THE REPRODUCTIVE PERFORMANCE, DEMOGRAPHY AND SPATIAL ECOLOGY OF AN EXTRALIMITAL WHITE RHINOCEROS POPULATION

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ABSTRACT

The white rhinoceros (*Ceratotherium simum*) (hereafter rhino) is under threat of becoming extinct due to continued poaching for its horns. In South Africa and elsewhere in Africa private landowners have, over the last few decades, contributed to the conservation of various species, including rhinos, even in areas where they have not occurred historically (i.e., where they are extralimital). Unfortunately, very few studies have investigated the conservation contribution of extralimital white rhinos on private reserves to the overall meta-population and/or their reproductive performance. The first aim of my study was therefore to determine whether or not the white rhinos introduced to a private game reserve in the Eastern Cape Province in 1992 have been successful from a reproductive perspective. I calculated inter-calving intervals, age at first calving, conception period, sex ratio, fecundity and fertility rates for white rhinos over this 28-year period. The average annual population growth rate for the rhinos was 10%, which is higher than the recommended 5% by the Rhino Management Group. Trends in density-dependent parameters such as age at first calving and inter-calving intervals also indicated that my study population is still well below carrying capacity for white rhinos and is contributing positively to white rhino conservation in South Africa. The second aim of my study was to investigate home range size and vegetation preferences of white rhinos. Home ranges were mostly larger for all age groups compared to rhinos in their native range. Previously cultivated lands (dominated by several grass species) were preferred by all rhino age groups. The rehabilitation of these previous agricultural-based pastures has likely contributed to the successful introduction of the white rhino as an extralimital megaherbivore in the Eastern Cape. I conclude that although extralimital white rhino populations in the Eastern Cape can be successful from a reproductive perspective, their potential impact on the indigenous biodiversity of the region should be a key future research priority.

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CHAPTER 1

GENERAL INTRODUCTION

The Eastern Cape Province of South Africa is known for its rich diversity of floristic communities (Lubke *et al*., 1986). The specific area in which my study was conducted forms part of the IUCN-recognised Albany *hot spot* for biodiversity, known for its rolling hills and deep valleys, predominantly covered by the subtropical thicket, known as valley bushveld (Lubke *et al*., 1986; Kerley *et al*., 2003). Valley bushveld is known for its spiny, impenetrable thickets of 3-5 m high, consisting of various succulent and woody shrubs, small trees, grasses, geophytes and forbs (Kerley *et al*., 2003). Due to this rich biodiversity of flora, comes an abundant variety of vertebrate herbivores such as African elephant (*Loxodonta africana*), black rhinoceros (*Diceros bicornis*), eland (*Tragelaphus oryx*), Cape buffalo (*Syncerus caffer*), greater kudu, (*Tragelaphus strepsiceros*), bushbuck, (*Tragelaphus scriptus*), bushpig, (*Potamochoerus porcus*) and common (*Silvicapra grimmia)* and blue duikers (*Philantomba monticola*) (Skead, 1987). Predators such as lions (*Panthera leo*), leopards (*Panthera pardus*), African wild dogs (*Lycaon pictus*), brown (*Parahyaena brunnea*) and spotted hyenas (*Crocuta crocuta*) coexist with the above-mentioned herbivores, and more than 300 bird species are found in the area (Kerley *et al*., 2003).

Since the arrival of the 1820 Settler's, the Eastern Cape has undergone severe degradation of natural veld, due to pastoralist activities with mostly cattle, sheep and goats (Smith & Wilson, 2002; Kerley *et al*., 2003; Mills *et al*., 2005; O'Brien, 2013). Alluvial soils, adjacent to permanent water were cleared to plant pastures, and grow crops such as barley, maize, rye, chicory and pineapples (O'Brien, 2013). Due to these past agricultural activities, some of the landscape has been transformed to more open savanna-like systems dominated by grass and only a few trees (Mills *et al*., 2005).

From the 1980's, this transformed landscape presented the region with a unique opportunity to diversify its farming operations to include more wildlife-based activities (Mills *et al*., 2005). The reasoning behind this shift in land-use was to make the land more ecologically and economically viable (Mills *et al*., 2005). Wildlife such as the white rhinoceros (*Ceratotherium simum*) (hereafter white rhino) and the diversity of animals present on a game reserve have been found to be a major contributing factor for tourists when considering which reserves to visit (Maciejewski & Kerley, 2014). According to Maciejewski and Kerley (2014), who investigated tourist preferences while on safari, white rhinos were initially not highly regarded as one of the preferred species to view. However, over time, the white rhino came third after lions and elephants, indicating that the white rhino is a highly valued species for tourists. Not only is the private wildlife sector of economic importance; it is estimated that 80% of biodiversity conservation takes place on private land in South Africa (Carruthers, 2008). Wildlife, including the white rhino, has been stocked in the Eastern Cape because of international ecotourism market (Pasmans & Hebinck, 2017), often without considering the possible impact that such an extralimital species (populations that fall outside of the historical distribution range of the species) could have on the natural vegetation (Spear *et al*., 2011).

Ex situ conservation involves the re-distribution of endangered species in and out-of-range areas as an additional measure to compliment current *in situ* conservation (Kasso & Balakrishnan, 2013). Since the arrival of European explorers and hunters in the early 1800s, the mass killing of white rhinos began and poaching for rhino horn started to escalate from the 1900s (Carruthers, 2005; Santos, 2017). These killings resulted in the eradication of white rhinos across various African countries, including Angola, Zimbabwe, Botswana, Namibia and northern sections of South Africa (Player, 1967; Emslie & Brooks, 1999). In 1930, only a small population of approximately 120 white rhinos were left in the area known today as the iMfolozi Game Reserve (Skinner & Chimimba, 2005). The Natal Administrators Executive Committee was issued with the task to make recommendations to save the white rhino from extinction (Player, 1967). The idea was to relocate white rhinos from the iMfolozi Game Reserve to other suitable reserves with the aim to increase numbers. The launch of "Operation Rhino" which resulted in the relocation of about 4 000 white rhinos to eight different African countries, various reserves around South Africa, including the Eastern Cape and zoos around the world was launched in 1960 (Player, 1967; Skinner & Chimimba, 2005). White rhino numbers gradually started to increase from a mere 437 in 1953 to 18 064 at the end of 2017 (Emslie, 2020). However, due to the escalating trend in rhino poaching since 2008, numbers of white rhino have recently started to decrease (Emslie, 2020).

The increase in white rhino numbers over the last few decades is remarkable and it is evident that the relocation programme was, and still is, a huge success (Castley & Hall-Martin, 2003). The survival of a population is dependent on its ability to reproduce and increase in numbers (Bradshaw & McMahon, 2008). Active monitoring, post-release, is therefore vital, to establish whether a population has successfully habituated and is able to contribute reproductively to the meta-population (Sheil & Kirkby, 2018; Balfour *et al.*, 2019a). Initial introductions involved mainly populations of low numbers which result (initially) in very slow population growth. However, once they have reached a certain point, they will suddenly increase exponentially until the ecological capacity is reached (Bothma & du Toit, 2016). Thereafter, various external factors such as competition for resources, lower fecundity and increased mortality may cause a reduction in population growth rates (Bothma & du Toit, 2016). Home range size, population density, age at first calving (Rachlow, 1997), conception rate and inter-calving intervals (Gaillard *et al.*, 1998; Kraai, 2010) all directly influence fecundity and population growth rates. For example, low density white rhino populations have a tendency to increase relatively slowly, due to females giving birth to their first calves at an older age (Rachlow, 1997). However, as the population increases, inter-calving intervals generally decrease which allows for increased population growth rates (Rachlow, 1997). In most introduced white rhino populations, the growth rate would initially be slow due to low numbers, however according to Rachlow (1997) lower densities of white rhino result in cows becoming reproductively active at an earlier age and also generally display shorter inter-calving intervals, resulting in the population growing at a faster rate. Once densities increase, the population growth rate will gradually start to decline (Rachlow, 1997; Rachlow & Berger, 1998)

Caution should, however, be exercised with the introduction of extralimital populations to ensure ecological sustainability and the conservation of biodiversity (Castley *et al.*, 2001). The introduction of extralimital species can pose a threat to sensitive microhabitats due to increased feeding pressure on the landscape (Castley *et al.*, 2001). Importantly, the white rhino is a megaherbivore (a herbivore > 1000kg) that feeds exclusively on grass (Owen-Smith, 1988) and they are known to have a high impact on mesic savanna systems (Waldram *et al.*, 2008). The wide mouth of the white rhino and its plucking ability, accompanied by its hard lower lip, enable it to feed as low as 2,5 cm from the ground (Owen-Smith, 1981). The result from this feeding action has led to the phenomenon of grazing lawns, also known as "rhino gardens" (Waldram *et al*., 2008; Hempson *et al*., 2015). McNaughton (1984) describes grazing lawns as grassland that has been severely over-utilized by large herbivores, resulting in a reduced canopy height of the grass sward. Due to the severity of utilization, grass species create tillers and develop dense canopies of nutritious bulk forage, which in turn attracts other herbivores (McNaughton, 1984; Hempson *et al*., 2015) such as impala (*Aepyceros melampus*), zebra (*Equus quagga*) and blue wildebeest (*Connochaetes taurinus*) (Cromsigt & Olff, 2008). Waldram *et al*., (2008) have described the white rhino as "ecological engineers" due to their feeding habits and impact.

Fire is another important driver in savanna systems and studies conducted by Waldram *et al.,* (2008) in iMfolozi Game Reserve, and Cromsigt and Beest (2014) in the Kruger National Park (hereafter KNP) have found that grazing lawns were unable to burn due to the reduced fuel load resulting in patch burns. These biological barriers are believed to contribute to increased heterogeneity (Cromsigt & Beest, 2014). Studies conducted in KNP have found that in high density white rhino areas, the creation of grazing lawns to be more prominent than in low density areas, thus describing the white rhino as an important ecological driver in savanna landscapes (Cromsigt & Beest, 2014).

In iMfolozi Game Reserve, Owen-Smith (1981) found that during periods of increased overgrazing, the feeding habits of the white rhino have a negative impact on climax grass species such as *Themeda triandra* which eventually dies off due to its inability to recover from rhino grazing. Owen-Smith (1981) also noticed an increase in the formation of soil erosion and increaser II grass species (grass species who are abundant in overgrazed veld) settling in the landscape.

Their ecological impacts notwithstanding, white rhinos are at risk of extinction as the cost of security for protecting these animals is starting to outweigh the benefits of conserving them (De Beer, 2016). In South Africa, there has been a trend to convert agricultural lands into more financially viable wildlife ranches since the inception of the Game Theft Act of 1991, empowering landowners with ownership rights over wildlife on their property. This trend has led to an increase in the number of game ranches for various reasons, including ecotourism, hunting, game breeding and meat production (Taylor *et al*., 2014). Due to the increase in these conservation establishments, various extralimital species such as the white rhino have been introduced onto many private game reserves to assist in the conservation of the species and to attract international tourists (Maciejewski & Kerley, 2014).

Large-bodied herbivores require large ranges to satisfy their foraging and reproductive needs. Many studies have investigated home range size and movement of either established (Rachlow *et al*., 1999; White *et al*., 2006; Hebbelman, 2013; Jordaan *et al*., 2014; Thompson *et al*., 2016) or newly introduced rhino populations (Pitlagano, 2007; Sheil *et al*., 2018; Pederson, 2009). However, none have investigated the space use of white rhinos outside of their native range or where they are considered extralimital (Skead *et al*., 2007).

My study therefore aimed to assess the overall reproductive success (Rachlow, 1997; Gaillard *et al*., 1998; Kraai, 2010) and spatial ecology and habitat use of an extralimital white rhino population in the Eastern Cape Province, South Africa.

CHAPTER 2

STUDY ANIMAL AND STUDY AREA

2.1 STUDY ANIMAL

2.1.1 Description

The white rhino is considered the third largest land mammal (Owen-Smith, 1988) with adult males reaching a weight of 2300 kg, and females 1700 kg (Figure 2.1) (Shrader *et al*., 2006). The white rhino has a relatively long head that carries both an anterior and posterior horn made out of keratin filaments, with the latter normally being shorter (Skinner & Chimimba, 2005). The horns on males are generally thicker at the base than those of the females and continue to grow throughout the animal's lifetime (Skinner & Chimimba, 2005). The female's horn is generally more slender than the male's, but not necessarily longer (Skinner & Chimimba, 2005). The shape and angle of the horn varies individually, with some having anterior horns pointing forward, making them parallel with the ground while feeding (Player & Feely, 1960).

The white rhino has wide, square-shaped lips specifically adapted for grazing (Skinner & Chimimba, 2005) and they move these around with their head held low to the ground while foraging (Shrader *et al*., 2006). Other features of the white rhino are its pointed ears and a distinct hump on the neck, and its thick skin is prominently folded on the front shoulders, on the upper part of the hind limbs and at the junction of the forelimbs and the body (Player & Feely, 1960; Skinner & Chimimba, 2005). The body appears to be hairless to the naked eye, however, it is sparsely covered in bristle hair. The skin can reach a thickness of about 20 mm around the shoulders and 50 mm on the forehead (Skinner & Chimimba, 2005).

The name white rhino is believed by many to have been derived from the Cape Dutch word "*weit*", meaning wide and was used to describe the mouth of the white rhino (Skinner & Chimimba, 2005). Others believe that some of the first white rhinos that were spotted were white due to the colour of the clay in which they wallowed (Player & Feely, 1960).

Figure 2.1. Photograph showing an adult female white rhino.

2.1.2 Taxonomy and distribution

The white rhino forms part of the Order *Perrissodactyla*, also known as odd-toed ungulates, within the family Rhinocerotidae which includes five species of rhino, namely: the white rhino; black rhino (*Diceros bicornis*); the Sumatran rhino (*Dicerorhinus sumatrensis*); the Indian rhino (*Rhinoceros unicornis*) and the Javan rhino (*Rhinoceros sondaicus*) (Steiner & Ryder, 2011). Two subspecies of white rhino occur, namely: the southern white rhino *(Ceratotherium simum simum)* and the northern white rhino (*Ceratotherium simum cottoni*).

Historical evidence suggests that the two sub-species had about 2000 km of land separating them, with the northern white rhino occupying northern sections of the Democratic Republic of the Congo, Uganda and southern Sudan, and the southern white rhino occurring north of the Orange River towards the north-eastern section of Namibia, south of the Zambezi River and western Mozambique (Pienaar, 1994). Diggings at Grassridge Dam between Hofmeyr and Middelburg (Eastern Cape Province, South Africa) have, however, revealed skeletal remains of a white rhino and these represent the only evidence of white rhinos occurring south of the Orange River (Furstenburg, 2013). It was noted in the early 1900s that the northern white rhino numbers were significantly greater than the southern white rhino, but due to an increased demand for meat, horns and skins, their numbers started to rapidly decline from the 1960s (Emslie & Brooks, 1999). In an attempt to reduce the slaughter and conserve the remaining northern white rhinos, Garamba National Park in the Democratic Republic of the Congo was formed in 1938, as well as the Southern National Park in Sudan in 1939 (Emslie & Brooks, 1999). Continued poaching for horn and skins resulted in the northern white rhino becoming extinct in Uganda during 1984, and years of civil and political unrest in the Democratic Republic of the Congo have resulted in the extinction of the remaining wild northern white rhinos (Emslie & Brooks, 1999; Skinner & Chimimba, 2005; Tunstall *et al*., 2018; Janssens & Trouwborst, 2018). There are now only two female northern white rhinos remaining in captivity (Tunstall *et al*., 2018; Janssens & Trouwborst 2018).

By the early nineteenth century, southern white rhino numbers had declined to a single relict population of between 10 - 20 animals in the KwaZulu-Natal Province of South Africa (Skinner & Chimimba, 2005). By the 1930's, an estimated 120 individuals were counted (Skinner & Chimimba, 2005). The first aerial count was conducted in 1953 and confirmed 437 individuals (Player & Feely, 1960). In 1961, Operation Rhino was initiated by the Natal Parks Board (see Chapter 1). Today, southern white rhinos can be found in five African countries in addition to South Africa; Botswana, Mozambique, Namibia, Swaziland and Zimbabwe (Figure 1.2). Extralimital populations (Spear *et al*., 2011) have also been established in Kenya and Uganda (Amin *et al*., 2006). In South Africa, extralimital populations have also been successfully established in the Eastern and Western Cape Provinces on private land (Castley & Hall-Martin, 2003). The numbers of southern white rhinos have increased significantly over the last few decades with an estimated number of 18 064 white rhinos in Africa in 2017 (Emslie *et al*., 2019). South Africa, Kenya, Zimbabwe and Namibia are responsible for the conservation of about 99% of the total population (Amin *et al*., 2006).

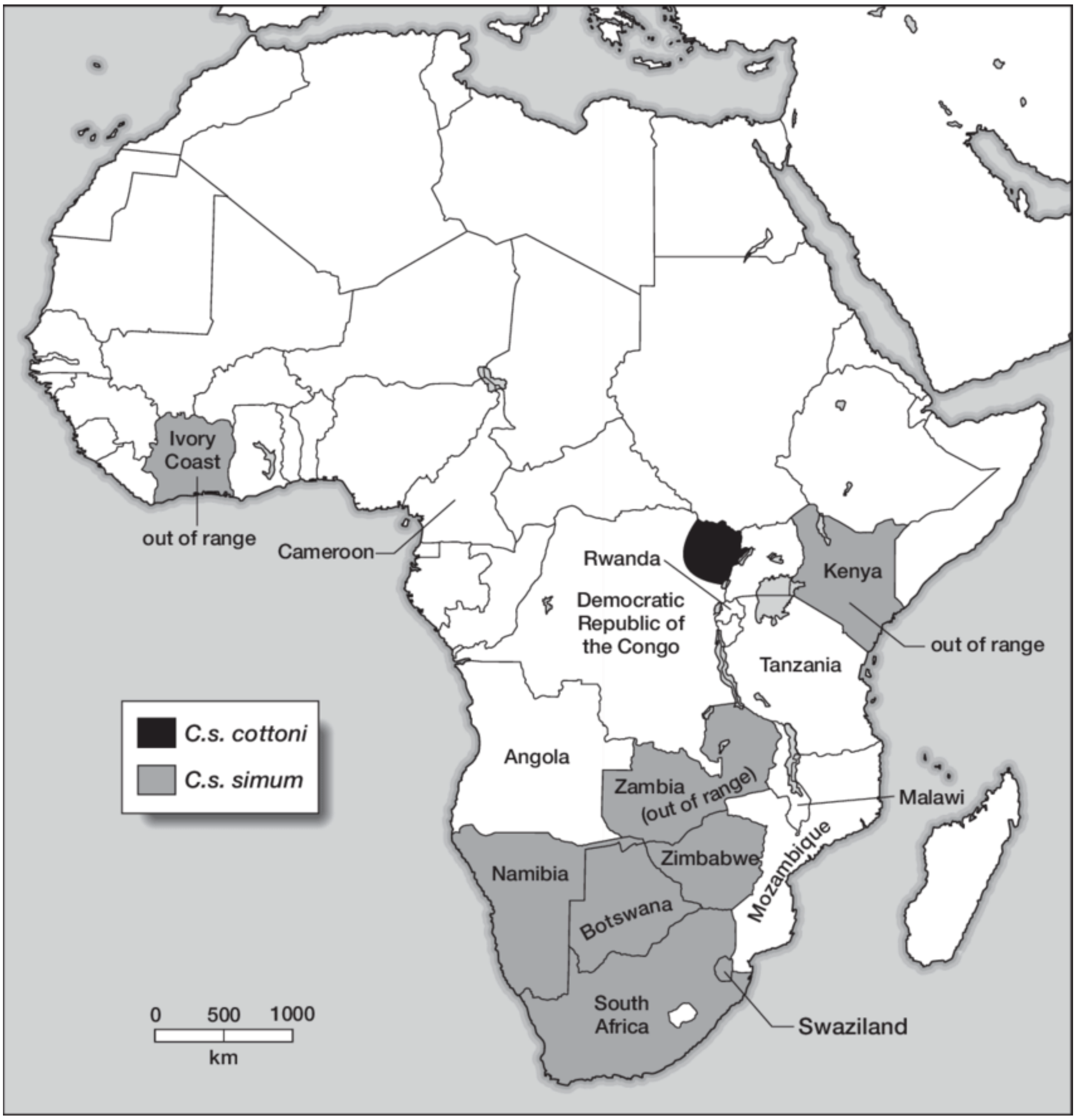

Figure 1.2. Map showing the current distribution of both white rhino sub-species in Africa (Emslie & Brooks, 1999). Note that wild *Ceratotherium simum cottoni* has since 2018 been declared extinct (Janssens & Trouwborst, 2018).

2.1.3 Habitat

Player and Feely (1960) identified four basic habitat requirements for white rhinos, namely: areas with short grass, water to drink and wallow, thickets to provide shelter and protection and a relatively flat topography. Steep slopes are generally avoided and only accessed to move between preferred foraging areas (Skinner & Chimimba, 2005).

According to Horne *et al*., (2008), habitat selection is dependent on accessibility and preference. White rhinos display seasonal preference towards certain habitats (Pienaar, 1994; Shrader *et al*., 2006; Hebbelmann, 2013; Chirenje, 2016). In the Pilansberg National Park, South Africa white rhinos preferred old, cultivated lands during the wetter season and wooded valley thicket during the drier season (Borthwich, 1986). By contrast, savanna, thornveld and shrubveld were mostly utilized by the white rhinos in the Willem Pretorius Reserve in the Free State Province, South Africa (Jordaan *et al*., 2015). Semi-arid savanna areas were preferred by rhinos in the Kruger National Park (hereafter KNP) (Pienaar, 1994). In iMfolozi Game Reserve it was noted that the white rhinos utilized a variety of specific grassland types throughout the year and this was season-dependant (Owen-Smith, 1988). Short grasslands were preferred during the wet season and this preference shifted more towards the woodland grassland when the green grass declined, eventually shifting towards less palatable hill slopes (Owen-Smith, 1988).

Access to water plays an important role in habitat selection in the white rhino and they will drink daily in the wetter seasons when water is readily available. However, during the dry season, when water is scarcer, it has been found that white rhinos will only drink every 2 – 4 days (Pienaar, 1994). Wallowing in mud is another important activity practiced by the white rhino and it has the dual purpose of thermoregulation and to rid the animals of various external parasites such as ticks when they rub on old fencing posts, trees and rocks (Pienaar,1994; Shrader *et al*., 2006).

2.1.4 Activity patterns, territoriality and home range

White rhinos are most active in the early mornings and again in the early to late evenings (Owen-Smith, 1988; Rachlow *et al*., 1999; Sheil & Kirkby, 2018). During these active periods, they are mostly found feeding or moving to waterholes. At midday, they tend to sleep and they are generally inactive from about 9:00 until 16:00 during the hot summer months (Owen-Smith, 1988). During the cooler seasons, evenings are spent mostly travelling to waterholes (Owen-Smith, 1988). Females with small calves were found to feed for more extended periods than other age or sex classes due to their increased nutritional demands (Monks, 1995). White rhinos were also found to be more active throughout the day during the wet season from October to December, also including periods when the weather was overcast (Owen-Smith, 1988).

Visits to waterholes are often characterized by wallowing where rhinos were often observed either just lying in a pool of water or actively rolling in the mud from side-to-side followed by rubbing of various body parts against stumps or termite mounds (Owen-Smith, 1973). Although mud-wallowing is important in the eradication of external parasites (Owen-Smith, 1973), Red-billed Oxpeckers (*Buphagus erythrorhynchus*) have also been found to favour white rhinos as their preferred hosts to feed on ticks (Ndlovu & Combrink, 2015).

White rhinos tend to be solitary animals (Skinner & Chimimba, 2005), however cows are normally associated with their offspring, and sub-adults will form temporary companionships during their most vulnerable period of development from adolescence to adulthood (Owen-Smith, 1988). These temporary social companionships are unique in the white rhino (Shrader & Owen-Smith, 2002). Companionships normally consist of sub-adults from both sexes and adult cows prior to giving birth or who have lost a calf (Shrader & Owen-Smith, 2002; Skinner & Chimimba, 2005). Companionship group sizes generally consist of between two to five individuals and can last from a few days to a few years (Skinner & Chimimba, 2005). Movement will predominantly be predicted by the adult cow until she gives birth to her first calf, when she will leave the remaining sub-adults (Shrader & Owen-Smith, 2002).

Spatial distribution and general movement of sub-adult white rhinos was found to be predominantly erratic, with some sub-adults utilizing certain areas only on a temporary basis, while others would hold fixed home ranges (Shrader & Owen-Smith, 2002). Home ranges varied from 2 - 7 km^2 in sub-adults (Shrader & Owen-Smith, 2002). White rhino bulls undergo various stages of maturity before they have any mating privileges (McKenzie *et al*., 2007). As in other species, bulls will reach sexual maturity from the age of six years but may only mate much later (see below). Only territorial bulls have mating privileges and, once they become territorial, they are referred to as socially mature bulls (Rachlow, 1997; McKenzie *et al*., 2007). As in other species, socially mature bulls are solitary and territorial, and sexually mature bulls hold non-overlapping territories which are shared and accepted by other bulls on condition that submissive behaviour is displayed towards the territorial bulls (Owen-Smith, 1988). Territorial bulls mark their territories using scent-marking by defecating in dung middens, followed by vigorous kicking of the dung using the rear legs (Rachlow *et al*., 1999). They also spray urinate onto vegetation or areas after it has been scraped by the dragging of their hind feet (Rachlow *et al*., 1999). Sub-ordinate or non-territorial bulls do not display any scent-marking activities (Rachlow *et al*., 1999).

Home range sizes of territorial bulls vary from 0.75 km² - 2.60 km² in Ndumu Game Reserve, KwaZulu-Natal, from 2.5 km² - 13.9 km² in the south-western side of the KNP, from 44.8 km² - 84.1 km² in the Pafuri section of KNP (Pedersen, 2009), from 6.37 km² - 8.13 km² in Willem Pretorius Reserve, Free State (Jordaan *et al*., 2015) and 2.62 km² - 8.95 km² in iMfolozi Game Reserve (White *et al*., 2007).

Home range sizes of adult cows vary from 1.97 km² - 5.05 km² in the Willem Pretorius Game Reserve (Jordaan *et al*., 2015), from 7.2 km² – 45.2 km² in the south-western side of KNP (Pienaar, 1994) to 17 km² - 84.1 km² in the northern Pafuri section of the KNP (Pedersen, 2009), and from 2. 9km² - 20 km² in iMfolozi Game Reserve (White *et al*., 2006).

Home range size is influenced by seasonality with white rhinos having larger home ranges during the dry season compared to the wet season (Rachlow *et al*., 1999; Jordaan *et al*., 2015). Home ranges of adult cows regularly overlap with other cows (Owen-Smith, 1988) and also incorporate various territorial bull home ranges (Skinner & Chimimba, 2005).

Communication among white rhinos is mostly dependant on olfactory signals and is conveyed at dung middens by means of urine and dung (Skinner & Chimimba, 2005, Marneweck *et al*., 2018). Dung middens act as information posts, providing information on past visitors regarding sex, age, social and reproductive status (Marneweck *et al*., 2018). Territorial males have a selection of dung middens of their own which they patrol on a regular basis and these are also frequently utilized by females and non-territorial males (Estes, 2012; Marneweck *et al*., 2018). According to Marneweck *et al*., (2018), the placement of the dung is meticulous, whereby the territorial bull will always defecate in the centre of the midden accompanied by vigorous kicking, while females and subordinate males will defecate around the midden periphery (Marneweck *et al*., 2018). These middens are frequently visited by territorial bulls (Marneweck *et al*., 2018).

Vocalization also forms part of their communication and a variety of sounds are used in various situations (Player & Feely, 1960; Skinner & Chimimba, 2005; Estes, 2012). Calves who are separated from their mothers or who are in distress will squeal in a pig-like fashion and will whine to get their mother's attention (Player & Feely, 1960; Estes, 2012). Adult cows are generally more silent with only an occasional puff or snarl at approaching bulls (Player & Feely, 1960). Adult bulls, on the other hand, are very noisy during aggressive encounters and mating sessions (Player & Feely, 1960). Bulls will squeal at females who are trying to evade their territories while in oestrus and vocally announce their frustrations when cows persistently refuse mating (Player & Feely, 1960). Snorting and snarling is a warning to other rhinos not to approach (Monks, 1995; Estes, 2012). Fighting between bulls is rare, however, they can be one of the main causes of mortality in high density areas (Rachlow, 1997).

White rhinos will often share feeding grounds with various other species without any aggression (Skinner & Chimimba, 2005), however, they can be susceptible to attack from delinquent African elephants (*Loxodonta africana*) in extraordinary situations (Figure 2.2) (Slotow & van Dyk, 2001). Lions (*Panthera leo*) and spotted hyenas (*Crocuta crocuta)* can pose a threat to vulnerable young calves (Skinner & Chimimba, 2005).

Figure 2.2. Photograph showing a young elephant bull chasing a sub-adult white rhino bull.

2.1.5 Reproductive behaviour

White rhinos breed throughout the year with birth peaks between March and July (Skinner & Chimimba, 2005). Females have been found to start breeding at four years old, while bulls started mating from six years (Skinner & Chimimba, 2005). Population density has been found to influence the age at first calving as was noted by Rachlow (1997) in Matobo National Park, Zimbabwe where high density areas of white rhinos resulted in a population growth rate decrease, and age at first calving increased to an average of 10.1 years.

Once a female is ready for mating, she enters a period of oestrus which can last up to 28 days (Bertschinger, 1994). During this period, the resident territorial bull will stay within close proximity (5 – 30 m) (Estes, 2012) for a few days until she is ready for mating. During this time, the bull takes active steps to prevent her from leaving his territory (Skinner & Chimimba, 2005). Cows become more irritable and will display their frustration by charging and snorting at the persistent bull (Skinner & Chimimba, 2005). Once the female is ready to be mated, she will allow the bull to approach her. The bull approaches by using a series of hick-throbbing sounds and will lay his chin on her rump (Owen-Smith, 1988). Copulation will last for about 15 – 28 minutes, with ejaculations being repeated every few minutes during the mounting session (Owen-Smith, 1988). Only territorial bulls are believed to breed successfully (Owen-Smith, 1988; Rachlow *et al*., 1999). However, studies done in Thaba Tholo Game Reserve, South Africa have found significant levels of kleptogamy in white rhinos by non-territorial males within the territorial bull’s range (Kretzschmar *et al*., 2020).

The gestation period lasts 16 months after which a single calf is born weighing about 40 kg (Skinner & Chimimba, 2005). The female will stay within close proximity to dense vegetation for the first few weeks after birth (Player & Feely, 1960). The calf will stay very close to its mother, but with time will wander further and further. Calf movement is guided by the mother’s touch from her horn (Player & Feely, 1960; Owen-Smith, 1988; Skinner & Chimimba, 2005). Calves start to feed on grass from about 2 months of age and will spend most of their time grazing from 3 – 4 months. Calves are weaned at about 12 months but will still suckle up to 18 months (Owen-Smith, 1988).

Inter-calving intervals vary significantly from 1 year and 10 months to 3 years and 5 months. However, the mean interval is 2 years and 6 months in iMfolozi Game Reserve (Owen-Smith, 1988), while intervals of between 2 years 3 months, and 3 years and 3 months have been recorded in Matobo National Park (Rachlow & Berger, 1998). Bonds between mother and calf are long-lasting, with some calves returning to their mothers (temporarily) years later (Owen-Smith, 1988).

2.1.6 Diet

The white rhino is a bulk grazer and therefore feeds primarily on grass. The quality of grass will determine utilization (Player & Feely, 1960), and forms part of their preferred feeding grounds, influencing their movement (Shrader *et al*., 2006).

The diet of the white rhino varies from wet to dry season, whereby short grass is preferred during the wet season and they gradually shifting to more medium to tall grasses such as *Themeda* spp. during the dry season (Owen-Smith, 1988; Shrader *et al*., 2006; Kraai, 2010). In iMfolozi Game Reserve it was found that *Panicum, Digitaria* (Figure 2.3) and *Urochloa* spp. were preferred, while *Themeda triandra* was only utilized after veldfires (Player & Feely, 1960). In the KNP, grass such as *Panicum maximum*, growing in the shade of trees was preferred along river banks, and a variety of short-grass species such as *Sporobolus nitens, Panicum coloratum, Urochloa mosambicensis, Dactyloctenium aegyptium* and *Digitaria* spp. were preferred when foraging elsewhere. Researchers found that during the drier seasons, the white rhinos would not shift their feeding habits to less palatable species, but rather extending their feeding time moving amongst more woodland terrain feeding on the *Panicum maximum* found under the trees (Pienaar, 1994). In the Willem Pretorius Game Reserve, the white rhinos preferred grass species during both dry and wet seasons was *Cynodon* species (Figure 2.4), being 47.4% of its total diet during the wet season and 31.4% in the dry season. Various other species such as *Enneapogon scoparius, Themeda triandra, Eragrostis curvula* and *Aristida congesta* contributed most of its remaining diet (Jordaan *et al*., 2015).

A Study done by Kraai (2010) on Shamwari Private Game Reserve, Eastern Cape Province, South Africa found that the white rhinos mostly consumed *Karoochloa curva, Panicum* spp.*, Eragrostis obtusa* and *Themeda triandra* as their preferred grass species, with *Themeda triandra* being utilized during both the dry and wet seasons.

Figure 2.3. Photograph showing a white rhino calf feeding on *Digitaria eriantha*.

Figure 2.4. Photograph showing an adult white rhino cow and calf feeding on *Cynodon dactylon*.

2.1.7 Conservation status

White rhinos are categorised as Near Threatened on the IUCN Red List (Emslie *et al*., 2019). According to Emslie *et al*., (2019), white rhino numbers at the end of 2017 were estimated to be 18 064 in Africa, with South Africa remaining the stronghold country, accounting for about 87% of the continental population. However, from 2012, white rhino numbers have started to decline annually due to the increase in highly specialised organised crime syndicates poaching the rhino for its horn (De Beer, 2016).

Private game reserves in South Africa contribute to rhino conservation in a positive manner by conserving natural areas, making them suitable to conserve threatened species (Cousins *et al*., 2008). Significantly, private game reserves are home to about 24% of the South African national population (Knight *et al.,* 2015). In the private sector, white rhino numbers have shown continued population growth. By contrast, state-owed parks and reserves have lost about 21% of their white rhino population since 2012 due to poaching (Emslie *et al*., 2019). Concerns over the monetary drop in the value of rhino declining yearly and the cost of security is concerning for the future of the white rhino (Taylor *et al*., 2014).

2.2 STUDY AREA

2.2.1 Location and history

My study was conducted on Shamwari Private Game Reserve (hereafter Shamwari), in the Eastern Cape Province of South Africa (Figure 2.5). The reserve is situated north of the N2 highway about 72 km north-east outside of Port Elizabeth on-route to Makhanda (previously known as Grahamstown). Shamwari was established in 1990 for both ecotourism and biodiversity conservation purposes (O’Brien, 2013).

Prior to the establishment of Shamwari, the land was predominantly utilized for agricultural practises, including raising of livestock and the growing of crops such as chicory, pineapples and vegetables (O’Brien, 2013). Most of the neighbouring land is still being used for agriculture.

During the period of my study, the reserve was divided in three different management zones, physically separated by fences namely Amanzi, Bayethe/Rippons and Main reserve.

Amanzi (2 219.2 ha) is managed as a semi-intensive breeding centre. Endangered species such as the cape mountain zebra (*Equus zebra zebra*) and disease-free buffalo (*Syncerus caffer*) are bred in the absence of any large predators. Excess antelope species are relocated to the main reserve or sold during annual game sales. Bayethe/Rippons consist of 4477 ha and doubles as a breeding centre with no large predators, however large herbivores such as elephants, buffaloes and hippos (*Hippopotamus amphibious*) were introduced from the main reserve during 2007. The main reserve, consisting of 13 742 ha is managed as a natural area and includes large herbivores, including both black- and white rhinos, elephants, buffalos and hippos and large predators such as lions (*Panthera leo*), cheetahs (*Acinonyx jubatus*) and leopards (*Panthera pardus*).

Prior to November 2017, the area in which the white rhinos were found was 13 742 ha in size. The available area increased to 18 219 ha after the north-eastern corner, dividing the main reserve and Bayethe/Rippons was opened and fences were removed. The additional 4477 ha of Bayethe/Rippons was not incorporated in this study as no rhinos have migrated to this section yet. However, during early 2018, a section of land consisting of 817 ha in the south-eastern section of the reserve was lost to a neighbouring reserve. This specific section formed an integral part of the rhino's home ranges and mostly consisted of open grassland.

Figure 2.5. Map showing the location of Shamwari Private Game Reserve within the Eastern Cape Province of South Africa.

2.2.2 Climate

Shamwari falls within the semi-arid coastal zone that receives unpredictable rainfall throughout the year, but with two bimodal peaks during March – April and again in October – November (Mucina & Rutherford, 2006). Due to the rainfall being unpredictable, droughts lasting several months are common (Mucina & Rutherford, 2006). The reserve experiences hot summers, often reaching 35°C and above and cold winters with maximum daily temperatures as low as 5°C and frost (Mucina & Rutherford, 2006).

The mean annual rainfall for Shamwari over the past 21 years has been 501 mm for the south, and 513 mm for the north (Figure 2.6) with the southern section generally receiving more rainfall during spring, and the north receiving more during summer (Figure 2.7a and b). The highest rainfall in the south was recorded in 2006 (789 mm) and for the north in 2001 (813 mm). The lowest in the south was in 2016 (247 mm) and in the north in 2018 (201 mm).

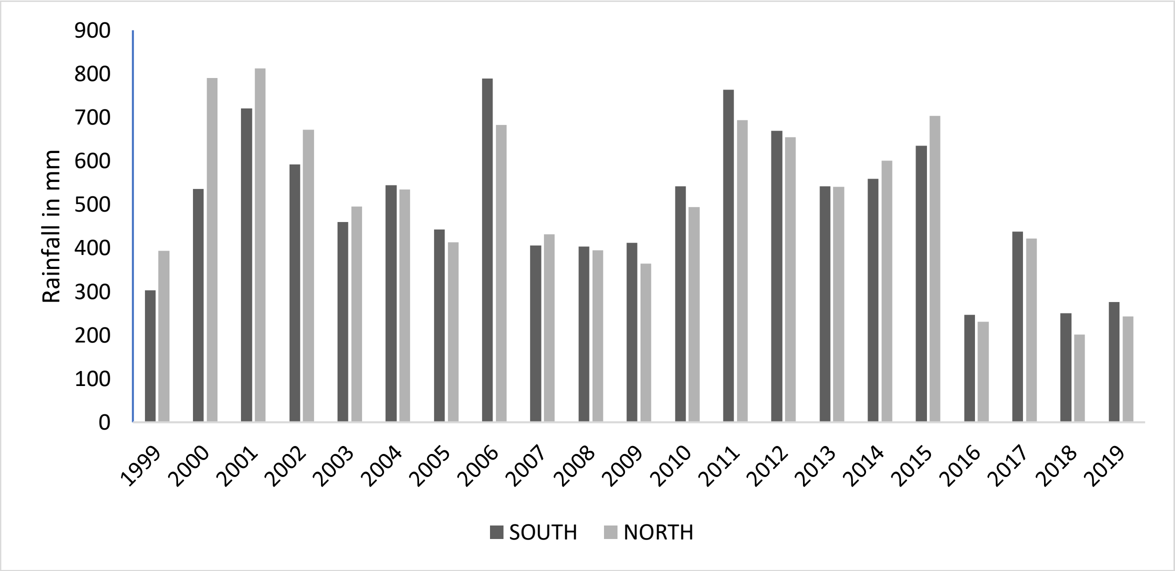

Figure 2.6. Total annual rainfall (mm) on Shamwari Private Game Reserve for the period 1999 – 2019.

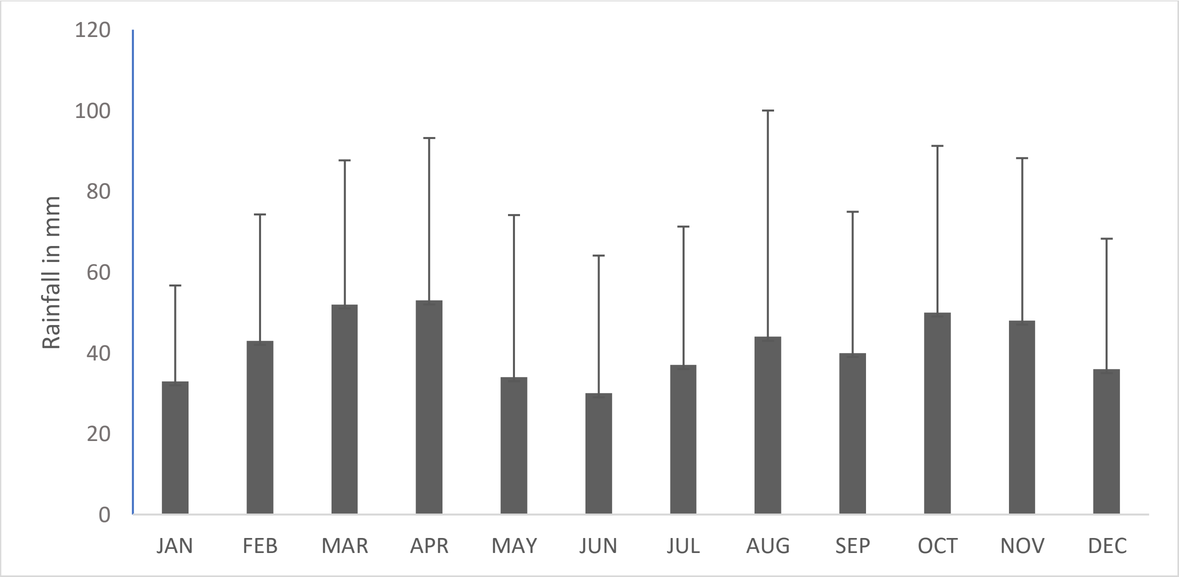

Figure 2.7a. Mean monthly average rainfall for the southern section of Shamwari Private Game Reserve for the period 1999 – 2019.

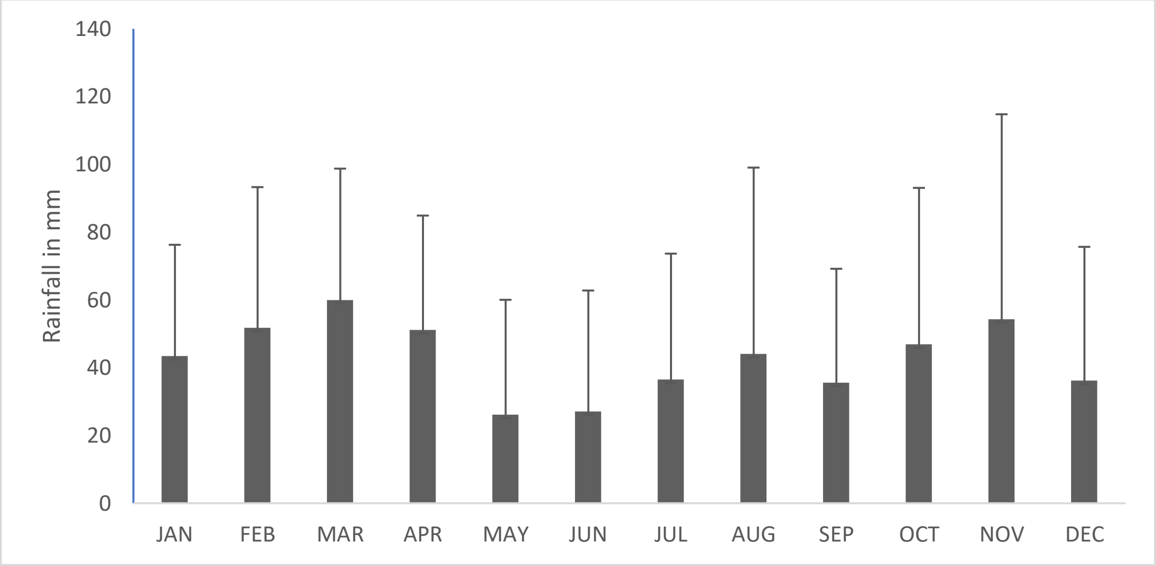

Figure 2.7b. Mean monthly average rainfall for the northern section of Shamwari Private Game Reserve for the period 1999 – 2019.

2.2.3 Geology and topography

The dominant geological formation around the northern section of the reserve is the east-west trending of the Cape fold mountains forming part of the Cape Supergroup (Mucina & Rutherford, 2006) and consist of the Bokkeveld Series shales, Witteberg quartzites, Karoo sandstones and Sundays River Formations (O'Brien, 2013). The quartzite ridges traverse the central and northern parts of the reserve, dividing it into distinct geomorphologic zones separated from one another by the ridges (Burroughs & Palmer, 1992). The northern section is characterised by rolling hills and deep valleys. The southern part of the reserve is dominated by the Sundays River Formation resulting in shallow soils underlain by calcrete. The elevation gradient of the reserve is significant from south to north and differs from 196 m above sea level in the south to 628 m in the north. The steep gradient elevation, in turn, influences the seasonal distribution of rainfall where the reserve experiences considerably more rainfall in the north-east compared to the southern sector (O'Brien, 2013).

The Bushmans River is semi-perennial and flows for 27.6 km through the reserve entering the reserve in the central west and exiting in the south-east (Parker & Bernard, 2005). Four major geological substrata are found, namely shale, sandstone, quartzite and calcrete and deep alluvial soils are found on the lower lying areas in the southern section of the reserve (O'Brien, 2013).

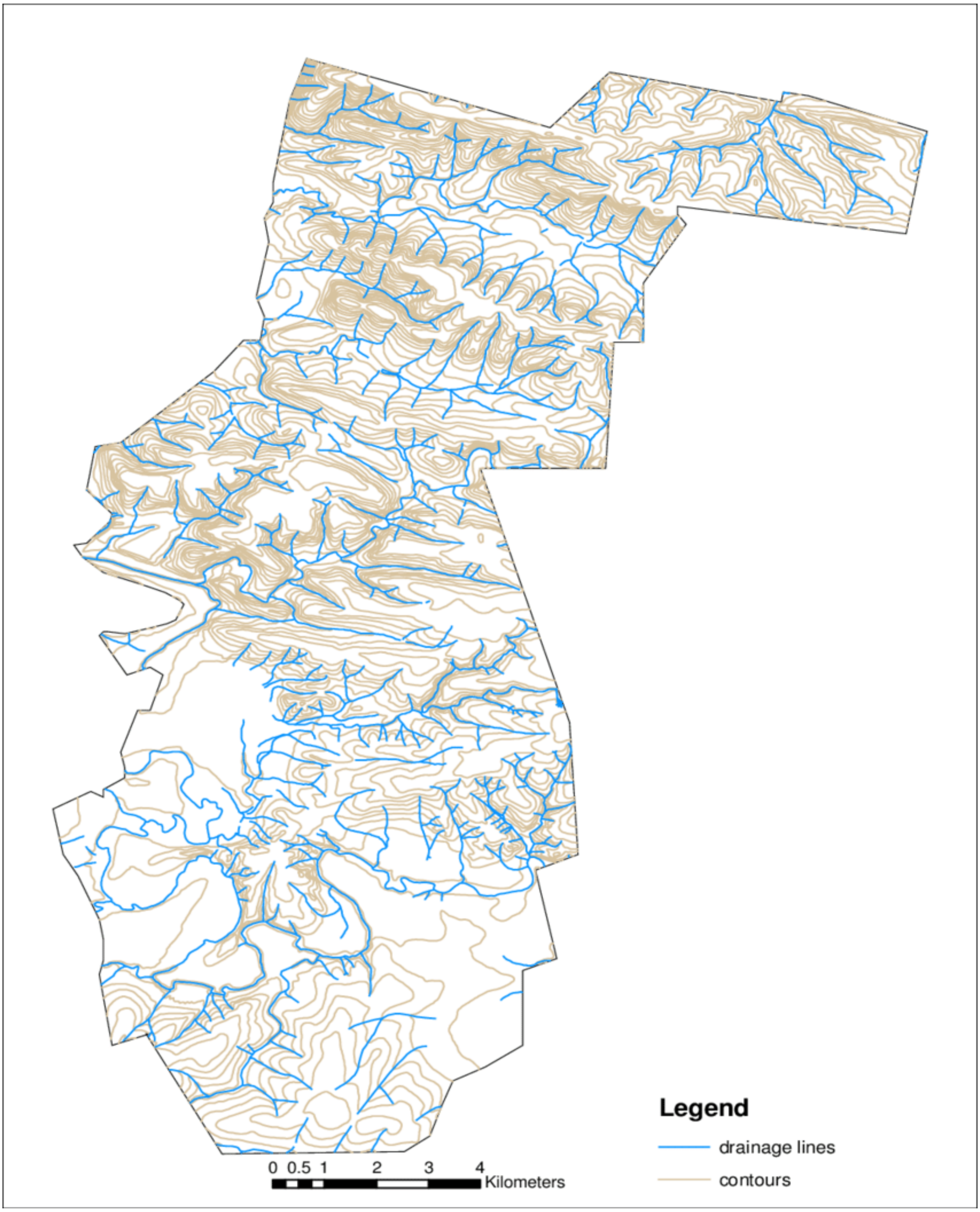

Figure 2.8. The topography and drainage lines of Shamwari Private Game Reserve (Roux, 2006)

2.2.4 Vegetation

South Africa is home to seven different biomes namely Fynbos, Grassland, Savanna, Thicket, Forest, Succulent Karoo and Nama-Karoo of which five are present on Shamwari, namely forest, thicket, savanna, grassland and fynbos (Lubke *et al*., 1986). Secondary vegetation, which include cultivated and old cleared lands were further identified by O'Brien (2004) (Figure 2.9). These cultivated lands have been seeded with *Panicum maximum, Digitaria eriantha* and *Cenchrus ciliaris* to improve grazing by the Shamwari Wildlife Department (O' Brien, 2004).

The vegetation of Shamwari is classified under the Albany thicket, savanna and fynbos biomes (Mucina & Rutherford, 2006). It includes the dominant Kowie thicket vegetation unit which occurs over most of the reserve. Bhisho thornveld, occurring in the central areas, and a small portion of Albany coastal belt occur in the extreme south-west of the reserve. The northern and north-eastern areas of the reserve are mostly dominated by Suurberg quartzite fynbos and smaller patches of Suurberg shale fynbos. The diversity within the vegetation units found on Shamwari is due to its transitional location, resulting in high levels of endemism (Kerley *et al*., 2003).

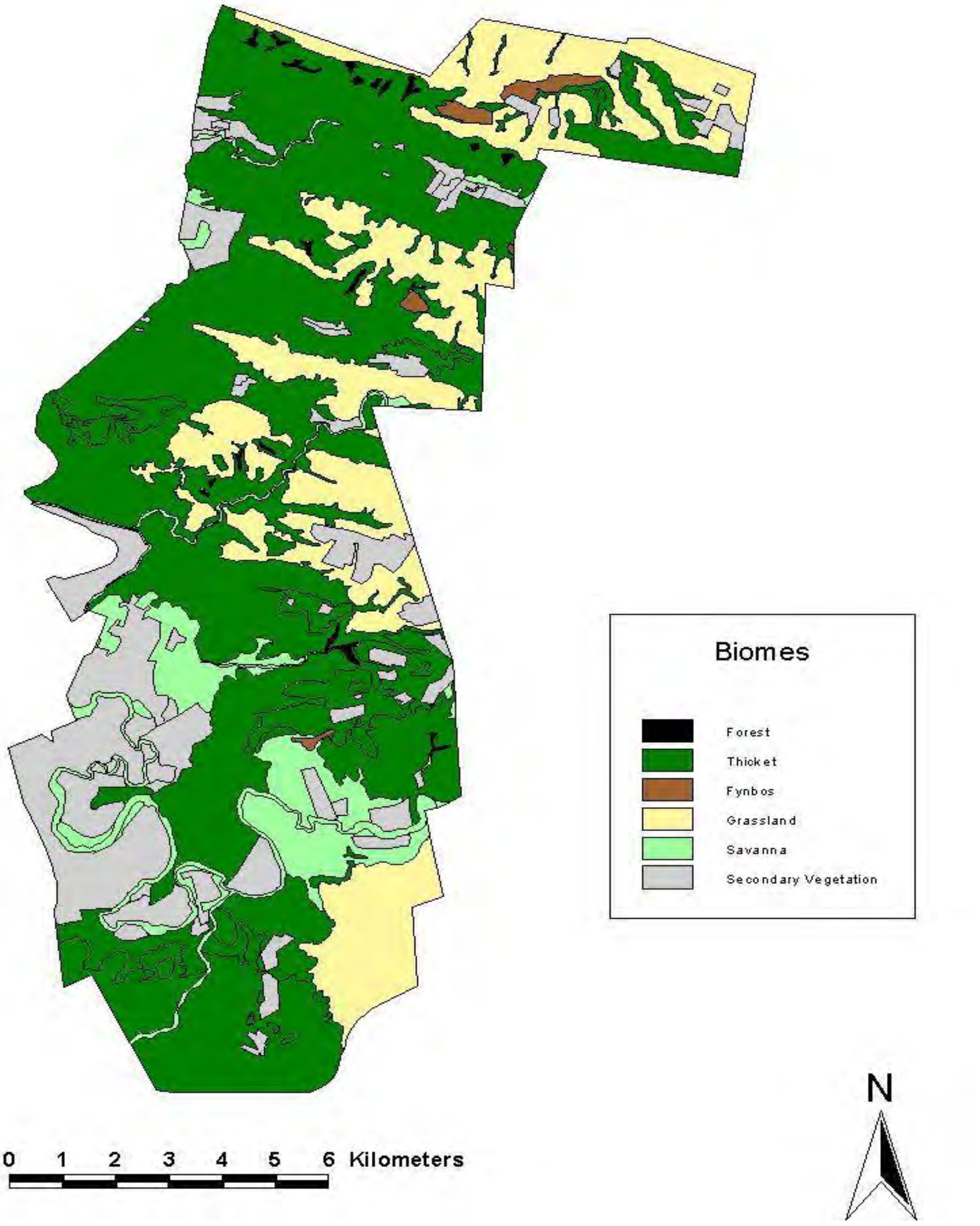

Figure 2.9. Map showing the different vegetation biomes found on Shamwari Private Game Reserve as identified by O’Brien (2004).

2.2.5 Study animals

Shamwari introduced their first white rhinos in 1992 and included four adult cows, followed by an additional two adult bulls and one sub-adult heifer in 1993, making it a total of seven animals (Joubert, *pers. comm.*). Additional white rhinos were introduced during 2002 (two heifers and one sub-adult bull) and 2006 (two adult cows, both accompanied by calves). All white rhinos originated from iMfolozi Game Reserve, except for the two adult cows and calves in 2006 which came from KNP.

Since 2007, Shamwari has sold 20 white rhinos, including nine adult bulls, four adult cows with calves at foot, three sub-adult bulls and three heifers. As in other species, these sales were to prevent inbreeding within the current population, prevent fighting and to supply newly established reserves with breeding stock (Benjamin-Fink & Reilly, 2017).

2.2.6 Monitoring and individual identification

Since the introduction of rhinos on Shamwari, a wildlife monitoring system has been in place. The anti-poaching team was originally responsible for the monitoring of the rhinos and collecting data on births, deaths, overall health and the locations of the rhinos (Balfour *et al.*, 2019b). However, from September 2007, I was appointed as the full-time animal monitor to monitor both the rhino and predator populations on Shamwari. Existing data were used to set up individual profile system for each rhino. Daily sightings and locations of specific rhinos were recorded (if no accurate identification could be made, it was not recorded as seen for that day), and records of any new births, deaths, and behaviours such as fighting, mating, dominant bull were recorded.

Rhinos can be identified in the field by unique ear notches. The white rhinos on Shamwari are routinely immobilized for DNA profiling (Harper, 2011). The DNA samples are used in poaching investigations and to trace horns back to the owner (Harper, 2011). During the immobilisation process, rhinos are microchipped in both horns and the tail, and notches are cut into the ears of un-notched individuals (Harper, 2011; Balfour *et al.*, 2019b). The number and location of notches is unique to every individual (Figure 2.10) to avoid confusion and to aid identification in the field.

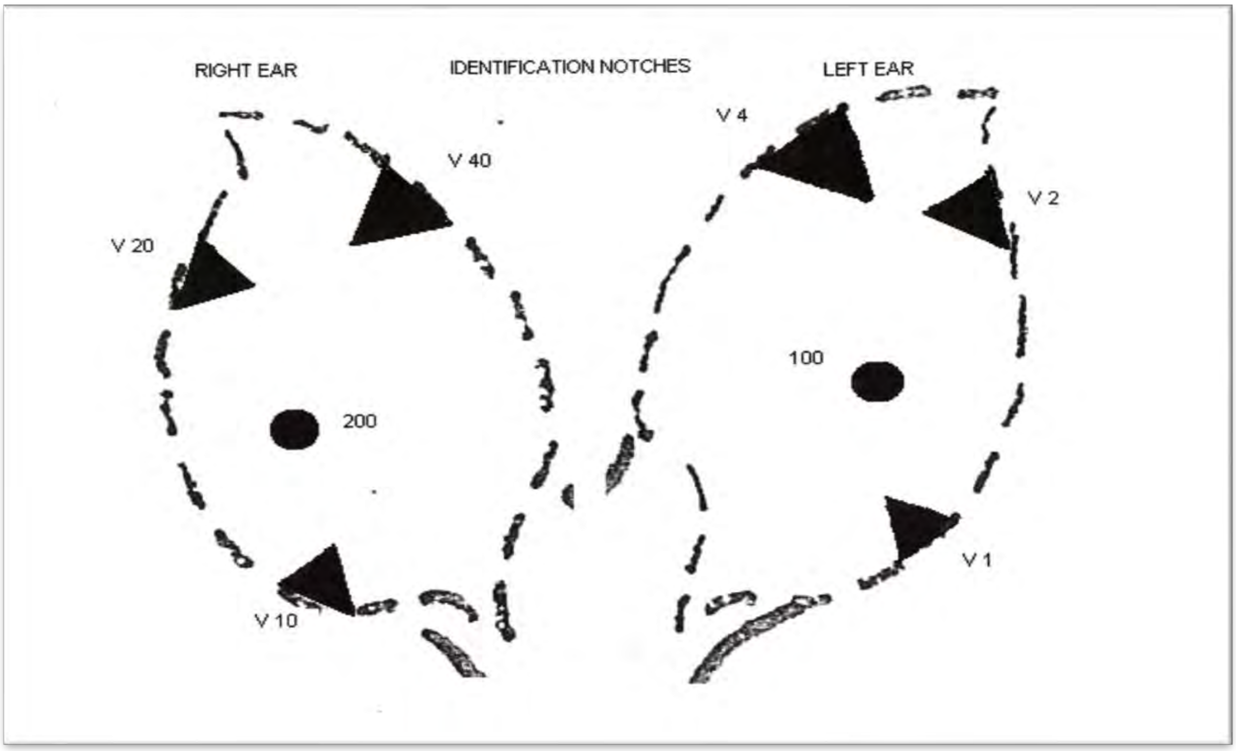

Figure 2.10. Picture of white rhino ears showing the location and numbering patterns that can used for ear notching (du Toit, 1998).

CHAPTER 3

DEMOGRAPHY AND REPRODUCTIVE SUCCESS

3.1 INTRODUCTION

White rhinos have been introduced as an extralimital species on various private game reserves within the Eastern Cape Province of South Africa for a variety of reasons, including conservation, hunting and ecotourism (Kraai, 2010). Most white rhino populations are managed as meta-populations under the guidelines set out by the Rhino Management Group to achieve certain demographic and genetic goals (Emslie & Brooks, 1999; Knight *et al*., 2015). The Rhino Management Group recommends a 5% annual growth rate for the national herd, however rhino managers on private reserves need to achieve a growth rate of between 7% – 9% to make removals and sales possible (Cousins *et al*., 2008; Knight *et al*., 2015; Balfour *et al*., 2019b). In this way, private rhino owners are able to contribute to rhino conservation through the ongoing range-expansion of white rhinos (Cousins *et al*., 2008; Knight *et al*., 2015).

Productivity is influenced by various reproductive parameters such as population growth rate, inter-calving interval, age at first calving, conception rate, sex ratio of the population, the proportion of females giving birth per year, and the survival rate of calves and mortalities (Owen-Smith, 1988; Rachlow, 1997; Gaillard *et al*., 1998; Rachlow & Berger, 1998; Kraai, 2010; Balfour *et al.,* 2019b). These parameters are also influenced by various environmental factors such as drought, disease, fire and floods that can result in a negative impact on the reproduction and population dynamics of white rhinos (Nhleko, 2014; Ferreira *et al*., 2019). The intensity of these factors influence various age groups in different ways (Ferreira *et al*., 2019). For example, droughts result in a lower nutritional value within grass species which negatively impacts adult female white rhinos, resulting in a decline in conception rates and fewer calves being born (Ferreira *et al*., 2019). The survival rate of calves also becomes unpredictable (Ferreira *et al*., 2019). Other mortalities associated with drought are mostly due to limited food availability, resulting in starvation (Owen-Smith, 1988; Monks, 1995; Anderson *et al*., 2016; Ferreira *et al*., 2019).

The above-mentioned parameters are mutually correlated by density-dependant factors (Rachlow & Berger, 1998). These parameters have a direct influence on how populations perform reproductively. Density plays a significant role in the reproductive success of a white rhino population, whereby high density rhino populations result in females giving birth to their first calves at an older age, and an increase in inter-calving intervals, resulting in a slower overall growth rates (Rachlow & Berger, 1998). By contrast, white rhinos at lower densities have a younger age at first calving, a decreased inter-calving interval and, ultimately, an increased or accelerated growth rate (Rachlow & Berger, 1998). To prevent density-dependant factors having a negative impact on population growth rates, it is important to keep rhino populations below the ecological carrying capacity (Trakolis, 2003; Bothma & du Toit, 2016). The carrying capacity will constantly change as resource availability and quality continue to be stochastic at different rainfall variables (Fike, 2011; Bothma & du Toit, 2016). These environmental factors are also believed to influence sex allocation of calves (Berkeley & Linklater, 2010). The physical condition of pregnant females when conceived will influence the sex of calves and is derived from the probability of the calf surviving once born (Berkeley & Linklater, 2010). These sex-biased populations could have challenging implications for rhino managers, whereby female-biased populations can significantly contribute to an accelerated population growth rate, while male-biased populations can severely depress the population growth rate (Okita-Ouma *et al.,* 2009; Berkeley & Linklater, 2010).

To determine how effective rhino populations are performing reproductively, it is important for the management of game reserves to implement effective monitoring systems as they provide vital information on inter-calving intervals, age at first calving, fecundity rate, home range size and distribution, mortality rates and causes, social behaviour and population performance (Balfour *et al.,* 2019b; Emslie, 2020). This information becomes essential for management to make informed decisions to ensure reproductive goals and objectives are achieved (Wittemyer *et al*., 2005; Coutts, 2009; Balfour *et al*., 2019b).

The objective of this chapter was therefore to investigate the reproductive parameters of an extralimital population of white rhinos on Shamwari Private Game Reserve (Shamwari) in the Eastern Cape Province. I asked the following research questions:

- What is the population growth rate of the white rhino population at Shamwari over the last 28 years and how does this compare to other reserves in similar studies?
- Have population parameters such as mortalities and sales had a negative influence on population growth over time?
- What is the age at first calving, conception period and inter-calving intervals of calves born within the population and is there any relationship between these parameters and density?
- Is there any relationship between conception period and rainfall?
- What is the sex ratio of rhino calves and its potential impact on population growth?
- What is the fecundity and fertility rates of the rhino population over the past 28 years?

3.1.1 Predictions

- I predicted that the population growth rate will be similar to other reserves.
- I predicted that mortalities and rhino sales will have a negative effect on population growth rates, however introductions may lead to a temporary artificial growth rate.
- I predicted that age at first calving will decrease as the population-density grows.
- I predicted that inter-calving intervals will decrease with an increase in density.
- I predicted that there will be a positive correlation between conception period and rainfall.
- I predicted that rhino calves born on Shamwari will be male-biased and this will have a negative influence on population growth rate.
- I predicted that the fecundity and fertility rates would be similar to other reserves.

3.2 METHODS

White rhino population monitoring on Shamwari was implemented in 1992 and the overall approach to the daily monitoring, and data collection is described in Chapter 2.

3.2.1 Population growth

To determine the population growth rate, annual growth percentages were calculated, whereby mortalities, sales and any additional rhino introductions were incorporated. Sales or the removal of white rhinos were done to prevent inbreeding within the current population, prevent fighting and to provide breeding stock for other game reserves. Of the total white rhino population, 20% have been sold on auction and re-located to other game reserves (Figure 3.2).

Population growth rate was calculated following Monks (1995) and calculated as follow: $r = (Pres\ pop/Prev\ pop)^{(1/N)}-1$ where r equals population growth rate; *Pres pop* equals total rhino present for specific year; *Prev pop* equals total rhino from previous year and N equals year

A Kruskal-Wallis test was conducted to examine the population growth rate over three periods (Period one 1992 – 1999; Period two 2000 – 2009; Period three 2010 – 2019). The periods were dived equally and was done to determine whether factors such as introductions could have contributed to any unusual artificial growth rates.

3.2.2 Mortality

A Chi-square goodness-of-fit test was used to determine whether there was a significant relationship between age structure and sex with respect to rhino mortalities.

3.2.3 Inter-calving interval

To calculate the inter-calving intervals, only adult cows who gave birth to two or more calves during the study period were used (Hitchins & Anderson, 1983). A total of eleven cows were used to analyse inter-calving intervals. A total of 54 inter-calving intervals were recorded (Table 3.3). Inter-calving intervals were calculated monthly, whereby the total months between any two successive births was calculated. To determine the average inter-calving interval, the total number of months was divided by the total inter-calving interval for each cow (Mostert *et al*., 2010).

3.2.4 Inter-calving interval and density

Density of white rhinos was calculated in relation to inter-calving intervals. Rachlow and Berger (1998) established a link between density and age at first calving, inter-calving intervals, and population growth. To determine whether or not there was a similar relationship in the Shamwari population a correlation coefficient test was conducted (Schober *et al*., 2018). The density of the white rhino in Shamwari was calculated as follows (Ottensmann, 2018): $D = P / A$ where D equals density; P equals the population total for the year under review and A equals to the size of the reserve in square kilometres.

Density was calculated annually between 1992 and 2019.

3.2.5 Sex ratio of calves born on Shamwari

To determine whether there was any relationship in the sex ratio of rhino calves born on Shamwari, a Chi-square goodness-of-fit test was used (Debella, 2004).

3.2.6 Conception rate and rainfall

To determine whether there was any relationship between conception period and mean monthly rainfall, a correlation coefficient test was conducted (Schober *et al*., 2018).

3.2.7 Fecundity and fertility rates

Fecundity rate represents the number of calves born and still alive at the end of the year as a proportion of adult females (females > 7 years old) in a population at the start of each year. The calculation was done following Nhleko (2014) as *FECt = Surviving births / Ad Ft-1* where *Surviving births* equals to the number of calves that survived under the year of review and *Ad Ft-1* equals to the number of adult females (>7 years old).

Fertility rate represents the number of calves born during a specific year in relation to mature adult females (females older than 7 years) at the start of each year and calculated following Nhleko (2014) as *FERt = Births / Ad Ft-1* where *Births* equals births of calves in the year under review and *Ad Ft-1* equals to number of females (> 7 years old) in the preceding year.

Both fecundity and fertility rates were calculated for the study period of 1992 – 2019. Data were tested for normality and a One-way ANOVA was used to determine any significant differences in the fecundity and fertility rates of the rhino population over time.

All statistical tests were conducted using various computer software programmes. The Kruskal-Wallis tests and the One-way ANOVA tests were both conducted using the statistical computer software R-Studio (Affero General Public Licence version 3, RStudio, PBC). The Correlation coefficient tests were calculated using Microsoft Excel 2007 (Version 16.0.13029.20232; Microsoft Corporation, United States).

3.3 RESULTS

3.3.1 Population growth rate

The white rhino population of Shamwari had a mean annual growth rate of 10% per annum (Figure 3.1). Compared to other studies that also investigated the mean annual growth rate, the population on Shamwari had a higher growth rate than all other reserves (Table 3.1) except for Whovi National Park. There were no significant differences in the growth rate over time (H = 1.87, *df* = 2, p = 0.39). This growth percentage includes mortalities, sales, and additional introductions over the entire 28-year period.

The white rhino population growth rate was at its highest during 2002 at 46% (Figure 3.1a). The reasons for this spike in growth were the introduction of additional rhinos and the highest number of births since their introduction in 1992 (Figure 3.1b). The average growth rate of white rhinos during 2007 to 2014 was at 1% and this is attributed to increased rhino sales (73% of all rhino sales) and mortalities (39% of the total mortalities) (Figure 3.1b).

Table 3.1 The annual population growth rates of white rhinos within reserves around South Africa and elsewhere.

Author	**Reserve/National Park**	**Growth per annum**
Castley *et al.,* 2001	Private Game Reserves	9%
	State Reserves South Africa	6%
Monks, 1995	Kyle National Park - Zimbabwe	-6.4%
Rachlow & Berger, 1998	Whovi National Park - Zimbabwe	10.4%
Pienaar, 1994	Kruger National Park	6-9%
Knight *et al.,* 2015	National herd (South Africa)	2%

Within the Shamwari population there have been regular mortalities recorded and represent 17% of the total population. The number of mortalities between 1996 – 2000 exceeded the number of births, resulting in a low 4% growth rate during the 5-year period (Figure 3.1b). However, as the population numbers started to increase exponentially, mortalities have had little effect on overall growth rates.

Regular sales of white rhino have taken place since 2004. The year following sales generally resulted in a negative growth rate, except for 2016 and 2017 (Figure 3.1a). This was due to the high number of births during this period. From 2009 to 2013, the growth rate decreased in four consecutive years due to sales (Figure 3.1a).

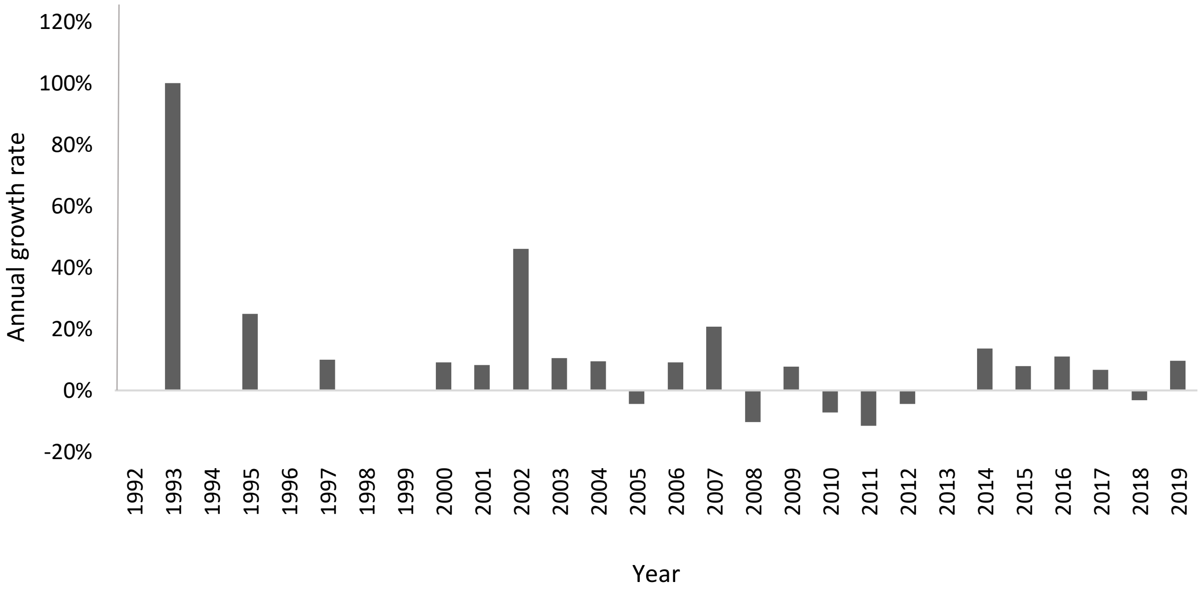

Figure 3.1a. White rhino population growth rates for the years 1992 – 2019 on Shamwari Private Game Reserve, Eastern Cape, South Africa.

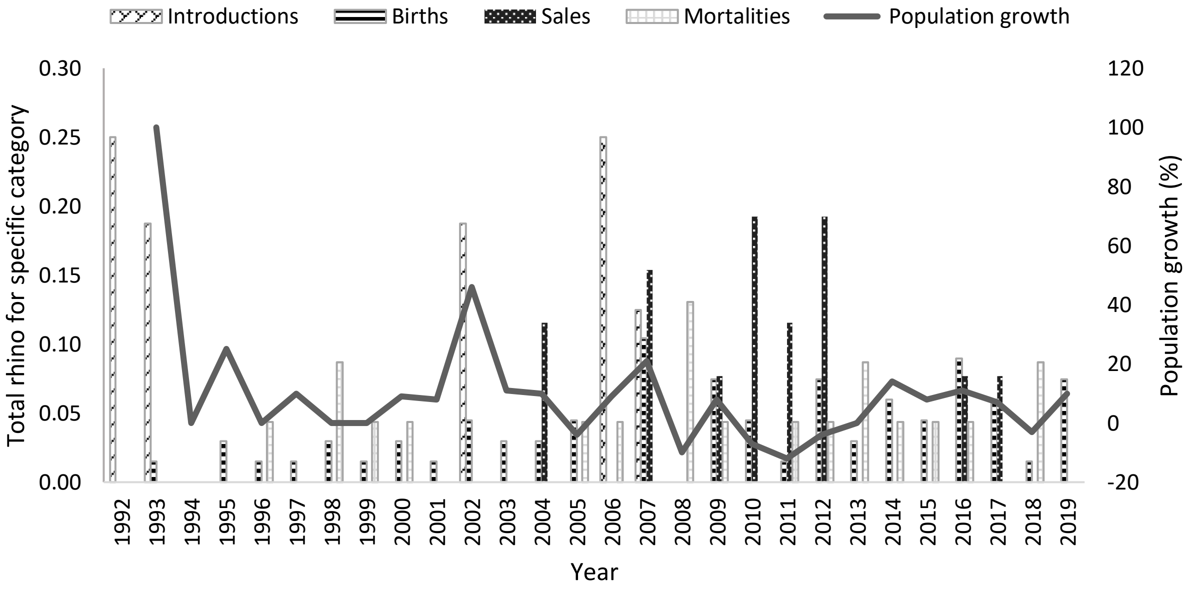

Figure 3.1b. White rhino population growth rates for the years 1992 – 2019 on Shamwari Private Game Reserve, Eastern Cape, South Africa (horizontal line), including rhino introductions; births of calves; rhino sales and mortalities.

3.3.2 White rhino mortality

Of the total mortalities recorded, 35% were due to fighting (Figure 3.2). The sex ratio included only male rhinos. The second highest cause of death was poaching, contributing to 17% of total deaths and comprised 50% female and 50% males. The third highest cause of death was paralysis including 13% of total mortalities recorded, followed by post-release causes and unknown causes, both contributing to 9% of total mortalities. The lowest percentage of 4% included birth related complications, elephant (*Loxodonta africana*) drought and a vehicle collision (Figure 3.2).

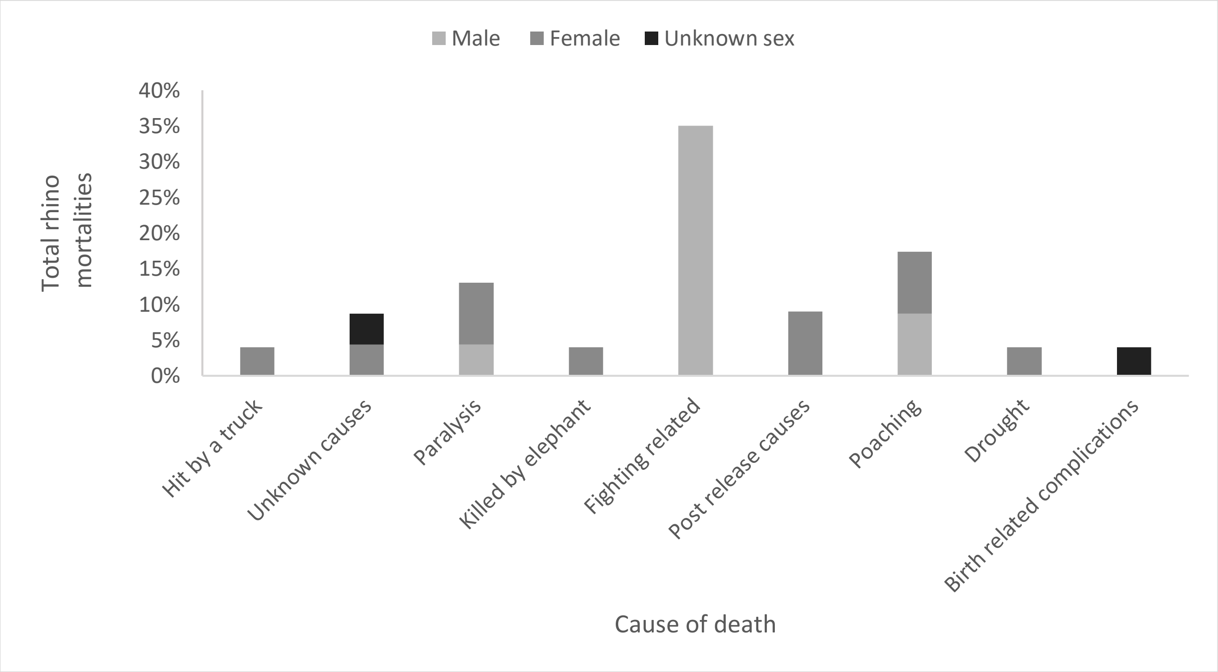

Figure 3.2. White rhino mortality record including cause of death and percentage of total mortalities recorded at Shamwari Private Game Reserve, Eastern Cape, South Africa. The sex ratio is indicated as a percentage for each total cause of death.

Mortalities for both male and female rhinos, including their age at the time of death was recorded (Table 3.2). Results indicated that there was no significant relationship between age class and sex of rhino (χ^2 = 4.35; *df* =13; p-value =0.83). The highest number of mortalities included male white rhino with a total of eleven (Table 3.2). Of the total male mortalities, two include males from the C-class (age between 1 to 2 years), one from D-class (age between 2 and 3 and a half years), two from E-class (aged between 3 and a half to 7 years) while the highest number of six include F-class (aged older than 7 years) male rhino. Of the total female mortalities, one included a female in the B-class (aged 3 months to 1 year), three included females from the C-class (age between 1 to 2 years), two from E-class (aged between 3 and a half to 7 years). The highest number of four include F-class (aged older than 7 years). Unknown sex included two rhinos from A-class comprising of calves between the ages of 0 – 3 months.

Table 3.2. Age structure of white rhino mortalities on Shamwari Private Game Reserve, Eastern Cape, South Africa between 1992 – 2019.

Age class	**Age category**	**Male**	**Female**	**Unknown sex**
A-class	0 - 3 months			2
B-class	3 months - 1 year		1	
C-class	1 - 2 years	2	3	
D-class	2 - 3 1/2 years	1		
E-class	3 1/2 - 7 years	2	2	
F-class	7 years and older	6	4	
Total		**11**	**10**	**2**

3.3.3 White rhino sales

During the study period, the total white rhino sales (Table 3.3), 62% consisted of male rhinos while 38% represented female rhinos. The highest percentage of sales was from F-class (7 years and older) males, followed by 19% E-class (3 and a half to 7 years) males. The remaining 12% of males were C-class (1 – 2years) and would have been accompanied by an F-class female. Of all female rhinos sold, 4% included C-class (1 – 2 years), 4% from D-class (2 years to 3 and a half years), 15% from E-class (3 and a half years to 7 years), while 15% was from F-class (older than 7 years).

Table 3.3. Age structure of white rhino sold from Shamwari Private Game Reserve, Eastern Cape, South Africa during the study period from 1992 – 2019. The age class and represented age (Age category) are indicated and include percentage of the total deaths under male, female and unknown sex.

Age class	**Age category**	**Male (%)**	**Female (%)**
A-class	0 - 3 months		
B-class	3 months - 1 year		
C-class	1 - 2 years	12	4
D-class	2 - 3 1/2 years		4
E-class	3 1/2 - 7 years	19	15
F-class	7 years and older	31	15
Total (%)		**62**	**38**

3.3.4 Inter-calving intervals

Inter-calving interval for Shamwari ranged between 1.11 – 3.6 years (23 –42 months) with an average of 2.6 years (30 months) (Table 3.4). The shortest inter-calving interval recorded on Shamwari was 17 months, this was from cow W54 who lost her second calf within a week after giving birth. It was suspected that the calf was killed by lions (*Panthera leo*). Although W54 had the shortest inter-calving intervals on Shamwari, it is not a true reflection of her reproductive ability as the loss of her second calf likely skewed the calculation of her inter-calving interval. W76 and W10 both had the second shortest inter-calving interval with an average of 24 months (2 years). Four cows had average inter-calving intervals longer than 30 months, including W3, W6, W51 and W52. W52 had an inter-calving interval of 31 months, followed by W51 with 32 months, W3 with 33 months and W6 with 34 months. W3 and W6 had one inter-calving interval exceeding 40 months. W3 had an interval of 46 months in 1997 when she gave birth to her second calf and W6 had an interval of 47 months during 2003 to her third calf.

The most calves born to a specific cow was W7 who gave birth to nine calves. The exact age of W7 is unknown and the only details available for her is that she arrived at Shamwari as a sub-adult in 1993. She gave birth to her first calf during May 1998 and could therefore be assumed that she was born between 1987-1990, making her between the ages of 30 - 33 years old. The second highest number of calves was eight to W3 (she died in 2019 following a poaching incident) and she was presumed to be the oldest white rhino on Shamwari.

Table 3.4. Inter-calving intervals of 11 female white rhinos on Shamwari Private Game Reserve, Eastern Cape, South Africa who had more than two calves. The table indicates adult cow, total calves born and average inter-calving interval of adult cow.

Rhino cow	Total calves	Average inter-calving interval
W 3	8	2 years. 9 months
W 5	5	2 years. 8months
W 51	7	2 years. 3 months
W 52	3	2 years. 7 months
W 54	3	1 year. 11 months
W 6	4	2 years. 10 months
W 7	9	2 years. 4 months
W 75	2	3 years. 6 months
W 76	3	2 years
W 8	4	2 years. 4 months
W 10	6	2 years

3.3.5 Inter-calving intervals and density

The density of white rhinos has decreased from one white rhino per average of 34.35 km^2 in 1992 to one rhino per 3.80 km^2 in 2019 (Figure 3.3). There was no significant relationship (r = - 0.48) between density and inter-calving intervals. However, the results indicated that with increased rhino density, the inter-calving interval tended to decrease. This is the opposite to what most other reserves have experienced.

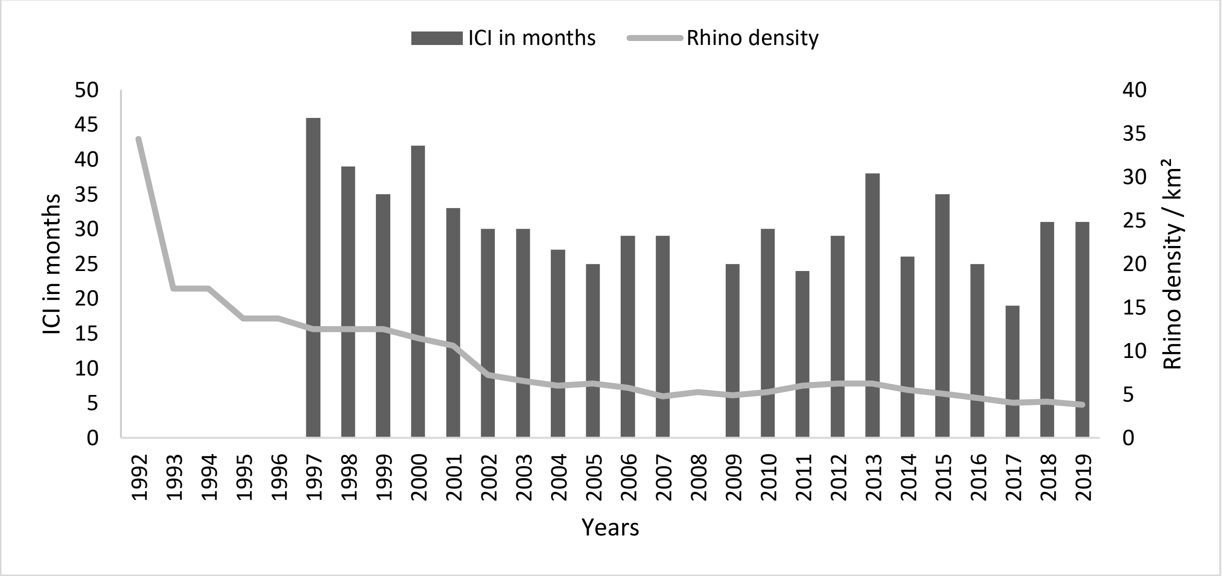

Figure 3.3. Average annual inter-calving (IC) intervals at Shamwari Private Game Reserve, Eastern Cape, South Africa over the period of 1992 to 2019 (indicated as bars) and density of rhino per square kilometre (indicated as the grey line).

3.3.6 Sex ratio of calves born on Shamwari

A total of 67 white rhino calves have been born on Shamwari since their introduction in 1992. Of the 67 calves born, 38 (56.7%) were males, 26 (38.8%) were females and 3 (4.5%) the sex was unknown (Figure 3.4).

The Chi-square goodness of fit results ($\chi^2 = 12.34$; *df* = 13; p-value = 0.11) indicated that the results were not significant and that there is no relationship between sex of calves and breeding cows.

Of the fourteen cows, four produced more male calves than females. Three cows had a 50:50 ratio. Three cows produced more female calves than males. Some of the cows produced calves of a specific sex. W52, W515, W75 and W103 only produced male calves. Both W515 and W103 have only produced one calf each thus far. W12 was the only cow to only produce female calves (Figure 3.5).

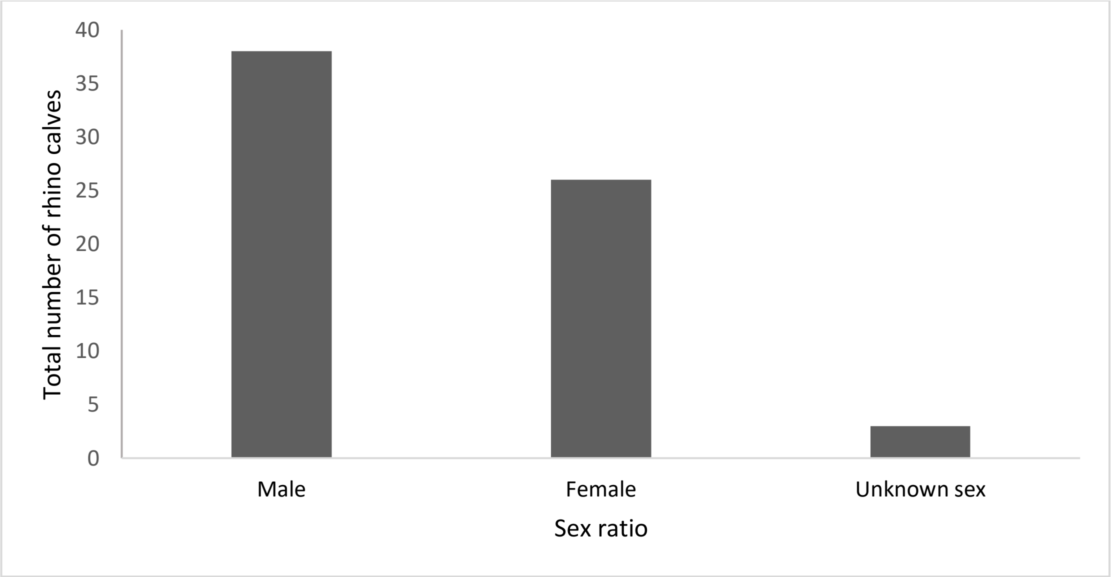

Figure 3.4. Sex ratio of 67 white rhino calves born at Shamwari Private Game Reserve, Eastern Cape, South Africa between the period 1992 – 2019.

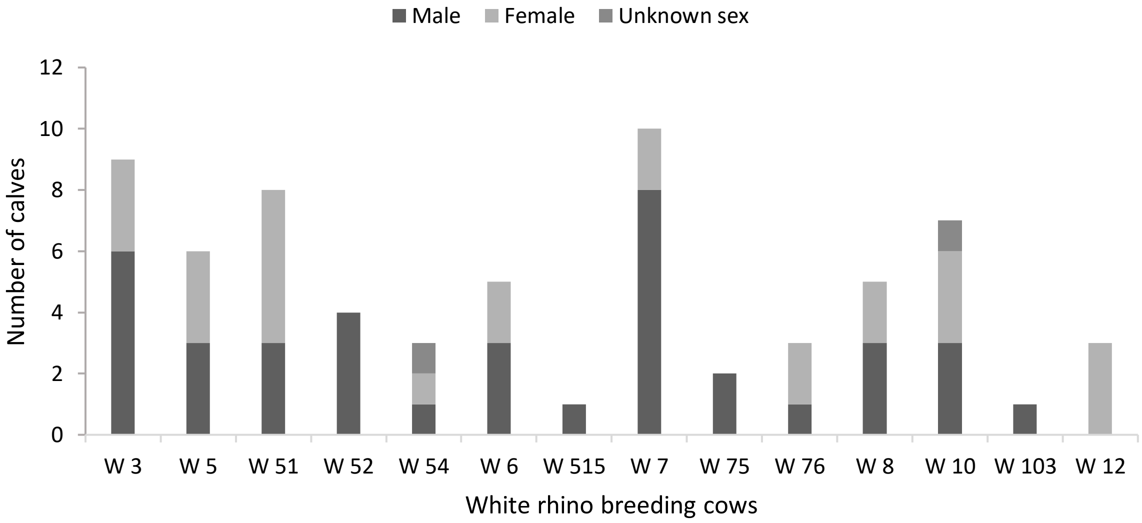

Figure 3.5. The sex ratio of 14 calves born to white rhino cows on Shamwari Private Game Reserve, Eastern Cape, South Africa during the study period from 1992-2019. A total of 67 calves were born.

3.3.7 Age at first calving

To determine the age at first calving (Table 3.5), only seven females were used as they were the only rhinos whose birth dates were known and who (during the period of study) had their first calves. Cows that were introduced during 1992 and 1993 exact birth dates are unknown and no information regarding previous calves prior to their arrival were known and therefore was not used.

The mean age at first calving was 84 months (7 years). The range was between 62 months (52 years to 109 months (9.1 years). The gestation period of a white rhino is 16 months (Player & Feely, 1960). The youngest age at first successful mating was of W515 at 46 months or three years, ten months and the oldest mating was of W54 at 93 months or seven years, nine months.

Table 3.5. Table showing seven female white rhinos and age at first calving. The female age at first calving is given in years and months, the year female conceived and the age in years and months and density of rhino per square km² at the specific year when conceived.

Female rhino	Age at first calf in years	Age at first calf in months	Year conceived	Age conceived in years	Age conceived in months	Density rhino/km²
W 51	7	84	Aug. 2001	5.8	68	1/10.57 km²
W 52	8.1	97	Oct. 2006	6.9	81	1/5.72 km²
W 54	9.1	109	Aug. 2012	7.9	93	1/6.25 km²
W 76	5.3	63	Nov. 2013	3.11	47	1/6.25 km²
W 515	5.2	62	Oct. 2015	3.10	46	1/5.09 km²
W 75	9	108	July. 2015	7.8	92	1/5.09 km²
W 103	5.11	70	Sept. 2015	2.6	54	1. 5.09 km²

3.3.8 Conception and seasonal rainfall influences

Rainfall in the Eastern Cape is bimodal, with peaks during early autumn and late spring which coincide with conception and birth peaks (Figure 3.6). There was no significant correlation between conception month and rainfall (*r* = - 0.40), nor was there any significant correlation between births and rainfall months (*r* = 0.46). However, the results do confirm that both correlations were positive, indicating an increase in conception (late spring from October) and births (early autumn between February to April), possibly as a consequence of increased rainfall (Figure 3.6). There was a peak in births between February to April. This was also the period when rain started to increase in autumn and represents a total of 28 births. April had the highest number of births with a total of 12 calves born. April also receives the highest mean rainfall of 53 mm recorded over the last 20-year period (see Chapter 2, Figure 2.7a). Only one calf was born during June. June also received the lowest mean monthly rainfall of 30 mm (see Chapter 2, Figure 2.7a), while conception during the same month was the second lowest of all months while only two calves were conceived in June.

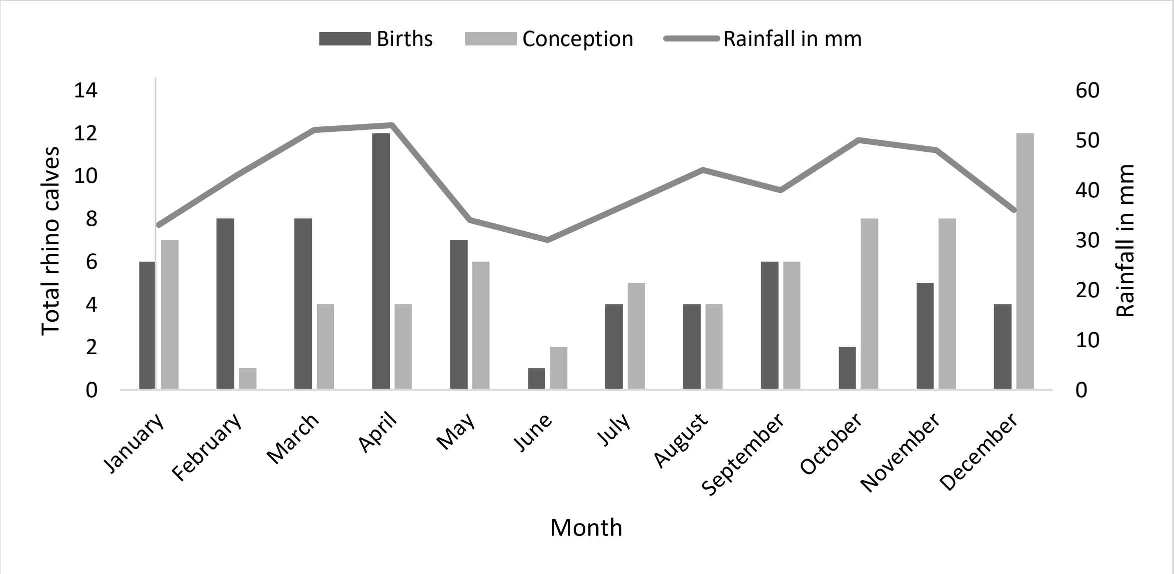

Figure 3.6. Graph showing total births and conception of calves for each month of the year in Shamwari Private Game Reserve, Eastern Cape, South Africa for the period of 1992 - 2019 in relation to the mean monthly rainfall over a period of 20 years.

3.3.9 Fecundity and fertility rate

Both the fecundity and fertility rate (Table 3.5) were lowest during 1994, 2006 and 2008 when no calves were born during those three years, followed by 2018 at 0.11 and 2011 at 0.14. Both the fecundity- and fertility rates were at their highest during 2007 at 0.88. However, there were no significant differences in both the fecundity rate ($F_{(2, 24)} = 1.38$; $P = 0.27$) and the fertility rate ($F_{(2, 24)} = 0.85$; $P = 0.44$) over time.

Table 3.6. Table showing the fecundity and fertility rates of the white rhinos on Shamwari Private Game Reserve, Eastern Cape, South Africa for the period of 1992 – 2019.

Year	Adult cows >7 years	Total calves born	Calves survived >1yr	Deaths >1 year	Fecundity rate	Fertility rate
1992	4					
1993	4	1	1		0,25	0,25
1994	4				0,00	0,00
1995	4	2	2		0,50	0,50
1996	4	1	1		0,25	0,25
1997	4	1	1		0,25	0,25
1998	4	2	1	**1**	0,25	0,50
1999	4	1	1		0,25	0,25
2000	4	2	2		0,50	0,50
2001	4	1	1		0,25	0,25
2002	5	3	3		0,60	0,60
2003	5	2	2		0,40	0,40
2004	5	2	2		0,40	0,40
2005	6	3	3		0,50	0,50
2006	7				0,00	0,00
2007	8	7	7		0,88	0,88
2008	8				0,00	0,00
2009	7	5	5		0,71	0,71
2010	7	3	3		0,43	0,43
2011	7	1	1		0,14	0,14
2012	7	5	5		0,71	0,71
2013	8	2	2		0,25	0,25
2014	8	4	4		0,50	0,50
2015	9	3	3		0,33	0,33
2016	10	6	5	**1**	0,50	0,60
2017	10	4	4		0,40	0,40
2018	9	1	1		0,11	0,11
2019	8	5	4	**1**	0,50	0,63
Average					**0,37**	**0,38**

3.4 DISCUSSION

Assessing the reproductive status of the white rhino population on a private reserve within the Eastern Cape Province of South Africa has indicated that extralimital populations can indeed contribute to the ongoing conservation of this threatened species (Castley & Hall-Martin, 2003; Kraai, 2010). Assessing the reproductive success of the white rhino population on Shamwari has been important to determine how the various reproductive parameters, density dependant factors and rainfall have thus far influenced the population and its growth.

3.4.1 Population growth rate

Newly established large herbivores in previously unoccupied environments generally result in a rapid growth rate following their introduction (Rachlow & Berger, 1998). According to the Rhino Management Group's white rhino biodiversity management plan (Emslie & Brooks, 1999; Knight *et al*., 2015), the preferred annual growth rate for rhino populations should be at 5% per annum. Balfour *et al*., (2019b) recommended that growth rates should be kept between 7-9%, including regular sales, however caution should be practiced to not exceed the Ecological Carrying Capacity. Game reserves and National Parks within South Africa show an annual growth rate of between 2-9% (Table 3.1) (Pienaar, 1994; Castley *et al*., 2001; Knight *et al*., 2015). Growth rates for the national herd have been consistent at 6,6% from 1991-2012, but has since been under enormous pressure due to the reawakening of poaching for rhino horn (Knight *et al*., 2015). The national population annual growth rate stands at 5%, however due to the continued high level of poaching, the annual growth rate after incorporating poached rhino is standing at a grim rate of only 2% (Knight *et al*., 2015).

On a continental level, white rhinos that were introduced into Kyle National Park, Zimbabwe during 1962 – 1966 have since 1973 been fluctuating with a general declining population growth trend of -6,4% during the early 1990's (Condy, 1973; Monks, 1995). In contrast, Whovi National Park, Zimbabwe introduced white rhinos during the same period as Kyle National park has demonstrated the highest documented annual population growth rate of 10.4% (Table 3.1) (Rachlow, 1997; Rachlow & Berger, 1998). White rhino in Whovi National Park increased exponentially between 1966-1974 at low density, followed by a stabilisation of growth, whereby a second increased growth rate followed again from 1988, however at a reduced growth rate of 6.6% (Rachlow & Berger, 1998). Other African countries such as Kenya and Namibia have also showed an increase in their white rhino populations while countries such as Botswana, Ivory Coast, Swaziland and Zimbabwe have had gradual decrease in their rhino populations (Emslie & Brooks, 1999). Although there was no significant difference in the growth rates of the white rhinos within the Shamwari population (P = 0.36) over time, the overall growth rate on Shamwari exceeds those of several other Reserves and National Parks in South Africa at an average annual growth rate of 10% for the past 28 years (Figure 3.1a). However, additional introductions during 2002, 2006 and 2007 likely contributed to an artificial growth rate not necessarily representing the true reproductive capability of the population.

3.4.2 White rhino mortality

Causes of mortality of white rhino were similar to what other reserves have documented. Fighting-related deaths contributed the highest percentage of deaths, and only involved male rhinos. This cause of death was a regular occurrence on other reserves where fighting-related mortalities contributed to the highest number of deaths and mostly involved adult males (Owen-Smith, 1988; Anderson, 1993; Monks, 1995; Rachlow, 1997). Fighting-related deaths is common in translocated white rhino populations and is mostly due to an increase in rhino density as population numbers start to increase (Rachlow, 1997). Increased density within fenced reserves leads to aggression amongst rhinos, resulting in increased fighting and deaths and could be due to competition for resources (Rachlow, 1997; Ferreira *et al*., 2019). Of the total fighting-related deaths (35%), 8.75% of the mortalities occurred during 2008, when Shamwari received its lowest total yearly rainfall for the period from 2000 -2015 (see Chapter 2, Figure 2.6), possibly increasing mortalities due to limited availability of food resources (Ferreira *et al*., 2019). In both Kruger National Park (hereafter KNP) and iMfolozi Game Reserve (hereafter iMfolozi) mortality rates increased during periods of drought (Owen-Smith, 1988; Ferreira *et al*., 2019).

Interaction between elephants and white rhinos resulting in death have been witnessed on numerous reserves. In Pilansberg National Park, an estimated 37 white rhino were killed by delinquent elephants (Slotow & van Dyk, 2001). The leading cause of death on private reserves was fighting (15.2%), followed by starvation due to drought (14.3%), poaching (12.4%) while other causes included disease, accidents, food contamination in bomas and unknown causes (Anderson, 1993). Managers should therefore be proactive to avoid such mortalities and initiate regular removals.

3.4.3 White rhino sales

Rhinos have been sold on live auctions for the past three decades (Van der Merwe & Saayman, 2003). Shamwari has been selling white rhinos on a regular basis since 2004. White rhino sales have thus far had a negative impact on the population growth rate for the subsequent year (Figure 3.1a and Figure 3.1b) resulting in either negative growth percentage or no growth. Sales in 2004 resulted in a -4% growth in 2005; sales in 2007 resulted in a -10% in 2008; sales in 2009, 2010, 2011 and 2012 resulted in consecutive -7% (2010), -12% (2011), -4% (2012) and 0% (2013) and sales in 2017 resulted in a -3% growth rate. The only exception was during 2016 where sales resulted in a positive 7% growth rate the following year (2017).

The biggest percentage of rhino sales includes males within the E- and F-class (50%). The remaining 12% of males was within the C-class and was sold as cow and calf combinations to other reserves. To prevent negative genetic impacts on the rhino, translocation becomes important (Coutts, 2009). Sales form an integral part of Shamwari's rhino management plan to prevent fighting-related mortalities, supplement new upcoming rhino owners with breeding stock and to decrease density within a population (Owen-Smith, 1981; Brodie *et al.,* 2011; Laubscher *et al*., 2015).

3.4.4 Inter-calving interval

White rhino calves are born after a gestation period of 16 months and weigh approximately 40 kg and will be dependent on its mother for milk up to 18 months (Skinner & Chimimba, 2005). Inter-calving intervals in white rhino vary between two to four years (Owen-Smith, 1981). Mean inter-calving intervals for cows in Shamwari was 2 years and 5 months, with the shortest being 1 year, 11 months (W54) and the longest being 3 years and 6 months (W76). The longest single inter-calving interval was from W5 in the year 2000, who had a 4 years and 3 months (51 months) interval. According to Hitchins and Anderson (1983), any inter-calving interval longer than 40 months or 3 years and 3 months could be assumed that the cow either lost the calf shortly after birth or that she aborted. In the Shamwari population, three cows (W3, W5 and W6) had inter-calving intervals longer than 40 months and can therefore be assumed that three additional calves were born and lost during the study period, which gives a total of 70 calves born during the study period from 1992 – 2019. According to Pienaar (1994), in KNP, age of white rhino cows influenced inter-calving intervals, and found that younger cows had shorter inter-calving intervals than older cows. However, it was not found to be the same at Shamwari as the younger cows both had the longest and shortest inter-calving averages as previously stated. Inter-calving intervals in Whovi National Park, Zimbabwe were similar to iMfolozi, KwaZulu-Natal, South Africa (Owen-Smith, 1981). However, it was found to be strongly influenced by density where in low density areas the average inter-calving interval was shorter at 2 years, 9 months, while in higher density areas the inter-calving interval was longer at an average of 3 years, 3 months (Rachlow, 1997; Rachlow & Berger, 1998). The mean inter-calving interval recorded for iMfolozi was 2 years, 6 months (Owen-Smith, 1988). The shortest inter-calving of 1 year, 8 months was also recorded in iMfolozi (Owen-Smith, 1981). Inter-calving intervals recorded by Kraai (2010) on various game reserves in the Eastern Cape ranged between 2 years, 3 months to 2 years and 6 months.

3.4.5 Inter-calving intervals and density

Inter-calving intervals is density-dependant in large herbivores (Owen-Smith, 1988; Monks, 1995; Rachlow & Berger, 1998). High density areas generally result in longer inter-calving intervals, while low density areas result in shorter inter-calving intervals (Owen-Smith, 1988; Rachlow & Berger, 1998). Within Shamwari, inter-calving intervals gradually decreased from an average of 46 months in 1997 to 19 months in 2017. However, within the last two consecutive years (2018 and 2019), intervals increased to 31 months. It is believed that the increase in inter-calving intervals could have either been due to the drought (below average rainfall was experienced during both years) or the 817 ha of land lost during early 2018, which incorporated an important area the rhino often utilized (see Chapter 2). Between 2002 and 2012, the inter-calving intervals was relatively consistent, varying between 24 – 30 months. After 2012, intervals started to fluctuate between 19 – 38 months. There were two exceptions in 2013 (from cow W52) and 2015 (from cow W3) where inter-calving intervals were higher than 30 months due to the following circumstances:

W52 - During 2011, the dominant bull in W52’s area was removed and replaced by a younger bull, who was still actively showing sub-ordinate behaviour. Towards the end of 2011, W52 was removed and relocated to a different part of the reserve to prevent poaching. This second disruption resulted in an unusual extended inter-calving interval during 2013.

W3 - There were three calves born during 2015 of which W3’s calf represented the only consecutive birth. The other two births were from young cows giving birth to their first calves (therefore no prior inter-calving interval data were available). W3 was at that time considered to be one of the oldest females on the reserve and could therefore be assumed that the long inter-calving interval contributed to her age. That specific calf was also the last calf she gave birth to.

According to Rachlow and Berger (1998), growth rates decrease in high-density areas due to a longer inter-calving interval while mean age at first calving increase to 10 years and 1 month. This is the opposite for low density areas where inter-calving intervals increase, thereby increasing growth rates and cows give birth to their first calf at a younger age of approximately 7 years and 4 months. By contrast, the results from the Shamwari population indicated a negative correlation (r = -0.48) between density and inter-calving intervals, meaning that with increased density, inter-calving intervals decreased. Although the results were not significant, it is unique in that all other reserves experienced the opposite trend (Owen-Smith, 1988; Pienaar, 1994; Monks, 1995; Rachlow, 1997; Rachlow & Berger, 1998), suggesting that the Shamwari population may not have yet reached its maximum density (or carrying capacity).

3.4.6 Sex ratio

Sex ratios in rhino populations influence the reproductive parameters within populations (Okita-Ouma *et al*., 2009). The Trivers-Willard hypothesis suggest that in a polygynous population, females will produce more male calves during favourable conditions than females (Cameron, 2004; Fike, 2011; Law *et al*., 2014). The hypothesis is that males would have a greater chance of mating (therefore contributing to the reproductive rate of the population) due to his physical advantage above other bulls to compete for mating rights (Fike, 2011; Law *et al*., 2014). Therefore, rainfall will most likely have a significant influence on the sex ratio of rhino calves (Fike, 2011). Factors such as density and vegetation condition will also influence condition of breeding females which could lead to skewed sex ratios (Okita-Ouma *et al*., 2009; Fike, 2011). Facultative adjustment to calf sex allocation has been suggested by Owen-Smith (1988) due to the rhino's adaptable inter-calving intervals and a seasonal conception period. Skewed sex ratios within populations that is female biased will result in an increased reproduction rate (Okita-Ouma *et al*., 2009). In a study conducted by White *et al*., (2007) in iMfolozi, they found that mothers invested more time in raising male calves than females and would normally be followed by an extended inter-calving interval period. The results of rhino calves born on Shamwari have indicated a skewed male-biased population. However, my study did not investigate whether rainfall and vegetation condition had any influence on the skewed sex ratio which would be worthwhile investigating. My results are, nevertheless, similar to Kraai's (2010) findings who reported that calves born in the Eastern Cape white rhino population tended to be male biased.

3.4.7 Age at first calving and density

Age at first calving is dependent on various factors such as density, body condition and rainfall (Rachlow & Berger, 1998; Fike, 2011; Hebbelmann, 2013; Law *et al*., 2013). In K-selected animals, fertility is directly linked to the physical condition of the female and will only reach sexual maturity once 80% of her bodyweight has been achieved (Fike, 2011). Rainfall has been found to be one of the main contributing factors influencing demographic parameters in megaherbivores (Law *et al*., 2013). Low rainfall generally had a negative effect on breeding rhino cows whereby conception periods would be delayed, resulting in prolonged inter-calving intervals and reduced population growth (Law *et al*., 2013). Density-dependence has been well documented and is considered to influence age at first calving to increase with increased density (Rachlow & Berger, 1998; Law *et al*., 2013). Female white rhinos who reproduce at an early age have a genetic advantage over other females and should produce more calves during her lifespan, resulting in an increased population growth rate (Rachlow & Berger, 1998). There was no clear evidence that the rhinos on Shamwari followed the same trend as described by Rachlow and Berger (1998). Six of the seven rhino's age at first calving was recorded at a higher density. During the six years of increased density there was a definite fluctuation where both the youngest age at first calving being W515 at five years, two months, and oldest age at first calving being W54 only calved at nine years, one month.

3.4.8 Conception and rainfall

Conception is dependent on factors such as density, climate and physical condition of the rhino (Fike, 2011). Conception peaked between October to December and could be due to a flush of green grass after good spring rains and increased nutritional value of grazing resulting in the birth peaks from February to April. The peaks in conception and births coincide with the bi-modal rainfall experienced on Shamwari. During these periods, grazing conditions should be at an optimal level, which in turn increase calf-survivorship. These results are similar to Pienaar (1994) who found that conception peaked after good rain. Monks (1995) had similar results in Kyle National Park, Zimbabwe where births peaked between March to June, with the highest number of calves born during April, while conception peaked from November to March.

3.4.9 Fertility and fecundity rates

Fecundity and fertility rates both can be used as an indicator to measure an individual's reproductive performance over time (Bradshaw & McMahon, 2008). Fertility rate is determined by the number of offspring a specific female produces within her lifetime, while fecundity measures the rate of survivorship of the offspring that was born (Bradshaw & McMahon, 2008). A decrease in calf survivorship can have a negative impact on growth rates in the long-term and is believed to be influenced by density (Rachlow & Berger, 1998). On Shamwari, both the fecundity rate (P = 0.27) and fertility rate (P = 0.44) did not change significantly over time, indicating that the population growth has been consistent over time, and that calf survivorship has probably contributed to the continued growth of the population (Rachlow & Berger, 1998).

3.5 CONCLUSIONS

The rhinos on Shamwari have thus far exceeded the objectives of the Rhino Management Group with an average annual growth rate of 10% over the last 28 years despite regular sales. Inter-calving intervals have decreased with increased density, indicating that the population is increasing at a steady pace. However, over the last two years, inter-calving intervals have begun to increase. Although the sex ratio of calves born on Shamwari was not significant, there were slightly more male calves born than females which could have a negative impact on the population growth rate in the future and careful management will be required to prevent inbreeding. Age at first calving was similar to what has been reported by other reserves. Conception period was not influenced by rainfall; however births did increase with higher rainfall indicating that rhino preferred to calf when conditions were favourable to ensure survival of the calf.

The reproductive performance of the white rhinos on Shamwari is comparable with other endemic populations, however the last two years of the study (2018 and 2019) have indicated a prolonged inter-calving interval. The loss of 817 ha of land may have contributed to this increase, however, rainfall was also at its lowest for the past 20 years during that time. The impact of the current drought situation accompanied by the loss of habitat may have serious repercussions in the reproductive success of the population and may be worth investigating in the future.

CHAPTER 4

SPATIAL ECOLOGY

4.1 INTRODUCTION

A home range is an area utilized by animals to satisfy their daily requirements such as food intake, water, mating and for nursing young (Pedersen, 2009; Hebbelmann, 2013). Home range size is often driven by both environmental factors and social structures within the populations (Pienaar *et al*., 1993b; Pedersen, 2009; Hebbelmann, 2013; Jordaan *et al*., 2015; Kretzschmar *et al*., 2020). Quality and quantity of food resources also often influence home range size (Beest *et al*., 2011). Large grazing herbivores must continually show behavioural flexibility to fluctuations in biomass and quality of grazing due to seasonal changes in rainfall (Birkett *et al*., 2012). During higher rainfall periods, rhinos, for example, utilize a larger variety of vegetation types (Joubert & Eloff, 1971; Kraai, 2010), and during the dry season, the quality and availability of food resources starts to decline (Hebbelmann, 2013; Janse van Rensburg *et al*., 2018). To compensate for the poor quality food, adult female white rhinos alter their movements to incorporate areas of grass with a high crude protein content (Hebbelmann, 2013). Female home range sizes, therefore, tend to be larger (core area 20 km^2) than those of males (core area of 5 km^2) and this is attributed to the additional nutritional requirements needed to ensure the survival of calves (White *et al*., 2007; Hebbelmann, 2013).

Home range size of male and female white rhinos varies between reserves and often correlates with seasonal rainfall and rhino density (Owen-Smith, 1988; Pedersen, 2009; Hebbelmann, 2013; Jordaan *et al*., 2015; Chirenje 2016; Thompson *et al*., 2016). In Matobo National Park, Zimbabwe, female (51.86 km^2) white rhinos generally had larger home ranges than males (45.97 km^2) during the dry season (Chirenje, 2016). During the wet season, results were the same with the average home range of males being 34.1 km^2 while females had their average home range size at about 44.4 km^2 (Chirenje, 2016). In the Willem Pretorius Reserve, South Africa adult females had mean home ranges of 3.78 km^2 in the wet season compared to 4.08 km^2 in the dry season, however only one adult bull was present on the reserve and could be the reason for the bull's home range being larger at 8.13 km² in the wet season and 6.37 km² in the dry season compared to females (Jordaan *et al*., 2015).

White rhino habitat requirements include accessible water, short grass, relatively flat terrain and sufficient shelter provided from trees and thickets (Player & Feely, 1960; Myers, 1998; Chabwela *et al*., 2017). White rhinos show preference for open grassland areas but avoid riverine terrain (Thompson *et al*., 2016) and dense woodlands (White *et al*., 2007). According to White *et al.,* (2007), male white rhino territories are predicted by a female's home range whereby the males incorporate as many female home ranges as possible to increase their chances of successful mating.

Large herbivores have been known to be selective towards palatable, highly nutritious grazing areas by regularly returning to them (Bailey *et al*., 1996). In iMfolozi, white rhinos preferred short grass during the wet season, but would shift to areas with more medium to tall grasses (such as *Themeda triandra*) in the dry season (Owen-Smith, 1988; Hebbelmann, 2013). The Eastern Cape regularly experiences drought and this severely limit the availability of suitable grazing (Kerley *et al*., 1995). To compensate for limited food resources during dry periods, white rhinos may need to increase quantity rather than the quality of grass to survive by either expanding, or increase the sizes of their home ranges (Owen-Smith, 1988; White *et al*., 2007).

The aim of this chapter was to establish how home range size differed between adult bulls, adult cows, and sub-adult white rhinos on Shamwari Private Game Reserve. In addition, I also wanted to establish whether or not yearly rainfall influenced white rhino spatial ecology. Lastly, I wanted to investigate the vegetation preferences of the three age classes.

RESEARCH QUESTIONS:

- How does the home range size differ between adult females, adult males, and sub-adults?
- How does home range size change during drier years compared to wetter years?
- What vegetation types were utilized by the rhinos?
- Is there any specific vegetation type that is preferred?
- Is there any relationship in vegetation types utilized and rainfall?

PREDICTIONS:

- The home ranges of adult females will be larger than adult males.
- I predicted that home ranges would be larger during the drier years compared to wetter years.
- I predicted that vegetation types dominated by short grass will be preferred.
- I predicted that vegetation types that are not normally utilized during wet and average rainfall years would be used during dry years.

4.2 METHODS

As discussed in Chapter 2, the monitoring of the rhinos was done daily by myself.

For a 12-year period (2008 – 2019), the rhinos have been directly observed. All sightings have been recorded manually on the rhino sightings sheets and information included date, location of the rhino (expressed as the area name) and the rhinos that were seen. Since not all rhinos were located every day over the 12-year period, the number of annual sightings (direct observations of individual rhinos) for each rhino varied (between 32 and 168). A total of 14 903 sightings was recorded from 26 different rhinos. In other words, 14 903 individual GPS locations for 26 rhinos were available over the 12-year period to investigate their spatial ecology. Rhinos that were used for the study were categorized as follows:

1. **Adult bulls** - Only adult bulls who were socially mature and actively breeding (Kretzschmar *et al.*, 2020) were used (n = 4). For the year 2008, no bulls were used. This was due to the breeding bull and another adult bull fighting. Both fell off a cliff into the river and drowned. From 2012, two breeding bulls were used for each year after breeding cows were re-introduced into the northern section.
2. **Adult cows** – Six adult cows were used and present throughout the study period, except for W3 who died in 2019. Cows that were sold or died during the period were not included.
3. **Sub-adults** – Various sub-adult animals (n = 18) from both sexes over the period 2008 – 2019 were used for the study. The reason for incorporating so many individuals was due to their short adolescent period from 3 – 7 years. Also note that

W102 and W64 were used both as sub-adults and adult bulls as they both transitioned from sub-adults to adult breeding bulls during the study period.

4.2.1 Home range size

4.2.1.1 Home range sizes

To determine the home range size of the rhinos, sightings recorded on the rhino sightings sheets were transferred onto Google Earth Pro as pin-locations. A folder for each rhino and year was created and saved containing all pin-locations (sightings). These folders were saved as a Keyhole Markup Language (hereafter KML) file. To establish home range size, QGIS, Version 3.10.11, Coruña was used to create a Minimum Convex Polygon (hereafter MCP). The MCP's were created by importing the KML folders as vector layers onto QGIS whereby the pin-locations of the rhinos would be displayed on a map as point-vertices. These point-vertices were then enclosed using the algorithm, Minimum Bounding geometry to create a Convex Hull (Downs & Horner, 2009). From the convex hull layer, information on area size (in km²) was recorded on the Attribute Table.

To statistically test whether there were any significant differences in the mean home range sizes of bulls, cows and sub-adults, a One-Way ANOVA was conducted (Wang *et al*. 2017) using the computer software R-Studio (Affero General Public Licence version 3, RStudio, PBC). Homogeneity of variance was not met using the One-Way Anova, therefore the Brown-Forsythe test was conducted instead using Microsoft Excel 2007 (Version 16.0.13029.20232; Microsoft Corporation, United States.

4.2.1.2 Influence of rainfall on home range size

Shamwari receives rain throughout the year with two bi-modal peaks during early autumn and late spring. The mean annual rainfall for the past 21 years recorded on Shamwari has been 501 mm. Historical records indicate a mean of 422 mm, east of the reserve (O'Brien, 2013), 394 mm to the west (Addo area – 40 km west of Shamwari) (SA Weather Service, 2008). Droughts is a regular occurrence in the Eastern Cape (Kerley *et al*., 1995). According to Low and Robelo (1996), and Stone *et al.,* (1998) the area receives approximately 550 mm of rainfall annually. Rainfall was therefore categorized as follows:

- Below average rainfall (i.e., a dry year) – rainfall between 0 – 419 mm
- Average – rainfall between 420 – 550 mm
- Above average rainfall (i.e., a wet year) – rainfall above 550 mm

To determine whether there was any relationship between rainfall and home range size, a correlation coefficient test was conducted for each rhino. I wanted to determine whether home range size increased during drier years compared to years of increased rainfall. The correlation coefficient tests were conducted using Microsoft Excel 2007 (Version 16.0.13029.20232); Microsoft Corporation, United States.

4.2.2 Vegetation utilization

4.2.2.1 Vegetation types utilized by rhinos

Thirteen vegetation types have been classified and identified by O' Brien (2004). The areas where rhinos were seen were recorded on the rhino sightings sheets (as described previously). The vegetation type was allocated to the area in which the rhino was seen in the rhino sightings sheets. I used a Chi-square goodness-of-fit test to determine whether vegetation types were randomly selected or preferred (Chabwela *et al*., 2017). The statistical analysis was done using Microsoft Excel 2007 (Version 16.0.13029.20232; Microsoft Corporation, United States.

4.2.2.2 Vegetation preferences of adult bulls, adult cows and sub-adults in relation to rainfall

To determine whether specific vegetation types were preferred (based on the percentage occurrence of each rhino's total sightings) at different precipitation levels, sightings of each specific rhino obtained through direct observations were recorded and the vegetation type identified, based on the location it was seen. The total sightings of every rhino seen in each vegetation type was used to determine what vegetation types were preferred during different precipitation levels by comparing vegetation use in dry, average, and wet years and by which age class. The percentage of preference for each different vegetation type was calculated by using the total sightings (one sighting equals to one direct observation and positive identification of rhino) a rhino was observed in a specific vegetation type and dividing this into the total sightings the rhino was seen.

4.3 RESULTS

4.3.1 Home range size

4.3.1.1 Home range size

Adult bulls - The mean home range size for the four bulls was 43.05 ± 10.42 km². Bulls from both the southern and northern section of the reserve were used as they held exclusive territories with only minor overlapping in the central-west section of the reserve (Appendix I). The largest mean home range size was held by W102 (57.63 ± 10.00 km²), followed by W64 (41.43 ± 7.79 km²), W34 (40.27 ± 8.08 km²) and lastly W21 (32.90 ± 7.32 km²) (Appendix I).

Cow and calf – Home range size for cows accompanied by calves was 39.74 ± 12.21 km². All cows utilized the entire reserve, except for W3 who utilized the central area of the reserve exclusively (Appendix I). W51, W7 and W8 utilized both the northern and southern areas of the reserve, however W10 was mostly found in the southern section while W54 was predominantly found in the northern section of the reserve. W3 occupied the smallest area with a mean home range size of 22.08 ± 4.33 km². The largest mean home range size was from W54 (57.95 ± 25.52 km²), followed by W51 (45.42 ± 16.79 km²), W7 (43.17 ± 12.35 km²), W8 (37.26 ± 6.27 km²) and W10 (32.55 ± 5.55 km²). The mean home range size for all cows was 39.74 km².

Table 4.3.1. Mean home range size of white rhinos from all age classes during the period 2008 - 2019 on Shamwari Private Game Reserve, Eastern Cape, South Africa. Sample size (N) is given as the total sightings recorded. Home range size was determined using the Minimum Convex Polygon (MCP) and calculated in km².

Rhino	Age class	N	MCP (km²)
W 21	Adult Bull	845	32.90
W 34	Adult Bull	408	40.27
W 64	Adult Bull	539	41.43
W 102	Adult Bull	276	57.63
W 3	Cow and calf	1217	22.08
W 51	Cow and calf	1210	45.42
W 54	Cow and calf	688	57.95
W 7	Cow and calf	1230	43.17
W 8	Cow and calf	1060	37.26
W 10	Cow and calf	1263	32.55
W 101	Sub-adult	361	39.74
W 512	Sub-adult	261	37.04
W 64	Sub-adult	261	41.32
W 74	Sub-adult	215	41.32
W 102	Sub-adult	449	49.66
W 75	Sub-adult	804	32.70
W 76	Sub-adult	424	37.69
W 103	Sub-adult	548	35.72
W 515	Sub-adult	372	23.72
W 38	Sub-adult	277	32.48
W 104	Sub-adult	277	32.48
W 523	Sub-adult	327	65.37
W 541	Sub-adult	223	66.47
W 516	Sub-adult	391	43.75
W 83	Sub-adult	305	51.28
W 105	Sub-adult	193	45.31
W 78	Sub-adult	170	36.59
W 82	Sub-adult	309	44.63

Sub-adults – Home range sizes for sub-adults was 41.55 ± 11.03 km². The largest home range was occupied by W541 of 66.47 ± 26.75 km² and can be attributed to the cow (W54 and his mother) who he temporarily re-joined after his mother lost her second calf shortly after birth. The smallest home range size was 23.72 ± 4.76 km² by W515. Overall, sub-adults occupied home ranges of below 50 km², except for three, namely W523 (65.37 ± 21.95 km²), W541 (66.47 ± 26.75 km²) and W83 (51.28 ± 29.69 km²) (Appendix I)

From a total of 14 903 sightings, the mean home range size for all age classes was similar, ranging between 39.74 – 43.05 km² with a mean of 41.37 ± 10.83 km² . There were no significant differences (H = 0.11, *df* = 2, p = 0.90) in home range size between the three different rhino age groups (Table 4.3.1).

4.3.1.2 Influence of rainfall

ADULT BULLS

Table 4.3.2. Home range size (in km²) of adult bulls over the period 2008 – 2019 on Shamwari Private Game Reserve, Eastern Cape, South Africa.

RHINO/YEAR	2008	2009	2010	2011	2012	2013	2014	2015	2016	2017	2018	2019
Rainfall in mm	**403**	**412**	**542**	**765**	**670**	**542**	**560**	**635**	**248**	**438**	**250**	**276**
W 21						31.13	25.24	29.65	29.39	47.17	37.81	29.91
W 34		40.59	48.86	42.22	29.40							
W 64					37.14	43.18	37.41	54.29	35.11			
W 102										54.79	68.74	49.35
Mean per year		40.59	48.86	42.22	33.27	37.15	31.33	41.97	32.25	50.98	53.27	39.63

Bulls in the north included W64 (2012 – 2016) and W102 (2017 – 2019). Bulls in the south included W34 (2009 – 2012) and W21 (2013 – 2019). Bulls in the northern section occupied larger home ranges (range 35.11 – 68.74 km²), than bulls in the southern section (range 25.24 – 48.86 km²). W102 had the largest mean home range size of 57.63 km², followed by W64 (41.43 km²), W34 (40.27 km²) and lastly W21 (32.90 km²). A correlation coefficient test revealed a mean correlation of r = -0.18, indicating a weak negative correlation between rainfall and home range sizes of the bulls, indicating that with increased rainfall, home range size tended to decrease. All bulls indicated weak negative correlations, except for W64 who showed a moderate positive correlation (*r* = 0.46). However, all the results were statistically insignificant (Table 4.3.2).

ADULT COWS

Table 4.3.3. Home range size (in km²) of Adult cows with calves and cows without calves over the period 2008 – 2019 on Shamwari Private Game Reserve, Eastern Cape, South Africa.

Rhino/Year	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**
Rainfall in mm	**403**	**412**	**542**	**765**	**670**	**542**	**560**	**635**	**248**	**438**	**250**	**276**
Cow and calf												
W 3	25.51	20.43	26.06	20.12	13.57	25.42	18.33	18.75	22.29	23.88	28.52	
W 51	33.28	58.10	51.48	53.35	27.25	40.76	20.73	58.17	24.16	41.20	63.21	73.40
W 54							38.61	61.77	78.61	95.99	30.83	41.87
W 7	33.65	59.50	53.02	54.19	54.01	62.23	32.34	32.44	35.41	39.78	32.38	29.05
W 8			42.33	40.20	31.55	31.49	30.11	35.62	34.21	33.92	48.28	44.91
W 10	28.08	27.99	44.12	32.83	34.18	22.36	30.64	29.00	34.83	33.72	38.01	34.86
Mean per year	30.13	41.51	43.40	40.14	32.11	36.45	28.46	39.29	38.25	44.75	40.20	44.82

For the period 2008 – 2019, W3 occupied the smallest home range size ranging between 13.57 – 28.52 km² suggesting that the different rainfall years had little influence on home range size, however results did indicate a moderate negative correlation (*r* = -0.60) suggesting that increased rainfall did result in a decreased home range size. W51's home range size varied between 20.73 – 63.21 km². Results indicated a very weak negative correlation (*r* = -0.18) suggesting that home range size was not influenced by rainfall, however the largest recorded home range size was during 2019 (73.40 km²) when below average rainfall was experienced. The most conspicuous change in home range size was for W54 (varied between 30.83 – 95.99 km²) and was also the largest home range size for a specific year (2017) when average rainfall was experienced. Results (*r* = 0.10) indicated no relationship between home range size and rainfall. W7's home range size varied between 29.05 – 62.23 km². Her home range was larger between 2009 – 2013 (mean 57.19 km²) after which her home range size declined yearly (mean 33.57 km²) with a fluctuation of 62.23 km² in 2013 when average rainfall (542 mm) was experienced, followed by a smaller home range of 32.34 km² in 2014 when above average rainfall (560 mm). There was a moderate positive correlation (*r* = 0.49) indicating that home range size for females with calves increased with increased rainfall. Both W8 (range 30.11 – 48.28 km²) and W10 (range 27.99 – 44.12 km²) also showed little fluctuation between the various rainfall years, however W8's largest home range was recorded in 2018 (below average rainfall). Correlation coefficient results indicated negative correlation for both W8 (*r* = -0.42) and W10 (*r* = -0.18). All correlation coefficient results for adult cows (mean *r* = -0.26) suggest that the influence of rainfall on home range size was insignificant (Table 4.3.3).

SUB-ADULTS

Table 4.3.4. Home range size (in km²) of sub-adult rhinos over the period 2008 – 2019 on Shamwari Private Game Reserve, Eastern Cape, South Africa.

Rhino/Year	**2008**	**2009**	**2010**	**2011**	**2012**	**2013**	**2014**	**2015**	**2016**	**2017**	**2018**	**2019**
Rainfall in mm	**403**	**412**	**542**	**765**	**670**	**542**	**560**	**635**	**248**	**438**	**250**	**276**
W 101		30.00	43.35	37.76								
W512	44.72	44.60	49.83	26.12								
W 64	44.72	44.60	49.83	26.12								
W 74	45.05	63.39	40.54									
W 102					34.34	30.73	33.02					
W 75			43.35	37.76	32.93	33.72	42.51	35.89				
W 76					29.06	43.78	42.51	27.53				
W103						34.59	42.51	42.54	21.12			
W 515							19.53	22.74	28.89			
W 38									34.26	23.74	39.43	
W 104									34.26	23.74	39.43	
W 523									62.06	95.99	43.84	59.60
W 541										95.99	43.84	59.60
W 516									21.15	40.51	28.49	84.85
W 83										40.51	28.49	84.85
W 105										47.31	43.30	
W 78										36.54	36.65	
W 82										40.96	48.84	44.09
Mean per year	44.83	45.65	45.38	31.94	32.11	35.70	36.01	32.18	33.62	49.48	39.14	66.60

Home range size during years when average rainfall was experienced (2008, 2009, 2010, 2013 and 2017) varied between 35.70 – 49.48 km² with a mean of 42.59 km². Home range sizes for above average rainfall years (2011, 2012, 2014 and 2015) varied between 31.94 – 36.01 km² with a mean of 33.98 km². Home range size for sub-adults during below average rainfall years (2016, 2018 and 2019) varied between 33.62 – 66.60 km² with a mean of 50.11 km², indicating that home range size tended to be larger during years of below average rainfall, and smallest during above average rainfall years. Results from the correlation coefficient tests revealed seven sub-adults showing positive correlations between home range size and rainfall; W101 (r = 0.45), W102 (r = 0.85), W103 (r = 0.95), W523 (r = 0.93), W541 (r = 0.98), W516 (r = 0.06) and W105 (r = 1) and eleven sub-adults showed negative correlations; W512 and W64 (r = -0.81), W74 (r = -0.60), W75 (r = -0.34), W515 (r = -0.86), W38 and W104 (r = -0.94), W83 (r = -0.19), W78 (r = -1) and W82 (r = -0.87) (Table 4.3.4).

4.3.2 Vegetation use

4.3.2.1 Vegetation types utilized by the white rhinos

The white rhinos utilized a total of twelve vegetation types (Table 4.3.6). The vegetation type that was not utilized was Grassy fynbos. The following vegetation types were utilized in order of preference; cultivated lands (38.5%), primary acacia thicket (18.8%), montane grassland (11.2%), bontveld (10.8%), cleared lands (5.1%), bushclump savanna (4.5%), open grassland (3.0%), riverine bush (2.6%), secondary acacia thicket (1.9%), subtropical thicket (3.2%), secondary acacia thicket (1.9%), calcrete fynbos (0.1%) and lastly afromontane forest (0.0%). Cultivated lands represent the most preferred vegetation type for 24 of the 26 white rhinos with one bull (W64), one cow (W54) and three sub-adults (W512, W64 and W541) showing high preference for montane grassland. primary acacia thicket represents the second highest preferred vegetation type by 20 of the 26 rhinos. Thirdly was bontveld (including 16 of 28 rhinos), followed by primary acacia thicket (5 of 28 rhinos), riverine bush (4 of 28 rhinos), bushclump savanna and montane grassland (both having 2 of 28 rhinos and lastly subtropical thicket (1 rhino).

A few vegetation types were not utilized by certain individual rhinos. W512 and W64 were never seen in bontveld, W515 and 82 were never seen in montane grassland, W21 and W82 were never seen in secondary acacia thicket and W64, W102, W3, W512, W38, W104 and W541 were never seen in open grassland and W64, W102, W3, W38, W104 and W82 were not seen in montane grassland.

Cultivated lands, primary acacia thicket, bontveld, cleared lands, montane grassland and bushclump savanna were preferred by the rhinos (Table 4.3.6). Afromontane forest, calcrete fynbos and grassy fynbos, all showed significant Chi-square values, indicating that their presence in these vegetation types was random (Table 4.3.7).

Table 4.3.6. Vegetation utilization according to preference of 26 white rhinos on Shamwari Private Game Reserve for the period 2008 – 2019.

Rhino	Afromontane forest	Bontveld	Bushclump Savanna	Calcrete Fynbos	Cleared lands	Cultivated lands	Grassy fynbos	Montane grassland	Open grassland	Primary acacia thicket	Riverine bush	Secondary acacia thicket	Subtropical thicket
W 21	0.0%	17.2%	0.6%	0.0%	7.7%	38.6%	0.0%	0.1%	4.9%	27.0%	2.8%	0.0%	1.2%
W 34	0.0%	7.8%	3.2%	0.2%	4.2%	45.6%	0.0%	2.5%	3.4%	28.9%	2.7%	0.7%	0.7%
W 64	0.0%	0.2%	5.6%	0.0%	8.3%	19.9%	0.0%	36.4%	0.0%	6.7%	0.9%	4.1%	18.0%
W 102	0.0%	12.0%	8.3%	0.0%	8.0%	27.9%	0.0%	18.5%	0.0%	11.2%	9.4%	3.6%	1.1%
W 3	0.0%	14.1%	11.3%	0.2%	12.3%	35.7%	0.0%	3.8%	0.0%	16.2%	0.7%	0.0%	3.1%
W 51	0.0%	9.7%	3.1%	0.2%	2.5%	40.2%	0.0%	7.0%	3.9%	27.7%	1.9%	1.2%	2.6%
W 54	0.1%	6.3%	5.1%	0.0%	6.8%	22.4%	0.0%	29.8%	0.4%	11.4%	1.9%	2.2%	13.7%
W 7	0.0%	9.2%	9.1%	0.0%	5.3%	33.2%	0.0%	15.2%	0.7%	19.4%	3.4%	1.6%	2.9%
W 8	0.0%	11.2%	3.4%	0.5%	4.4%	37.5%	0.0%	1.2%	4.6%	25.3%	0.7%	0.5%	1.2%
W 10	0.0%	13.4%	2.6%	0.1%	9.8%	35.4%	0.0%	1.8%	2.9%	30.3%	1.2%	1.6%	1.0%
W 101	0.0%	12.5%	4.4%	0.0%	1.7%	39.9%	0.0%	3.3%	5.3%	29.1%	2.2%	0.8%	0.8%
W 512	0.0%	0.0%	9.2%	0.0%	7.7%	18.0%	0.0%	55.2%	0.0%	2.7%	0.0%	0.8%	6.5%
W 64	0.0%	0.0%	9.2%	0.0%	7.7%	18.0%	0.0%	55.2%	0.0%	2.7%	0.0%	0.8%	6.5%
W 74	0.0%	10.7%	7.4%	0.0%	4.2%	35.8%	0.0%	10.7%	3.3%	21.9%	3.3%	1.4%	1.4%
W 102	0.0%	11.8%	1.1%	0.2%	7.1%	38.1%	0.0%	0.2%	6.5%	33.4%	0.9%	0.2%	0.4%
W 75	0.0%	12.4%	3.4%	0.0%	2.4%	39.3%	0.0%	1.5%	6.6%	31.2%	1.4%	1.2%	0.6%
W 76	0.0%	8.0%	6.1%	0.0%	4.5%	42.7%	0.0%	0.2%	4.7%	31.6%	1.2%	0.5%	0.5%
W 103	0.0%	12.2%	2.0%	0.2%	2.6%	43.1%	0.0%	0.2%	7.1%	29.0%	1.3%	1.5%	0.9%
W 515	0.0%	10.8%	0.0%	0.3%	7.8%	43.5%	0.0%	0.0%	6.7%	26.1%	2.4%	1.1%	1.3%
W 38	0.0%	4.0%	2.9%	0.4%	1.8%	58.1%	0.0%	2.2%	0.0%	11.9%	7.2%	6.9%	4.7%
W 104	0.0%	4.0%	2.9%	0.4%	1.8%	58.1%	0.0%	2.2%	0.0%	11.9%	7.2%	6.9%	4.7%
W 523	0.0%	3.7%	4.6%	0.0%	3.7%	39.8%	0.0%	26.3%	3.4%	4.6%	6.4%	3.7%	4.0%
W 541	0.0%	2.2%	4.5%	0.0%	3.1%	30.9%	0.0%	34.5%	0.0%	6.3%	9.0%	5.4%	4.0%
W 516	0.0%	26.9%	1.3%	0.0%	1.0%	47.8%	0.0%	1.3%	4.1%	14.6%	0.5%	1.3%	1.3%
W 83	0.0%	24.1%	0.6%	0.0%	1.3%	46.6%	0.0%	2.2%	7.2%	15.0%	0.6%	1.6%	0.9%
W 105	0.0%	21.2%	4.1%	0.0%	7.3%	38.3%	0.0%	0.5%	4.7%	19.2%	1.6%	2.6%	0.5%
W 78	0.0%	12.9%	7.6%	0.0%	4.1%	44.1%	0.0%	0.6%	3.5%	22.9%	0.6%	0.6%	2.9%
W 82	0.0%	25.2%	1.3%	0.0%	2.9%	58.3%	0.0%	0.0%	1.6%	8.1%	1.6%	0.0%	1.0%
Total	**0.0%**	**10.8%**	**4.5%**	**0.1%**	**5.1%**	**38.5%**	**0.0%**	**11.2%**	**3.0%**	**18.8%**	**2.6%**	**1.9%**	**3.2%**

Table 4.3.7. Chi-square values based on the vegetation preference of 26 white rhinos on Shamwari Private Game Reserve from the period 2008 – 201

Rhino	**Afromontane forest**	**Bontveld**	**Bushclump Savanna**	**Calcrete Fynbos**	**Cleared lands**	**Cultivated lands**	**Grassy fynbos**	**Montane grassland**	**Open grassland**	**Primary acacia thicket**	**Riverine bush**	**Secondary acacia thicket**	**Subtropical thicket**
VEGETATION PRESENT (%)	**0.5**	**8.1**	**3.6**	**0.1**	**1.4**	**11.9**	**0.7**	**17.0**	**3.7**	**5.7**	**2.5**	**2.1**	**42.8**
BULLS													
W 21	0.00	0.17	0.01	0.00	0.08	0.39	0.00	0.00	0.05	0.27	0.03	0.18	0.01
W 34	0.00	0.00	0.00	0.00	0.06	0.96	0.01	0.12	0.00	0.94	0.00	0.01	0.41
W 64	0.00	0.08	0.01	0.00	0.35	0.05	0.01	0.22	0.04	0.00	0.01	0.02	0.14
W 102	0.00	0.02	0.06	0.00	0.31	0.22	0.01	0.00	0.04	0.05	0.19	0.01	0.41
COWS													
W 3	0.00	0.14	0.11	0.00	0.12	0.36	0.00	0.04	0.00	0.16	0.01	0.00	0.03
W 51	0.00	0.10	0.03	0.00	0.02	0.40	0.00	0.07	0.04	0.28	0.02	0.01	0.03
W 54	0.00	0.06	0.05	0.00	0.07	0.22	0.00	0.30	0.00	0.11	0.02	0.02	0.14
W 7	0.00	0.09	0.09	0.00	0.05	0.33	0.00	0.15	0.01	0.19	0.03	0.02	0.03
W 8	0.00	0.11	0.03	0.00	0.04	0.38	0.00	0.01	0.05	0.25	0.01	0.00	0.01
W 10	0.00	0.13	0.03	0.00	0.10	0.35	0.00	0.02	0.03	0.30	0.01	0.02	0.01
SUB-ADULTS													
W 101	0.00	0.12	0.04	0.00	0.02	0.40	0.00	0.03	0.05	0.29	0.02	0.01	0.01
W 512	0.00	0.00	0.09	0.00	0.08	0.18	0.00	0.55	0.00	0.03	0.00	0.01	0.07
W 64	0.00	0.00	0.09	0.00	0.08	0.18	0.00	0.55	0.00	0.03	0.00	0.01	0.07
W 74	0.00	0.11	0.07	0.00	0.04	0.36	0.00	0.11	0.03	0.22	0.03	0.01	0.01
W 102	0.00	0.12	0.01	0.00	0.07	0.38	0.00	0.00	0.06	0.33	0.01	0.00	0.00
W 75	0.00	0.12	0.03	0.00	0.02	0.39	0.00	0.01	0.07	0.31	0.01	0.01	0.01
W 76	0.00	0.08	0.06	0.00	0.04	0.43	0.00	0.00	0.05	0.32	0.01	0.00	0.00
W 103	0.00	0.12	0.02	0.00	0.03	0.43	0.00	0.00	0.07	0.29	0.01	0.01	0.01
W 515	0.00	0.11	0.00	0.00	0.08	0.44	0.00	0.00	0.07	0.26	0.02	0.01	0.01
W 38	0.00	0.04	0.03	0.00	0.02	0.58	0.00	0.02	0.00	0.12	0.07	0.07	0.05
W 104	0.00	0.04	0.03	0.00	0.02	0.58	0.00	0.02	0.00	0.12	0.07	0.07	0.05
W 523	0.00	0.04	0.05	0.00	0.04	0.40	0.00	0.26	0.03	0.05	0.06	0.04	0.04
W 541	0.00	0.02	0.04	0.00	0.03	0.31	0.00	0.35	0.00	0.06	0.09	0.05	0.04
W 516	0.00	0.27	0.01	0.00	0.01	0.48	0.00	0.01	0.04	0.15	0.01	0.01	0.01
W 83	0.00	0.24	0.01	0.00	0.01	0.47	0.00	0.02	0.07	0.15	0.01	0.02	0.01
W 105	0.00	0.21	0.04	0.00	0.07	0.38	0.00	0.01	0.05	0.19	0.02	0.03	0.01
W 78	0.00	0.13	0.08	0.00	0.04	0.44	0.00	0.01	0.04	0.23	0.01	0.01	0.03
W 82	0.00	0.25	0.01	0.00	0.03	0.58	0.00	0.00	0.02	0.08	0.02	0.00	0.01
Average	0.00	0.11	0.04	0.00	0.05	0.38	0.00	0.11	0.03	0.19	0.03	0.02	0.03

4.3.2.2 Vegetation preferences in relation to rainfall

ADULT BULLS

Table 4.3.7. Vegetation use of all bulls on Shamwari Private Game Reserve for the period 2008 – 2019 indicating rainfall in mm for each year. Rainfall was categorized as average (410 – 550 mm), wet (above 550 mm) and dry (below 410 mm) years.

Year	Rainfall in mm	Afromontane forest	Bontveld	Bushclump Savanna	Calcrete Fynbos	Cleared lands	Cultivated lands	Grassy fynbos	Montane grassland	Open grassland	Primary acacia thicket	Riverine bush	Secondary acacia thicket	Subtropical thicket
2008	403	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%	0%
2009	412	0%	6%	0%	0%	4%	40%	0%	0%	3%	39%	7%	1%	1%
2010	542	0%	8%	3%	0%	3%	59%	0%	6%	2%	16%	2%	1%	1%
2011	765	0%	8%	4%	1%	5%	40%	0%	0%	5%	34%	1%	1%	1%
2012	670	0%	5%	7%	1%	5%	29%	0%	22%	1%	13%	0%	4%	11%
2013	542	0%	9%	2%	0%	9%	20%	0%	29%	3%	14%	2%	2%	11%
2014	560	0%	6%	2%	0%	11%	20%	0%	20%	3%	20%	1%	2%	15%
2015	635	0%	4%	6%	0%	13%	43%	0%	2%	2%	27%	1%	0%	1%
2016	248	0%	13%	3%	0%	5%	44%	0%	14%	6%	14%	0%	0%	3%
2017	438	0%	14%	6%	0%	5%	40%	0%	7%	1%	24%	3%	1%	1%
2018	250	0%	13%	0%	0%	9%	36%	0%	11%	0%	22%	6%	1%	2%
2019	276	0%	25%	7%	0%	3%	33%	0%	10%	0%	11%	6%	4%	1%

The vegetation types utilized by the adult bulls during years of average rainfall was Cultivated lands, followed by primary acacia thicket, montane grassland and bontveld. Other vegetation types showed less than 5% utilization, resulting in the least variety of vegetation types being utilized. Wet years represents the highest variety of vegetation types being utilized with cultivated lands still being most preferred, followed by primary acacia thicket, montane grassland, cleared lands, subtropical thicket, bontveld and bushclump savanna (Table 4.3.7). During 2012 – 2014 the reserve experienced both average (2013) and above average (wet) rainfall (2012 and 2014) and represents the only years where subtropical thicket and montane grassland were utilized above average from other years. During years

2016, 2018 and 2019 when the reserve experienced below average (dry) rainfall the preferred vegetation type remained cultivated lands, followed by bontveld, primary acacia thickets, montane grassland and cleared lands. Afromontane forest and grassy fynbos was not utilized by the adult bulls while calcrete fynbos only contributed to 1% utilization during 2011 and 2012 when above average rainfall was experienced.

ADULT COWS

Table 4.3.8. Vegetation use of all cows on Shamwari Private Game Reserve for the period 2008 – 2019 indicating rainfall in mm for each year. Rainfall was categorized as average (410 – 550 mm), wet (above 550 mm) and dry (below 410 mm) years.

Year	Rainfall	Afromontane forest	Bontveld	Bushclump Savanna	Calcrete Fynbos	Cleared lands	Cultivated lands	Grassy fynbos	Montane grassland	Open grassland	Primary acacia thicket	Riverine bush	Secondary acacia thicket	Subtropical thicket
2008	403	0%	2%	6%	0%	12%	37%	0%	16%	0%	19%	1%	4%	3%
2009	412	0%	7%	7%	0%	6%	33%	0%	11%	3%	28%	1%	2%	2%
2010	542	0%	8%	5%	0%	3%	48%	0%	15%	1%	17%	0%	1%	2%
2011	765	0%	16%	5%	0%	5%	38%	0%	1%	4%	25%	1%	1%	4%
2012	670	0%	10%	8%	0%	6%	36%	0%	3%	6%	27%	0%	0%	2%
2013	542	0%	13%	4%	1%	11%	32%	0%	1%	2%	30%	1%	2%	3%
2014	560	0%	7%	4%	0%	7%	30%	0%	7%	2%	32%	0%	2%	9%
2015	635	0%	7%	6%	0%	11%	41%	0%	5%	2%	25%	1%	1%	2%
2016	248	0%	15%	6%	0%	2%	43%	0%	7%	2%	16%	2%	4%	2%
2017	438	0%	22%	6%	0%	5%	38%	0%	5%	2%	21%	1%	0%	1%
2018	250	0%	19%	5%	0%	9%	32%	0%	7%	0%	16%	7%	2%	4%
2019	276	0%	19%	16%	1%	3%	23%	0%	21%	0%	8%	6%	2%	22%

Adult cows utilized a larger variety of vegetation types during all the rainfall years. During years of average rainfall cultivated lands was most preferred, followed by primary acacia thicket, bontveld, montane grassland, cleared lands and bushclump savanna. Other vegetation types represent below 5% utilization. Wet years represented the same order of vegetation preference than average rainfall years, with cultivated lands and primary acacia thicket representing nearly 65% of total utilization while other vegetation types were only marginally used. During dry rainfall years, a larger variety of vegetation types were utilized with cultivated lands still being most preferred, followed by bontveld, primary acacia thicket, montane grassland, bushclump savanna, subtropical thicket, and riverine bush. The highest presence for subtropical thicket was during 2019, which was the second consecutive year below average rainfall. Other vegetation types represent below 5% utilization. Afromontane forest and grassy fynbos were not utilized by the cows in any rainfall years, while calcrete fynbos contributed less than 1%.

SUB-ADULTS

Table 4.3.9. Vegetation use of all sub-adults on Shamwari Private Game Reserve for the period 2008 – 2019 indicating rainfall in mm for each year. Rainfall was categorized as average (410 – 550 mm), wet (above 550 mm) and dry (below 410 mm) years.

Year	**Rainfall**	**Afromontane forest**	**Bontveld**	**Bushclump Savanna**	**Calcrete Fynbos**	**Cleared lands**	**Cultivated lands**	**Grassy fynbos**	**Montane grassland**	**Open grassland**	**Primary acacia thicket**	**Riverine bush**	**Secondary acacia thicket**	**Subtropical thicket**
2008	403	0%	0%	16%	0%	13%	31%	0%	20%	1%	12%	0%	0%	7%
2009	412	0%	10%	5%	0%	4%	27%	0%	22%	4%	21%	2%	1%	4%
2010	542	0%	8%	8%	0%	3%	39%	0%	24%	0%	12%	3%	1%	2%
2011	765	0%	9%	4%	0%	4%	28%	0%	21%	6%	24%	1%	2%	2%
2012	670	0%	13%	4%	0%	5%	34%	0%	0%	6%	35%	0%	1%	1%
2013	542	0%	15%	2%	0%	3%	36%	0%	0%	8%	33%	2%	0%	0%
2014	560	0%	6%	1%	0%	10%	38%	0%	0%	6%	33%	2%	1%	1%
2015	635	0%	9%	3%	0%	2%	53%	0%	0%	5%	27%	0%	1%	0%
2016	248	0%	17%	3%	0%	1%	55%	0%	2%	6%	9%	2%	1%	2%
2017	438	0%	13%	4%	0%	3%	46%	0%	9%	4%	18%	0%	1%	2%
2018	250	0%	14%	3%	0%	4%	48%	0%	5%	0%	12%	6%	5%	3%
2019	276	0%	24%	2%	0%	2%	39%	0%	13%	0%	8%	5%	4%	3%

Sub-adult rhinos showed similar preference to vegetation types as the adult cows and bulls with cultivated lands remaining the most favoured vegetation type in all rainfall years, except during 2012 (wet year) when primary acacia thicket was marginally preferred. During years of average rainfall, the largest variety of vegetation types was utilized, namely; cultivated lands, primary acacia thicket, montane grassland, bontveld, bushclump savanna and cleared lands, while other vegetation types represent less than 5% utilization. In contrast to adult cows who utilized the largest variety of vegetation during dry years, sub-adults utilized the least variety. Nearly half the time (47%) was spent in cultivated lands, followed by bontveld, primary acacia thicket and montane grassland while other vegetation types showed less than 5% preference. Wet years showed similar preference to average years. All other vegetation types contributed to less than 10% of the overall presence for all years. Afromontane forest, grassy fynbos and calcrete fynbos were not utilized by the sub-adults.

4.4 DISCUSSION

4.4.1 Home range size

4.4.1.1 Home range sizes

The mean home range size for all age groups was similar, however there were notable variability between individual rhinos. Home ranges of adult bulls were slightly larger than adult cows and sub-adults and could be attributed to the management strategy of regularly selling bulls before they reach social maturity to prevent fighting-related injuries and deaths (Owen-Smith, 1981; Laubscher *et al*., 2015; Kretzschmar *et al*., 2020). Due to this management strategy, two breeding bulls (one north and one south) were always present on the reserve and, for this reason, each adult breeding bull had to cover large areas. Home range sizes of adult bulls on Shamwari were generally larger in size (range 32.90 – 57.63 km²) compared to bulls in iMfolozi: 2.62 – 8.95 km² (White *et al*., 2007), Welgevonden Game Reserve: 1.14 – 5.17 km² (Thompson *et al*., 2016), Willem Pretorius Game Reserve: 6.3 -8.1 km² (Jordaan *et al*., 2015) and KNP in the south-western area where bulls mean home range size was 9.86 km². Results from the Pafuri area of Kruger National Park (hereafter KNP) indicated a mean adult bull home range of 29.9 km² (Pedersen, 2009), Matobo National Park: 15 – 50 km² (Rachlow *et al*., 1999; Chirenje, 2016) showed similar result to Shamwari, however Kretzschmar *et al.,* (2002) recorded the largest home range sizes for breeding bulls of between 61 – 116 km² for a private reserve in the northern parts of South Africa.

Home range size of adult cows with calves on Shamwari varied between 22.08 – 57.95 km². The mean home range size of 39.74 ± 12.21 km² was the smallest of the three age classes on Shamwari. In contrast to adult bulls, adult cow home range size was found to be similar to other reserves; iMfolozi: 6.52 – 66.80 km² (White *et al*., 2007), Whovi National Park – Zimbabwe: 0.6 – 40 km² (Rachlow *et al*., 1999), Ithala Game Reserve: 27 – 32 km² (Hebbelmann, 2013), Matobo National Park: 51.86 km² (Chirenje, 2016) and Pafuri (KNP): 17 – 84 km² (Pedersen, 2009). Other reserves showed much smaller home range sizes in Welgevonden Game Reserve: mean 3.46 km² (Thompson *et al*., 2016), Kyle Recreational Park: 3.2 – 4.7 km² (Monks, 1995) and in Willem Pretorius Game Reserve: 1.9 – 5 km² (Jordaan *et al*., 2015).

Home range size for sub-adults varied between 23.72 – 66.47 km² with a mean of 41.55 ± 11.03 km². Relatively few other studies included sub-adult rhino to determine home range size. In Kyle Recreational Park, the mean home range size for sub-adults was 7.7 km² (Monks, 1995) and between 0.4 – 7.19 km² in Welgevonden Game Reserve (Thompson *et al*., 2016). The home range size for sub-adults was larger than recorded on other reserves. The largest mean home range size was from a sub-adult bull (W541) from the north, who's large home range size may be attributed to his choice of companionship when he re-joined his mother (W54), shortly after she lost her calf in 2017 (Shrader & Owen-Smith, 2002). These companionships are often led by an adult female (if present) and during this period W54 travelled to the southern part of the reserve in search of a breeding bull as the northern bull was sold the previous year and the bull W102 who was from the south only travelled as far north during 2018.

Home range sizes for rhinos of all age classes on Shamwari were mostly larger than what other reserves have reported (Pienaar *et al*., 1993b; Monks, 1995; Hebbelmann, 2013; Jordaan *et al*., 2015). The larger home range sizes of the Shamwari rhinos could be due to the characteristic presence of subtropical thicket on Shamwari, covering 42.8% of the landscape, making almost half the reserve unsuitable for white rhinos (O' Brien, 2004). The subtropical thicket is dominated by spiny impenetrable thicket and a poorly developed grass layer (Kerley *et al*., 1995). Being a megaherbivore, and an extralimital species in this grass-poor habitat, the limited grass cover could have challenging consequences for the rhino to find food (Owen-Smith, 1988).

The non-overlapping territories of the adult bulls on Shamwari was prominent. The management strategy to have only two breeding bulls on the reserve (one north and one south) and removing young bulls prior to reaching adulthood may have contributed to the larger home range sizes of the bulls.

4.4.1.2. Influence of rainfall

Changes in rainfall result in the uneven distribution of resources such as water and food and could result in shifts of home range area (Hebbelmann, 2013). In both iMfolozi and the Willem Pretorius Game Reserves no significant differences in home range size during wet and dry seasons were reported (White *et al*., 2007; Jordaan *et al*., 2015). In Whovi National Park and Pafuri (KNP), home range size was found to be larger during dry seasons (Pedersen, 2009; Chirenje, 2016), while in Ithala Game Reserve and KNP South-western area it was found that in wetter seasons, female white rhino home ranges were larger (Pienaar *et al*., 1993b; Hebbelmann, 2013). According to the results from the correlation tests for the Shamwari rhinos, ten rhinos showed positive correlations compared to eighteen that showed negative correlations. These results indicate that 64.3% of rhinos on Shamwari had larger home range sizes during drier years and smaller home range sizes in wetter years. The larger home range sizes during drier years could be attributed to the reduced presence of available resources during periods of decreased rainfall, contributing to the need to increase traveling in search of food. The larger home range sizes could also be attributed to waterholes on the southern section of the reserve drying up during drought periods, resulting in the Bushmans River being the only source of water for long periods. Understanding home range sizes of the rhinos enables managers to determine carrying capacity and can aid in the decision-making of off-takes during prolonged periods of drought (Balfour *et al*., 2019b; Ferreira *et al*., 2019).

4.4.1 Vegetation preference by rhino

Vegetation and habitat use have been well recorded for white rhinos where they are found to be endemic, however only Kraai (2010) investigated the diet of white rhino in the Eastern Cape Province where they are extralimital. Nearly 43% of Shamwari is dominated by subtropical thicket, a vegetation type that is dominated by impenetrable evergreen trees and spiny shrubs (O' Brien, 2004). Other than providing shelter, these subtropical thickets do not contribute to the diet of the white rhinos due to the limited presence of grass, and therefore rapidly decrease area-suitability for the white rhinos as in other species within Shamwari (Rueda *et al*., 2008; Kraai, 2010; O'Brien, 2013).

Cultivated lands were the most preferred by all rhino age classes, however W64, W512, W54 and W541 most preferred vegetation type was montane grassland. These four rhino were found in the northern section of the reserve at higher altitude where the geological characteristics consisted of rolling hills and valleys (O' Brien, 2004).

In contrast, the southern section is dominated by low lying areas where previous land practices mostly involved crops. These old crop-lands were rehabilitated and seeded with palatable grass species and then classified as cultivated lands by O' Brien (2004). The Bushman's River runs through the southern section of the reserve and rhino presence in this vegetation type was mostly random indicating that these areas were possibly only utilized to access water and for shelter (Pienaar, 1994).

Open grassland was only found in the south-eastern corner of the reserve consisting of 572 ha. W64, W512 and W541' s home range were in the northern part of the reserve, while W3, W38, W104 and W102 traversed the middle section of the reserve. For this reason, these seven rhinos were never seen in open grassland. Bontveld is only found in the southern section of the reserve and for this reason W64 and W512 did not utilize it as they were only ever found in the northern section of the reserve.

4.4.2.2 Vegetation preferences in relation to rainfall

Kraai (2010) indicated that the grass quality on Shamwari was very poor and that extralimital large herbivores such as the white rhino were increasingly placing pressure on the limited available grass-rich habitats. Cultivated lands was mostly preferred in all rainfall periods, suggesting that the palatable grass-species that were planted in these areas have contributed to this preference. During dry periods, the rhino could have a negative impact on grass habitats due to the mowing-action of rhino's lips, grazing as low as 2.5 cm from the ground which could result in denuding the soil (Owen-Smith, 1981). Cultivated lands was the most preferred vegetation type in all rainfall variables, however during dry years the second most utilized vegetation type was bontveld where *Themeda triandra* is the dominant grass species. According to Owen-Smith (1981) *Themeda triandra* was mostly utilized during periods of drought and was found to be similar on Shamwari.

Adult cows generally utilized a broader variety of vegetation types during dry years, compared to average and wet years when cultivated lands and primary acacia thicket incorporated more than 60% of their vegetation preference. To compensate for the limited food availability during dry years, adult cows expand their diets by incorporating a larger variety of vegetation types to increase food intake (Hebbelmann, 2013). It was also noted that a large proportion of subtropical thicket was incorporated within the adult cow's home range towards the latter part of the dry years and could be driven by their search for higher quality grass species such as *Panicum maximum* found in these thickets. In general, the subtropical thicket was more favoured by cows than other age groups and could be due to the thick bush providing shelter for cows with calves during times of vulnerability (Owen-Smith, 1988).

Adult bulls utilized a wider variety of vegetation types during wet years, however the order of preference remain the same as in other age classes. During wet years, the bulls increased their utilization of montane grassland and subtropical thicket during three consecutive years from 2012 to 2014. According to O' Brien (2004) most of the grass species found in montane grassland consist of both unpalatable grass species such as *Eragrostis curvula, Heteropogon contortis* and palatable species, *Themeda triandra* and *Sporobolus fimbriatus*. However, the increased utilization of the grass species found in montane grassland on Shamwari during wet years is similar to what Jordaan *et al.,* (2015) found in the Willem Pretorius Reserve. Subtropical thicket also showed an increased usage by adult bulls during wet years, which contrasts with adult cows and is believed to be due to past pastoralism practices that have damaged some of the subtropical thicket on the reserve, promoting the establishment of grass (O' Brien, 2004).

Riverine bush was also more frequently utilized by all age classes during dry years and could be due to waterholes drying up during dry periods. The rhino's main source of water in the southern section of the reserve is from the Bushman's river, which could have resulted in increased utilization of the riverine vegetation in dry periods.

4.5 CONCLUSIONS

The home range sizes of the white rhinos on Shamwari was generally larger than most other reserves (Pienaar *et al*., 1993b; Rachlow *et al*., 1999; White *et al*., 2007), however they were similar to rhinos re-introduced into a Pafuri-section of KNP (Pedersen, 2009). Most of the reserve is covered in subtropical thicket which does not provide sufficient foraging opportunities for white rhinos (Owen-Smith, 1988; O' Brien, 2004), resulting in the rhinos likely needing to travel greater distances to access food resources. Cows and sub-adult rhinos generally utilized a larger variety of vegetation types during average and dry years by shifting their home range, rather than increasing the size to supplement their nutritional requirements (Hebbelmann, 2013). However, it was the opposite for bulls, they incorporated less vegetation types within their home range, suggesting that food may not be an indicator for rhino bulls home range use, but rather reproductive strategies (White *et al*., 2007). Cultivated lands represented nearly 40% of preferred vegetation type of the white rhinos. The rehabilitation of old cultivated lands with palatable grass species in the southern section of the reserve have contributed to the successful reintroduction and reproductive success of the white rhinos on Shamwari as was discussed in Chapter 3.

CHAPTER 5

SUMMARY AND MANAGEMENT RECOMMENDATIONS

5.1 Introduction

Actively protecting and conserving endangered species such as the rhino has been a priority for conservationists over the last few decades (Amin *et al*., 2006). To ensure the long-term survival of the rhino, various strategies have been implemented, including the relocation of rhinos into areas where they occurred historically (Anderson, 1993), and areas where they did not occur historically and are considered extralimital (Castley *et al.,* 2001). The white rhino is predominantly a grazer and therefore has specific dietary requirements, but also has certain habitat preferences such as access to surface water and thicket for shelter to be successful (Pienaar *et al*., 1992; Skinner & Chimimba, 2005). To meet all the above-mentioned requirements is not an easy task as most areas are limited in these resources (Kerley & Landman, 2006). Other restrictions may include diseases and parasites (Taylor, 1986; Balfour. *et al*., 2019b), drought (Ferreira *et al*., 2019) and landscape suitability (Pienaar *et al*., 1993a).

The Eastern Cape Province regularly experiences drought, resulting in the degradation of grass species (Kerley *et al*., 1995). The area where Shamwari is located is characterised by the dominant subtropical thicket biome which lacks a substantial grass layer (Mucina & Rutherford, 2006). However, due to past pastoralism practices, the landscape has been transformed significantly over the last few decades, with thickets being gradually replaced by ephemeral grasslands, thereby potentially improving the suitability of some areas for large grazers (Mills *et al.,* 2005). White rhinos on private reserves around the Eastern Cape have become a prominent feature (Maciejewski & Kerley, 2014) presumably because of these changing habitat conditions, and their popularity with ecotourists (Langholz & Kerley, 2006).

I have been actively monitoring the white rhino for just over a decade on Shamwari and felt the need to utilize the information gathered over this period to firstly investigate the reproductive status and demography of an extralimital white rhino population in the

Eastern Cape to determine whether or not they were contributing to the conservation of the meta-population. Secondly, I wanted to determine home range size and vegetation preference of the white rhinos on Shamwari to compare how these differ from other reserves where the rhino is endemic.

5.2 Reproduction

In chapter 3, I wanted to investigate various reproductive parameters of white rhinos to determine how successful they are as an extralimital species in the Eastern Cape in relation to other reserves where rhinos are endemic. Parameters such as population growth rate, inter-calving intervals, age at first calving, sex ratio, fecundity and density were investigated (Rachlow & Berger, 1998; Sibly & Hone, 2002; Okita-Ouma *et al*., 2009). The average population growth rate for the white rhinos on Shamwari averaged 10%, higher than the recommended 5% by the Rhino Management Group (Emslie & Brooks, 1999; Knight *et al*., 2015) and the 7-9% suggested by Balfour *et al.,* 2019a), and 1% higher than the 9% annual growth rate recorded by several other private rhino owners (Castley & Hall-Martin, 2003). The higher growth percentage makes the live sale of rhinos possible, enabling Shamwari to contribute to the ongoing range expansion objectives of the Rhino Management Group (Emslie & Brooks, 1999; Knight *et al*., 2015; Balfour *et al*., 2019a).

Mortalities were mostly fighting-related, similar to what other reserves have experienced (Owen-Smith, 1988; Monks, 1995; Rachlow, 1997). The sale of white rhinos did, however, have a negative effect on population growth, characterised by a negative percentage growth the year following any live sales. However, sales of rhinos form an integral part of the reserve’s rhino management plan to mitigate fighting-related injuries/deaths amongst bulls (Monks, 1995), and to contribute to the ongoing conservation of the rhino by removing breeding stock (Ferreira *et al*., 2012).

Inter-calving intervals and the age at first calving have been known to be influenced by density-dependant parameters, whereby high density rhino populations are characterised by cows giving birth to their first calf at an older age and longer inter-calving periods, whereas low density rhino populations result in younger age at first calving with shorter inter-calving periods (Rachlow, 1997; Rachlow & Berger, 1998). White rhino density on

Shamwari is slowly increasing and has fluctuated annually with a gradual, decreasing trend over time as the population has grown. The inter-calving interval for white rhinos on Shamwari varied between 1 year and 11 months, and 4 years and 3 months with an average of 2 years and 5 months. Age at first calving in seven cows decreased with increased density, except for two cows (of which one cow, W54 was moved to a different area, disrupting her reproductive cycle). The results indicated a negative correlation between the density of rhinos and that of inter-calving intervals and age at first calving, suggesting that the population has not yet reached any of the density-dependent factors, predicting a slower reproductive trend of rhino (Rachlow & Berger, 1998).

Sex ratio of calves born on Shamwari were slightly male biased with 57% being males. It could be suggested that the Shamwari population is following the Trivers-Willard hypothesis where cows that are in poor condition invest in female offspring, while cows in good condition invest in male calves (Trivers & Willard, 1973), since both births and conceptions peaked during the bimodal rainfall periods. Cows on Shamwari appeared to have their peak in conceptions from October to December (spring rainfall), which coincided with births the following rainfall peak (autumn rainfall peak) from February to April. These data suggest that cows on Shamwari would generally be in good condition at both conception and for parturition (Trivers & Willard, 1973; White *et al.,* 2007; Fike, 2011). However, additional research would be required to determine how closely the white rhinos on Shamwari fit the Trivers-Willard model. Nevertheless, my overall assessment of the reproductive success and demography of the Shamwari white rhino suggests that this extralimital population is positively contributing to rhino conservation in South Africa.

5.3 Spatial ecology

I predicted that the home range sizes of cows would be larger than bulls, however my results indicated that the average home range sizes of the bulls were slightly larger than those of the cows and the sub-adults. The home range sizes of bulls on Shamwari were mostly larger than those found on other reserves (Pienaar *et al*., 1992; White *et al*., 2007; Jordaan *et al*., 2015; Thompson *et al*., 2016), but were similar to those estimated in Matobo National Park (Rachlow, 1997; Chirenje, 2016). Management strategies have manipulated the home ranges of bulls on Shamwari where only two breeding bulls are maintained to service all females from the northern or southern sections of the reserve. Home range size of cows with calves was mostly similar to other reserves (Rachlow *et al*., 1999; White *et al*., 2007; Pedersen, 2009; Hebbelmann, 2013; Chirenje, 2016), while sub-adult ranges were larger (Monks, 1995; Thompson *et al*., 2016). To determine whether rainfall variables influenced home range size, correlation tests revealed that 64.3% of rhinos on Shamwari increased their home range size during dry years, compared to wet years.

Vegetation utilization by white rhinos on Shamwari indicated clear preference for cultivated lands (areas where subtropical thicket has historically been cleared), followed by primary acacia thickets (also disturbed habitats), montane grassland and bontveld. Other vegetation types only contributed marginally to the rhino's vegetation preferences. During dry years, bontveld was favoured after cultivated lands and this could be due to the presence of *Themeda triandra* in the bontveld which is favoured during dry periods (Owen-Smith, 1981). Cows broadened their utilization of various vegetation types during dry years, whereas bulls were the opposite. Sub-adult's vegetation preferences were similar to the cows.

5.4 Recommendations

Reproductive success is dependent on various demographic parameters (Bonenfant *et al*., 2009). In large herbivores, reproductive success is believed to be predicted by density dependent factors, whereby population growth will become restricted in response to a population's increased density (Bonenfant *et al*., 2009). Environmental stochasticity also influences population growth and severely limits predictability of future population sizes (Hempson *et al*., 2015). In order for populations to be successful, they need to reproduce, therefore it is vital for wildlife managers to ensure that the various demographic parameters are monitored (Fike, 2011; Balfour *et al.,* 2019a).

In the past, very few conservation-based relocations considered the possible repercussions such introductions may have on the native biodiversity (Spear & Chown, 2009). The establishment of extralimital species poses a threat to the endemic biodiversity of an area and should only be considered under suitable habitat conditions which would be ecologically sustainable (Castley *et al*., 2001). About 28% of private landowners are disinvesting in rhinos due to the ongoing rhino poaching crisis (Clements *et al*., 2020). The presence of white rhinos in the Eastern Cape is mostly as a result of opportunistic introductions for economic benefit through eco-tourism and conservation incentives, however the impact on the biodiversity of the native vegetation is potentially at risk (Castley *et al*., 2001; Maciejewski & Kerley, 2014). Maintaining the reserve below the maximum carrying capacity will prevent deterioration of the vegetation, soil and biodiversity (Foran *et al*., 1978; Rachlow & Berger, 1998). The distribution of large herbivores in specific vegetation types is predicted by quality and quantity of the food resources and access to water (Bailey *et al*., 1996). Monitoring and assessing vegetation condition is therefore crucial to establish its current ecological status and stage of succession (Schirmel *et al*., 2011).

Vegetation utilization data in this study were severely limited due to the observational method of collecting data (Aguiar & Moro-Rios, 2009). Tracking and monitoring equipment have evolved over the years, making it easier to locate and study animal behaviour, their use of space and vegetation preference more precisely (Pienaar *et al*., 1992; Hofmeyr, 1998; Foley & Sillero-Zubiri, 2020). The use of GPS- and VHF collars will enable for more accurate data regarding use of vegetation types without having to physically see the rhino (Morgan, 2010), as the observational data in this study required a positive identification of the rhino for a confirmed sighting (Balfour *et al*., 2019b). The use of collars for future research purposes will provide better insights regarding vegetation preference and the movements of the rhinos.

The current monitoring programme on Shamwari is effective for determining the population status, trends, reproductive objectives and conservation achievements (Ferreira *et al*., 2011; Balfour *et al*., 2019b). However, there is much room for improvement to invest in digital-based applications to capture data in real-time (Liebenberg *et al*., 1999). Looking at the current data on reproductive parameters it seems that the white rhinos on Shamwari have thus far not reached any density dependence limitations as age at first calving and inter-calving intervals and fecundity rates are in relation by low density populations.

Although extralimital, white rhinos on Shamwari have contributed to the ongoing expansion and conservation efforts to protect rhinos in South Africa. Poaching remains a great threat to the species (Clements *et al*., 2020) and requires continued dedicated protection. In addition, the population needs to be monitored and managed in such a way that the reproductive parameters are met for optimum growth and the vegetation utilized in a sustainable manner. I believe that my work has provided the initial foundation for future work on the population viability and conservation of white rhinos in the Eastern Cape.

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APPENDIX I: Maps indicating home ranges of the white rhino on Shamwari Private Game Reserve.

Figure Ia. Home range of adult bulls on Shamwari Private Game Reserve indicated as individual sightings.

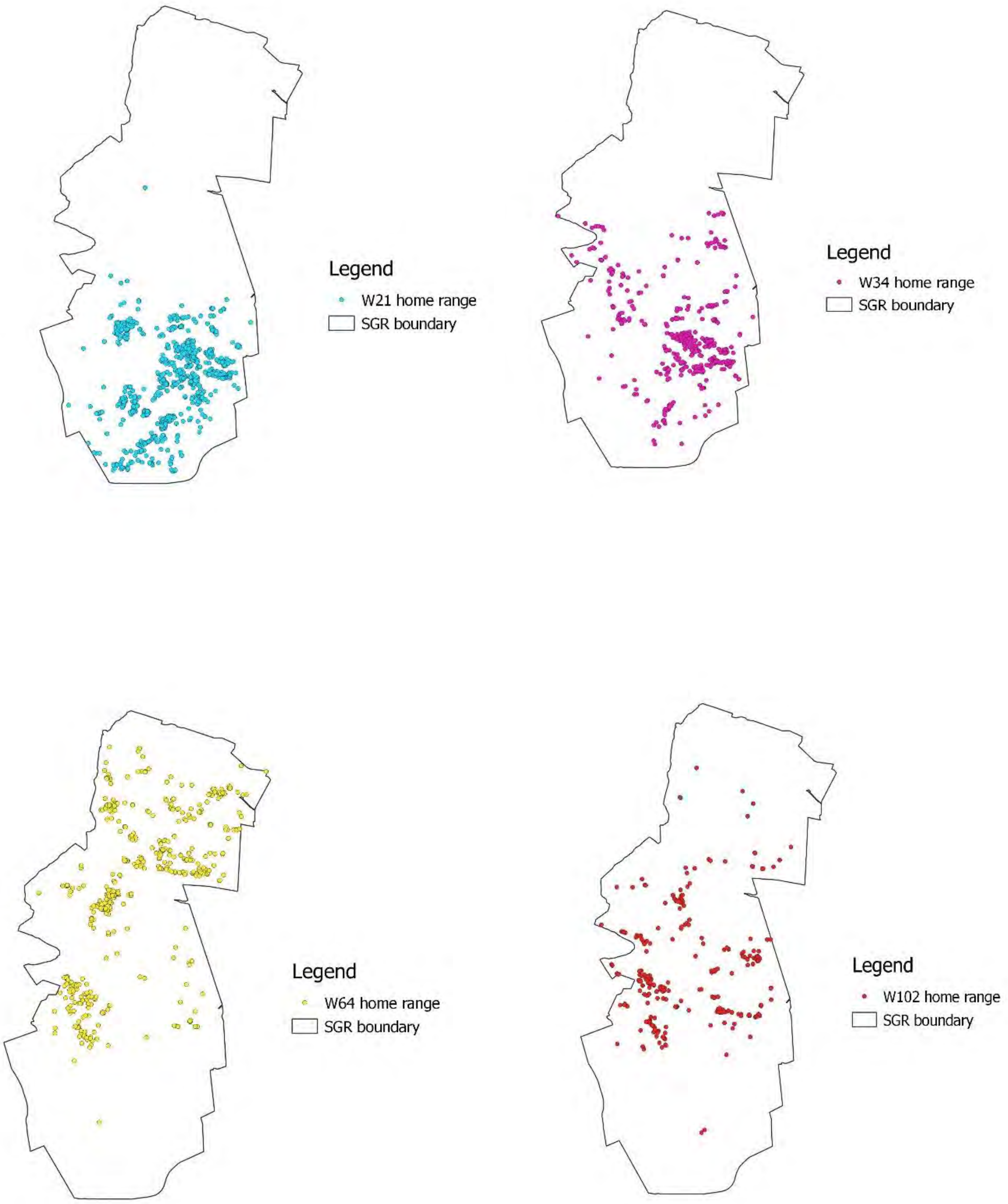
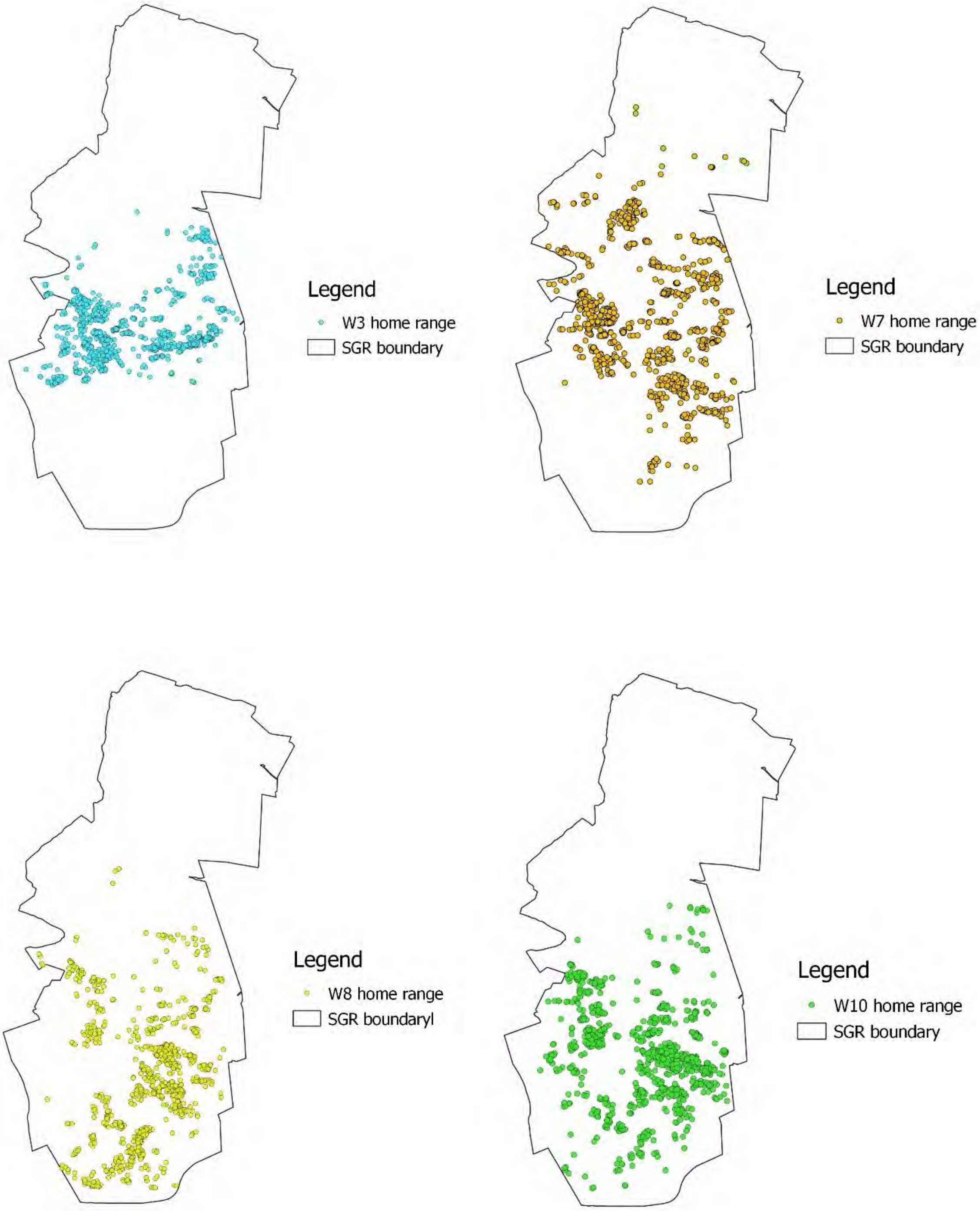


Figure Ib. Home range of adult cows on Shamwari Private Game Reserve displayed as individual sightings.



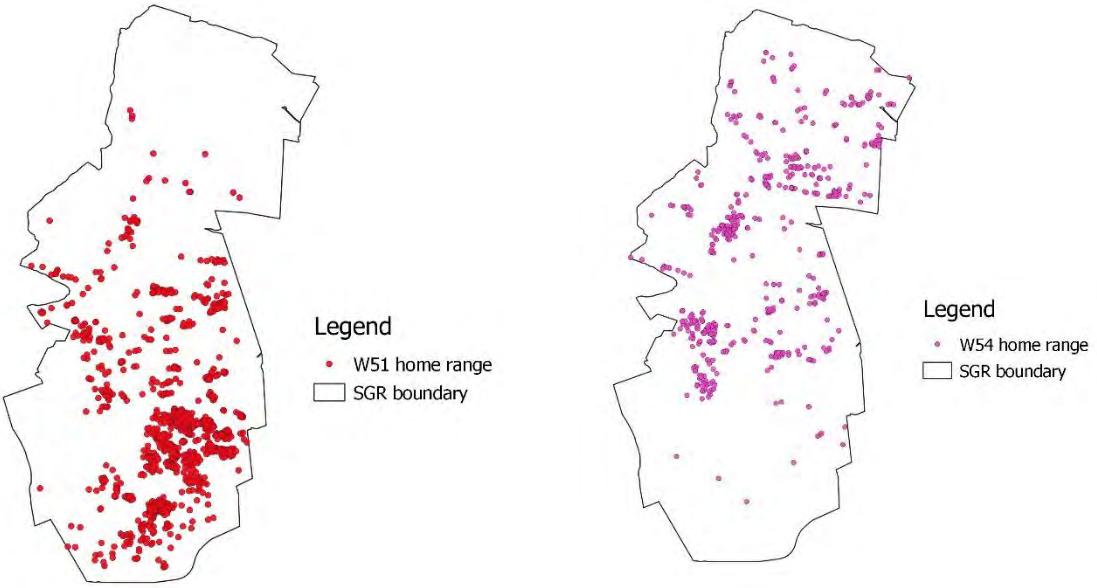
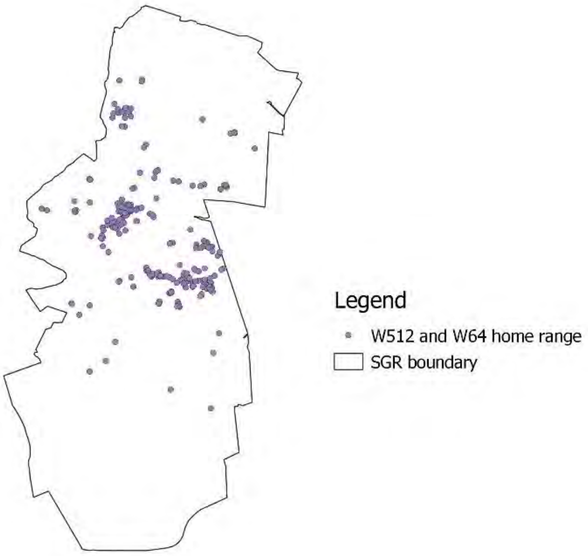
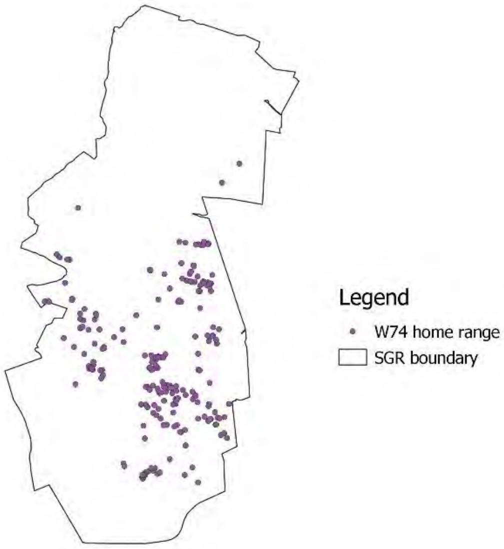
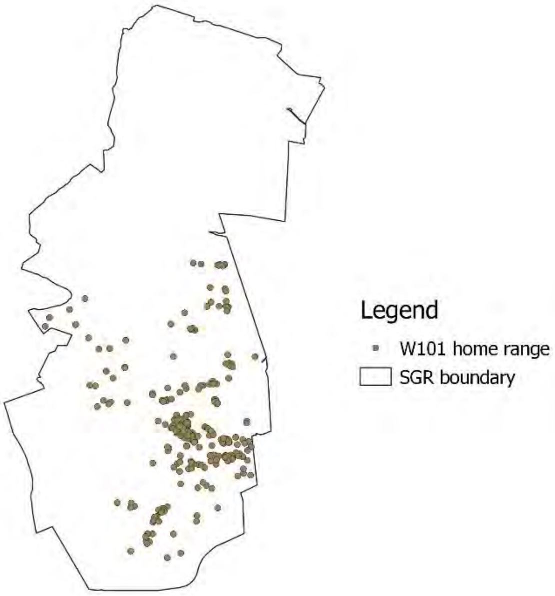
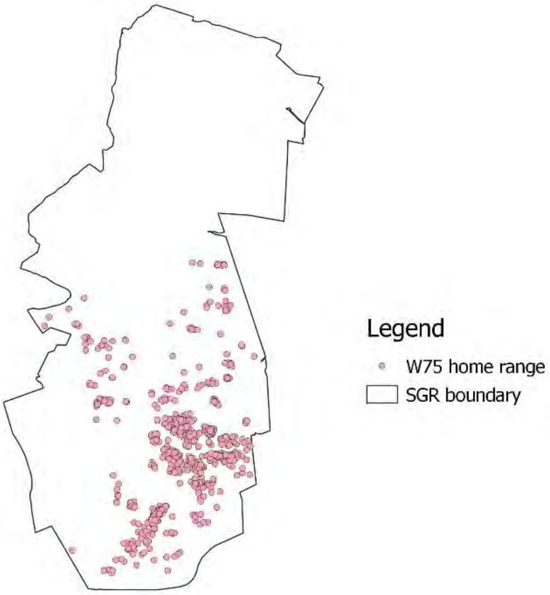


Figure Ic. Home range of sub-adults on Shamwari Private Game Reserve indicated as individual sightings.






Legend
● W101 home range
☐ SGR boundary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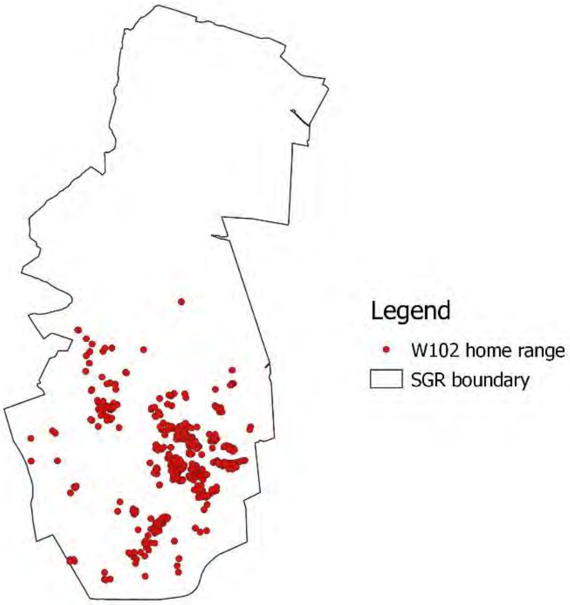
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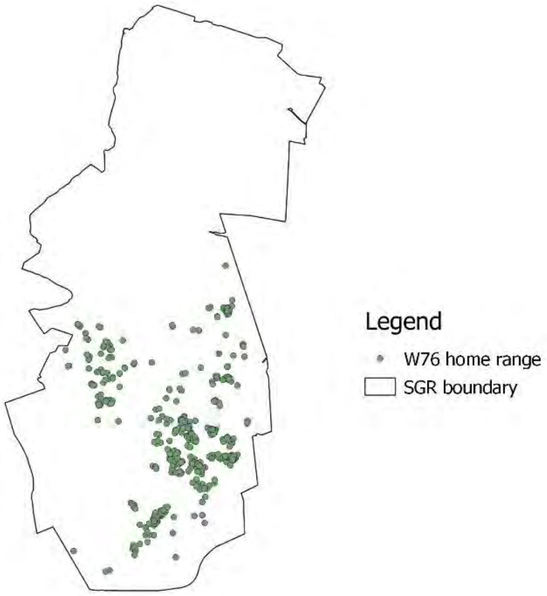
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● W76 home range
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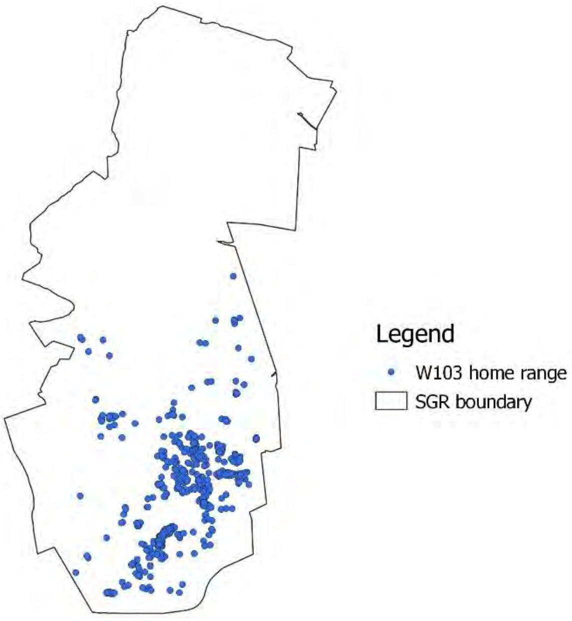
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● W103 home range
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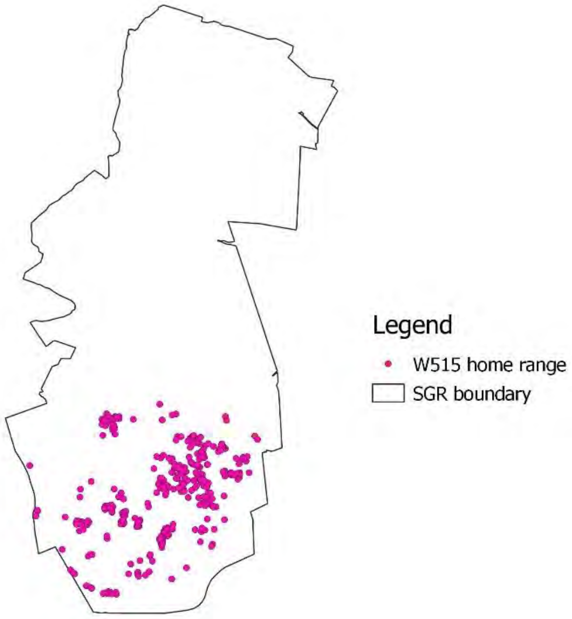
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● W515 home range
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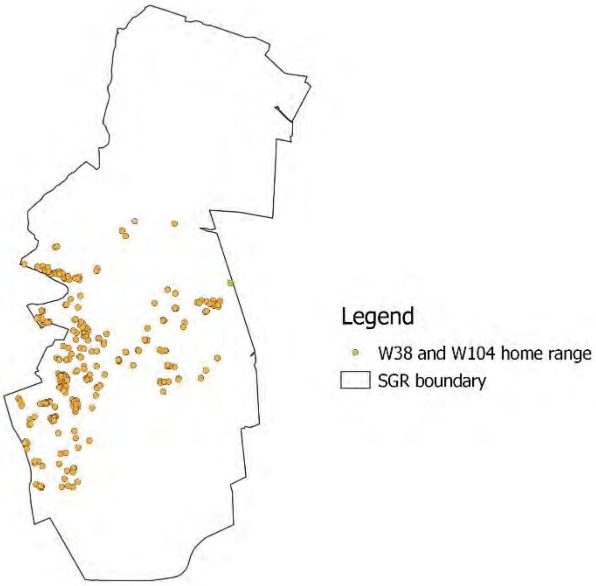
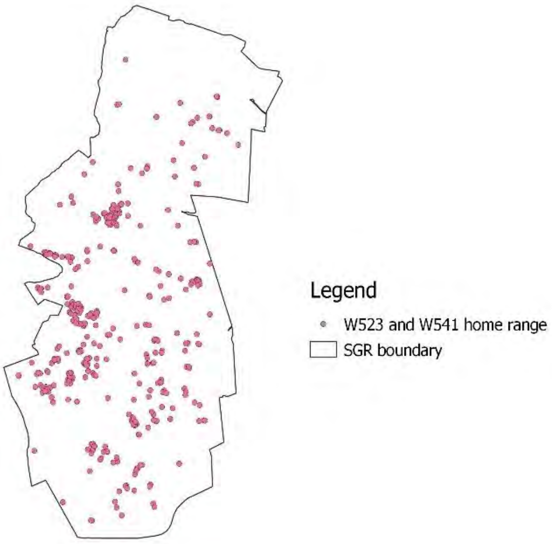

Legend
● W38 and W104 home range
☐ SGR boundary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● W523 and W541 home range
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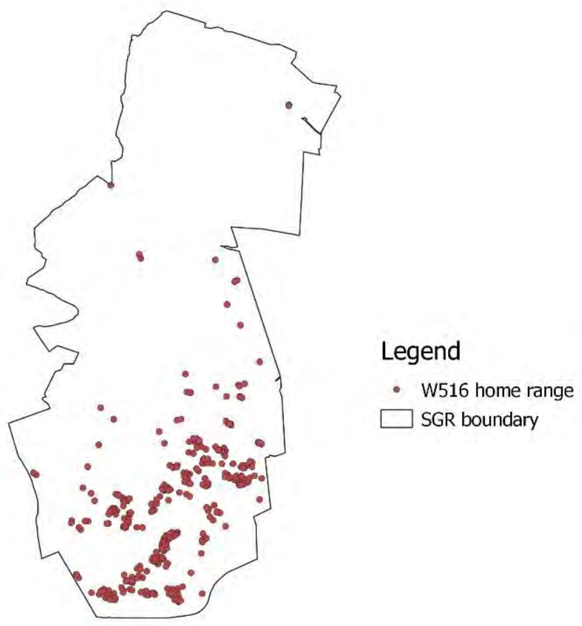
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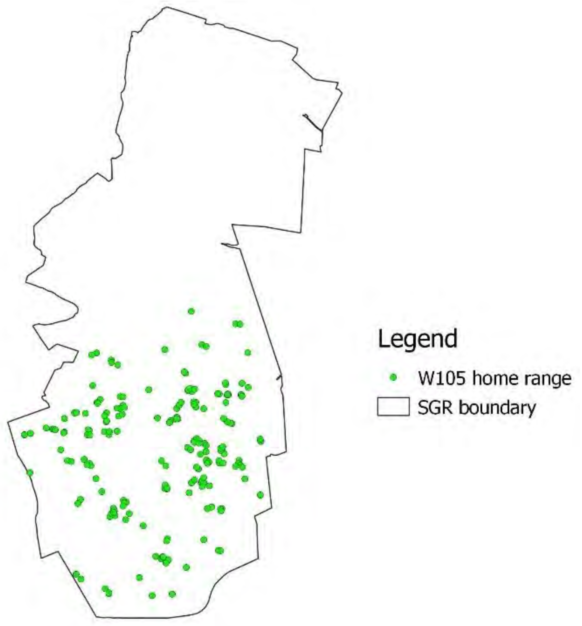
W516 home range
SGR boundary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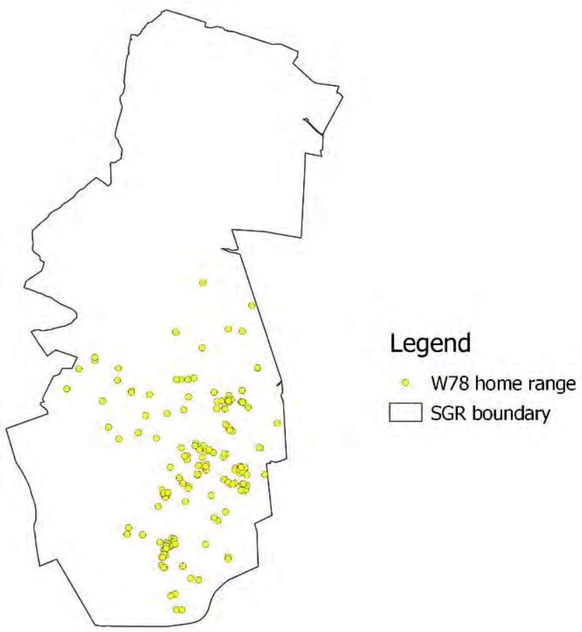
W105 home range
SGR boundary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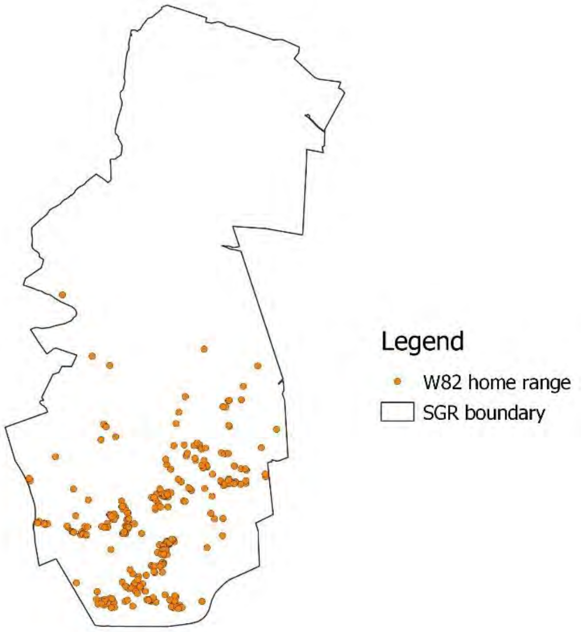
W78 home range
SGR boundary


Legend
W82 home range
SGR boundary