2010).

The focus of many rewilding projects is the formation of a self-sustaining population (Sandom *et al.*, 2013; Seddon *et al.*, 2014; Soorae, 2018). However, for the long-term survival of wildlife populations it is crucial that protected areas remain connected and ecologically functional (Lindenmayer *et al.*, 2008; Bartlam, 2010; Sandom *et al.*, 2013). Sinclair (2003) showed how it is possible to measure the direct and indirect effects of the presence or absence of guilds within the Serengeti community. Keystone species can act as both ‘umbrella species', where the conservation of these species and their habitats also helps to protect other members of the community (Sinclair, 2003; Breckheimer *et al.*, 2014), and 'indicator species' where they can be used to monitor trends and the health of the ecosystem (Rapport & Hildén, 2013; González *et al.*, 2014). Combining monitoring methods builds more resilience in determining the stability and health of ecosystem functions (Roberge & Angelstam, 2004). Ultimately determining how reintroduced keystones regulate other species and how ecosystems are affected by their introduction enables improved ecosystem management and species conservation (Sinclair, 2003).

6.4 Concluding remarks

The bonnox boma in this research did not halt long distance dispersal and although more research is needed, hard releases or a boma build of solid pole construction is advisable for future translocations. Rhino released into a novel environment must find resources while avoiding risks such as predators and aggressive territorial males. Rhino should be released in the vicinity of grassland areas, while offering refuges for further acclimation after release. The re-wilding of the Okavango Delta through the reintroduction of rhino may restore ecosystem functions and services, so further long-term research is needed. The Okavango Delta offers vast areas of food, water and shelter for rhino, and so is capable of sustaining a population in their thousands.

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Supplementary information 2

Figure S2.1. Histogram of the frequency of observed distances between rhino dyads during observations in the boma.

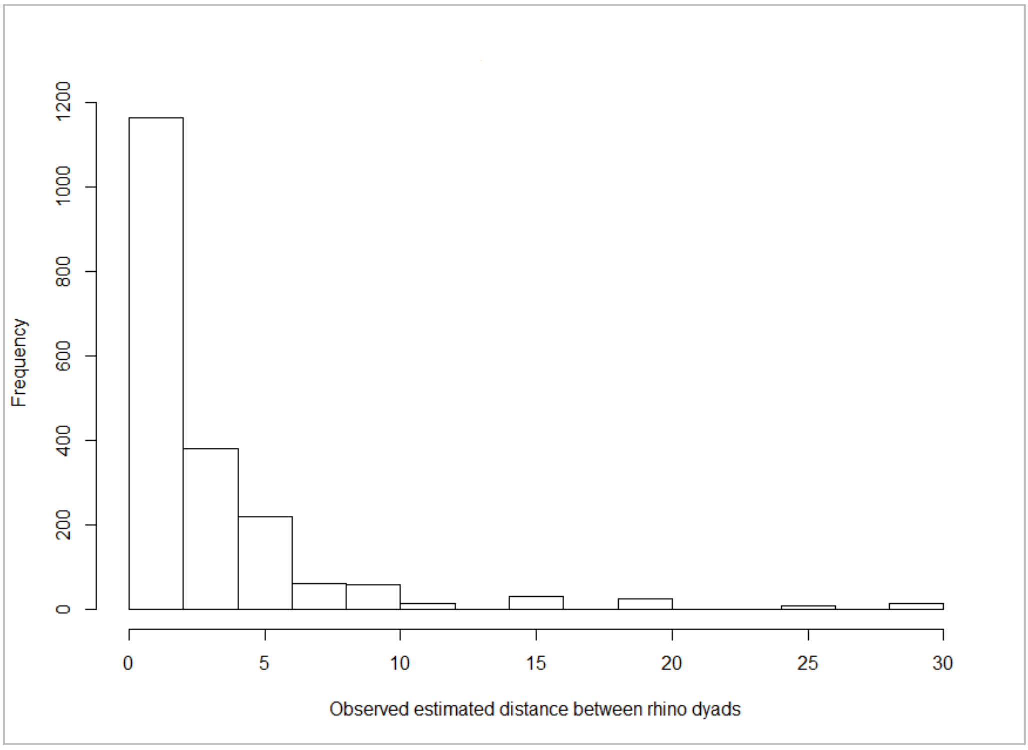


Figure S2.2. Histogram of the frequency of Euclidean distance (<1000 m) between rhino dyads in the Okavango Delta, Botswana.

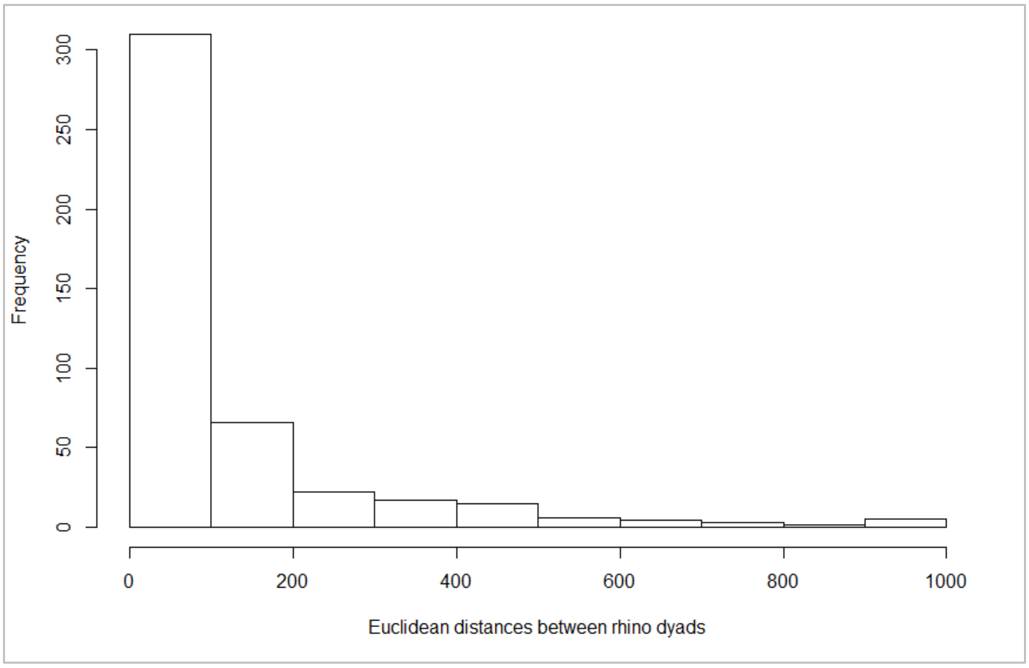


Table S2.1. Ethogram of the observed behaviours of white rhino: reprinted from Metrione et al. *(2007).*

Vocalisation or behaviour	**Purpose**	**Description**
Vocalisation		
Snort	Mild keep away warning	Nasal exhalation or inhalation
Snarl	More powerful distance increasing tool	Gruff roar or rumbling with mouth open, ears laid back
Pant	Contact seeking or maintaining call	Chesty exhalation or inhalation
Hic	Signifies bulls intent to court	Repetitive wheezy exhalations with throb at each inhalation
Squeal	Signifies actions of bull towards cow	High pitched then falling off
Shriek	Attack inhibiting	Intense/Shrill: ears back head thrust forward
Whine	Calf seeking udder or adolescents moving back towards companions	Thin mewing tone, rises and falls in pitch
Squeak	Distress signal used by calves	Abrupt and high pitched
Gruff squeal	Emphasises presence of bull	Throaty, rumbling squeal
Gasp-puff	Response to sudden fright	Sudden inhalation or exhalation
Behaviour		
Pinning ears back	Distance increasing display	Ears back usually with head thrust and snort/snarl
Advancing steps	More powerful distance-increasing effect than snarl or snort alone	Actor steps forward to recipient & gives snarl/snort/shriek
Horn prod	Ritualised attack movement	Head lowered jabbing movement
Horn clash	Gesture to repel encroachment	Horn lowered parallel to ground & hit sideways at horn of recipient
Charge	Intimidation display	Rapid advance
Head flings	Play invitation	Head swung up & down rapidly
Presenting the side	Act of appeasement	Turning head away from other rhino
Horn against horn stare	Intimidation display	Horns of two bulls pressed together, heads raised & ears forward
Horn wiping	Assertion of presence/status	Sideways/twisting movement of horn on the ground
Scraping	May be related to deposition of scent marks	Hind legs and forelegs dragged with nail pressed against ground
Tail curled	General autonomic stimulation – nervousness	Curling of tail may be held or repeated
Nasonasal meeting	Identification of individuals	Movements slow and relaxed, allowing noses to meet
Attack	Drive opponent away	Horn jabbing moments toward body of recipient
Fight	Opponents attempt to drive each other away	Attack gestures by both opponents
Acceptance of tactile contact	To strengthen bonds	Expression of close bond through nonaggressive physical contact
Urine/dung smelling	Identification	Smelling or urine or dung, sometimes followed by flehmen
Smelling of vagina	Estrus identification, courtship	Bulls smells cows vaginal area, may be followed by flehmen
Chin resting	Courtship	Bull rests his head on rump or back of cow
Mounting	Breeding	Bulls straddles cow with forelegs while standing on hind legs, may or may not be preceded by erection

*Table S2.2. Dynamic association indices for part-flood season (May –June 2013). * denotes significance at p < 0.05. Half-weight Association Index (HWAI) >0.5 represents preferred association within shared area, HWAI<0.5 equates to avoidance within shared area, Coefficient of association (Ca) >0.5 signifies attraction, Ca<0.5 relates to avoidance, Benhamou's IAB Index where p-Avoid represents the probability of significant avoidance, p-Attract represents the significance of attraction, Proximity Index (Prox) indicates the proportion of fixes within time and distance thresholds.*

Dyad		HWAI	Ca	IAB		Prox
				Avoid	Attract	
F1	F2	0.917	0.828	1	0.028*	1
F1	F3	0	0	0.750	0.286	0
F1	M1	0	0	0.606	0.424	0
F1	M2	0	0	0.606	0.424	0
F1	M3	0	0	0.75	0.286	0
F2	F3	0	0	0.818	0.212	0
F2	M1	0	0	0.641	0.385	0
F2	M2	0	0	0.641	0.385	0
F2	M3	0	0	0.818	0.212	0
F3	M1	0	0	0.027*	0.811	0
F3	M2	0	0	0.027*	0.811	0
F3	M3	1	1	1	0.024*	1
M1	M2	1	1	1	0.022*	1
M1	M3	0	0	0.027*	0.811	0
M2	M3	0	0	0.027*	0.811	0

*Table S2.3. Dynamic association indices for the hot dry season 2013. * denotes significance at p < 0.05. Half-weight Association Index (HWAI) >0.5 represents preferred association within shared area, HWAI<0.5 equates to avoidance within shared area, Coefficient of association (Ca) >0.5 signifies attraction, Ca<0.5 relates to avoidance, Benhamou's IAB Index where p-Avoid represents the probability of significant avoidance, p-Attract represents the significance of attraction, Proximity Index (Prox) indicates the proportion of fixes within time and distance thresholds.*

Dyad		HWAI	Ca	IAB		Prox
				Avoid	Attract	
F1	F2	0.9167	0.612	1	0.016*	0.968
F1	F3	N/A	0	0.014*	0.254	0
F1	M1	0	0.008	0.897	0.115	0.128
F1	M2	0	0.008	0.896	0.117	0.130
F1	M3	N/A	0	0.014*	0.232	0
F2	F3	N/A	0	0.018*	0.339	0
F2	M1	0	0.010	0.954	0.062	0.154
F2	M2	0	0.010	0.954	0.062	0.154
F2	M3	0	0	0.179	0.340	0
F3	M1	0	0	0.012*	0.183	0
F3	M2	0	0	0.847	0.165	0
F3	M3	0.952	0.919	1	0.009*	0.947
M1	M2	0.970	0.922	1	0.008*	0.941
M1	M3	0	0	0.011*	0.416	0
M2	M3	0	0	0.736	0.275	0

*Table S2.4. Dynamic association indices for the rainy season 2013/14. * denotes significance at p < 0.05. Half-weight Association Index (HWAI) >0.5 represents preferred association within shared area, HWAI<0.5 equates to avoidance within shared area, Coefficient of association (Ca) >0.5 signifies attraction, Ca<0.5 relates to avoidance, Benhamou's IAB Index where p-Avoid represents the probability of significant avoidance, p-Attract represents the significance of attraction, Proximity Index (Prox) indicates the proportion of fixes within time and distance thresholds.*

Dyad		HWAI	Ca	IAB		Prox
				Avoid	Attract	
F1	F2	N/A	N/A	N/A	N/A	N/A
F1	F3	0	0	0.667	0.370	0
F1	M1	0	0	0.053	1	0
F1	M2	0	0	0.083	0.958	0
F1	M3	0	0	0.667	0.370	0
F2	F3	0	0	0.870	0.152	0
F2	M1	0	0	0.783	0.239	0
F2	M2	1	0.768	1	0.014*	1
F2	M3	0	0	0.887	0.132	0
F3	M1	0	0.018	1	0.014*	0.029
F3	M2	0	0	0.808	0.205	0
F3	M3	1	0.968	1	0.010*	1
M1	M2	0	0	0.788	0.227	0
M1	M3	0	0.018	1	0.013*	0.026
M2	M3	0	0	0.824	0.188	0

*Table S2.5. Dynamic association indices for flood season 2014, animals were recollared between May 25-27 2014. * denotes significance at p < 0.05. Half-weight Association Index (HWAI) >0.5 represents preferred association within shared area, HWAI<0.5 equates to avoidance within shared area, Coefficient of association (Ca) >0.5 signifies attraction, Ca<0.5 relates to avoidance, Benhamou's IAB Index where p-Avoid represents the probability of significant avoidance, p-Attract represents the significance of attraction, Proximity Index (Prox) indicates the proportion of fixes within time and distance thresholds.*

Dyad		HWAI	Ca	IAB		Prox
				Avoid	Attract	
F2	F3	N/A	0	0.048*	0.048*	0
F2	M1	0	0	0.077	0.077	0
F2	M2	0.042	0.495	1	0.042**	1
F2	M3	0	0	0.053	0.053	0
F3	M1	0.016	0.453	1	0.014**	0.658
F3	M2	0	0	0.020*	0.020*	0
F3	M3	0.120	0.546	1	0.011**	0.670
M1	M2	0	0	0.031*	0.031*	0
M1	M3	0	0.493	1	0.013**	0.671
M2	M3	N/A	0	0.022*	0.022*	0

*Table S2.6. Dynamic association indices for the hot dry season 2014, * denotes significance at p < 0.05. Half-weight Association Index (HWAI) >0.5 represents preferred association within shared area, HWAI<0.5 equates to avoidance within shared area, Coefficient of association (Ca) >0.5 signifies attraction, Ca<0.5 relates to avoidance, Benhamou's IAB Index where p-Avoid represents the probability of significant avoidance, p-Attract represents the significance of attraction, Proximity Index (Prox) indicates the proportion of fixes within time and distance thresholds.*

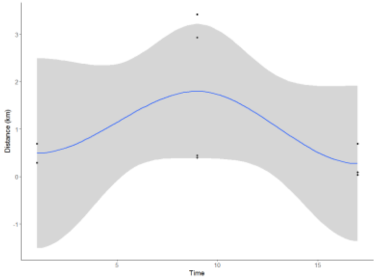
Dyad		HWAI	Ca	IAB		Prox
				Avoid	Attract	
F3	M1	0	0.529	1	0.013*	0.769
F3	M3	0	0.588	1	0.015*	0.985
M1	M3	0	0.515	1	0.013*	0.790

*Table S2.7. Dynamic association indices for rainy season 2014/15, * denotes significance at p < 0.05. Half-weight Association Index (HWAI) >0.5 represents preferred association within shared area, HWAI<0.5 equates to avoidance within shared area, Coefficient of association (Ca) >0.5 signifies attraction, Ca<0.5 relates to avoidance, Benhamou's IAB Index where p-Avoid represents the probability of significant avoidance, p-Attract represents the significance of attraction, Proximity Index (Prox) indicates the proportion of fixes within time and distance thresholds.*

Dyad		HWAI	Ca	IAB		Prox
				Avoid	Attract	
F3	M1	0	0.358	1	0.020*	0.653
F3	M3	0	0.328	1	0.022*	0.644
M1	M3	0	0.394	1	0.019*	0.698

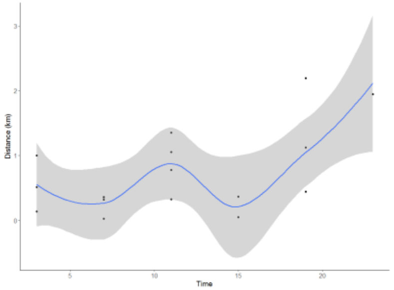
Figure S2.3. Movement estimates for the 5 day period after a recollaring attempt. Predictive data were used to generate distances corresponding to GPS collar time intervals, and these predicted distances were used to plug gaps in the data. Shaded areas represent standard errors.

a) M1 predicted daily distance 5 days after recollaring attempt, number of GPS fixes=10



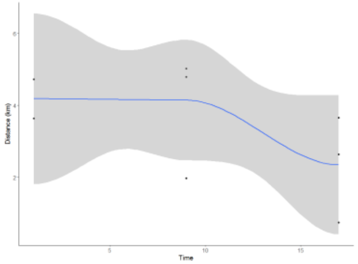
Time interval	Predicted distance (km)
01:00	0.4938
09:00	1.8001
17:00	0.2760

b) M2 predicted daily distance 5 days after recollaring attempt, replaced, number of GPS fixes =17



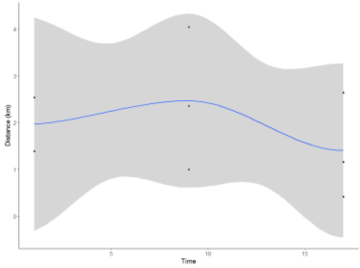
Time interval	Predicted distance (km)
03:00	0.5501
07:00	0.2634
11:00	0.8749
15:00	0.2069
19:00	1.0439
23:00	2.1144

c) M3 predicted daily distance 5 days after recollaring attempt, number of GPS fixes =9



Time interval	Predicted distance (km)
01:00	4.183
09:00	4.148
17:00	2.349

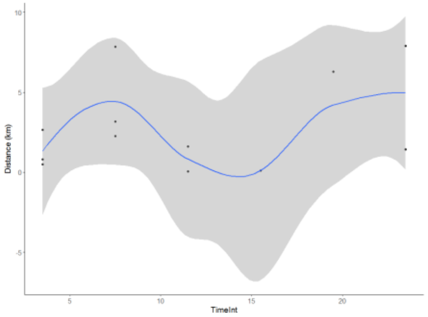
d) F3 predicted daily distance 5 days after recollaring attempt, number of GPS fixes =10



Time interval	Predicted distance (km)
01:00	1.967
09:00	2.469
17:00	1.407

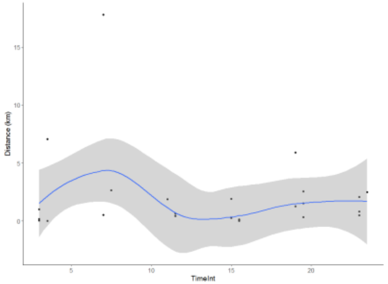
Figure S2.4. Movement estimates for the 5 day period after herding. Predictive data were used to generate distances corresponding to GPS collar time intervals, and these predicted distances were used to plug gaps in the data. Shaded areas represent standard errors.

a) M1 predicted 5 daily distance from 1 herding event, number of GPS fixes =12



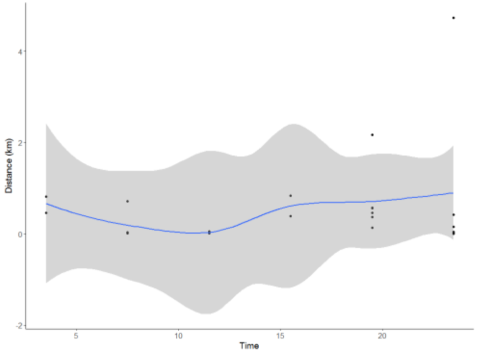
Time interval	Predicted distance (km)
03:30	1.3106
07:30	4.4252
11:30	0.8199
15:30	0.1043
19:30	4.1954
23:30	4.9522

b) M2 predicted 5 daily distance from 3 herding events, total number of GPS fixes =29



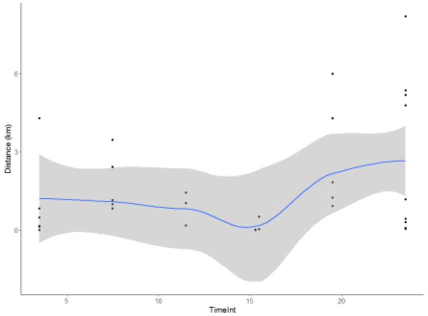
Time interval	Predicted distance (km)	Time interval	Predicted distance (km)
03:00	1.5215	15:00	0.3262
03:30	2.1435	15:30	0.4507
07:00	4.3363	19:00	1.4775
07:30	4.3348	19:30	1.5474
11:00	1.1614	23:00	1.7168
11:30	0.7084	23:30	1.6909

c) M3 predicted 5 daily distance from 2 herding events, number of GPS fixes = 21



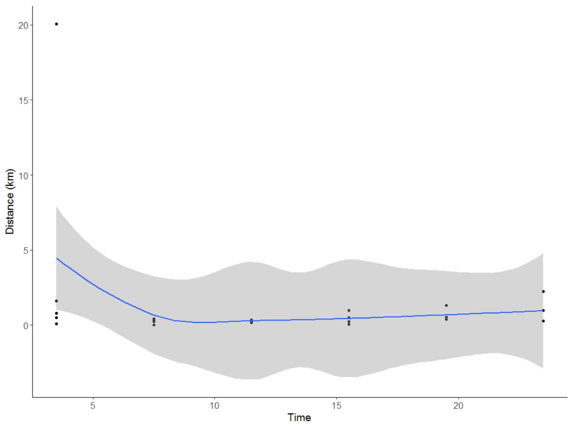
Time interval	Predicted distance (km)
03:30	0.66590
07:30	0.19071
11:30	0.03061
15:30	0.61226
19:30	0.71059
23:30	0.89920

d) F2 predicted 5 daily distance from 3 herding events, total number of GPS fixes = 33



Time interval	Predicted distance (km)
03:30	1.2005
07:30	1.0820
11:30	0.8143
15:30	0.1610
19:30	2.1620
23:30	2.6504

e) F3 predicted 5 daily distance from herding 2 events, n= 27

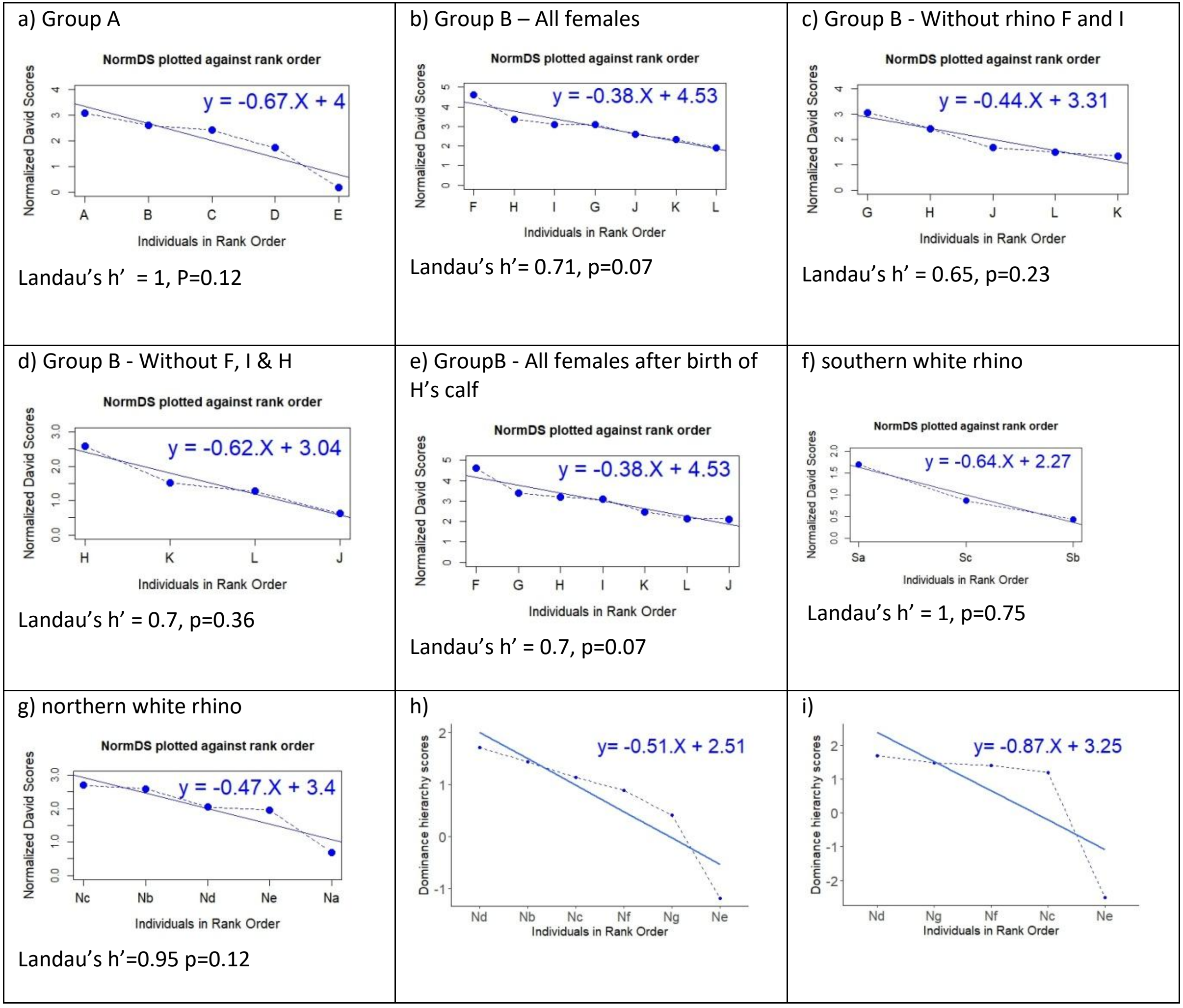


Time interval	Predicted distance (km)
03:30	4.4755
07:30	0.6849
11:30	0.2867
15:30	0.4392
19:30	0.6781
23:30	0.9585

Table S2.8. Rhino ID's from Metrione et al. (2007), Kuneš and Bičík (2002), and Cinkova and Bičík (2013), for use in dominance hierarchy tests (see Figure S2.5).

Publication authors	Publication rhino ID	allocated ID
Metrione et al. (2007)	Linda	A
	Kit	B
	Kathy	C
	Natalie	D
	Helen	E
	Half-Ear	F
	Long horn	G
	Maggie	H
	Notch	I
	Julie	J
	Mamma	K
	Karla	L
Kuneš and Bičík (2002)	Saut	Na
	Nesari	Nb
	Nabire	Nc
	Najin	Nd
	Dan	Sa
	Sasa	Sb
	Zamba	Sc
Cinkova and Bičík (2013)	Nesari	Nb
	Nabire	Nc
	Najin	Nd
	Suni	Ne
	Nasi	Nf
	Fatu	Ng

Figure S2.5. Normalised David's scores (NormDS) plotted against rhino in rank order, with linear regression lines fitted through NormDS based on proportion of wins (Pij). Landau's dominance tests h' indicate linearity index (where 1=complete linearity), and the p-value from simulations. a) to e) were calculated using data from dominance matrices in Metrione et al. (2007), f) estimates northern white rhino hierarchy and g) southern white rhino hierarchy, both using matrices from Kuneš and Bičík (2002), h) and i) represent dominance hierarchy scale plots from data in Cinkova and Bičík (2013).



a) Group A

Landau's h' = 1, P=0.12

b) Group B – All females

Landau's h'= 0.71, p=0.07

c) Group B - Without rhino F and I

Landau's h' = 0.65, p=0.23

d) Group B - Without F, I & H

Landau's h' = 0.7, p=0.36

e) GroupB - All females after birth of H's calf

Landau's h' = 0.7, p=0.07

f) southern white rhino

Landau's h' = 1, p=0.75

g) northern white rhino

Landau's h'=0.95 p=0.12

h)

i)

Supplementary information 3

Table S3.1. Flood season 2013 proportion of range overlap calculated in ArcGIS10 and mean estimated using formula 3.2.

ID	M1	M2	M3	F1	F2	F3	Mean *(total/5)
M1	*	99	49	31	35	49	53
M2	99	*	49	31	35	45	52
M3	88	89	*	66	74	93	82
F1	83	84	97	*	100	98	92
F2	84	84	97	90	*	98	91
F3	93	86	98	71	78	*	85

Table S3.2. Hot dry season 2013 proportion of range overlap calculated in ArcGIS10 and mean estimated using formula 3.2.

ID	M1	M2	M3	F1	F2	F3	Mean *(total/5)
M1	*	88	0	74	0	78	48
M2	100	*	0	80	86	0	53
M3	0	0	*	0	0	92	18
F1	95	91	0	*	98	0	57
F2	92	90	0	90	*	0	54
F3	0	0	99	0	0	*	20

Table S3.3. Rainy season 2013/14 proportion of range overlap calculated in ArcGIS10 and mean estimated using formula 3.2.

ID	M1	M2	M3	F1	F2	F3	Mean *(total/5)
M1	*	52	60	15	58	59	49
M2	6	*	6	2	99	6	24
M3	26	21	*	6	24	97	35
F1	100	100	95	*	100	100	99
F2	7	98	95	2	*	7	24
F3	26	24	98	7	25	*	36

Table S3.4. Flood season proportion of range overlap calculated in ArcGIS10 and mean estimated using formula 3.2.

ID	M1	M3	F3	Mean *(total/2)
M1	*	76	91	84
M3	35	*	95	65
F3	31	72	*	52

Figure S3.1. Range size based on six rhino for each season, where horizontal lines denote median, boxes span interquartile ranges, and 'whiskers' reach to the first data point within 1.5 inter-quartile ranges of the box edge. Any points outside the whiskers are indicated with circles.

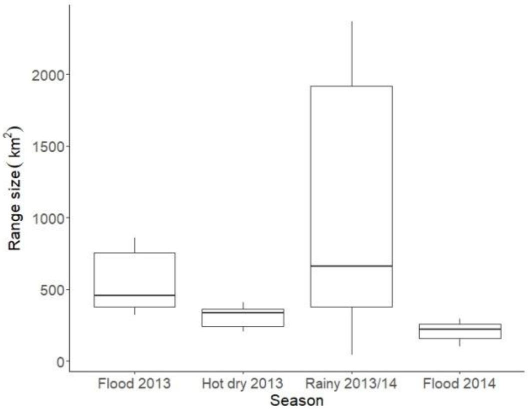


Figure S3.2 Percentage of range overlap based on six rhino for each season, where horizontal lines denote median, boxes span interquartile ranges, and 'whiskers' reach to the first data point within 1.5 inter-quartile ranges of the box edge. Any points outside the whiskers are indicated with circles.

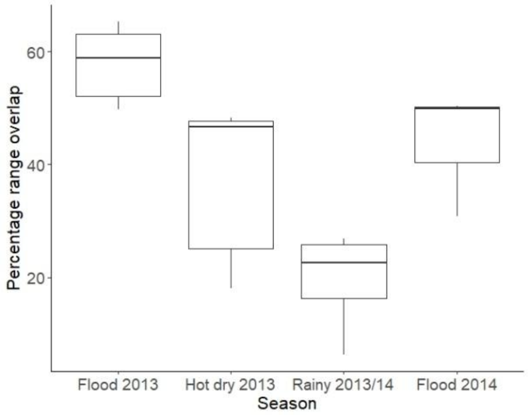


Figure S3.3. Range size by sex (n=11 for males, and n=10 for females), where horizontal lines denote median, boxes span interquartile ranges, and 'whiskers' reach to the first data point within 1.5 inter-quartile ranges of the box edge. Any points outside the whiskers are indicated with circles.

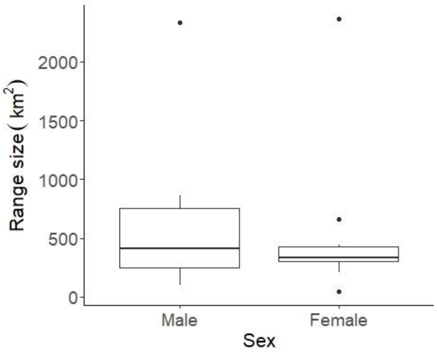
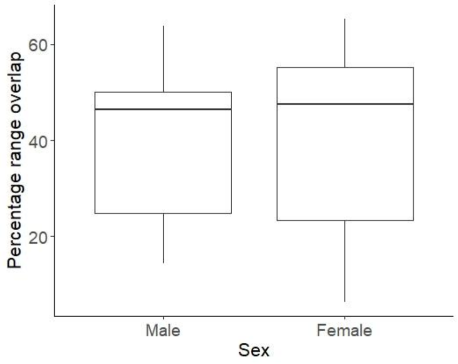


Figure S3.4. Percentage of range overlap by sex (n=11 for males, and n=10 for females), where horizontal lines denote median, boxes span interquartile ranges, and 'whiskers' reach to the first data point within 1.5 inter-quartile ranges of the box edge. Any points outside the whiskers are indicated with circles.



Supplementary information 4

Figure S4.1. Fitted GAMM plot of net squared displacement movements for rhino M1. Continuous line represents the fitted model and dashed lines represent 95% confidence intervals. Tick marks signify periods of data collection.

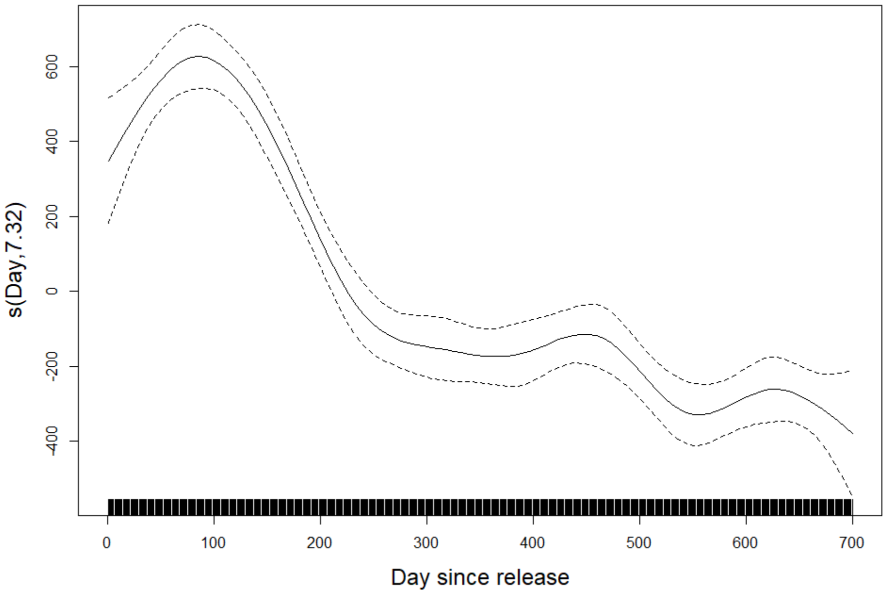


Figure S4.2. Net squared displacement movement behaviour for rhino M1. Black boxes indicate areas to be used for resource extraction utilisation distribution mapping and to generate landscape and habitat parameters. Blue boxes indicate seasons, F-flood, HD-hot dry, R-rainy

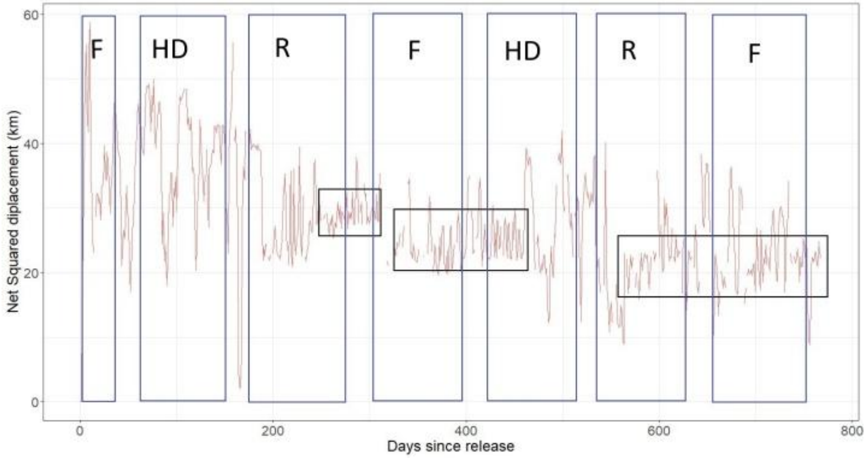


Figure S4.3. Fitted GAMM plot of net squared displacement movements for rhino M2. Continuous line represents the fitted model and dashed lines represent 95% confidence intervals. Tick marks signify periods of data collection.

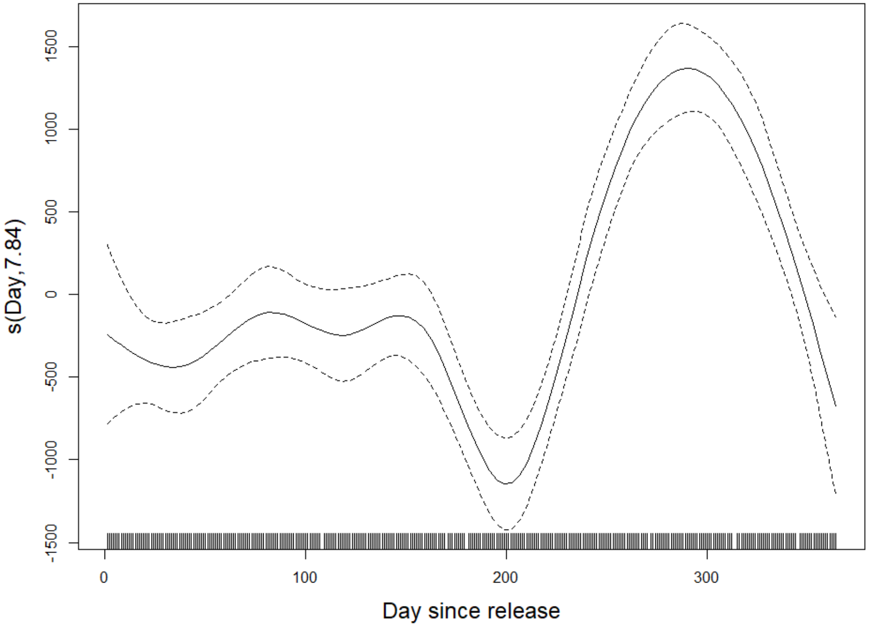


Figure S4.4. Net squared displacement movement behaviour for rhino M2. Black boxes indicate areas to be used for resource extraction utilisation distribution mapping and to generate landscape and habitat parameters. Blue boxes indicate seasons, F-flood, HD-hot dry, R-rainy

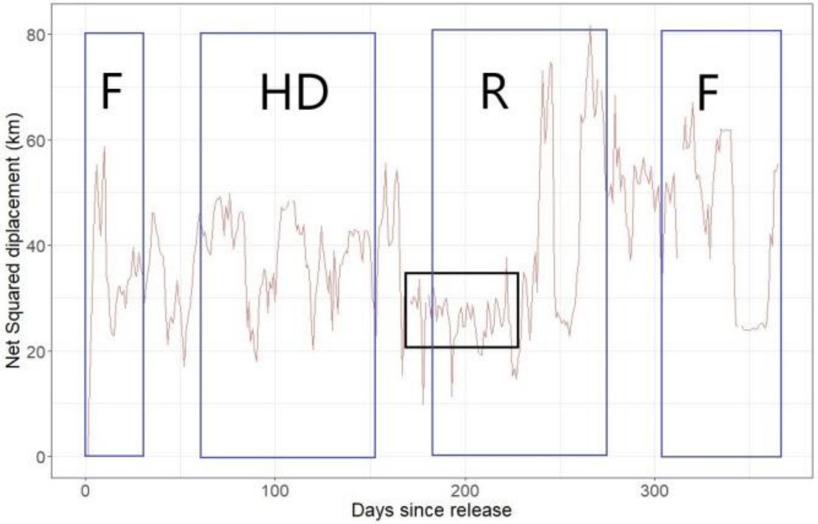


Figure S4.5. Fitted GAMM plot of net squared displacement movements for rhinos M3 and F3. Continuous line represents the fitted model and dashed lines represent 95% confidence intervals. Tick marks signify periods of data collection.

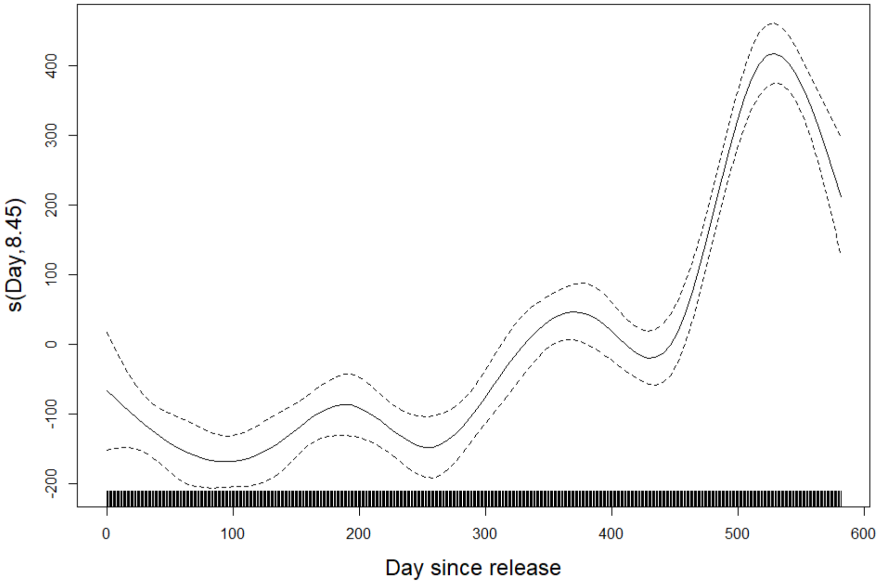


Figure S4.6. Net squared displacement movement behaviour for rhino M3 and F3. Black boxes indicate areas to be used for resource extraction utilisation distribution mapping and to generate landscape and habitat parameters. Blue boxes indicate seasons, F-flood, HD-hot dry, R-rainy

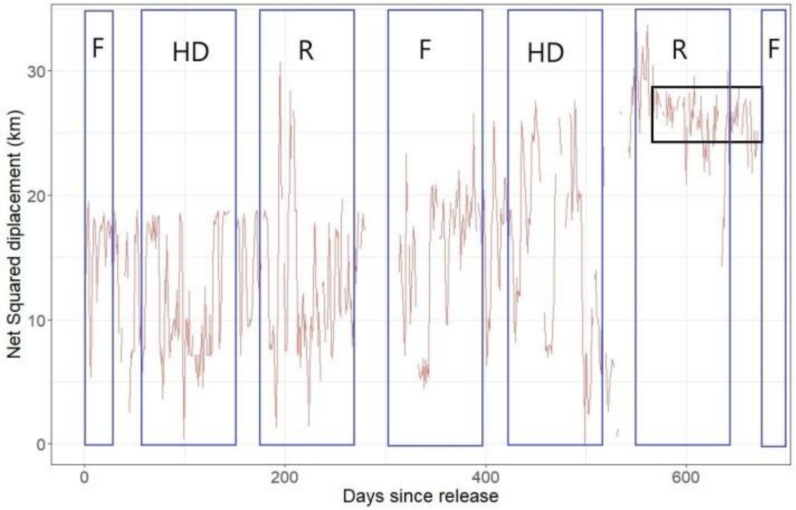


Figure S4.7. Fitted GAMM plot of net squared displacement movements for rhino F1. Continuous line represents the fitted model and dashed lines represent 95% confidence intervals. Tick marks signify periods of data collection.

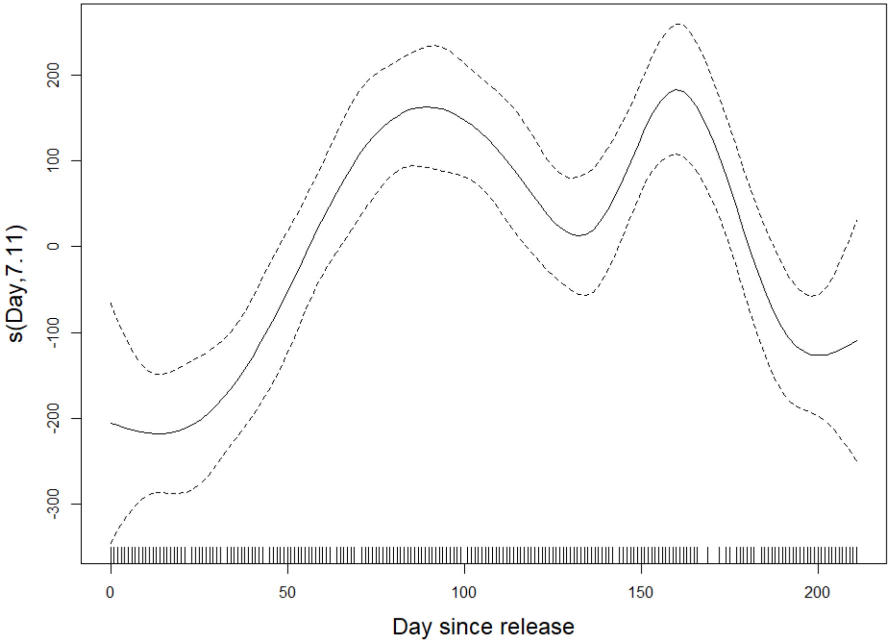


Figure S4.8. Net squared displacement movement behaviour for rhino F1. Black boxes indicate areas to be used for resource extraction utilisation distribution mapping and to generate landscape and habitat parameters. Blue boxes indicate seasons, F-flood, HD-hot dry, R-rainy

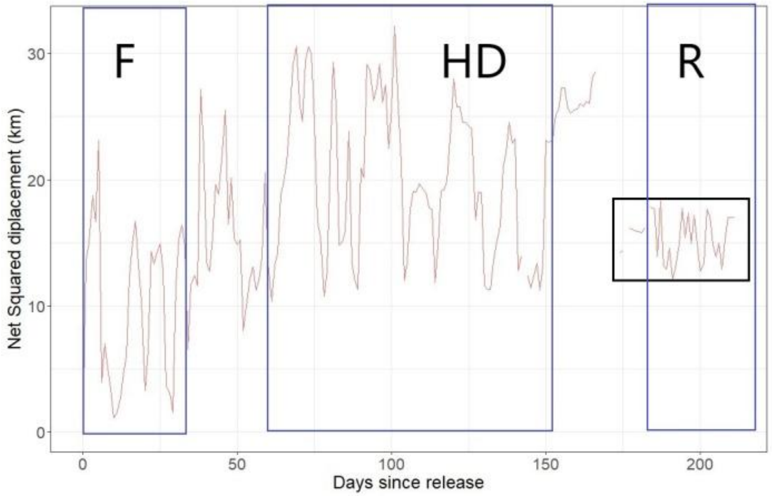


Figure S4.9. Fitted GAMM plot of net squared displacement movements for rhino F2. Continuous line represents the fitted model and dashed lines represent 95% confidence intervals. Tick marks signify periods of data collection.

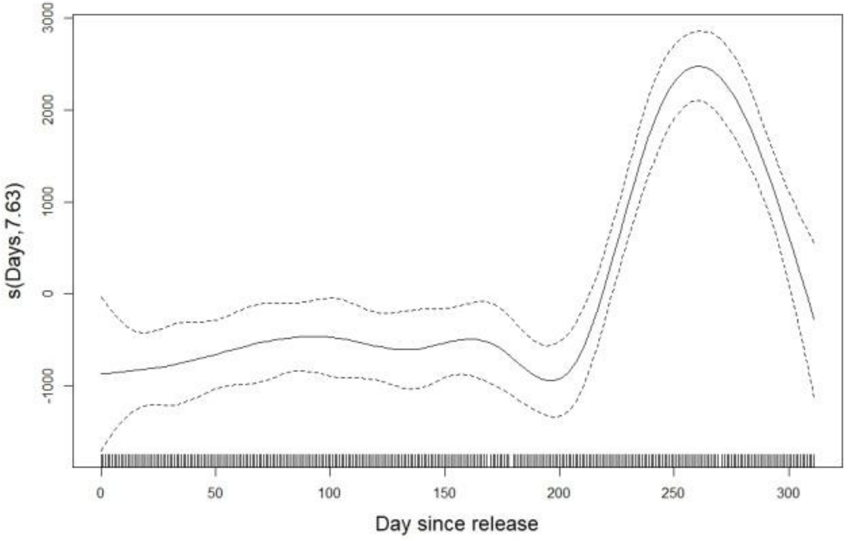


Figure S 4.10. Net squared displacement movement behaviour for F2. Black boxes indicate areas to be used for resource extraction utilisation distribution mapping and to generate landscape and habitat parameters. Blue boxes indicate seasons, F-flood, HD-hot dry, R-rainy

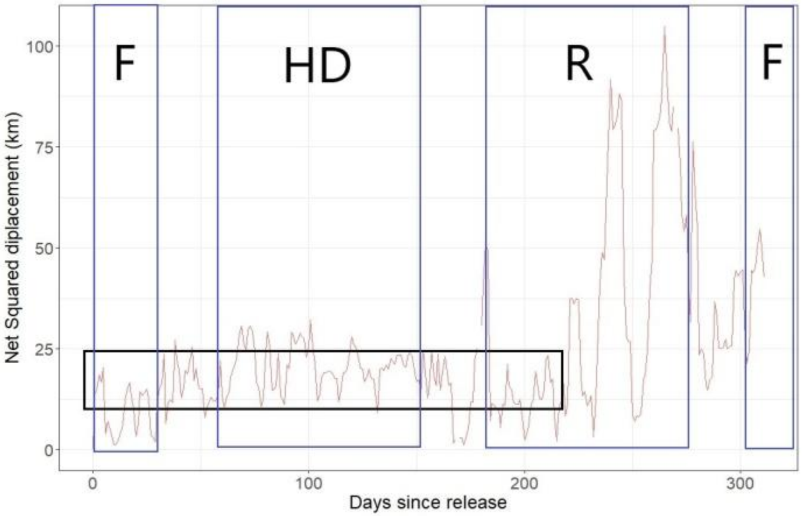


Table S4.1. Relative importance of habitat classes with resource utilisation function (RUF) coefficients for each resource extraction (RE) site. Positive signs indicate an increase of use relative to habitat availability and negative signs a decrease.

Habitat Class	RE site						
	1	2	3	4	5	6	7
Acacia (intercept)	-0.504	-4.571	-6.216	-6.639	-6.126	-4.592	-7.124
Dry floodplains	-0.468	-0.230	0.441	-0.315	0.176	0.244	-0.204
Shrubbed grassland on former floodplain	0.160	-0.759	-0.002	0.279	-0.325	0.015	0.229
Grassland with wild sage	-0.967	-1.582	-0.311	-0.837	N/A	1.413	0.062
Riparian woodland	-0.520	-0.481	-0.171	-0.407	-0.560	-0.310	-0.586
Mopane woodland	-0.432	-1.063	0.340	-0.650	0.501	-0.983	-0.294
Swamp vegetation	-0.288	-1.152	-0.117	-0.430	-0.073	-0.986	-0.515

Supplementary information 5

Table S5.1. All recorded grass species in Okavango Delta study area.

Habitat	**Grass species**
Dry floodplain and island interiors	*Aristida adscensionis*
	Cenchrus ciliaris
	Chloris gyana
	Chloris virgata
	Cynodon dactylon
	Digitaria eriantha
	Eragrostis rigidior
	Eragrostis trichophora
	Eragrostis viscosa
	Pogonarthria squarrosa
	Schmidtia pappophoroides
	Sporobolus ioclados
	Stipagrostis hirtigluma
	Stipagrostis uniplumis
	Urochloa mosambicensis
Shrubbed grassland former floodplain	*Aristida congesta*
	Cenchrus ciliaris
	Chloris virgata
	Cynodon dactylon
	Eragrostis rigidior
	Eragrostis trichophora
	Schmidtia pappophoroides
	Sporobolus ioclados
	Stipagrostis hirtigluma
	Urochloa mosambicensis
Grassland with wild sage	*Cynodon dactylon*
	Cyperus fulgens
	Oxycaryum cubense (sedge)
Acacia woodland	*Aristida adscensionis*
	Brachiaria nigropedata
	Cenchrus ciliaris
	Chloris virgata
	Cynodon dactylon
	Digitaria eriantha
	Echinochloa colona
	Eragrostis lehmanniana
	Eragrostis rigidior
	Eragrostis superba
	Eragrostis trichophora
	Eragrostis viscosa
	Panicum repens
	Stipagrostis hirtigluma
	Stipagrostis uniplumis
	Urochloa mosambicensis
Swamp vegetation	*Cenchrus ciliaris*
	Cynodon dactylon
	Eragrostis rigidior
	Sporobolus fimbriatus
Riparian woodland	*Aristida adscensionis*
	Aristida congesta
	Cenchrus ciliaris
	Chloris virgata
	Cynodon dactylon
	Dactyloctenium giganteum
	Eragrostis lehmanniana
	Enteropogon macrostachyus
	Eragrostis rigidior
	Eragrostis superba
	Panicum maximum
	Sporobolus fimbriatus
	Urochloa mosambicensis
Mopane woodland	*Aristida adscensionis*
	Aristida congesta
	Cenchrus ciliaris
	Cynodon dactylon
	Dactyloctenium giganteum
	Digitaria eriantha
	Eragrostis lehmanniana
	Eragrostis rigidior
	Eragrostis trichophora
	Eragrostis viscosa
	Hyperthelia dissoluta
	Pogonarthria squarrosa
	Schmidtia pappophoroides
	Setaria Sphacelata var. sericea
	Stipagrostis uniplumis
	Urochloa mosambicensis
	Urochloa trichopus

Figure S5.1. Number of dominant grass species categorised by hot dry and rainy season and habitat class. Habitat classes are represented by dummy categories (section 5.2.4) grassland (GR) and woodland (WD). Dominant grass species were defined as the species that had the largest proportion of ground cover (%) within the sample site.