THE DEMOGRAPHY, SPATIAL ECOLOGY AND REPRODUCTIVE SUCCESS OF THE BLACK RHINOCEROS, *DICEROS BICORNIS*, IN HLUHLUWE- iMFOLOZI PARK, KWAZULU-NATAL, SOUTH AFRICA

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ABSTRACT

Black rhinoceroses (*Diceros bicornis*) are endangered; there are only ~5000 individuals remaining worldwide. Consequently, black rhinos are managed as a metapopulation in southern Africa. This means that even though several sub-populations of black rhinos are geographically separated, they are managed as a single population. This is achieved by interchanging genetic material between the sub-populations. The main aim of the metapopulation management approach is to increase black rhino numbers in the sub-region. The Rhino Management Group (RMG), formed in 1989, was tasked with setting scientifically defensible demographic targets for the remaining black rhino sub-populations in southern Africa. In the same year, the RMG set fecundity rate at 25% and stated that each black rhino sub-population should achieve a minimum growth rate of 5% per year. The black rhino population in the Hluhluwe-iMfolozi Park (HiP), KwaZulu-Natal, South Africa, is of international importance as it has historically been a significant donor population for the translocation of black rhinos to establish new sub-populations elsewhere in the sub-region. However, the black rhino population at HiP is performing poorly in terms of reproductive success.

My study was initiated to assess the reproductive life-histories of the black rhino population at HiP and to determine whether the population was meeting the demographic targets set by the RMG. I also wished to assess the use of space by black rhinos in HiP as a potential explanation for the observed reproductive output. Detailed life-history information for known black rhinos (n = 120) was used to investigate reproductive success between 1998 and 2012. The mean age at sexual maturity (ASM) was determined as 12 years, which is higher than the ASM found in black rhino populations that are considered to be performing poorly (ASM = ~ 7 years). The intercalving interval (ICI) was three years, nine months; this was also longer than the ICI of most black rhino populations. Further, the 2012 black rhino population at HiP had a growth rate of 6.4%, and the population comprised 60% adults, 23% sub-adults and 13% juveniles. Such demographics are usually observed in stable populations and it is possible that poor habitat quality could be resulting in the delayed ASM and longer ICI's at HiP. In addition, 5% of the population is removed annually as part of the Black Rhino Range Expansion Program (BRREP) to establish new sub-populations. This could also be negatively influencing the reproductive performance of the HiP population.

To determine the home range and habitat use of black rhinos at HiP, field data from 13 individual adult black rhinos (n = 9 females and 4 males) over a two-year period (2011-2012) were analyzed. Black rhino female home ranges were slightly smaller (15.4 ± 12.9 km^2) than the home ranges of males (23.3 ±14.0 km^2) and both sexes utilized similar habitats in the centre of the park. In addition, both the male and female black rhinos were found closer to rivers and drainage lines than expected. However, the assessment of black rhino space use in HiP was limited by a small sample size, making inferences of the impact of space use on reproductive success difficult. Nevertheless, my study suggests that food availability likely influences the location and sizes of black rhino home ranges at HiP. I believe that my study forms the first step in understanding the factors that influence the reproductive success and habitat use patterns of the current black rhino population at HiP. The information produced by my study should enable park management to identify future research to be conducted at HiP, which will yield more robust data for making informed black rhino management decisions at HiP and elsewhere.

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CHAPTER ONE

GENERAL INTRODUCTION

1.1. Description

The black rhinoceros (hereafter black rhino) (*Diceros bicornis* Linnaeus, 1758; Mammalia: Pachyderm) is a close relative of the white rhinoceros (*Ceratotherium simum*) (Milliken *et al.,* 2009). An adult black rhino is 1.6 m at the shoulder and can weigh as much as 1 000 kg (Skinner and Chimimba, 2005). The average adult male weight at the Hluhluwe-iMfolozi Park (HiP) in KwaZulu-Natal, South Africa was 852 kg, whilst an average female in the same park was 884 kg (Figure 1.1) (Skinner and Chimimba, 2005). The black rhino has a prehensile upper lip which is used to grasp twigs from woody plants. This is one of the features that separate the black rhino from the white rhino. Other distinguishing features include a shorter head, a longer neck, smaller rounded ears and a back which lacks the nuchal hump found in white rhinos (Milliken *et al.,* 2009). The black rhino has a dark grey skin like that of the African elephant (*Loxodonta africana*), whilst the white rhino generally takes on the colour of the soil on which they live (Milliken *et al.,* 2009).

Figure 1.1. Photograph showing a male (right) and female (left) black rhino. *Photo: G. Wienekus.*

Black rhinos have eyelashes and hairy fringes on the ears and the ends of their tails (Skinner and Chimimba, 2005). Their skin is scattered with sweat glands which excrete sweat droplets and have a red tinge when an individual is under stress (Skinner and Chimimba, 2005). Black rhinos have two horns composed of a mass of tubular filaments which are similar to hair (Skinner and Chimimba, 2005). The horns grow from the skin and are not attached to the bone under the skin (Skinner and Chimimba, 2005). The anterior horn is usually longer than the posterior horn. Age and horn size are related and males usually have greater horn sizes than females (Stuart and Stuart, 2007). In the KwaZulu-Natal black rhino population, the maximum anterior horn recorded measured at 1.05 m, whilst the longest posterior horn was 0.52 m (Skinner and Chimimba, 2005).

Adult black rhinos in KwaZulu-Natal suffer from skin lesions caused by filarial infestations of the parasite *Stephanofilaria dinniki* (Hitchings and Keep, 1970; Skinner and Chimimba, 2005). These lesions appear as black, blood-encrusted areas that ulcerate and haemorrhage. The lesions appear on the skin behind the shoulders and may also appear on the chest, neck and forelegs (Skinner and Chimimba, 2005). Both flies and ticks are associated with the transmission of the parasite. Flies from the genus *Musca* (*M. lusoria* and *M. xanthomelas*) and ticks from the *Rhipicephalus* genus (*R. maculates*, *R. appendiculatus* and *R. muhlensi*) have been recorded carrying the parasite

(Hitchings and Keep, 1970). Parasitic lesions are absent in the black rhino populations of Central Africa, Namibia and other parts of South Africa. This is attributed to the absence of the flies that serve as vectors for the parasite (Hitchings and Keep, 1970). Black rhino calves only get the lesions when they are about 6 months old and the reason for this has not yet been determined (Skinner and Chimimba, 2005). The lesions are not related to the health of the individual as they have also been noted to occur on perfectly healthy individuals (Skinner and Chimimba, 2005).

1.2. Taxonomy, distribution and habitat

The black rhino belongs to the *Rhinocerotidae* family, subfamily *Dicerotinae* (Owen-Smith, 1988, Dinerstein, 2011). It is one of five rhino species that remain on the planet. With the recent extinction of the northern white rhino *Ceratotherium Simus cottoni* in the wild, the black and the larger white rhino are the only two rhino species remaining in Africa (Fyumagwa and Nyahoyo, 2010; Emslie, 2011). The other three rhino species are found in Asia, they are the Javan rhino (*Rhinoceros sondaicus*), the Indian rhino (*Rhinoceros unicornis*) and the Sumatran rhino (*Dicerorhinus sumatrensis*) (Owen-Smith, 1988; Fyumagwa and Nyahoyo, 2010).

The International Union for the Conservation of Nature and Natural Resources (IUCN) recognises four subspecies of black rhinos in Africa (Skinner and Chimimba, 2005) (the recent extinction of the north-western *Diceros birconis longipes* has brought this number to three (Emslie, 2011). These subspecies are defined by where they occur; the eastern *Diceros bicornis michaeli,* the south-western *Diceros bicornis bicornis* and the south-central *Diceros bicornis minor* (Brooks and Adcock, 1997; Skinner and Chimimba, 2005). The black rhino population found at HiP is of the *Diceros bicornis minor* subspecies (Brooks and Adcock, 1997).

In the 19th century, the black rhino was distributed from the south-western Cape to Somalia and the northern Cameroon-Ivory Coast border (Figure 1.2) (Owen-Smith, 1988; Skinner and Chimimba, 2005). The black rhino was absent from the equatorial forest region of Central Africa (Figure 1.2), this absence is due to the highly unpalatable, nutrient poor and chemically defended plant species found in these forests (Dinerstein, 2011). In the 1900s, the black rhino was the most numerous of the world's rhino species with between 300 000 to 1000 000 individuals roaming the continent (Emslie and Brooks, 1999; Dinerstein, 2011). The black rhino suffered catastrophic declines in both numbers and the extent of its range between the 1970s and 1980s (Okita-Ouma *et al.,* 2006). The cause of the decline in the distribution of black rhinos can be attributed to a combination of factors, including habitat destruction to make way for the ever increasing human population and poaching (see 1.6. conservation status; Brooks and Adcock, 1997). Numbers declined from 65 000 in 1970 to less than 2 500 in 1992 (Okita-Ouma *et al*., 2006). Today, black rhinos occur in scattered population fragments throughout their historic range (Owen-Smith, 1988). Black rhinos are native to Angola, Kenya, Mozambique, Namibia, South Africa and Zimbabwe; they were re-introduced to Botswana in the early 1980s, Malawi in the early 1990s, Swaziland in 1987 and Zambia in 2003 (Chomba and Matandiko, 2011; Emslie, 2011). The re-introductions were done to maximize population growth rates and to stimulate local community conservation awareness (Emslie and Brooks, 1999). Black rhinos still occur in Kenya (*Diceros birconis michaeli)*, Tanzania (*Diceros birconis michaeli* and *Diceros birconis minor*), Rwanda (*Diceros birconis michaeli*), Malawi (*Diceros birconis minor*) and Mozambique north of the Zambezi River (*Diceros birconis minor*) (figure 1.3) (Skinner and Chimimba, 2005). Black rhinos are extinct in Ethiopia and regionally extinct in Cameroon and Chad (Emslie, 2011).

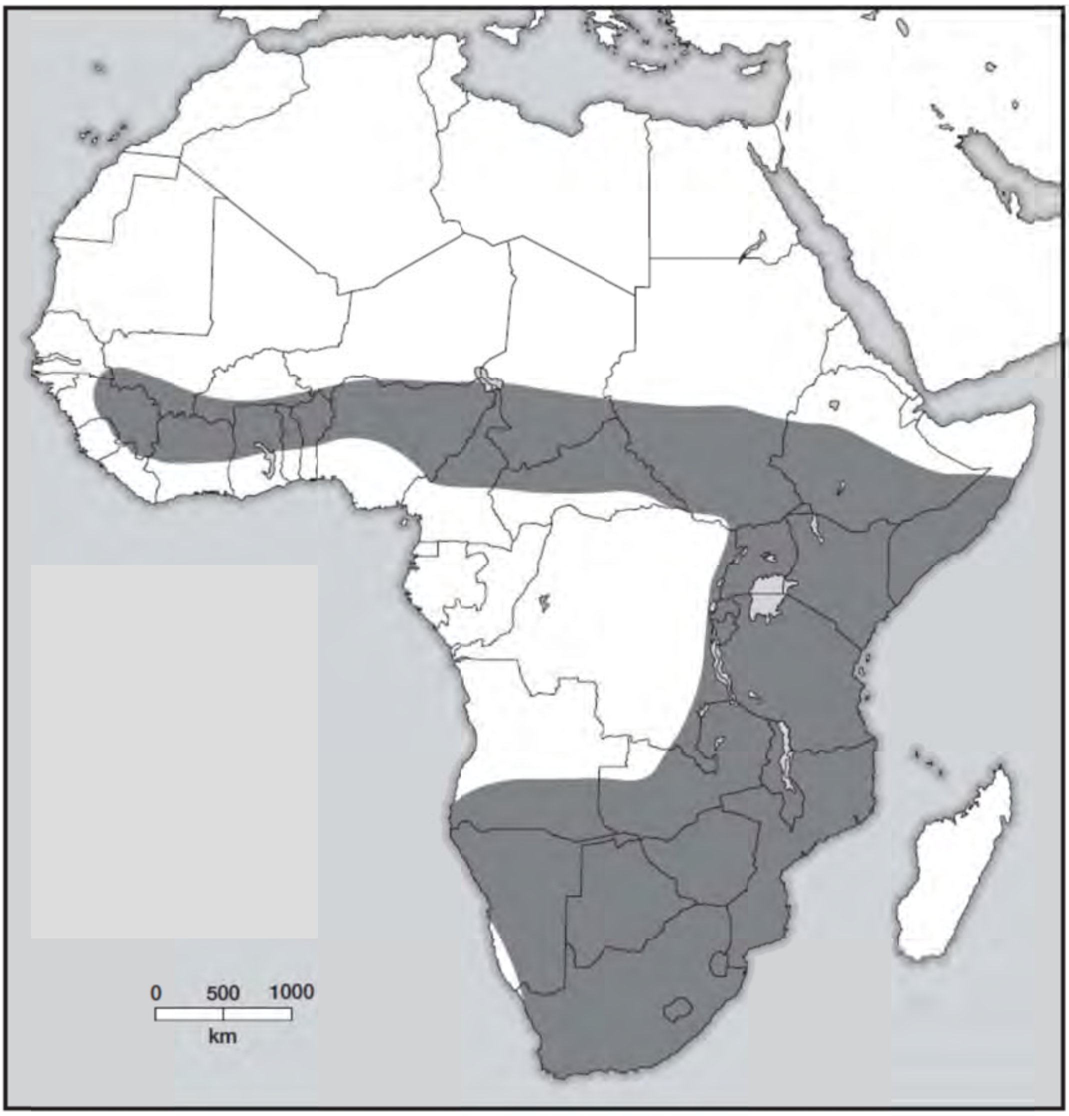

Figure 1.2. The historical distribution of the black rhino c. 1700 (from Emslie and Brooks, 1999).

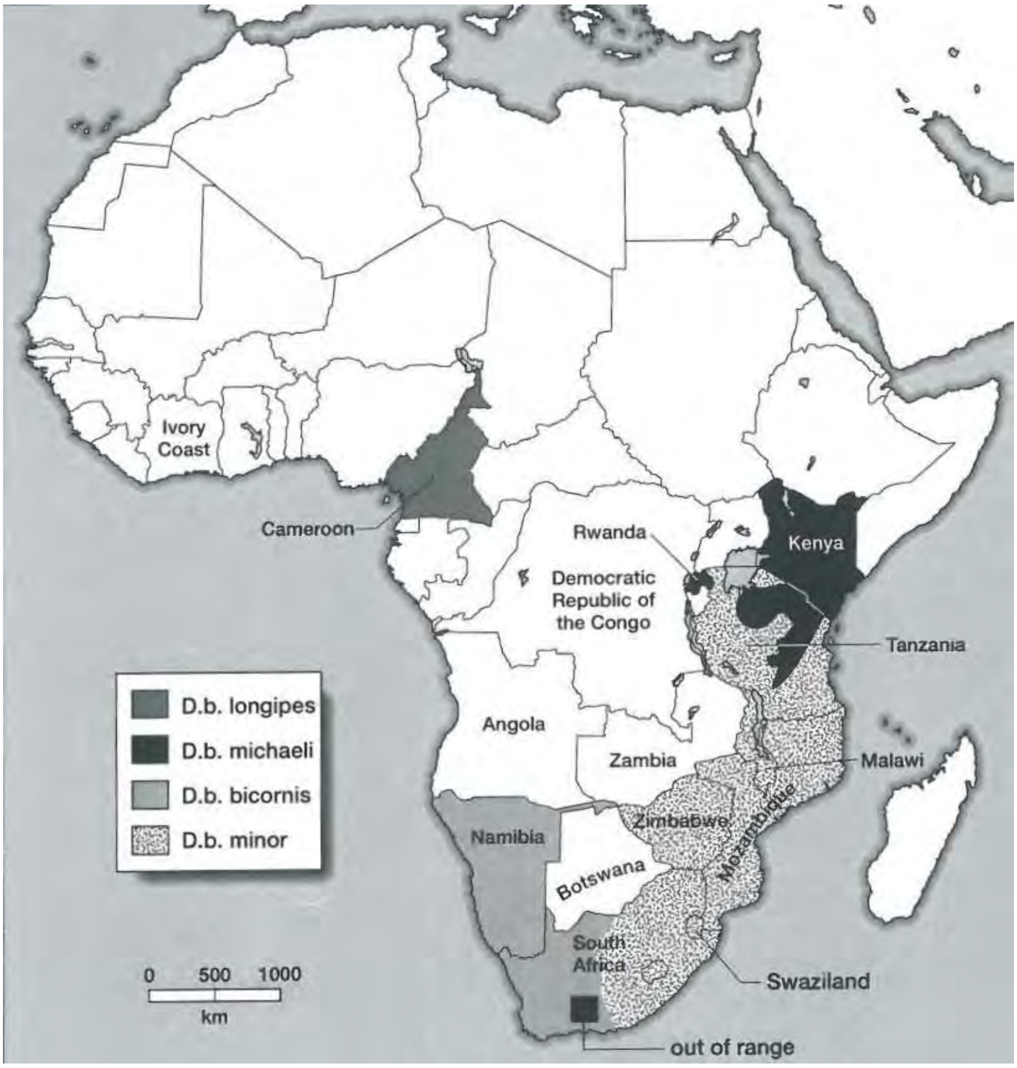

Figure 1.3. The current distribution of the four black rhino subspecies in Africa (see text). *D.b. longipes* has since been listed as extinct in 2011 (Emslie and Brooks, 1999).

The black rhino's habitat ranges from forest to savannah woodland and scrub (Skinner and Chimimba, 2005). Black rhino occur at sea level and up to an altitude of about 1 500 m in the southern African sub-region and up to 2 700 m in East Africa (Skinner and Chimimba, 2005). Black rhino habitat requirements include adequate shrubs and young trees (up to 4 m tall) as forage, and areas with well-developed woodland or thickets to provide shelter during hot and cold weather conditions (Skinner and Chimimba, 2005). Water is also an important requirement as it is not only used for drinking but also for bathing and mud wallowing (Skinner and Chimimba, 2005). Black rhinos are seldom found more than 15 km from a water source (Skinner and Chimimba, 2005). In East Africa during the dry season, the maximum distance from water was 25 km (Skinner and Chimimba, 2005).

Bush encroachment, which is the suppression of palatable grasses and herbs by encroaching unpalatable woody species (Wiegand *et al.,* 2005), favours black rhinos in its early successional stages (Skinner and Chimimba, 2005). This is because black rhinos have the ability to feed on species considered unpalatable such as *Euphorbia* spp., and *Euclea divinorum* (Oloo *et al.,* 1994). However, later successional stands may lead to reduced foraging success because the bush density prevents black rhinos from gaining access to the majority of the palatable species and therefore reduces habitat quality (Emslie and Adcock, 1994; Skinner and Chimimba, 2005). These dense areas do, however, provide good sheltering areas where black rhinos can keep cool during the heat of the day (Emslie and Adcock, 1994). Habitat changes which occurred between the 1950s and 1960s and resulted in the emergence of *Euclea schrimperi; Berchemia zeyheri* and *Searsia pentheri* (Figure 1.4) at HiP reduced the habitat quality and may have contributed to the decline of the species at this site over the last two decades (Emslie and Brooks, 1999; Skinner and Chimimba, 2005).

Figure 1.4. A photograph of a *Searsia pentheri* thicket which is believed to have contributed to the decline in the habitat quality and preferred black rhino browse species at HiP.

1.3. Activity patterns, territoriality and home range

Black rhinos are most active between 06:00 - 07:00 when they are either feeding or walking (Hitchins, 1971). There is generally a decrease in activity around midday (12:00), but activity increases steadily after 14:00 (Hitchins, 1971). The majority of the black rhino population in the Hluhluwe section of HiP, KwaZulu-Natal, South Africa, was found to be active at night (Hitchins, 1971). At HiP, females were active for 47% of the day and 95% of the night, while males were active for 33% of the day and 93% of the night (Owen-Smith, 1988). In East Africa, 30% of the daylight hours were spent eating while 20% was spent walking (Owen-Smith, 1988). During the hottest parts of the day, black rhinos spend more time resting under the shade of thickets or woodland (Skinner and Chimimba, 2005). Females spend at least 6 hours (between 10:00 - 16:00) under shade, while males spend around 5 hours (between 10:00 - 15:00) under shade (Hitchins, 1971). Black rhinos may spend this time standing motionless or lying down (Skinner and Chimimba, 2005). Black rhinos usually rest on ridges facing away from the oncoming wind to take advantage of the cooling breeze that occurs at ridge crests (Dinerstein, 2011). Black rhinos may also lie in dusty hollows or at water holes or mud wallows (Skinner and Chimimba, 2005).

Black rhinos are usually solitary animals (Skinner and Chimimba, 2005). However, long term bonds exist between a female and her calf (Skinner and Chimimba, 2005). These female and calf bonds end when the female is about to give birth to a new calf (Skinner and Chimimba, 2005). The older calf may re-join the cow and her new calf once the younger calf is more active (Skinner and Chimimba, 2005).

Animals engage in a number of daily activities, from travelling between feeding areas, to and from water, resting and other maintenance behaviours such as drinking, wallowing, grooming and social interactions (Owen-Smith, 1988). These activities are generally restricted to a particular segment of the available habitat; the area referred to as the home range because it contains most, if not all, of the resources needed by the black rhino to conduct these routine activities (Owen-Smith, 1988). Black rhinos are not strictly territorial

(Skinner and Chimimba, 2005) as the term territory is only applied to areas that are defended or used by one particular individual or group at the exclusion of others (Owen-Smith, 1988). The home range size of black rhinos differs depending on the sex and age of the individual and the habitat type Skinner and Chimimba, 2005). In areas with a high proportion of thickets and dense stands of woody plants, black rhino home ranges were usually smaller (3.0 km^2) than in more open areas (4.9 km^2) (Hitchins, 1969 ; Owen-Smith, 1988). In addition, male home ranges (5.3 – 51.8 km^2) are usually smaller than females (3.6 – 90.6 km^2) (Goddard, 1967). This is because female home ranges often overlap with other female home ranges and adult bulls seldom have overlapping home ranges (Mukinya, 1973) due to intersexual competition for females (Owen-Smith, 1988; Linklater *et al.,* 2009). In the Masai Mara Game Reserve, Kenya, females with calves had larger home ranges (22.68 km^2) than males (18.60 km^2) (Mukinya, 1973; Reid, 2004) and single females (12.72 km^2) (Goddard, 1967). This may be because both single males and females are solitary and spend most of their day resting, restricting their movements to areas close to shelter (Mukinya, 1973). Moreover, females with calves move greater distance searching for food and perhaps to acquaint the calf with other areas in the home range (Mukinya, 1973). Black rhinos tend to move over wider areas during the wet season (25.1 km^2) than in the dry season (21.1 km^2) (Owen-Smith, 1988; Reid *et al.*, 2007). This may be due to the increased availability of leguminous forbs in grassland areas at this time of the year (Owen-Smith, 1988).

Biotic and abiotic characteristics of the habitat influence habitat selection in black rhinos (Melton, 1987). The abiotic factors that determine whether a habitat is suitable or not include; water availability, altitude, gradient and climate (Melton, 1987). The biotic factors include the distribution of food, presence of competitors and the density and distribution of predators (Melton, 1987). In adult black rhinos, predation is irrelevant and so habitat selection is generally influenced by the other factors. The factors that influence habitat selection may be different for the two sexes due to sex specific requirements (Melton, 1987). Male black rhinos select their home ranges based on the location water points and the presence of females whilst the females base their home range selection decision on forage, water and cover availability (Emslie, 1999; Skinner and Chimimba, 2005).

Lions (*Panthera leo*) and spotted hyaenas (*Crocuta crocuta*) have been reported to attack adult black rhinos (Skinner and Chimimba, 2005). However, of the seven encounters between lions and black rhinos recorded in the Ngorongoro Crater, Tanzania, black rhinos were favoured on all seven occasions. The lions moved away when the female black rhino was about 10 m away (Goddard, 1967). Female black rhinos are more aggressive than males towards predators (Skinner and Chimimba, 2005). Consequently, predation on calves is generally rare (Skinner and Chimimba, 2005). It has been suggested that sub-adult black rhinos that have just left their mothers are more susceptible to predation by lions than adults (Skinner and Chimimba, 2005). A small number of black rhino individuals in the Kruger National Park (KNP), Mpumalanga, South Africa, population have been reported to have ears or pieces of tail missing (Skinner and Chimimba, 2005). This is because some black rhinos lose parts of their pinnae due to interactions with predators, but some rhinos are known to be born without ears (Gwynne, 1969).

1.4. Reproductive behaviour

Black rhinos breed throughout the year with minor peaks in births during January and April-August, and October-November (Hillmann-Smith and Grove, 1994; Skinner and Chimimba, 2005). This suggests that rainfall may be an important cue for reproduction (Hillmann-Smith and Grove, 1994). Females produce their first calves when they are about six years, six months old (Skinner and Chimimba, 2005). In the Great Fish River Reserve, Eastern Cape, South Africa, a female gave birth at four years, one month old (Skinner and Chimimba, 2005). In KwaZulu-Natal, pro-oestrus was found to last 6-7 days, a time characterized by the frequency of tail erecting in females (Skinner and Chimimba, 2005). The length of the oestrus cycle can be up to 35 days (Skinner and Chimimba, 2005). Copulation occurs between two and seven times with each copulation event lasting between 12 and 43 minutes (Skinner and Chimimba, 2005). The number of ejaculations per copulation event range from two in two minutes to nine in 43 minutes (Skinner and Chimimba, 2005). The gestation period is ~478 days (14-16 months), after which a calf weighing ~40 kg is born (Bertschinger, 1994; Hillmann-Smith and Grove, 1994; Skinner and Chimimba, 2005). The calf is able to walk and suckle within 3 hours of birth (Skinner and Chimimba, 2005). Calves only start browsing a few weeks after birth, but continue to suckle until they are about a year old (Skinner and Chimimba, 2005).

The intercalving interval (ICI), the time between one calf and another (Adcock, 2009), is usually two years, six months (Owen-Smith, 1988). The shortest ICI recorded was one year, eight months and this occurred in the adjoining corridor and iMfolozi section of HiP (Owen-Smith, 1988).

1.5. Diet

Black rhinos are predominantly ground feeders that prefer forbs and low growing woody shrubs (Owen-Smith, 1988). Black rhinos use their prehensile upper lip to manoeuvre food into their mouths. Black rhinos use their premolars to bite off shoots and molars are used to grind the food (Skinner and Chimimba, 2005). Black rhinos are selective feeders, often rejecting dry plant material and woody browse is often eaten after fires have occurred and the herb layer has been removed (Skinner and Chimimba, 2005). It is hypothesized that black rhinos prefer browsing on burnt trees because fire alters the smell and taste of twigs by denaturing the chemical composition of plants and decreasing the physical defences used by the plants (Emslie & Adcock, 1994; Weladji and Laflamme-Mayer, 2001). For some plants, black rhinos eat the outer tips of the shoots, while in others they also eat the twigs (Skinner and Chimimba, 2005). Small forbs are often eaten and small quantities of grass may also be taken during the wet season (Skinner and Chimimba, 2005).

In areas where herbaceous plants are less available such as in Namibia and the Addo Elephant Park, Eastern Cape, South Africa, woody plants become the preferred species (Owen-Smith, 1988). Woody plants become less preferred as they grow in size (Skinner and Chimimba, 2005). Owen-Smith

(1988) found that the preferred browsing level of black rhinos is between 0.5m and 1.2 m, with a maximum of 1.5 m. Stem succulents like *Euphorbia* spp. are an important food source during the dry season in most parks (Skinner and Chimimba, 2005). At HiP, *Acacia* spp. such as *A. gerrardii, A. Senegal, A. borleae* and their close relatives make up the bulk of the diet (Skinner and Chimimba, 2005). Young tamboti (*Spirostachys africana*) trees (Figure 1.5) form the dominant food item in the black rhino summer diet (Skinner and Chimimba, 2005). In the Hluhluwe section of HiP, the black rhinos preferred the riverine bush, tamboti thickets and lowland forest margin vegetation, whilst in the iMfolozi section the black rhino preferred habitat that was previously heavily grazed: short grass country with scattered, small acacias (Skinner and Chimimba, 2005). The main species preferred by black rhinos in iMfolozi included *A. karroo, A. nilotica* (Figure 1.6)*, A. gerrardii, A. tortilis, A. borleae* and *Dichrostachys cinerea* (Figure 7) (Emslie and Adcock, 1994). In the Ithala Nature Reserve, KwaZulu-Natal, South Africa, *A. nilotica* and *A. karroo* were the most preferred species (Skinner and Chimimba, 2005).

Figure 1.5. Photograph of the young tamboti (*Spirostachys africana)* trees, a dominant food item in the black rhino summer diet in the Hluhluwe section of HiP.

Figure 1.6. Photograph of the *Acacia nilotica*, a preferred browse species by black rhino in the iMfolozi section of HiP.

Figure 1.7. Photograph showing *Dichrostachys cinerea,* a preferred browse species by black rhino in the iMfolozi section of HiP.

1.6. Conservation status

The black rhino was listed as endangered by the IUCN in 1990 and critically endangered by 2003 (Emslie, 2011). This was due to an estimated 97.6% decrease in the population since 1960 (Emslie, 2011). The main cause for the decline was poaching followed by the clearing of land for human settlements and agricultural needs (Emslie, 2011). However, since 1995 the black rhino population, on a continental level, has been on a slow increase (Emslie, 2011). The South African and Namibian populations have increased the most during this period. In 1980, the South African and Namibian populations were estimated at 630 and 300, respectively (Emslie, 2011). In 2010, the numbers had increased to 1915 and 1750, respectively (Emslie, 2011). The increased numbers in South Africa and Namibia are likely attributed to increased investment in conservation programmes such as intensive rhino monitoring and law enforcement (Emslie, 2011). Nevertheless, poaching for rhino horn continues to plague the species across the continent (Emslie, 2011).

1.7 Rationale for the study

At HiP, poaching is not believed to be a high threat to the black rhino population (Adcock, 2009), yet the population appears to continue to decline in numbers (Adcock, 2009). A black rhino population under suitable conditions (i.e. suitable vegetation/habitat, adequate water supply and rainfall) should have a growth rate of approximately 9% per year (du Toit, 2006) but should achieve at least a minimum of 5% per annum (du Toit, 2006; Goodman, 2013). However, between 1999 and 2002 the HiP black rhino population had growth rates of <5%. The growth rates increased to above 5% between 2003 and 2005; this period was followed by four years of below minimum growth rates. The population recovered in 2010 and has since grown at rates above the minimum 5% growth rate. The periods of below minimum growth rates are significant because the HiP black rhino population is considered an important donor population for the Black Rhino Range Expansion Programme (WWF, 2012). Since 1962, individuals from HiP have contributed to the creation of at least 15 new populations in Africa (Brooks and Adcock, 1997; Skinner and Chimimba, 2005). It is thus extremely important to accurately investigate the demographic and reproductive parameters of the HiP black rhino population in order to begin to understand which factors may be affecting the reproductive success of the population.

The large scale habitat changes which occurred in the early 1950s at HiP (see section 1.2 above) are believed to have resulted in the reduction of the park's estimated black rhino carrying capacity. This is because the amount of black rhino browse recorded in the Hluhluwe in 1990 was much lower than that recorded between 1969 and 1971 (Emslie, 1999). This decline in browse availability corresponded with a decline in black rhino densities in the same period from 0.80 rhinos/km^2 to 0.26 rhinos/km^2 (Emslie, 1999). The black rhino carrying capacity in Hluhluwe was estimated to have declined from 1.45 rhinos/km^2 before the 1950s to 0.4 rhinos/km^2 in the 1990s (Emslie, 1999; Reid, 2004). The changes in vegetation composition in the park could have led to black rhinos increasing the sizes of their home ranges (from 3-7.5 km^2 in the 1960s to 15 km^2 in 1999) in order to meet their nutritional needs (Emslie, 1999; Reid *et al.,* 2007).

While it is well-known that black rhino spatial ecology (like most large herbivores) changes seasonally and is also influenced by factors such as sex and age (see section 1.3 above; Goddard, 1967; Reid *et al.,* 2007), the link between space use and reproductive success is less formally understood. Furthermore, most of the studies have focused on the population patterns of black rhinos (Goddard, 1967; Joubert and Eloff, 1971; Mukinya, 1973; Conway and Goodman, 1989; Kiwia, 1989); they have not investigated reproductive parameters in detail.

1.9. Objectives

The main objectives of this study were to:

- Determine how the reproductive parameters (age at sexual maturity, intercalving interval, fertility and fecundity rates) of the HiP black rhino population compared to other black rhino populations within the southern African region and the rest of Africa;

- Assess whether the HiP black rhino population is achieving the genetic and demographic targets set by the RMG and to;
- Investigate the spatial ecology of black rhino at HiP and how this relates to reproductive success.

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CHAPTER TWO

STUDY SITE

2.1 Location and history

The Hluhluwe and iMfolozi Game Reserves were founded in 1895; are located 280 km North of Durban, South Africa and are the oldest protected areas in Africa (Brooks, 2000; Ezemvelo, 2011). The two reserves were amalgamated in 1989 to form the Hluhluwe-iMfolozi Park (HiP) which is ~960 km^2 in size (Figure 2.1) (Brooks, 2000). HiP is a sanctuary for black rhino and has the world's second largest population of white rhino (Brooks, 2000; Ezemvelo, 2011). It was at HiP that the world acclaimed Operation Rhino was introduced during the 1960s and is credited with bringing the white rhino back from the brink of extinction (Brooks, 2000; Ezemvelo, 2011). The park is divided into five management sections, namely Manzimbomvu, Nqumeni, Masinda, Mbhuzane and Makhamisa (Figure 2.2). HiP is under the management of Ezemvelo KwaZulu-Natal Wildlife (Ezemvelo, 2011). Ezemvelo KZN Wildlife is a provincial nature conservation and tourism organization responsible for the conservation of biodiversity and associated activities for the province of KwaZulu-Natal in South Africa (Ezemvelo, 2011).

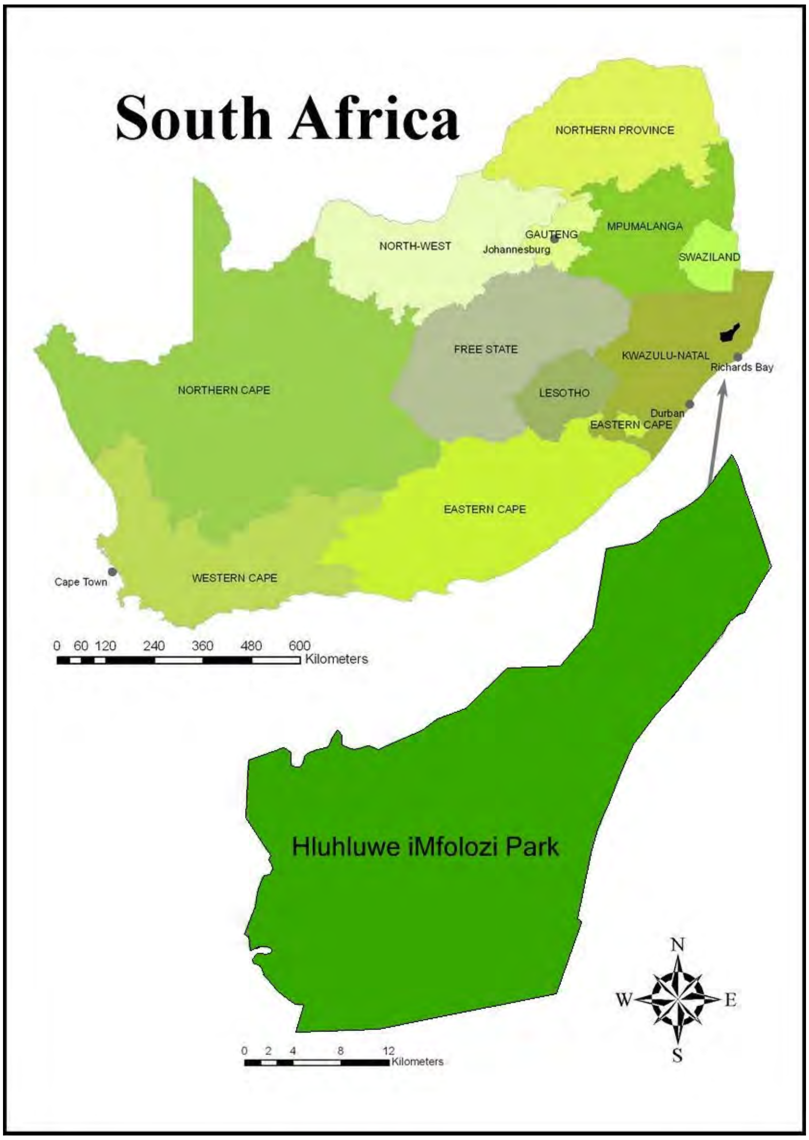


Figure 2.1. Map showing the location of Hluhluwe-iMfolozi Park in relation to South Africa.

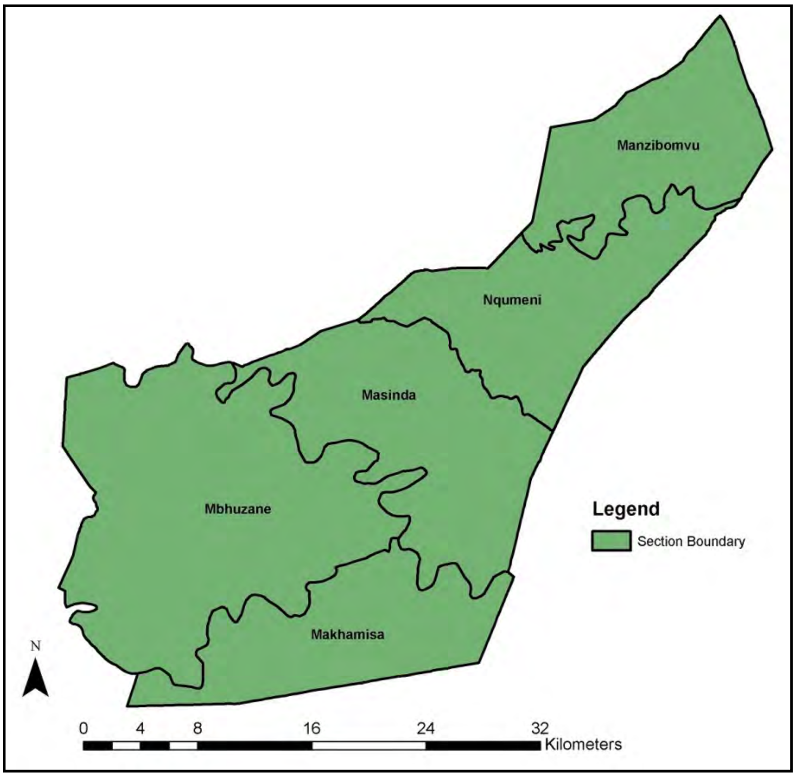


Figure 2.2. Map showing the five management sections of Hluhluwe-iMfolozi Park.

2.2. Climate

The climate at HiP is influenced by the St Lucia coast and the differences in the local weather are related to topography (Ezemvelo, 2011). HiP receives seasonal annual rainfall between October and March (Ezemvelo, 2011). The mean annual rainfall ranges from 650 mm in the low-lying areas of the western part of the park to 985 mm in the high altitude areas found in the north of the park (Ezemvelo, 2011).

HiP has a warm, temperate climate with annual temperatures ranging from ~13 °C to ~35 °C (Ezemvelo, 2011). Thunderstorms are a common summer feature with a few hail storms each year (Ezemvelo, 2011). The park receives north-easterly to easterly winds during the summer which bring moisture laden air and mist (Ezemvelo, 2011). The dry westerly winds received during the autumn and winter seasons have a strong evaporative effect on vegetation and enhance the flammability of the vegetation during the dry season (Ezemvelo, 2011).

Weather data for Riverview, a suburb of Mtubatuba (~ 25 kms North HiP), provided by the South African Weather Service was used to describe the weather trends of HiP.

The mean annual rainfall for the study period (April 2012 – March 2013) was 83.8 mm (Figure 2.3). September experienced the highest rainfall during the study period at approximately 217 mm, followed by December with 205 mm. The hottest day during the study period had a maximum temperature of 38 ºC, while the coldest day had a minimum temperature of 6.8 ºC. The mean monthly temperatures ranged between 11.1 ºC to 30.2 ºC (Figure 2.4).

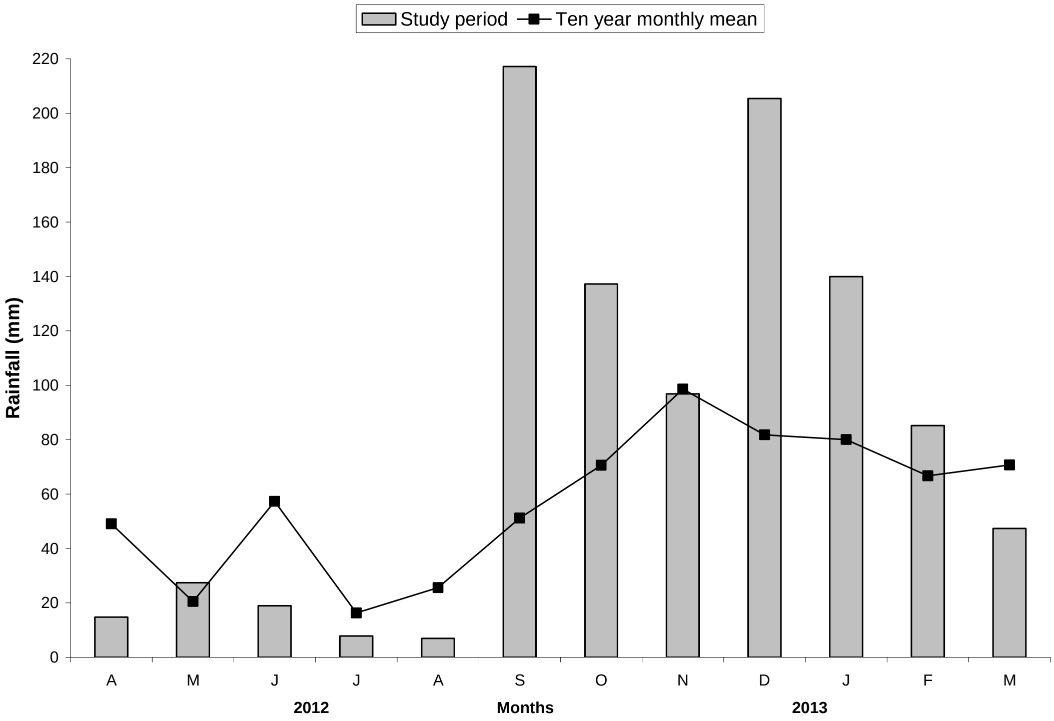


Figure 2.3. Total monthly precipitation during the study period (2012-2013) at Riverview in relation to the ten-year monthly mean.

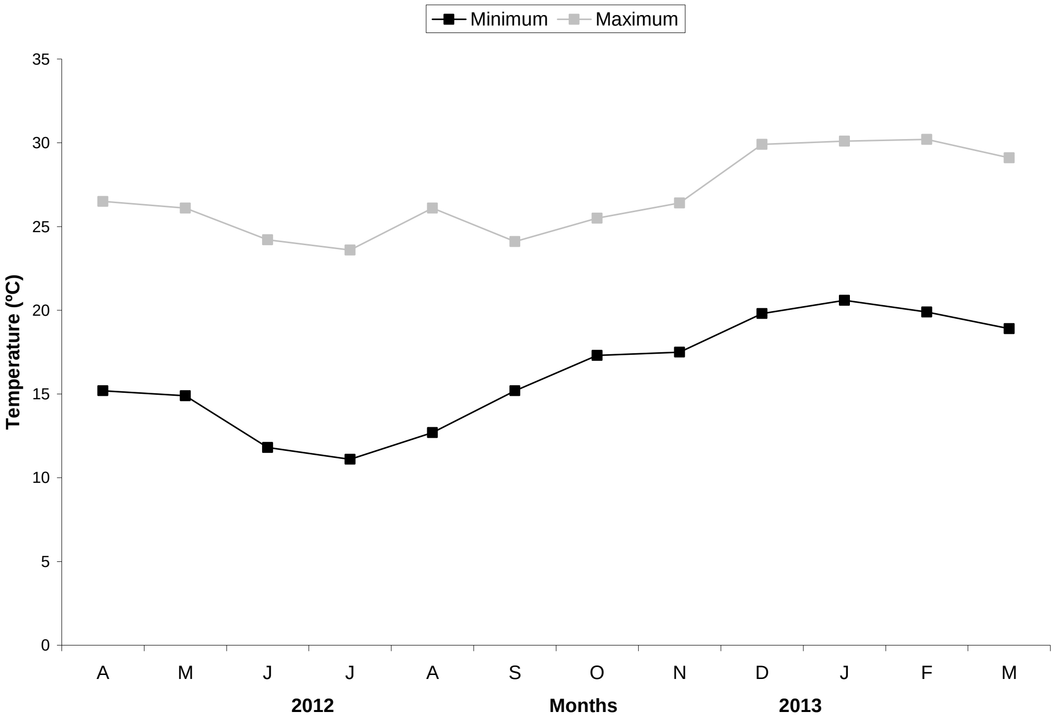


Figure 2.4. The mean monthly minimum and maximum temperatures for Riverview during the study period (2012-2013).

2.3. Topography, geology and hydrology

The HiP topography (Figure 2.5) consists of gentle, rolling hills at higher altitudes, which become steeper valleys and end up as undulating lowlands that carry the Umfolozi rivers and their floodplains (Ezemvelo, 2011). The geology of the park is diverse and is representative of the geological structure of the KwaZulu-Natal region (Ezemvelo, 2011). The stratigraphy composition of the park is made up of the following geological formations; the Nseleni Gneiss, which is the oldest formation that forms the basement granite of the KwaZulu-Natal region (Ezemvelo, 2011). Natal Group Sandstone overlies the Nseleni Gneiss (Ezemvelo, 2011). The Dwyka Formation overlies the Natal Group Sandstone (Ezemvelo, 2011). The Ecca Group rocks form the most dominant surface geology in the park and overlies the Dwyka formation (Ezemvelo, 2011). The Vryheid formation overlies the Ecca Group rocks and is the most widespread and common rock in the park (Ezemvelo, 2011). Overlying the Vryheid formation is the Ntabene formation, followed by Sabi

River Basalt Formation and finally the dolerites of the Rooi Rand Dyke Swarm (Ezemvelo, 2011).

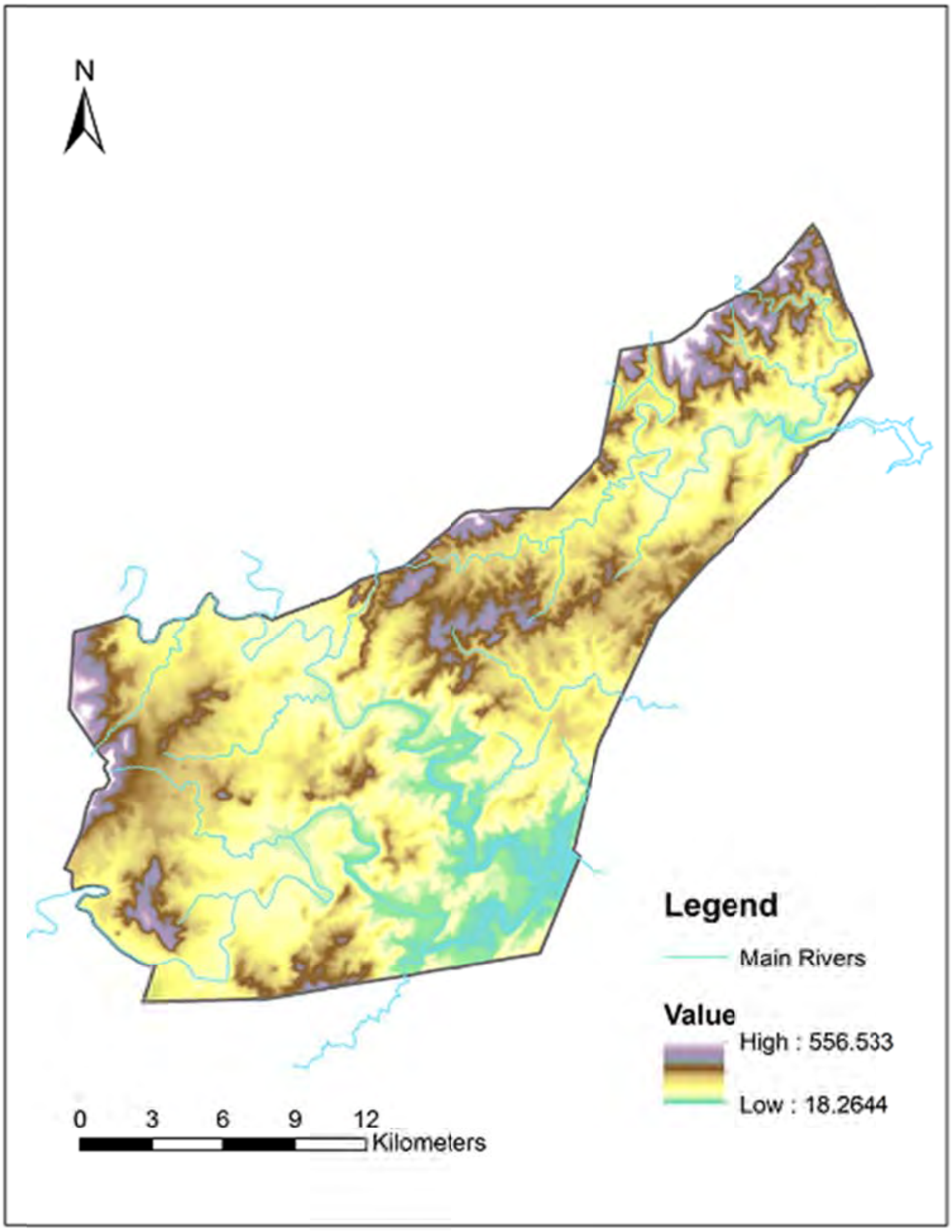


Figure 2.5. The topography and drainage patterns of the Hluhluwe-iMfolozi Park (ArcGIS 9; map units decimal degrees; not projected).

HiP is trisected by three main watercourses (Figure 2.5), the White Umfolozi River which flows through the iMfolozi section of HiP in a west-east direction (Ezemvelo, 2011). The Black Umfolozi River also flows through the iMfolozi section of HiP but in a north-west to south-east direction (Ezemvelo, 2011). The Hluhluwe River flows through the Hluhluwe section of the park in north-east direction (Figure 2.5) (Ezemvelo, 2011). These rivers have water throughout the year, but most of the streams and smaller rivers in the park are non-perennial (Ezemvelo, 2011).

2.4. Vegetation

The park covers a vast and diverse landscape, consisting mainly of steep wooded hills, grass-covered slopes and riverine woodland along the many rivers and streams (Brooks, 2000). The park is situated in the Savanna biome, a tropical vegetation type that is characterized by woody plants and grasses (Cowling *et al*., 1997). Savannas are the most abundant vegetation types in Africa and cover at least 54% of southern Africa (Cowling *et al*., 1997). HiP contains 60% of the savanna found within protected areas in KwaZulu-Natal (Ezemvelo, 2011). The park lies within two broad veld types; the Lowveld subcategory that occurs in the Tropical Bush and Savanna Types category and the Zululand Thornveld subcategory that falls into the Coastal Tropical Forest Types category (Whateley and Porter, 1983; Acocks, 1988).

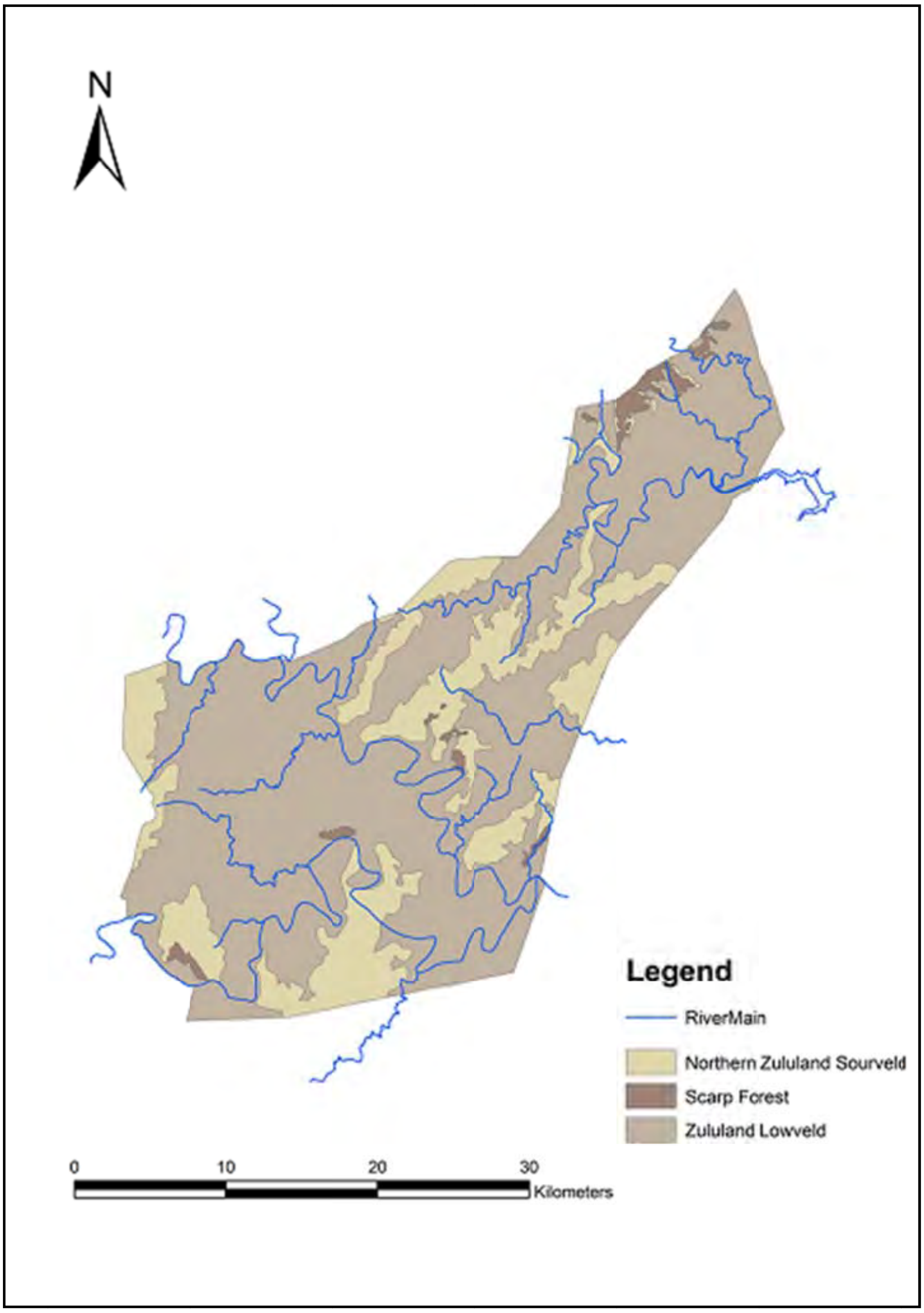


Figure 2.6. Distribution of the vegetation types at Hluhluwe Game Reserve according to Mucina and Rutherford (2006). (ArcGIS 9; map units decimal degrees; not projected).

From these two broad veld types, three vegetation types can be distinguished (Figure 2.6); the Northern Zululand Sourveld, Zululand Lowveld and the Scarp Forest (Mucina and Rutherford, 2006).

Northern Zululand sourveld

This vegetation type (Figure 2.7) consists of wooded grasslands, pure sour grassland and rare occurrences of bushveld thickets (Mucina and Rutherford, 2006). Northern Zululand sourveld generally occurs on low terrain with undulating mountains and well-drained and shallow soils (Mucina and Rutherford, 2006). It occurs in areas with summer rainfall and occurs at high altitudes of between 450 and 900 m in HiP (Mucina and Rutherford, 2006). Small *Acacia* sp. trees such as *Acacia woodii* and *A. nilotica* are the important tree species found in this vegetation type (Mucina and Rutherford, 2006).

Figure 2.7. Photograph showing the Northern Zululand sourveld vegetation that can be found at Hluhluwe-iMfolozi Park. *Photo L.W. Powrie*

Zululand lowveld

This vegetation type (Figure 2.8) occurs at lower altitudes, between 50 and 450 m in slightly undulating landscapes with black-clay and well-drained soils (Acocks, 1988; Mucina and Rutherford, 2006). It occurs in areas with summer rainfall of about 500 – 750 mm and also receives some winter rain (Acocks, 1988; Mucina and Rutherford, 2006). It supports a variety of bushveld units such as dense thickets of *Dichrostachys cinerea* to park-like savanna of *A. tortilis* and woodland dominated by *A. nigrescens* trees (Mucina and

Rutherford, 2006). This vegetation type is characterized by mosaic tall grassland types scattered with solitary trees and shrubs and typical savanna thornveld and thicket patches (Mucina and Rutherford, 2006). Important plant species found in this vegetation type include *A. burkei, A. nigrescens*, *A. nilotica, D. cinerea* and *A. robusta* along rivers (Acocks, 1988; Mucina and Rutherford, 2006).

Figure 2.8. Photograph showing the Zululand lowveld vegetation found at Hluhluwe-iMfolozi Park. *Photo L. Mucina.*

Scarp forest

Scarp forest (Figure 2.9) occurs at low altitudes, between 20 and 600 m on nutrient poor, leached and shallow soils (Mucina and Rutherford, 2006). This vegetation type is typically tall (15-25 m), species rich, structurally diverse, and multilayered (Mucina and Rutherford, 2006). The canopy and understorey tree layers are well developed but the herb layers are not (Mucina and Rutherford, 2006). The most important plant species in this vegetation type include *Buxus macowanii* and *B. natalensis* (Mucina and Rutherford, 2006).

Figure 2.9. Photograph showing the Scarp forest vegetation found at Hluhluwe-iMfolozi Park. HiP. *Photo A. Riley*

2.5. History of the HiP black rhino

Black rhinos were formerly widespread throughout South Africa but declined due to poaching and habitat destruction, to between 100 – 150 individuals by 1930 (Hitchins and Brooks, 1986; Brooks, 1989; Brooks and Adcock, 1997). The remaining black rhinos were all found in the Hluhluwe-iMfolozi and Mkhuze Game Reserves, KwaZulu-Natal, South Africa (Brooks, 1989). Efforts put in place by staff at these reserves led to the population recovery (Brooks, 1989). These included complete fencing of the reserve, so that animals could no longer wander outside the park boundaries (Emslie and Brooks, 1999). An intensive population monitoring programme was also initiated and included regular patrolling as well as increased anti-poaching law enforcement (Emslie and Brooks, 1999). By 1961, there were ~300 black rhinos in HiP; double the number from the 1930 count (Hitchins, 1968). Despite an unexpected die-off of about 46 black rhinos in 1961, the population had recovered to such an extent that in 1962 the Natal Parks Board (now Ezemvelo KZN Wildlife) conducted translocations of black rhinos (Brooks, 1989). The black rhinos were translocated to at least five other reserves including Ndumo Game

Reserve, KwaZulu-Natal, South Africa and the Kruger National Park, Mpumalanga, South Africa, to establish new populations (Hitchins *et al*., 1972; Brooks, 1989). Between 1962 and 1992, almost 200 black rhinos were translocated to other protected areas in southern Africa (Brooks, 1989).

2.6. **Individual identification**

Black rhino at HiP are routinely immobilized and individually ear-notched to allow for the identification of each individual in the field (Hitchins, 1990; Brooks and Adcock, 1997). The process involves several incisions (~2 cm triangles) into the ears of the black rhinos to generate unique number combinations (Hitchins, 1990). The number and location of each notch creates a unique notch pattern for each individual (Figure 2.10) and it is important that black rhinos within the same reserve receive a unique ear notch pattern (Hitchins, 1990; Brooks and Adcock, 1997). The notch patterns are kept simple to allow for easy identification in the field (Hitchins, 1990). Examples of the notching patterns and how they can create unique number combinations for each black rhino can been seen in Figure 2.11 (A and B). The notching pattern in Figure 2.11 (A) gives a total notch number of 112 while the pattern in Figure 2.11 (B) gives a total notch number of 341.

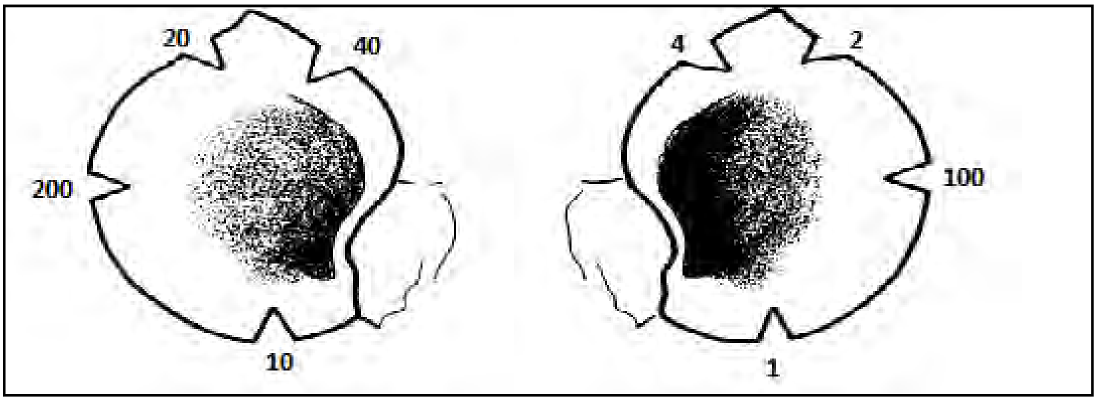


Figure 2.10. Picture of black rhino ears showing the location and numbering pattern for notches (modified from Hitchins, 1970).

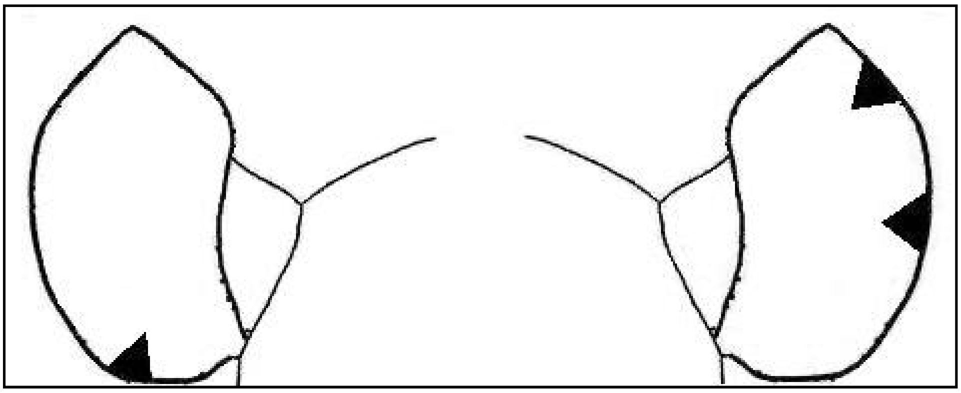
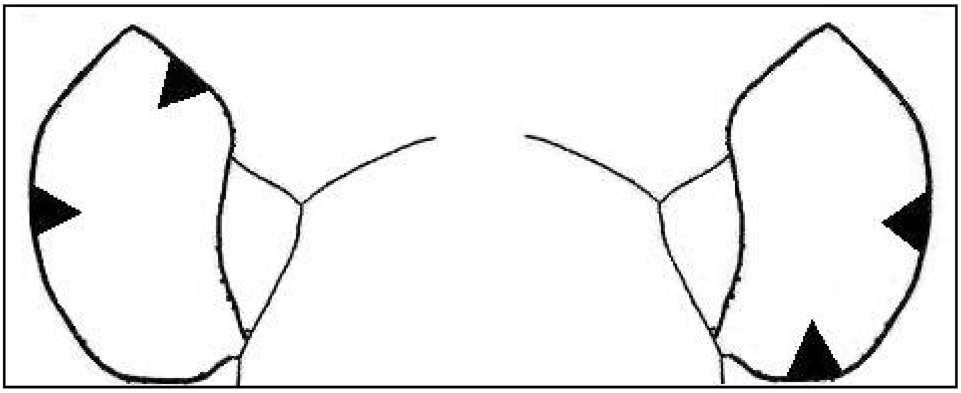


Figure 2.11. Picture of black rhino ears showing the location and numbering pattern for notches that A) give a notch number of 112 and B) give a notch number of 341.



Sexing of black rhinos in the field is achieved by looking at the external genitalia (Mukinya, 1976). It is easy to distinguish the genitalia of an individual when its tail is lifted (Mukinya, 1976). The age criteria used to age black rhino in the field was developed in 1970 by Hitchins (Appendix A) and modified by Emslie *et al.* (1993). This is a system recommended by the Rhino Management Group (RMG) (Emslie *et al*., 1993). The aging system involves measuring the height of a calf relative to that of an adult individual (usually its mother) (Appendix A). Calves between the ages of 0- 5 months fall into the A age class, calves between 5 months to 1 year fall into B age class, 1- 2 years are in C age class, 2 – 3.5 years are in D age class, 3.5 years to 7 years are in E age class and individuals 7 years and older are in the F age class (Appendix A) (Hitchins, 1970; Emslie *et al*., 1993; Adcock, 1996).

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CHAPTER THREE

THE DEMOGRAPHY AND REPRODUCTIVE SUCCESS OF BLACK RHINOCEROS (*DICEROS BICORNIS)* IN THE HLUHLUWE-IMFOLOZI PARK, KWAZULU-NATAL, SOUTH AFRICA

3.1 Introduction

The Hluhluwe-iMfolozi Park (HiP) black rhinoceros (hereafter black rhino) population is one of the most important black rhino populations in southern Africa (Brooks and Adcock, 1997; Emslie and Brooks, 1999), as it serves as a donor population for the Black Rhino Range Expansion Programme (BRREP) (WWF, 2012). The BRREP was initiated in 2003 to extend the range of the black rhino and to start new populations where black rhino occurred historically, mainly within the KwaZulu-Natal province of South Africa (WWF, 2012). It is therefore important to maintain the HiP population at maximum productivity to ensure that the BRREP is sustained.

As a donor population, 5% of the HiP black rhino population is removed and translocated to new areas annually (Clinning *et al.,* 2009). For these translocations to be possible, a high annual population growth rate of at least 5% is required to ensure that the species does not become locally extinct (Hrabar and du Toit, 2005; du Toit, 2006). Consequently, it is important to understand the factors which can affect this productivity (Hrabar and du Toit, 2005).

Population dynamics in herbivorous mammals are governed by the differences between births, deaths, emigration and immigration (Fowler, 1981). Vital rates such as the age at sexual maturity (ASM), conception rate, gestation length and intercalving interval (ICI) all influence fecundity, growth potential and turnover or generational time (Gaillard *et al.,* 1998; 2000).The minimum age at first conception indicates the potential for the population to increase because the earlier the minimum age at sexual maturity, the longer the lifetime productivity (Owen-Smith, 1988). Thus, if females attain sexual maturity and start reproducing at an early age, the growth rate for the population could increase as long as nothing else changes.

Longer ICIs reduce the number of calves born each year and therefore result in a reduction in the growth rate. Significantly, long-lived animals (such as black rhinos) can also be heavily influenced by stochastic environmental events such as drought, flood, fire and disease (Fowler, 1981; Gaillard *et al.,* 1998; 2000; Hrabar and du Toit, 2005; Greaver *et al*., 2013). Mortalities by fire are generally indiscriminate of age and sex because smoke inhalation (which is the main cause of death from fires) affects all animals (Singer *et al*., 1989). Drought leads to shortages of food, which result in starvation (Singer *et al*., 1989). Moreover, starvation may lead to increased susceptibility to disease (Singer *et al*., 1989). Predation does not seem to affect adult black rhinos due to their large size and, as such, predation does not influence the population dynamics of black rhinos (Schenkel and Schenkel-Hulliger, 1969; Pianka, 1970; Hrabar and du Toit, 2005). However, there are suggestions that lions may depredate black rhino calves (Plotz and Linklater, 2009).

To maintain high productivity rates in black rhino, it has been suggested that populations should be kept at 75% of the ecological carrying capacity (ECC; du Toit, 2006). ECC is a concept that looks at the number of individuals of a species that an area can comfortably sustain at a given time, in a way that available resources such as water and food are sufficient to keep the population fairly constant (du Toit, 2006). The estimated carrying capacity for a species in an area does not remain constant but changes temporally as changes in vegetation occur. The reason for keeping populations at 75% is to maintain a balance between the potential for high growth rates and to avoid density dependent effects (Hrabar and du Toit, 2005).

Most protected areas with black rhinos in Africa are enclosed (i.e. fenced) and it becomes impossible for the black rhinos to migrate and avoid environmental, demographic and genetic stochasticity (Hrabar and du Toit, 2005; Greaver *et al*., 2013). This increases the vulnerability of small populations to extinction (Greaver *et al*., 2013). Consequently, the Rhino Management Group (RMG) has suggested that the southern African black rhino population should be managed as a metapopulation (Hrabar and du Toit, 2005). A metapopulation is defined as geographically separated groups of one species which is managed and/or conserved as a single population (Patton *et al*., 2008). This is achieved by interchanging genetic material between sub-populations through the exchange of breeding animals or their semen, ova or embryos (Hall-Martin and Knight, 1994; du Toit, 2006; Patton *et al.*, 2008; Greaver *et al*., 2013). Managing black rhinos as a metapopulation ensures that genetic diversity is not lost as this is essential for the long-term evolutionary potential of black rhinos (Patton *et al.*, 2008).

To facilitate meta-population management for black rhinos in the southern African region, the RMG has set clearly defined genetic and demographic targets for all four sub-populations (South Africa, Namibia, Swaziland and Zimbabwe) (du Toit, 2006). Together, these sub-populations make up 94% of all black rhinos in Africa (du Toit, 2006). The targets for the metapopulation include overall population size targets for all provinces within South Africa (set at 740 for KwaZulu-Natal), a minimum population growth rate of 5% per annum and a minimum fecundity rate of 25% for each sub-population (Goodman, 2013). The growth rate target is set high enough to ensure that black rhino populations do not experience a genetic bottleneck (du Toit, 2006). A genetic bottleneck happens when populations are decimated by disease, predation or habitat destruction in such a way that the remaining individuals are no longer genetically representative of the original population (McCouch *et al*., 2007). In an attempt to further prevent the possibility of a genetic bottle neck, fecundity rates of 25%, together with ICIs of at least three years or less, were set as additional reproductive targets (du Toit, 2006).

While the overall reproductive biology of black rhino is well documented; i.e. they have a long gestation period of ~15 months (Goddard, 1967), calves suckle for 12-19 months (Goddard, 1967; Schenkel and Schenkel-Hulliger, 1969), the ASM is between six and nine years (Bertschinger, 1994; Hrabar and du Toit, 2005; Fike, 2011), and ICIs are generally two years, six months (Hrabar and du Toit, 2005); detailed information on the reproductive biology and demographics of individual sub-populations is generally sparse (but see Hrabar and du Toit, 2005; Fike, 2011). This detailed information is imperative for the management planning that will ensure that populations achieve the reproductive targets laid down by the RMG and for the overall conservation of black rhinos in Africa. Thus, the objective of this study was to better understand the reproductive biology and demographics of the HiP black rhino population. The specific aims of the study were to:

- Determine how the reproductive parameters (age at sexual maturity, intercalving interval, fertility and fecundity rates) of the HiP black rhino population compare to other black rhino populations within the southern African region and the rest of Africa; and to
- Assess whether the HiP black rhino population is achieving the genetic and demographic targets set by the RMG.

3.2 Methods

Population estimates of black rhinos at HiP were derived from the field recognition of individual animals. Individual black rhinos were divided into three categories; green, orange and red. Green animals included recognisable animals, animals known by association and known, clean animals (i.e. individual black rhinos that had not been ear-notched but were recognisable by other physical features, location or by association with notched animals), which were re-sighted during the year under review. Orange animals were recognisable animals that had not been re-sighted in the year under review but had been seen in the two years prior to the year under review. The red category was used for recognisable animals that had not been re-sighted in the year under review and had also not been seen in the two years prior to the year under review. However, these animals would have been seen in the four years prior to the year under review. For this study, only animals from the green and the orange categories were used to calculate population estimates as they were more likely to give an accurate representation of the actual black rhino population in HiP (Goodman, 2013).

Five percent of the black rhino population at HiP is removed annually as part of the BRREP. The number of black rhinos removed each year (H_t) was calculated using the following formula:

$$\mathbf{h_t = H_t / N_{t-1}}$$

Where, h_t = the harvest rate, Ht = the number of animals removed in year t and N_{t-1} is the population estimate in the preceding year (Goodman, 2013). For example, to work out how many animals must be removed in 2011 (H_t), h_t would be 0.05 and N_{t-1} = 200, the formula would be used as follows:

$$N_{t-1} \text{ x } h_t = H_t$$

$$200 \text{ x } 0.05 = 10$$

Where, 10 is the number of animals that must be removed in 2011.

Population age structure information for the black rhino population at HiP was only available from 2009 to 2012. This was because a detailed population status report (i.e. demographics and status), compiled on the 31st of December each year, was only initiated in 2009. No similar information was available prior to 2009.

Information on black rhino sex ratios was also only available for the last four years (2009-2012), due to changes in population status reporting. The sex ratio of calves born to females that had given birth to more than four calves each was used to determine whether individual females tended to produce calves of only one sex (Hrabar and du Toit, 2005).

To calculate the age at sexual maturity (ASM), a sub-sample of 120 individual female black rhinos was used (21 % of the adult female population at HiP). These females had the most complete lifehistory records (i.e. their birthdates and the birthdates of their first and subsequent calves were known).

The same sub-sample of 120 females was also used to calculate inter-calving interval (ICI). ICIs longer than 40 months can be omitted from calculations of births per year, births per lifetime and when plotting the distribution of ICIs for a population (Hitchins and Anderson, 1983). This is because it can be assumed that ICIs longer than 40 months (three years, three months) are a sign of a female aborting a calf or that a neonate died soon after birth and before it could be recorded (Hitchins and Anderson, 1983).

Fertility rate (FER_t), which is the number of calves born per year as a proportion of mature females (i.e. females ≥7 years old) in the population at the beginning of each year was calculated as follows:

$$\mathbf{FER_t = Births_t / Ad\ F_{t-1}}$$

Where, $Births_t$ is the number of births in the year under review and $Ad\ F_{t-1}$ is the number of adult females (i.e. females ≥7 years old, F class) in the preceding year (Goodman, 2013).The fertility rate at HiP was calculated from 1998 to 2012.

Fecundity rate (FEC_t), which is the number of calves born in a year and still alive at the end of that year as a proportion of adult females (i.e. females ≥7 years old, F class) in the population at the beginning of each year was calculated as follows:

$$\mathbf{FEC_t = Surviving\ births_t / Ad\ F_{t-1}}$$

Where, surviving $births_t$ is the number of calves that survived in the year under review and $Ad\ F_{t-1}$ is the number of adult females (i.e. females ≥7 years old, F class) in the preceding year (Goodman, 2013).The fecundity rate at HiP was calculated from 2010 to 2012 when the relevant information was available.

Population growth rate (r) for a population that is being harvested was calculated as:

$$\mathbf{r = (\mathit{N}t_{x} - \mathit{N}t_{x-1} + Rem_{t} - Intro_{t}) / \mathit{N}t_{x-1} * 100}$$

Where, *N*tx is the population size in year x and *N*tx-1 is the population size in the preceding year. Rem_t is the number of black rhino removed in the year under review and Intro_t is the number of introduced black rhinos in the year under review (Goodman, 2013). The growth rate of black rhinos at HiP was calculated from 1999 to 2012. The growth rate for 1998 was not calculated because information from 1997 was needed to calculate r and this was not available.

The density (D) of black rhinos at HiP was calculated using the formula:

$$\mathbf{D = Ntx / \text{Size of park } (km^2)}$$

Where, Ntx is the population estimate in the year under review. The density of black rhinos at HiP was calculated from 1998 to 2012.

Mortality rate was calculated as the number of black rhinos that died per year divided by the number of animals alive at the beginning of that year (Sinclair *et al.*, 2006). The mortality rates were calculated from 2009 to 2012, a period when all mortalities were investigated and properly recorded.

Statistical analyses

A student’s T-test was used to determine the difference between the number of black rhinos removed from the population prior to 2008 and those removed post-2008. This was done to test whether the changes in data management and the subsequent correct population estimates influenced the number of black rhino removals post-2008. A Kruskal-Wallis test was used to assess the differences among the number (and proportions) of black rhinos in each age class. A T-test was also used to test for any differences between the sex ratio of the calves born on HiP in each year. Because the data did not satisfy the assumptions of a parametric test, the difference between the number of male and female calves born to each of the 12 females which had each had more than four calves was tested using a Mann-Whitney U- test. All statistical tests were completed using Statistica (version 11; StatSoft inc. Tulsa, OK, USA).

3.3 Results

The black rhino population at HiP decreased from 253 in 1998 to a low of 217 in 2001 (Figure 3.1). The population increased to 217 in 2004 before decreasing to another low of 211 in 2009. There has been a steady recovery since 2009 (Figure 3.1). Due to historical inaccuracies in the estimation of the size of the black rhino population at HiP (Clinning *et al*., 2009), the number of black rhinos removed in some years was higher than 5% (Clinning *et al.*, 2009). Between 1998 and 2000, 57 black rhinos were removed (Figure 3.2). In 2002, only one animal was removed. The inaccuracies in the population estimates were detected and rectified in 2008, and the number of black rhinos removed since then has stabilized. Forty four black rhinos were removed between 2008 and 2012 compared to the 57 which were removed between1998 and 2000 (Figure 3.2). However, there was no significant difference in the annual number of black rhinos removed pre-2008 compared to those removed post-2008 (Figure 3.2; $t = 1.29$, $df = 13$, $P>0.05$).

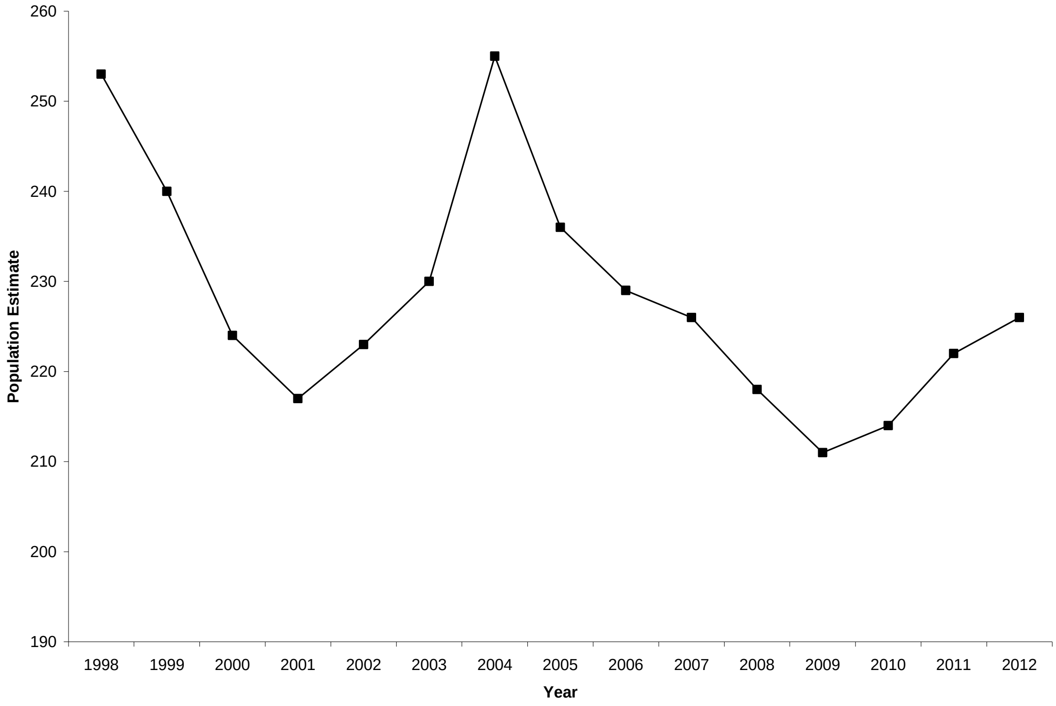

Figure 3.1. Annual changes in the black rhino population size estimates at HiP between 1998 and 2012.

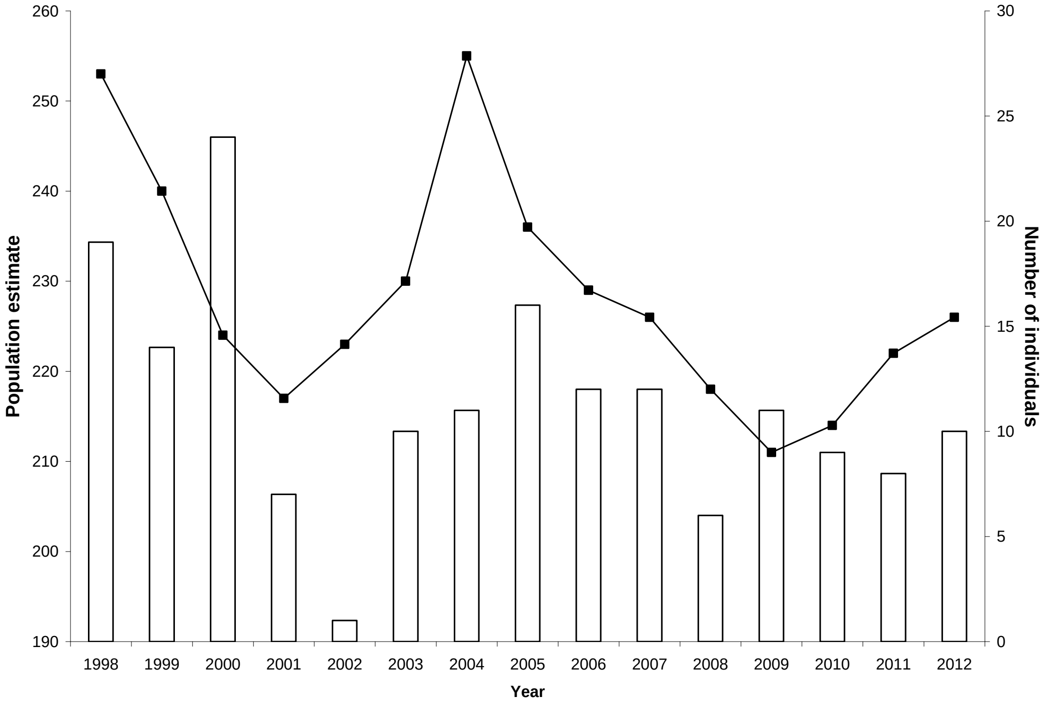

Figure 3.2. Annual changes in the black rhino population at HiP (black line on the primary axis) from 1998 to 2012, with removals shown for the same period (open bars on the secondary axis).

Population age structure

There were significant differences in the proportions of the age classes of the overall black rhino population at HiP (Table 3.1; $H_{(2, 24)} = 11.\ \ 4$; $P<0.05$). Juveniles (A, B and C class) made up the lowest proportion of the population in all years, with a minimum of 12.1% in 2010 when the population was 214 and a maximum of 13.3% in 2012 when the population was 226 (Table 3.1). Sub-adults (D and E classes) made up the second lowest proportion of the population in all years, with a minimum of 23% in 2012 and a maximum of 27.9% in 2011 (Table 3.1). Adult black rhinos (F class) comprised over half of the population between 2009 and 2012 (Table 3.1). There were significantly more adult than juvenile black rhinos (Table 3.1). However, there was no significant difference in the proportions of juvenile and sub-adult black rhinos, nor between sub-adults and adults (Table 3.1).

There was a significant difference in the proportion of male black rhinos in each age class (Figure 3.3; $H_{(2, 24)} = 14.3$, $P < 0.05$). There were more male juveniles than female juveniles between 2009 and 2010, with a maximum of 7.6% males in 2009 (Figure 3.3), compared to a maximum of 5.8% females in 2011 (Figure 3.4). The highest proportion of male sub-adults was 13.1% in 2011 and the highest proportion of male adults was 28.8% in 2012 (Figure 3.3). There were significantly more adult than juvenile males. However, there was no significant difference in the proportions of juvenile and sub-adult males, nor between sub-adults and adult males (Figure 3.3).

There was a significant difference in the proportion of female black rhinos in each age class (Figure 3.4; $H_{(2, 24)} = 15.7$, $P <0.05$). The maximum proportion of sub-adult females was 15.4% in 2010 and the maximum proportion of adults was 34.5% in 2012 (Figure 3.4). There were significantly more adult than juvenile females. In addition, there were significantly more sub-adult than juvenile females. The difference between adult and sub-adults was not significant (Figure 3.4).

Table 3.1. Age structure of the black rhino population at HiP on 31 December between 2009 and 2012. Data are numbers of animals in each age class, the proportions are given in brackets. A (< 3 months), B (4 months – 1 year), C (1-2 years), D (2-3.5 years), E (3.5-7 years), F (>7 years).

Class	Age category	2009	2010	2011	2012
A	< 3 months	3(1.4)	6(2.8)	0	2(0.9)
B	4months < 1 year	9(4.3)	7(3.3)	16(7.2)	14(6.2)
C	1 < 2 years	15(7.1)	13(6.1)	11(5.0)	14(6.2)
D	2 < 3.5 years	12(5.7)	16(7.5)	15(6.7)	10(4.4)
E	3.5 < 7 years	43(20.4)	43(20.1)	47(21.2)	42(18.7)
F	> 7 years	129(61.1)	129(60.3)	133(59.9)	143(63.6)
Total population		211	214	222	225

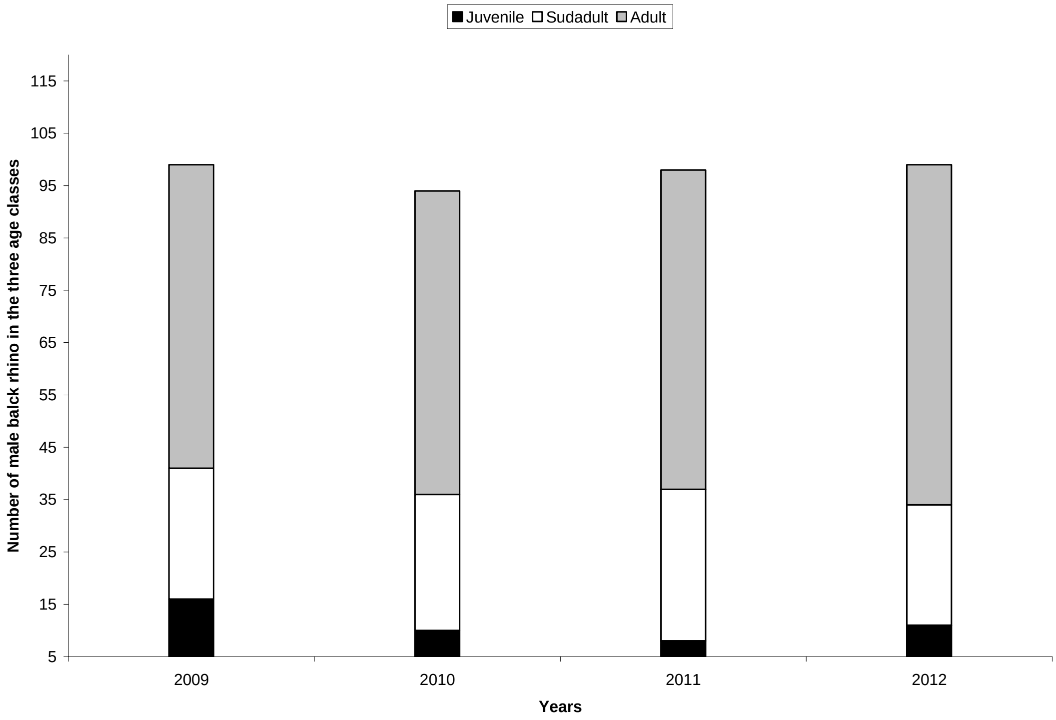

Figure 3.3. Annual changes in the proportion of male black rhinos in each of three age classes (juvenile, sub-adult and adult) at HiP on 31 December between 2009 and 2012.

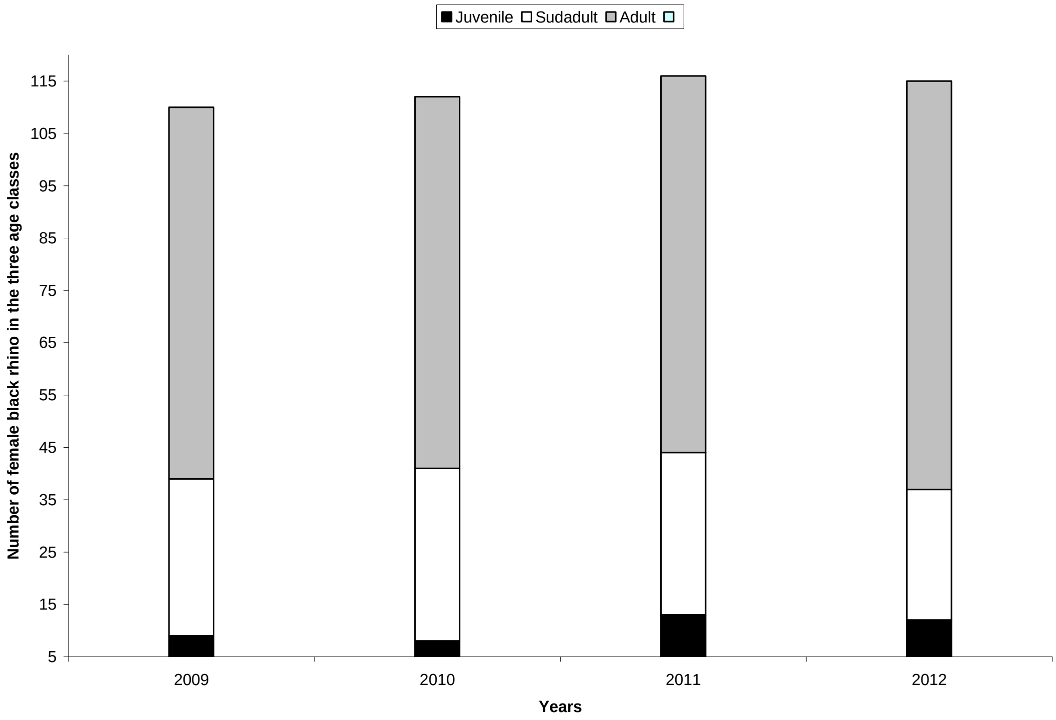

Figure 3.4. Annual changes in the proportion of female black rhinos in each of three age classes (juvenile, sub-adult and adult) at HiP on 31 December between 2009 and 2012.

Sex ratio

Between 2009 and 2012, the HiP black rhino population had significantly more females than males (Table 3.2, t = -8.1, df= 6, P < 0.05), and the E&F class had a slight female bias (1.2:1) (Table 3.2). Twelve females had more than four calves each and these animals tended to produce male calves. Three females produced more female calves than males, nine females produced more male than female calves and no female produced equal numbers of male and female calves (Table 3.3). However, the differences between the sexes of the calves produced were not significant (Table 3.3; z = 1.7, df = 22, P> 0.05).

Table 3.2. Sex ratio of the entire black rhino population at HiP between 2009 and 2012. Sex ratio is female to male. The sex ratio for both E&F classes combined is also provided.

Year	Males	Females	Sex ratio F:M	Sex ratio F:M (E&F)
2009	99	110	1.1:1	1.2:1
2010	94	112	1.2:1	1.2:1
2011	98	116	1.2:1	1.3:1
2012	100	115	1.2:1	1.1:1

Table 3.3. The sex ratios of the black rhino calves of 12 females which each had more than four calves in their lifetime at HiP for the period ending in 2012.

Female	Total Calves	Female	Male	Sex Ratio F:M
1	6	2	4	0.5:1
2	6	2	4	0.5:1
3	5	2	3	0.7:1
4	5	2	3	0.7:1
5	5	2	3	0.7:1
6	5	2	3	0.7:1
7	5	2	3	0.7:1
8	5	3	2	1.5:1
9	5	2	3	0.7:1
10	5	2	3	0.7:1
11	5	3	2	1.5:1
12	5	4	1	4:1

Age at sexual maturity (ASM)

The mean age at sexual maturity for the entire black rhino population at HiP was 12 years (145 ± 12 months). The range in ASM was four years to 23 years. Assuming a gestation length of 15 months (Goddard, 1967), the mean age of first mating and conception was 130 ± 12 months (10 years). The earliest mating (back dated from birth) recorded was of a female that was two years, eight months (34 months) old and the latest recorded mating was of a female aged 22 years, five months (269 months).

Inter-calving interval (ICI), births per year and births per lifetime

Of the 120 black rhino females for which adequate records were available, 78 had more than one calf. This gave a subset of 190 ICIs (Figure 3.5). The mean ICI was three years, nine months (45 ± 6 months). The shortest ICI was one year, six months (18 ± 2 months) and the longest ICI was nine years (108 ± 21 months). When ICIs longer than 40 months were removed from the dataset (Hitchins and Anderson, 1983), 105 individual ICIs remained and the calculation of the overall ICI for the HiP became two years, five months (29 ± 1 month)

Using an ICI of 45 months, the births per year per female were 0.27 and when using an ICI of 29, births per year increased to 0.4 per female.

The oldest female recorded to give birth at HiP between 1998 and 2012 was 31 years old. However, the mean age at parturition was 12 years, one month (146 ± 12 months). Thus, if 31 years is assumed to be the age at which female black rhinos at HiP cease reproductive activity, the reproductive lifetime of the population is approximately 19 years. A female black rhino may therefore be expected to have between five and eight calves in her lifetime. On average, females in HiP had 2.6 calves during their lifespan. However, one female had eight calves during the study. In addition, three other females had seven calves each.

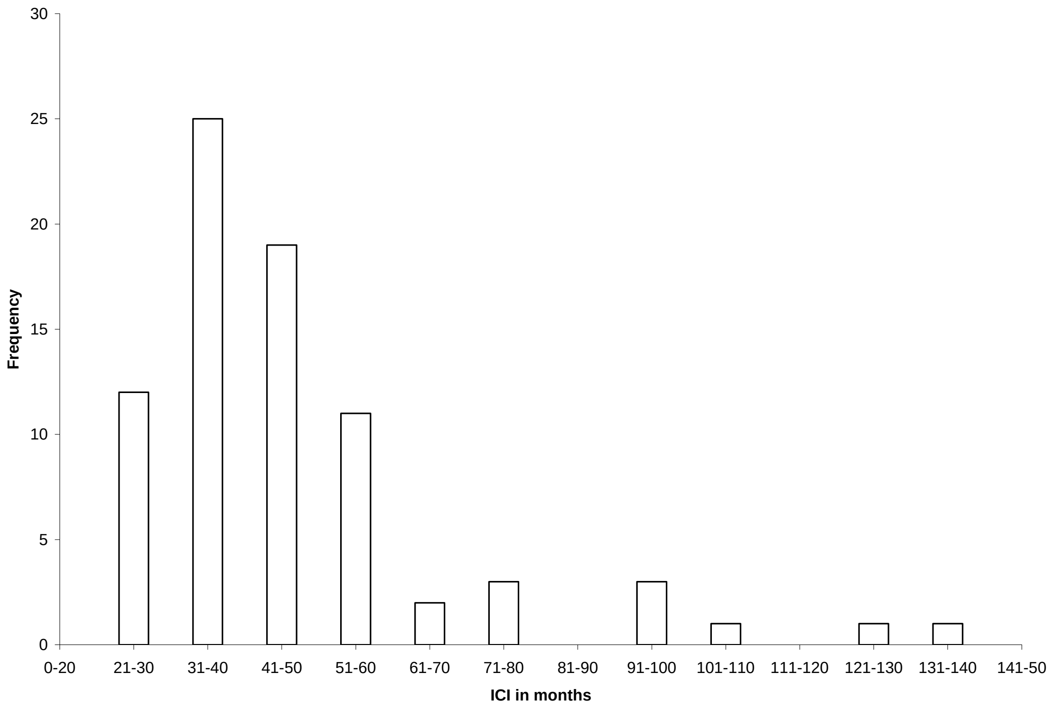

Figure 3.5. Histogram showing the frequency distribution of intercalf intervals for the 78 black rhino females which each had more than one calf at HiP from when each female had her first calf ending in 2012.

Fertility rate, fecundity, population growth rate and density

The fertility rate of black rhinos at HiP was lowest in 2006 and 2009 (0.17 for each year) and highest in 2000 (0.34). In the 15 years between 1998 and 2012, the fertility rate increased initially but declined slowly after that (Figure 3.6). The population growth rate at HiP was at its lowest in 2009 when it was -2.6%, the highest growth rate occurred in 2011 when it reached 7.5% (Table 3.4). The period between 2003 and 2005 had an average growth rate of 7.3% (Table 3.4). The fecundity of the black rhino population at HiP was below 0.25 between 2010 and 2012. The lowest fecundity rate was 0.18 in 2010, whilst the highest rate 0.23 in 2011. In 2012, the fecundity rate decreased to 0.22.

The black rhino population density at HiP was highest in 1998 (0.29/km^2), but decreased to a low of 0.23/km^2 in 2010 (Figure 3.7). There was a slight increase after that but the density remained lower than the period between 1999 and 2009 when the density was between 0.24 and 0.28 km^2.

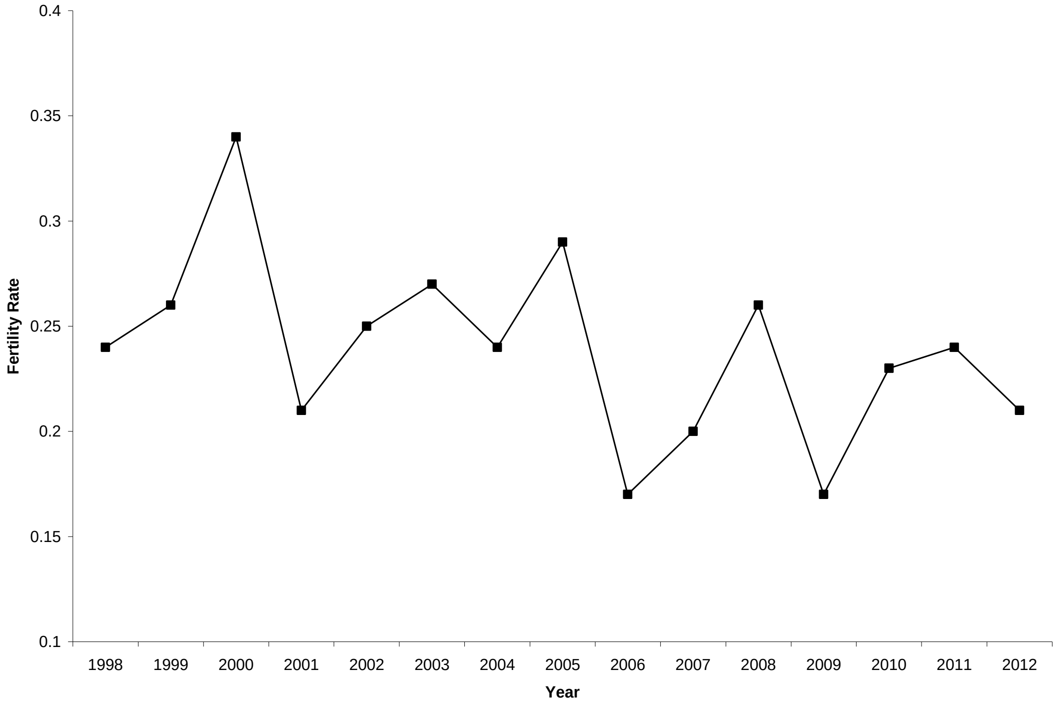

Figure 3.6. The fertility rate of the black rhino population at HiP from 1998 to 2012.

Table 3.4. The growth rate of the black rhino population at HiP from 1999 to 2012.

Year	**Growth Rate**
1999	0.4
2000	3.3
2001	0
2002	3.2
2003	7.6
2004	7
2005	7.2
2006	2.1
2007	3.9
2008	-0.9
2009	-2.6
2010	5.7
2011	7.5
2012	6.3
Ave growth rate	**3.6**

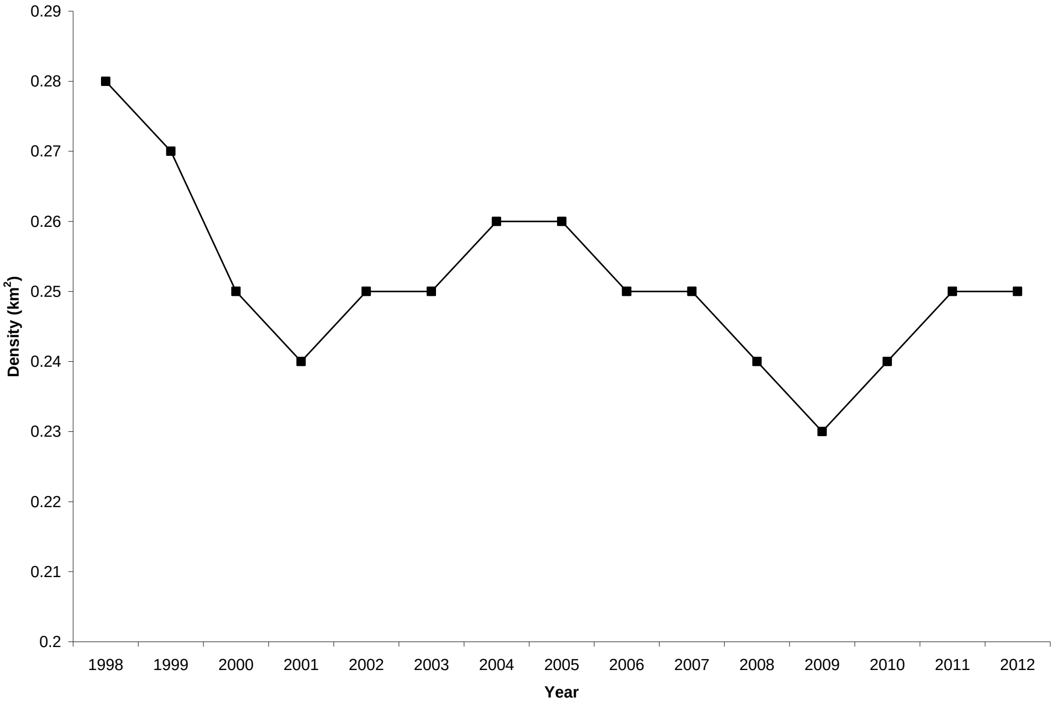

Figure 3.7. The density of the black rhino population at HiP between 1998 and 2012 after removals in each year.

Mortality

The mortality rate of black rhinos at HiP was relatively low. The highest mortality rate was recorded in 2010, when 0.07 % of the population died. The total number of dead rhinos was 15, with nine of these being calves (A and B class). The remaining six deaths were three female sub-adults, three male sub-adults and one unknown calf (A class). Calf mortalities made up almost half of all mortalities.

3.4 Discussion

Assessing the carrying capacity for black rhinos in HiP has never been easy due to the large size of the park and the different vegetation types found in the different sections of the park (Adcock, 2001). The park is divided into five sections which each have different climates, main soils and vegetation types (see Chapter 2; Adcock, 2001). The sections also have different rhino densities and removal histories (Adcock, 2001). To get around this problem and estimate the carrying capacity for HiP, the two sections of the park were treated separately. Historically the northern section of the park, Hluhluwe, was managed as a separate park to the southern section of the park, which was called Umfolozi (Brooks, 2000). The carrying capacity based on the percent area available to black rhinos, temperature, average annual rainfall, water availability, browse availability and quality was estimated for the northern section and for the southern section, respectively (Adcock, 2001). When these estimates were combined, the ecological carrying capacity for black rhinos at HiP was estimated to be 0.43 rhinos/km^2 (Adcock, 2001).

To ensure increased rhino productivity and to prevent density dependent declines, black rhinos need to be managed below the estimated carrying capacity for a particular period (Adcock, 2001; du Toit, 2006), ideally around 75% of the carrying capacity (Adcock, 2001). Seventy five percent is the maximum density at which density-dependent factors do not affect rhino productivity (Adcock, 2001). My results show that the current population at HiP (0.25 rhinos/km^2) has not yet reached 75% of the carrying capacity of the park (0.43 rhinos/km^2) and so the population should not be experiencing density dependent effects (Hrabar and du Toit, 2005).

Population estimates

There was no significant difference in the number of individuals removed on an annual basis from HiP pre-2008 compared to post-2008. Nevertheless, removals and translocations may disrupt the social structure of a population by leading to shifts in home ranges which create conflicts between individuals (Patten *et al*., 2008; Greaver *et al*., 2013). This may ultimately reduce population productivity (Patton *et al*., 2008; Weladji and Laflamme-Mayer, 2011; Greaver *et al*., 2013) as more energy would be used creating new home ranges instead of for reproduction (Patton *et al*., 2008; Weladji and Laflamme-Mayer, 2011; Greaver *et al*., 2013). To avoid the above problems, removals should be planned so that they bring about minimum disruption to the social network of black rhinos (Patton *et al*., 2008; Weladji and Laflamme-Mayer, 2011; Greaver *et al*., 2013). The sex and age structure of the donor population must also be considered before removals. Removing only young females over a long period can result in a skew in the sex and age structure of the donor population. This will reduce the future reproductive ability of the population (Patton *et al*., 2008; Weladji and Laflamme-Mayer, 2011; Greaver *et al*., 2013). Removing sub-adult males from well-established populations (50 or more) provides the least disruption to the population social structure because this is the age class most likely to disperse (Patton *et al*., 2008; Weladji and Laflamme-Mayer, 2011; Greaver *et al*., 2013). Therefore, a balance should be maintained in the social organization of the donor population by selecting from all sections of the reserve and not only removing rhinos from areas that are easily accessible (Patton *et al, 2008;* Greaver *et al*., 2013). By removing rhinos from all sections of a reserve, vacuum areas (unoccupied habitats due to lack of dispersal in species) can also be avoided (Patton *et al*., 2008).

Population age structure

In large, predator-free systems, the population growth of herbivorous mammals is most sensitive to adult survivorship (Gaillard *et al.,* 1998; 2000). However, high temporal variation in juvenile survival typically drives variability in population growth rates (Gaillard *et al.,* 1998; 2000) and is thus an important factor in determining fluctuations in the populations of large mammalian herbivores (Owen-Smith and Mason, 2005). The variability in growth rates occurs both during stochastic environmental conditions such as adverse weather, and density dependent situations like food limitation (Gaillard *et al.,* 1998; 2000). The survival rate of breeding-age adult female ungulates generally remains constant over time, while that of juveniles undergoes wide annual variability (Owen-Smith and Mason, 2005). It has been suggested that the constant survival of adult females could be due to the fact that adults are able to sacrifice offspring survival under food resource scarcity and adverse environmental conditions (Skogland, 1985; Owen-Smith and Mason, 2005). In wild reindeer (*Rangifer tarandus tarandus*), a pregnant doe may abandon its foetus or young in order to ensure its own future reproductive prospects (Skogland, 1985; Owen-Smith and Mason, 2005). The adult survival of black rhinos in my study has remained constant over the last four years (2009-2012) and is thus similar to situations found in other areas and other ungulate species (Owen-Smith and Mason, 2005).

In mammalian populations that are expanding, the proportion of juveniles and sub-adult animals will be higher and the mean age of the population will be low (Owen-Smith, 1988; Couslon *et al.*, 2004). Populations that are close to carrying capacity have a higher proportion of adult animals and a reduced juvenile survival and fecundity (Couslon *et al.*, 2004). Stable populations of megaherbivores (those species that attain a body size in excess of 1000 kg) are made up of about 60-70% reproductively mature adults, whilst increasing populations have 45-55% mature adults (Owen-Smith, 1988). For example, an increasing black rhino population in the Great Fish River Nature Reserve (GFRNR), Eastern Cape, South Africa, comprised 20% juveniles, 36% sub-adults and 44% adults (Fike, 2011). By contrast, the Thomson’s gazelle (*Eudorcas thomsonii*) population in the Serengeti, Tanzania was shown to be in rapid decline when the population was made up of 12% juveniles and 70% adults (Borner *et al.*, 1987). Owen-Smith (1988) demonstrated that an East African black rhino population which consisted of about 60% adults was categorized as stable. This study shows that the current black rhino population at HiP consists of about 60% adults, 23% sub-adults and 13% juveniles, in theory this suggests that the population is stable (Owen-Smith, 1988), however my results point to a population in decline. In order to reduce the number of adults and thus promote an increase in the number of juveniles, the park may want to consider removing the older individuals which have already contributed to the population reproductively but are still able to reproduce. This may allow much younger animals to attain the body mass required for reproduction much faster and possibly breed much earlier and thus increase the number of calves in the population. Another recommendation would be to not remove any individuals at all until the population grows to at least 75% of the carrying capacity and then restart removals.

Sex ratio

Sex ratio is an essential factor influencing the growth rates and population dynamics of many large mammal populations (Okita-Ouma *et al.*, 2009; Weladji and Laflamme-Mayer, 2011). This is because it affects the reproductive potential of a population, which is the relative capacity of a species to reproduce under favourable conditions (Okita-Ouma *et al.*, 2009; Weladji and Laflamme-Mayer, 2011; Merriam-Webster, 2013). A population with a female skew, under favourable conditions, is expected to demonstrate high growth rates (Okita-Ouma *et al*., 2009).The favourable conditions will allow females to reach the body mass required for reproduction sooner and ASM will then be attained earlier (Gaillard *et al.,* 2000).

Rainfall and range conditions at the time of conception have been found to influence conception rates, and seasonal and annual progeny sex ratios in black rhinos (Berkeley and Linklater, 2010). More female black rhino offspring are born during years with below average rainfall and more males are conceived in the years with above average rainfall (Hrabar and du Toit, 2005; Weladji and Laflamme-Mayer, 2011). The extrinsic modification hypothesis suggests that offspring sex can be influenced by the environmental conditions experienced by the mother (Weladji and Laflamme-Mayer, 2011). In horses (*Equus caballus*), the birth sex ratio varies depending on the body condition of the mother at conception (Cameron and Linklater, 2007). More males are born to females which are gaining body condition during conception, compared to more females when females are losing body condition at conception (Cameron and Linklater, 2007). However, the assessment and comparison of female body condition at the time of conception and calf sex was not possible during my study.

Nevertheless, research has shown that male foetuses are affected by poor maternal resources and weather experienced by the mother prior to conception and during mid to late gestation (Gaillard *et al.*, 2000; Berkeley and Linklater, 2010; Weladji and Laflamme-Mayer, 2011). This is because females eating food with poor nutrient source have poor body condition and poor body condition in black rhinos affects the sex of the calf (Hrabar and du Toit, 2005). Thus, it is possible that male biased foetal loss which is pregnancy failure through the loss of the embryo (Bechner *et al*., 2006) occurs to conceptions during the wet season, because a calf conceived in the wet season is in gestation through the dry season and a calf conceived in the dry season is in late gestation during the wet season (Berkeley and Linklater, 2010). The male biased foetal loss may reduce the male bias at parturition (Berkeley and Linklater, 2010; Weladji and Laflamme-Mayer, 2011). Owen-Smith (1988) found that the flexibility in the time of conception in black rhinos could also allow females to selectively abort embryos of the less advantageous sex during unfavourable conditions (Owen-Smith, 1988). Higher male birth rates at HiP in the past have been associated with conception periods which occurred during wetter seasons and this resulted in a relatively large male bias in the sex ratio of calves (Berkeley and Linklater, 2010).

In general, more male black rhino calves than females are born (du Toit, 2006), but because large herbivore male survival is lower than female survival (Gaillard *et al*., 2000), the adult sex ratio is usually, but not always, skewed towards females (du Toit, 2006). Large areas, open or fenced, of greater than 1000 km^2 where black rhino can undergo their natural patterns of distribution and movement (Hall-Martin and Knight, 1994), usually have a sex ratio of 1.3 to1.5 females per male (du Toit, 2006). However, in Mkuze Game Reserve, KwaZulu-Natal, South Africa the male biased sex ratio was related to the amount of rainfall during pregnancy and population sizes (Weladji and Laflamme-Mayer, 201). Females tended to give birth to male calves as the population size increased during pregnancy and preconception periods (Weladji and Laflamme-Mayer, 2011). They also had more male calves as the rainfall increased (Weladji and Laflamme-Mayer, 2011). An increase in population size could bring about increased competition for food resources and it would be advantageous to produce male calves that could potentially disperse away from the mother's habitat (Weladji and Laflamme-Mayer, 2011). The sex ratio for the black rhino population at the GFRNR in the Eastern Cape, South Africa was 1.3 females per male (Fike, 2011). This could be indicative of the lower than average rainfall experienced at GFRNR, Eastern Cape, South Africa which resulted in more female calves being born (Hrabar and du Toit, 2005). In HiP, the overall sex ratio was close to parity but the adult (E&F classes) sex ratio was slightly female biased (1.2:1). Of the females that had more than four calves, nine had more male than female calves; however, the difference in the sexes was not significant. The same was true in Pilanesberg National Park (PNP), North West, South Africa (Hrabar and du Toit, 2005). There was no evidence that primiparous females (those who have only given birth once) produce a calf of a certain sex or that individual females tend to produce one sex other the other (Hrabar and du Toit, 2005).

Age at sexual maturity

The ASM in mammals differs between populations and even within the same species (Bronson, 1989). The genetic makeup of each individual accounts for the differences in the ASM for females in the same population (Bronson, 1989). Environmental factors such as food availability, ambient temperature and, to a lesser extent, humidity can influence reproductive development (Bronson, 1989). These factors also influence ASM by influencing the rate of growth for each individual female (Bronson, 1989). Evidence shows that underweight females and those on nutrient poor diets may fail to ovulate (Hrabar and du Toit, 2005). In addition, low rainfall reduces the quality and quantity of the food supply, negatively affecting the body condition of black rhino females (Hrabar and du Toit, 2005).

A threshold mass must be attained by mammalian females before young females can attain sexual maturity and thus reproduce (Gaillard *et al.,* 2000). In deer (*Cervus elaphus*), for example, the female body mass during rut is usually the main factor determining the age at which females have their first calf (Gaillard *et al.,* 2000). The nutrition of young females, which is independent of both population density and climate, causes the differences in the ASM of young females (Gaillard *et al.,* 2000). Black rhino populations in poor habitats may attain sexual maturity and thus reproduce much later than black rhino populations in better habitats (Gaillard *et al.,* 2000). This is because body mass affects female fecundity and poor nutrition depresses fecundity and delays the onset of puberty (Gaillard *et al.,* 2000; Greaver *et al*., 2013). An interaction between body mass and population density can regulate reproduction by decreasing the possibility of females of a certain body weight from conceiving at high densities (Gaillard *et al.,* 2000). This is a reproductive strategy aimed at minimizing risks to females (Gaillard *et al.,* 2000).

Low population growth rates and long ICIs for black rhinos were observed at the Solio Game Reserve, central Kenya (Patton *et al.*, 2008). The main reasons for this poor performance were; foetal deaths caused by poor nutritional conditions which stemmed from habitat degradation and because the poor nutrition delayed the females in attaining the sufficient body condition and weight required for them to conceive and raise calves (Patton *et al.*, 2008).

In PNP in the North West, South Africa, ASM tended to increase with increasing density (Hrabar and du Toit, 2005). Thirty three percent of females calved before they were seven years old, 83% of females had calves before they were eight years old and 100% of breeding-aged females had calves by the time they were nine years old (Hrabar and du Toit, 2005). At the GFRNR in the Eastern Cape, South Africa, the ASM ranged from four years, 10 months to nine years and three months, the mean ASM was six years and eight months (Fike, 2011). The ASM of the black rhino population in Ithala Game Reserve, KwaZulu-Natal, South Africa, was six years and six months (Greaver *et al*., 2013). A study similar to the current one, also conducted at HiP in 1983, yielded an ASM of between five years, 10 months and six years, five months (Hitchins and Anderson, 1983). My data show that the ASM of black rhinos at HiP ranged between three and 23 years. The mean ASM was 12 years. The ASM for the current HiP population exceeds the seven years and five months quoted in du Toit (2006) for poor performing populations and is almost double that of the 1983 HiP estimate and GFRNR and PNP populations. The differences in the ASM found in my study and the study done by Hitchins and Anderson (1983) could be due to different methods is which data were collected for the studies. However, this is unlikely and could thus be due to changes in forage availability and changes in predator effects on juvenile black rhinos. The reasons for the longer ASM in the current study could be poor habitat (Gaillard *et al.,* 2000) and poor nutrition (Patton *et al*., 2008). Poor nutrition in black rhino can lead to a delay in attaining the body weight required for reproduction (Patton *et al*., 2008). The black rhino females in the current HiP population could be conceiving much earlier but may be losing their calves before they are born due to poor body condition (Patton *et al*., 2008).

Inter-calving Interval

The variation in the length of black rhino ICIs depends on the age of the female and the quality of food within her home range (du Toit, 2006). Under favourable conditions, black rhino females can produce successive calves every two to three years (du Toit, 2006). During unfavourable conditions, the length of the ICI can be in excess of three years, six months (du Toit, 2006). ICIs are not restricted to yearly time increments because reproduction in black rhinos is asynchronous (Hrabar and du Toit, 2005). Significantly, female megaherbivores can lengthen their ICI as an ecological response to food restrictions which occur when populations are close to carrying capacity (Owen-Smith, 1988). Female black rhinos that are 28 years or older take longer to regain body condition after weaning calves and tend to have longer intervals between calves (du Toit, 2006).

The ICI at PNP, North West, South Africa tended to decrease with increasing rainfall, and it ranged between one year, seven months and five years, two months, (Hrabar and du Toit, 2005). At HiP, in 1983, the black rhino ICI was between one year, eight months and seven years, five months (Hitchins and Anderson, 1983). In the Ngorongoro Crater, Tanzania the ICI was four years, in the Tsavo National Park it is was three years, four months and in Amboseli, Kenya it was four years (Goddard, 1967). At the Addo Elephant Park in South Africa, the ICI was two years, two months (Hall-Martin and Penzhorn, 1977). In the GFRNR, Eastern Cape, South Africa the mean ICI was two years, five months (Fike, 2011). The shortest ICI at GFRNR was one year, 10 months and the longest ICI was three years, six months long (Fike, 2011). In my study, the mean ICI was three years, nine months. The shortest ICI was one year, six months and the longest ICI was eight years, 11 months. The mean ICI at HiP, including ICIs longer than three years, four months, falls into the category of poor to very poor fecundity. This could be due to unfavourable conditions in the park, because black rhino and other megaherbivore females can extend their ICIs as a response to food scarcity (Owen-Smith, 1988). Low rainfall could also be a cause of the longer ICIs as was the case in PNP, North West, South Africa where ICIs decreased with increasing rainfall (Hrabar and du Toit, 2005).

Births per year and lifetime productivity

Using the mean ICI and the knowledge of when reproduction in black rhinos terminates, estimation of the births per year for females and the reproductive lifetime can be calculated. Reproduction in black rhinos and elephants (*Loxodonta africana*) in captivity may cease 15 years before wild populations (Hermes *et al.*, 2004). Reproduction in black rhinos in the wild may cease between 30-35 years (Schenkel & Schenkel-Hulliger, 1969, Garnier, 2001) or at 40 years old (Owen-Smith, 1988).

With a mean ICI of three years, nine months the births per year for black rhino females at HiP was 0.3, this was less than the births per year of 0.41 found at GFRNR, Eastern Cape, South Africa (Fike, 2011). This is due to the much longer ICI found at HiP. Using 35 years as the age at which reproduction ceases and a typical ASM of six years gives a reproductive lifespan of 29 years. A typical female in this situation would then be expected to produce between 11 and 12 calves in her lifetime. At GFRNR, Eastern Cape, South Africa the oldest black rhino female to give birth was 24 years old and the ASM in the park was six years and eight months (Fike, 2011). The reproductive lifespan estimate was 18 years and a typical female was expected to give birth to seven calves. However, two females gave birth to nine calves each (Fike, 2011). The oldest female to have a calf at HiP was 31 years old, and if this age is taken as the age at which black rhino females at HiP cease reproducing then the reproductive lifetime for females at HiP can be estimated to be approximately 19 years. The number of calves produced by a typical female per lifetime would be between five and eight. The average number of calves per female at HiP was 2.6. The reproductive lifespan of black rhino females in HiP is almost the same as that in GFRNR, Eastern Cape, South Africa, a population that is on an increase (Fike, 2011). However, my results show that the population is in fact declining.

Fertility rate

ICI and the gestation period determine the number of females that give birth each year (Owen-Smith, 1988). ICI is affected by both density dependent and independent factors, and these factors also influence the fertility rates (Hrabar and du Toit, 2005). At high densities, the ICI increases and this causes a decline in the number of females that give birth each year (Hrabar and du Toit, 2005). Under favourable conditions, ICI is at a minimum and this causes the fertility rates to increase (Hrabar and du Toit, 2005; Fike, 2011). In the GFRNR, Eastern Cape, South Africa the fertility rate was 41% for the F class females and 33% for the E and F classes, combined (Fike, 2011). PNP, North West, South Africa had fertility rates of between 16 and 45% (Hrabar and du Toit). At HiP, the highest fertility rates were reached in 2000 when 34% of adult females gave birth. The lowest fertility rates were observed in 2006 and 2009 when only 17% of adult females gave birth. The fertility rate for the current population was 21% and this is lower than the GFRNR, Eastern Cape and the PNP, North West, South Africa black rhino populations. This is likely to be an effect of the long ICI.

Population growth rate

Large herbivorous mammals generally have lower population growth rates than smaller mammals (Gaillard *et al*., 2000) because growth rates decrease with an increase in body size (Fenchel, 1974). Growth rate depends on environmental factors such as food availability, temperature and humidity which influence the size of a species (Fenchel, 1974). The amount of energy used for body maintenance increases with an increase in body size (Fenchel, 1974). In mammals, most of the energy is allocated for growth and maintenance (Brown *et al*., 1993). Once an individual has reached the body weight required for reproduction, energy is then allocated to reproduction. This is why large mammals have lower growth rates because they put less effort into reproduction than small mammals (Blueweiss *et al*., 1978; Brown *et al*., 1993). Black rhino populations with a higher proportion of females are expected to have high growth rates (du Toit, 2006). In black rhino populations approaching carrying capacity, mortality usually involves infants, calves and sub-adults and it can exceed 4% (du Toit, 2006). The ASM and ICI in these populations tend to increase and population growth rates decline (du Toit, 2006). Black rhino populations that have exceeded carrying capacity exhibit growth rates lower that 5% per year due to the reduction in the available browse per rhino (du Toit, 2006).

Due to annual variation in calving rates and the long gestation period in black rhino, population estimates can usually be analyzed over periods of three or five years so that an overall estimate of growth rates can be calculated (du Toit, 2006). Between 1999 and 2012, the population growth rate at HiP was below the 5% average for six out of the 14 years. The average growth rate for the period between 2003 and 2005 was 7.3% and for the period between 2010 and 2012 it was 6.5%. The lowest growth rate was observed in 2009 when it was -2.6%. The growth rate for the current black rhino population at HiP was 6.3%. The 5% minimum growth rate target for the southern African metapopulation (du Toit, 2006) refers to the population growth rate after removals, introductions and poaching events (du Toit, 2006). This target is below the 9% maximum growth rate estimate for populations with typical age and sex structures (du Toit, 2006). The HiP population has only started reaching the minimum growth rate target in the last three years. However, despite having a slight female bias, the HiP population is not showing growth rates of 9% which are expected for female biased population living under favourable conditions (du Toit, 2006).

Density

Most studies agree that density dependent changes in mammal populations occur when their populations are close to reaching carrying capacity (Fowler, 1981). This is because population sizes close to or at carrying capacity lead to food resource limitations (Skogland, 1985). Food limitation is the main factor that regulates the population sizes of herbivores because it leads to a number of demographic responses such as disease, decrease in infant survival and fecundity (Skogland, 1985). Black rhinos fall into the K-selected group of species; those species whose demographic patterns are influenced by variations in densities (Rachlow and Berger, 1998). Population density is known to influence habitat and forage selection (Weladji and Laflamme-Mayer, 2011). Resource availability is reduced at high population densities and this will force individual rhinos to disperse to other areas to look for food and places to create home ranges (Skogland, 1985; Hrabar and du Toit, 2005). Density dependence can play an important regulatory role by regulating the population dynamics in many mammal species (Hrabar and du Toit, 2005; Okita-Ouma *et al.*, 2009). Increasing population densities can reduce resource availability and can result in a decline in birth rates and an increase in mortality, emigration rates (Rachlow and Berger, 1998; Okita-Ouma *et al.*, 2009; Weladji and Laflamme-Mayer, 2011) and ASM (Hrabar and du Toit, 2005). Calf and adult mortality increases with decreasing resource availability and fecundity decreases due to the increase in the ASM and increasing ICI (Hrabar and du Toit, 2005). Density dependent effects act by slowing down population growth rates and lengthening the ASM and start of reproduction (Rachlow and Berger, 1998; Adcock, 2001). In African elephants, females show longer intercalving intervals in high density populations compared to those in low density populations which show low intercalving intervals (Rachlow and Berger, 1998).

Different vital rates (which include; ASM, ICI, fecundity rates, population growth rates, adult and juvenile survival and gestation) have different sensitivities to changes in population density (Gaillard et *al.,* 1998). This results in a sequence of responses by the vital rates. Juvenile survival responds first, followed by ASM, adult fecundity and then adult survival (Gaillard *et al.*, 1998; Eberhardt, 2002; Couslon *et al.,* 2004; Greaver *et al*., 2013). Juvenile survival is the most sensitive vital rate (Gaillard *et al.*, 1998; Greaver *et al*., 2013). It is sensitive to limiting factors whether they are caused by density increases or by stochastic environmental conditions (Gaillard *et al.*, 1998). Increased density has demographic and spatial effects that can persist in a population even 30 years after the density has stabilized (du Toit, 2006). The density for the black rhino population at HiP has been decreasing since 1998. The carrying capacity of HiP might have decreased over the years because even though the density of the current population is lower than the estimated carrying capacity, the sequential responses that one would predict from an increase in density are being observed. The population appears to be responding as if it is experiencing density dependant effects. A possible explanation for this is that the carrying capacity for the park might have decreased from the 0.43 rhino.km^2 it was estimated to be and the black rhino population at HiP has in fact reached carrying capacity. However, the data from this study cannot confirm nor rule this out.

Mortality

Black rhino calf mortality rates within the first year after birth in South Africa and Namibia range between 8-14% (du Toit, 2006). Sub-adult mortalities are between 2-4%, less than 2% in young and prime adults and 4% and over in much older adults (du Toit, 2006). Males have higher mortality rates than females because males are involved in fights more often than females. Fighting wounds are the main cause of death in males whereas most females die of old age (du Toit, 2006). Mortality at HiP was relatively low and deaths were mostly of calves. The highest mortality in the four years between 2009 and 2012 was 0.07 in 2010. Most calf mortalities occur within the first month of birth and are linked to maternal care in cases where predation on calves is not high (Gaillard *et al.,* 2000). Maternal age, size and reproductive experience also have a strong influence on calf survival (Gaillard *et al.,* 2000). Where predators are present, predation can account for about 50% of calf deaths. Maternal experience can lower calf vulnerability to predation (Gaillard *et al.,* 2000). Malnutrition is the main cause of early mortality and may cause females to abandon their young. Malnutrition also increases the juvenile’s susceptibility to other sources of mortality such as disease due to a weak immune system (Gaillard *et al.,* 2000). Calf mortalities made up most of the mortalities at HiP between 2009 and 2012. It is possible that the better monitoring methods employed from 2009 increased the chances of detecting calf births and mortalities than in previous years. It could also be a result of predation on the calves by lions (*Panthera leo)* and hyaenas (*Crocuta crocuta)* or malnutrition. Undernourished mammal females are unable to provide enough nutrition in the milk for their offspring and this can increase callf susceptibility to diseases (Gaillard *et al.,* 2000). Calf mortalities in Ithala Game Reserve, KwaZulu-Natal, South Africa were caused by exposure to cold weather conditions (Greaver *et al*., 2013).

Conclusion

The black rhino population at HiP is an important donor population for the BRREP. This means that this population must perform well both genetically and demographically in order to continue contributing to the BRREP. The RMG targets set for black rhino sub-populations in the southern Africa region include a minimum of 5% growth rates per year and 25% fecundity (Goodman, 2013). The current black rhino population at HiP attained and exceeded the 5% growth rate target. It did not, however, attain the 25% fecundity target as it had a fecundity rate of 22%. The difference between the fecundity rate of the HiP population and the RMG target is small. Therefore, it can tentatively be concluded that the current HiP black rhino population is almost at the minimum performance level according to RMG standards. However, the delayed ASM and longer ICIs are concerning as they point to problems with the habitat quality at HiP. The delayed ASM and longer ICIs mean that the KwaZulu-Natal population size target of 740 individuals will take longer than expected to be reached. This, in turn, means that the southern

African regional target of reaching 2 000 (or ideally 5 000) individuals for each sub-species will also take longer to be achieved. For a critically endangered species such as the black rhino any delay in increasing numbers could have serious implications for the conservation of the entire species.

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CHAPTER FOUR

BROAD HOME RANGE AND HABITAT USE OF BLACK RHINOCEROSES (*DICEROS BICORNIS)* IN THE HLUHLUWE-IMFOLOZI PARK, KWAZULU-NATAL, SOUTH AFRICA

4.1. Introduction

Home range is the area utilized by an individual animal or a group of animals while conducting routine activities such as those associated with foraging, resting and reproduction (Harestad and Bunnel, 1979; Owen-Smith, 1988; Powell, 2000; Börger *et al.,* 2006; Börger *et al.,* 2008; van Beest *et al.,* 2011; Monterroso *et al.,* 2013). All parts of the home range are not used equally and core areas are areas within a home range that are utilized more often than others as they contain abundant supplies of food and water (Owen-Smith, 1988). In the scientific literature, the words territory and home range are sometimes used interchangeably. However, a territory is an area which is aggressively defended by individuals because it may contain a limited resource such as water or food (Börger *et al*., 2008), while a home range refers to the entire area utilised by the animal (Börger *et al*., 2008). Territories are fixed areas where animals use advertising displays, such as scent-marking, to deter intruders (Börger *et al*., 2008). Space use is rarely fixed and varies between and within species with time. This variation in space use will include both the size of the space used and its location. A wide range of factors interact to influence space use and these are introduced below.

The availability and variability of forage are the driving forces behind the use of space by herbivores (van Beest *et al*., 2011). For black rhinos, habitat features such as food, water, the availability of cover and the absence of human disturbance all influence home range size and the location (Goddard, 1967; Tatman *et al*., 2000). Black rhinos in areas with abundant food and water such as in the Lerai Forest of the Ngorongoro Crater, Tanzania, have relatively small home ranges (~2.6 – 26.2 km^2) and occur at high densities (1 rhino / 3.1 km^2; Goddard, 1967). However, at the Olduvai of the Ngorongoro Crater, Tanzania, where food and water are scarce, black rhino home ranges are much larger (3.6 – 90.6 km^2) and densities lower (1 rhino / 6.4 km^2; Goddard, 1967). Black rhino population densities can also influence the habitat selection and home range size (Linklater *et al*., 2009; Shaw, 2011). Black rhinos are known to increase their home range sizes in response to decreasing population densities (Linklater *et al*., 2009). This is because intra-sexual competition restricts range overlap and it is better for males to extend their home ranges into newer unoccupied areas than to have home ranges that overlap with other males (Linklater *et al*., 2009).

Black rhinos use dense bush for shade during the hot parts of the day, and so the availability of suitable cover will also influence the location of their home ranges (Mukinya, 1973). In addition, black rhinos tend to avoid areas with human disturbance, which could be an evolutionary behaviour that came about as a response to mass poaching by humans that occurred in the early history of black rhinos or just to avoid the noise associated with human settlements (Mukinya, 1973; Mills *et al.,* 2003). In the Masai Mara Game Reserve, Kenya, black rhinos did not occupy areas where the Masai tribesmen and their livestock were present (Mukinya, 1973).

At an individual black rhino level, factors such as age and sex also influence the size and location of black rhino home ranges (Goddard, 1967; Shaw, 2011). Immature black rhinos of both sexes generally have larger home ranges than adult black rhinos of both sexes (Goddard, 1967). Adult bulls generally have smaller, mutually exclusive home ranges than adult females, which tend to have overlapping home ranges (Goddard, 1967). Competition for breeding mates is the main social pressure exerted on black rhino males and this in turn influences their location and size of the black rhino male home ranges (Owen-Smith, 1988). Nutritional requirements, and not social pressure, are the main factors influencing the location and size of female ungulate home ranges (Owen-Smith, 1988). As a result, black rhino females are able to share home ranges and the resources that occur in these ranges by having overlapping home ranges (Owen-Smith, 1988).

The home range can be interpreted as a crude measure of the energy available to an animal, so the size of the area in which an animal forages is roughly proportional to the animal's metabolic requirements (Lindstedt *et al.,* 1986). Aspects of an animal's morphology, physiology and ecology are affected by body size (Harestad and Bunnel, 1979). Therefore, the size of an animal's home range is related to its body size- as the animal gets bigger, so home range size increases (Harestad and Bunnel, 1979; Lindstedt *et al*., 1986).

Some animals have annual home ranges, because they move between different core areas within their home ranges seasonally (Owen-Smith, 1988). Elephants (*Loxodonta africana)*, for example, exhibit shifts in the sizes of their core areas during the dry and wet season (Owen-Smith, 1988). The dry season core areas of elephants are much smaller than the wet season core areas (Owen-Smith, 1988). Due to the patchy distribution of woody plants and surface water, the dry season core areas of elephants and other large herbivores are generally smaller or more focused on those areas retaining important resources (Owen-Smith, 1988). By contrast, forage and water availability are normally not limiting in the wet season and this allows large herbivores to range over larger areas (Owen-Smith, 1988; Shaw, 2011). Obligate grazers generally do not range as widely as browsers because grass is usually much more evenly distributed across the landscape (Owen-Smith, 1988). Animals may defend the entire area of their home range or only a small portion within the home range (Börger *et al*., 2008). In addition, not all individuals of a species display territoriality (Powell 2000). For example, black rhinos in Pilanesberg National Park (PNP), North West, South Africa demonstrated territorial behaviour (Adcock *et al.,*1998) but black rhinos in the Serengeti, Tanzania did not (Frame, 1980). This could be because the black rhinos in the Serengeti tolerated each other because resources were not limiting, whereas in PNP permanent water sources were limited and thus influenced the location of adult male ranges (Adcock *et al*., 1998). A similar situation was observed in the Ndumo Game Reserve, KwaZulu-Natal, South Africa, where seven black rhinos shared a home range that was 4.3 km^2 in size. This is likely due to the rhinos making use of the highly productive moist woodland habitat present at this reserve (Conway and Goodman, 1989).

Home range behaviour has important implications for the regulation of ungulate populations, their distribution, abundance and community structure (Börger *et al.,* 2008). Long-term studies on the seasonal selection of habitats in black rhinos can provide useful information on the quality and the carrying capacity of the habitat (Shaw, 2011). It can also indicate whether a black rhino population has reached or exceeded the carrying capacity of that habitat (Shaw, 2011).

The objective of this chapter was to investigate the broad spatial ecology of black rhino at Hluhluwe-iMfolozi Park (HiP) and the specific aims were to:

- Examine the space use and habitat selection of black rhinos at HiP; and
- Analyze the factors that may be influencing habitat selection and space use.

4.2 Methods

Rhino sightings

The data used to estimate home range sizes and determine habitat use were collected over a 12 month period; which commenced in April 2012 and ended in March 2013. These data were supplemented with other data collected in 2011 and 2012 during the routine monitoring of black rhinos by field staff in each of the five sections of HiP and a designated black rhino monitor (Druce, 2012, pers. comm.). Both the 2011 and 2012 sightings data were used in this study and were collected in a similar manner. The reason for limiting black rhino sightings to a two year period was because it has been argued that black rhino home ranges shift inter-annually (Lent and Fike, 2003; Linklater *et* *al*., 2009). Thus, there is an increased possibility of overestimating the home range sizes if the sampling period is too long (Linklater *et al*., 2009).

Individual black rhinos were recognised using the unique ear marking done during a procedure called ear notching (See Chapter 2). Re-sighting black rhinos is a continuous process at HiP and all field staff were involved in black rhino monitoring on a daily basis. In addition, every second day I went out to two of the management zones; Nqumeni and Masinda (See Chapter 2) to find black rhinos. The two study sections were chosen because they have historically had the highest numbers of black rhinos (Clinning *et al*., 2009). Further, a previous black rhino study concentrated on these two sections and this potentially allowed for comparisons to be made between my study and the previous one (Plotz and Linklater, 2009). However, the proposed comparison was ultimately not possible because the results from the previous study had not yet been published and I was not able to obtain the raw data.

Field observations of black rhinos were initially made from vantage points; hills, valleys and plains were scanned for signs of black rhinos (Balfour and Howison, 1997). When sighting a black rhino, it was approached cautiously until close enough (~30-50 m) to see its ear notches. At each sighting, the number of individuals present, their age and sex were recorded. The locations of the notches on the individuals' ears were recorded and the location of the sighted black rhino was determined using a handheld Garmin eTrex 10 GPS device. For sightings where an adult female with a calf was sighted, the sex of the calf was also recorded and its age estimated using the black rhino age class system (Appendix A) (Hitchins, 1970). The age estimation was used in order to estimate the calf's date of birth to calculate the intercalving intervals of females with more than one calf (See Chapter 3). A photograph of the individual(s) at each sighting was also taken in order to confirm the location of the ear notches and the identity of the individual. These data were then entered into a black rhino database which is managed by HiP's GIS technician. The database was updated with new black rhino sightings monthly.

Home range size estimates

To estimate the home range sizes for black rhino in HiP, only data from individuals with more than 10 sightings during the study period were used (Conway and Goodman, 1989). A total of 13 individual black rhinos (four males and nine females) satisfied this criterion. Since the Minimum Convex Polygon (MCP) method for estimating home range size is relatively insensitive to small sample sizes, it was deemed most appropriate for estimating black rhino home range size (Harris *et al.*, 1990). Ninety five percent MCPs were constructed using the location points for each individual (Lent and Fike, 2003; Borger *et al*., 2006) which gave a crude estimate of the size of each individual black rhino's home range. The reason for the choice of the 95% polygons was to exclude any outlying sightings which could unnecessarily inflate the home range estimates (Borger *et al*., 2006). In addition, 95% MCPs have been used successfully in other space use assessments of black rhinos (Goddard, 1967; Hitchins, 1969; Mukinya, 1973; Conway and Goodman, 1989; Tatman *et al*., 2000; Lent and Fike, 2003). Home Range Tools for ArcMap (version 9.3; ESRI, California) was used to construct and estimate the area of the 95% MCPs.

The total area of overlap between the home ranges of individual black rhinos was determined for both males and females using ArcMap (version 9.3; ESRI, California). The MCP layers for the individuals that had overlapping home ranges were overlaid on top of each other. The union feature on the analysis tools was used to clip the shapes onto each other. This created a new layer with the joined home ranges showing the total area of overlap. By calculating the geometry of the overlap area the size of the overlap area was determined. To calculate the percentage overlap between the home ranges of black rhino A and black rhino B the following formula was used (Poole, 1995):

Percentage Overlap = 100 x (2 x Area of overlap) / Area A x Area B

To determine general habitat use by male and female black rhino at HiP, all location points from the nine female (n = 109) and four male (n = 52) black rhinos over the study period (2011-2012) were overlaid on a vegetation map of the park (Balfour and Howison, 1997; Bissett, 2004). To calculate the proportion of black rhino sightings that occurred in each vegetation type the spatial join feature in ArcMap was used to join the black rhino sightings and the vegetation layer (Balfour and Howison, 1997; Bissett, 2004). By running the intersect analysis, a column was created in the attribute table which indicated the vegetation type in which each location point occurred.

Random points equal to the number of observed sighting points were created to estimate the expected vegetation use for both males and females. The sightings for the 13 black rhinos' shapefiles were overlaid on the park boundary shapefile. Using the feature class function in the data management tools, random points were created. The random points layer was spatially joined to the vegetation layer and the intersect analysis run to determine the vegetation type in which the random points occurred. To calculate the percentage habitat use for all vegetation types, the following equation was used (Tatman *et al*., 2000):

Habitat use (%) = No. of points in veg. type/ total number of location points x 100

Where the No. of points in veg. type = the number of observed location points occurring in a particular vegetation type, and total number of location points = the total number of location points for the four male or the nine female black rhinos (Tatman *et al*., 2000).

ArcMap was also used to determine the use of slope and aspect by the 13 black rhinos and the randomly generated fixes. Location points for the four males and nine females were overlaid separately onto the slope and aspect layers of the park. An extract values to point analysis was run and this created a new column for the slope and aspect in the attribute table. By selecting the new column and using the statistics function, the mean aspect and slope for each black rhino sighting was calculated.

The mean distance to roads and rivers was also calculated for each of the 13 black rhinos and the random points. The proximity feature was used for this analysis. The black rhino sightings layer was overlaid onto the rivers and drainage line layer, distance was set to meters and a near analysis run. This created a new column for the “near_distance” in the attribute table. By using the statistics function, the mean distances to roads and rivers were calculated.

Statistical analyses

A Chi-square test of independence was conducted to determine whether the differences between observed and expected habitat use were significantly different (Tatman *et al*., 2000). In addition, a student’s T-test was conducted to determine whether there was a statistical difference in mean slope values for the two sexes. However, because the mean distances to roads and rivers for each rhino sighting did not satisfy the assumptions of a parametric test (Statistica; version 11; StatSoft inc. Tulsa, OK, USA), a Mann Whitney U-test was conducted to determine whether there were any significant differences in the mean distances to rivers and to roads between the two sexes. All statistical tests were completed using Statistica (version 11; StatSoft inc. Tulsa, OK, USA).

4.3 Results

Of the 13 black rhino individuals that had sufficient sightings, males tended to have larger home ranges than females, (Table 4.1; Figure 4.1 A; Figure 4.1 B). However, there was no significant difference in the mean home range sizes of males and females ($t=0.99$; $df = 11$; $p > 0.05$). In addition, there was between 1.8% and 54.4% (mean overlap = 9.7 ± 16.9 %) overlap in the home ranges of females and between 24.8% and 64.2% (mean overlap = 30.5 ± 26.8 %) overlap in the home ranges of the four males. The overlap of female home ranges with male home ranges was between 7.5% and 98% (mean overlap = 17.2 ± 25.6 %).

Table 4.1: Home range sizes of 13 black rhino at Hluhluwe-iMfolozi Park as determined by the 95% minimum convex polygon method. Where n is the number of valid location points. Data covers two years: 2011 and 2012.

AREA (km^2) **Females**	**Age (yrs)**	**Home range size**	**Males**	**Age (yrs)**	**Home range size**
Female A (n=15)	26	32.7	Male A (n=14)	13	30.7
Female B (n=12)	32	4.5	Male B (n=10)	11	19.7
Female C (n=15)	26	5.4	Male C (n=14)	7	37.3
Female D (n=18)	8	32.7	Male D (n=14)	3	5.4
Female E (n=10)	4	12.2			
Female F (n=11)	23	6.5			
Female G (n=10)	17	13.1			
Female H (n=14)	4	1.2			
Female I (n=11)	4	30			
Average		**15.4 ± 12.9**			**23.3 ± 14.0**

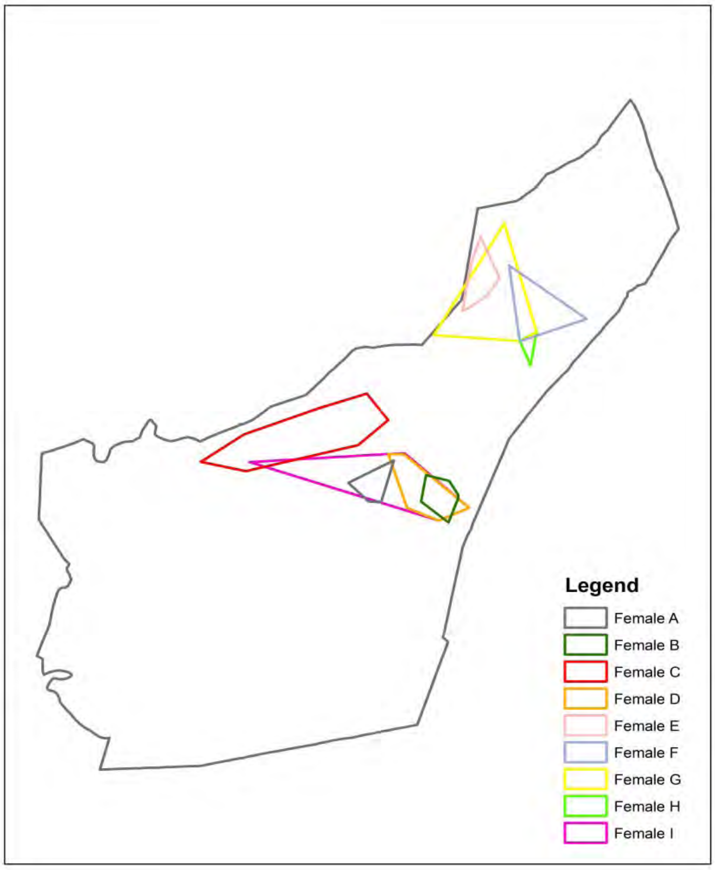

Figure 4.1 (A): Home range area for nine female black rhinos at HiP as determined by the minimum convex polygon method. (ArcGIS 9; map units: meters; projected).

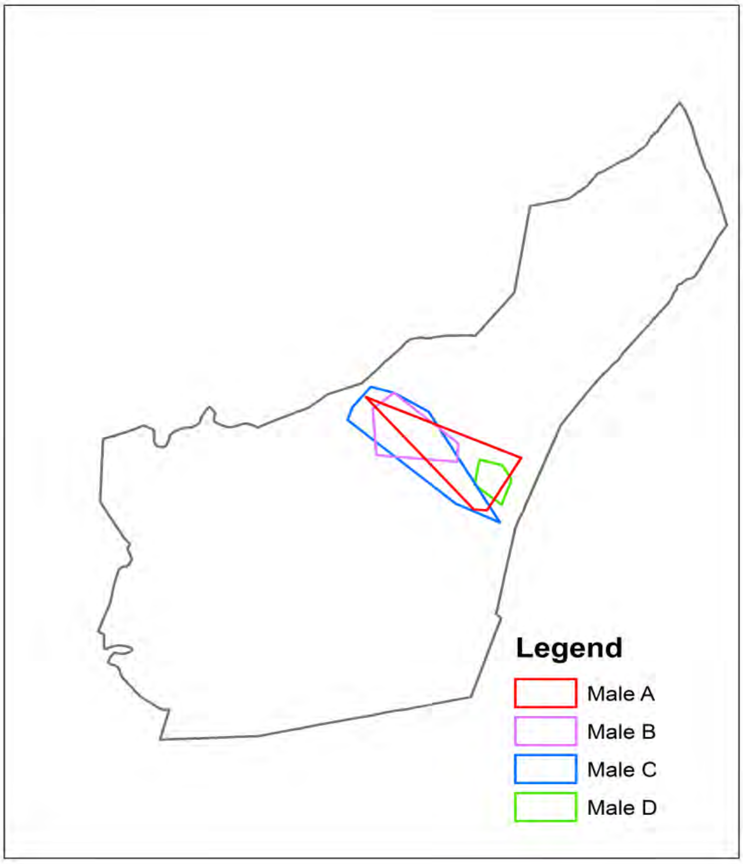

Figure 4.1 (B): Home range area for four male black rhinos at HiP as determined by the minimum convex polygon method. (ArcGIS 9; map units: meters; projected).

Habitat use

Both the male and female black rhinos used the Northern Zululand Sourveld (NZS) and Zululand Lowveld (ZL) vegetation types (Table 4.2). The males were found in the ZL vegetation 75% of the time, while the females were found in the ZL vegetation almost 90% of the time (Table 4.2). Male black rhinos utilized the NZS vegetation 25% of the time and the females utilized the NZS vegetation only 10% of the time (Table 4.2). There was no significant difference in the observed and expected use of vegetation for males (Table 4.3; $\chi^2 = 0.1$; df=2; $p>0.05$). The use of vegetation by males and females was similar to that of the randomly generated fixes (Table 4.2).

The female black rhinos were generally found on slopes of 2.7º ± 3.6º, while males were found on slightly steeper slopes of 3.2º ± 3.6º. These were slightly lower slopes than those for male and female random fixes. However, there was no significant difference in the use of slope by the sexes (Table 4.2; t=0.57; df=11; p>0.05). Both male and female black rhinos were found in close proximity to rivers and the difference in the mean distance to rivers between males and females was not significant (Table 4.2; Z= 0.69; df = 11; p>0.05). The distance of male and female black rhinos to rivers was similar to the random fixes. Male and female black rhinos were found further from roads than they were to rivers (Table 4.2). Males had a mean distance of 441.1 ± 330.2 m, while females had a mean distance of 473.5 ± 439.2 m (Table 4.2; Z= 0.08; df = 11; p>0.05). Random fixes of both male and female black rhinos were found further from roads than the observed black rhino positions.

Table 4.2: Characteristics of the home ranges (95% MCP) of 13 individual black rhinos at HiP and an equal number of randomly generated fixes. Data are means ± sd.

Characteristics	Males	Females	Random males	Random females
Vegetation Types (%)				
NZS	25	10.1	19.2	18.4
ZL	75	89.9	78.8	79.8
Distance (m)				
Rivers	185.0 ± 95.4	189.0 ± 145.6	117.8 ± 100.8	166.81 ± 132.3
Roads	444.1 ± 330.2	473.5 ± 439.2	898.2 ± 1138.9	1245.2 ± 1218.52

Vegetation types are described in chapter 2: NZS = Northern Zululand Sourveld; ZL= Zululand Lowveld

Table 4.3: The vegetation composition of the habitats selected by 13 black rhinos at HiP. The observed figure is the actual number of locations per vegetation type. The expected figure was determined using an equal number of random points.

Sex	NZS	ZL	χ^2 Results
Male			
expected	10	41	$\chi^2 = 0.9$, df=2; $p > 0.05$
observed	13	39	
Female			
expected	20	87	$\chi^2 = 5.4$, df=2; $p > 0.05$
observed	11	98	

Vegetation types are described in chapter 2: NZS = Northern Zululand Sourveld; ZL= Zululand Lowveld

4.4 Discussion

The home range estimation method selected needs to be appropriate for the data and the question being asked (Powell, 2000). Estimates for home ranges are sensitive to the methods used to collect and analyze the data and the length of the data collection period (Linklater *et al*., 2009). The MCP is a common and internationally accepted method for estimating home range size in animals (Anderson, 1982; Burgman and Fox, 2003). It allows for comparisons between new studies and those done in the past (Hansteen *at al.*, 1997; Grant, 2012) and it is relatively insensitive to small sample size (Harris *et al*., 1990). Polygons are drawn by joining peripheral points for all animal sightings and then calculating the area of the polygon (Frame, 1980; White and Garrott, 1990; Lent and Fike, 2003).

However, the MCP is not without disadvantages. Firstly, the home range size estimate increases with an increase in sample size and the home range shape is constrained to a convex shape, even if that is not the case in reality (Anderson, 1982; White and Garrot, 1990; Burgman and Fox, 2003). Secondly, the MCP often incorporates large areas that the animal hardly ever uses and assumes that the use of home ranges is evenly distributed (White and Garrott, 1990; Powell, 2000).

Due to the small sample size of individual black rhino sightings and the method used to collect the sightings data, it was not possible to use other home range estimation techniques such as the Kernel density and Harmonic mean methods in this study (Harris *et al*., 1990; Seaman *et al*., 1999). This is because these two methods require much large sample sizes; e.g. at least 30 sightings per individual for the kernel density estimator (Seaman *et al*., 1999). The simple nature of the MCP method, its ability to facilitate comparisons between different studies and its insensitivity to small sample size makes the MCP method the most applicable method for most situations (Seaman *et al*., 1999; Harris *et al.*, 1990; Grant, 2012). Despite the known limitations of the MCP method, it was considered an appropriate method to use for analysing home range data in this study (Anderson 1982). Nevertheless, the data presented in this study should be interpreted with caution.

The low observation rates of black rhino (Linklater and Hutcheson, 2010) may have contributed to the low number of black rhinos sightings in this study. Consequently, it is important to interpret all home range size estimates as crude minimum areas (Lent and Fike, 2003). The home range sizes cited in my study therefore describe black rhino activity areas and not necessarily absolute home range sizes (Linklater and Hutcheson, 2010). These estimates allow for comparison between the activity areas of male and female black rhinos (Linklater and Hutcheson, 2010). The black rhino home range sizes in my study are within the normal range of black rhino home ranges found in other studies (Owen-Smith, 1988, Tatman *et al*., 2000). However, the smallest home range in my study (1.2 km^2) was much lower than the smallest home range found in a Kenyan sanctuary (2.25 km^2) and in the Ngorongoro Crater, Tanzania (2.6 km^2; Goddard, 1967; Tatman *et al*., 2000). The possible reason for such a small home range could be to the low number of black rhino sightings which led to the underestimation of home range size.

At an interspecific level, variations in home range size are driven by body size and metabolic requirements (van Beest *et al.,* 2011). Home range size increases with increasing body mass; this is because absolute metabolic requirements increase with an increase in body mass (Owen-Smith, 1988). As a result, large animals require larger home ranges to fulfil their metabolic requirements (Owen-Smith, 1988). Smaller ungulates, like impala (*Aepyceros melampus*) have lower absolute metabolic requirements and can thus exist in relatively small home ranges (0.8 – 1.8 km^2) (Owen-Smith, 1988). By contrast, elephants are extremely large (>2800 kgs) and have higher absolute metabolic rates, thereby requiring significantly larger home ranges (200-700 km^2) (Owen-Smith, 1988).

At an intraspecific level, the variations in home range size are driven by extrinsic and intrinsic factors such as the individual involved, forage availability and climate (van Beest *et al.,* 2011). For moose (*Alces alces)*, home range sizes decrease with an increase in browse density (van Beest *et al.,* 2011). Moreover, the spatio-temporal changes in the abundance and quality of this food resulted in varying home range sizes - the home range sizes decreased with an increase in browse abundance in summer and increased during periods of food scarcity in winter (van Beest *et al.,* 2011). Reproductive status of ungulate species is also known to affect the use of habitat and thus home range size (van Beest *et al.,* 2011). Pregnant female ungulates often restrict their movements due to changes in their mobility and their increased vulnerability to predators (van Beest *et al.,* 2011). However, while lactating, female ungulates can either enlarge their home ranges *sensu* roe deer (*Capreolus capreolus*) due to the high energetic and nutritional demands, or reduce their home range sizes *sensu* white-tailed deer (*Odocoileus virginianus*) due to the increase in vulnerability to predation as a result of having a young offspring (van Beest *et al.,* 2011). In my study three female black rhinos had calves aged two years and younger during the study period; these were female A, female C and female G. The sizes of their home ranges may be because they had dependant young (van Beest *et al*., 2011).

The ages of animals can also result in the variation of home range sizes within a species (Lindstedt *et al.,* 1986). For example, sub-adults of most ungulate species (and black rhinos) may live as nomads due to dispersals from their natal range until they are socially established, therefore they have large home ranges (Lindstedt *et al.,* 1986). Also, because sub-adults generally require more nutrients to grow, but may lack proper food gathering skills, they may have larger home ranges in order to satisfy their dietary requirements (Lindstedt *et al.,* 1986). However, adult black rhinos of both sexes generally have smaller home ranges than sub-adults (Goddard, 1967). Sub-adults are nomadic and their ranges often overlap with those of adults of both sexes and incorporate ranges of the adults they associate with and so the sizes of their home ranges are larger until they are socially established and start reproducing (Goddard, 1967; Lindstedt *et al.,*1986; Adcock *et al*., 1998), while adults settle into smaller home ranges once they start reproducing (Adcock *et al*., 1998).

Male black rhinos are known to hold mutually exclusive territories, while females have home ranges that generally overlap with home ranges of adult males and other females (Shaw, 2011). The location and sizes of female home ranges is greatly influenced by food supply and high quality habitats suitable for raising offspring (Bailey, 1993). By contrast, male black rhino home range size and location is influenced by intra-sexual competition for breeding mates (Linklater *et al*., 2009). The lack of competition between females means that black rhino females can occupy home ranges that overlap with those of other individuals. The overlap in mammal female home ranges could also occur to reduce predation on their offspring (Owen-Smith, 1988). The age and sex of the individual black rhino were the main factors influencing the sizes of home ranges at PNP, North West, South Africa (Adcock *et al.,*1998). The location of male home ranges at PNP, North West, South Africa, was influenced by the location of permanent water sources and, as a result, male black rhinos were found exclusively in one part of the park (Adcock *et al.,* 1998). Hitchins (1969) found that the location and size of the black rhino home ranges at HiP were influenced primarily by food availability. The location and size of both female and male black rhinos in my study were possibly influenced by the availability of food and water. All black rhino home ranges occurred close to rivers and drainage lines and the overlapping of the home ranges means that those areas probably contained sufficient food resources (Conway and Goodman, 1989). The proximity of the black rhinos to water in my study was further than randomly distributed fixes suggesting that water is probably not the main factor influencing the location of home ranges in this study. It is then possible that the central location of home ranges in my study is an artefact of the concentration of field work in these central areas. The occurrence of overlapping home ranges in both the males and the females in my study could be pointing to the abundance of food in the areas where these home ranges are situated (Conway and Goodman, 1989). This is because male black rhinos generally do not hold overlapping home ranges and for them to do so could mean that the abundance of food in these areas is adequate to supply all the black rhinos in that area and that competition for food resources amongst the males is minimal (Conway and Goodman, 1989; Tatman *et al*., 2000). It could also mean that male dominance systems, rather than territoriality, govern the location of male home ranges (Owen-Smith, 1988). In male dominance systems, the high ranking male has dominance over subordinate males and can thus tolerate the subordinate males in his territory so long as he remains the dominant individual (Owen-Smith, 1988). It could also mean that the availability of resources is a much greater influence on the location and sizes of male home ranges than competition for mates (Conway and Goodman, 1989). Another possible reason for the occurrence of overlapping home ranges could be that the black rhinos used in the analysis were related (Adcock *et al., 1998*). It is known that the home ranges of sub-adult black rhinos (mostly males) are similar to those of their mothers (Adcock *et al., 1998*). However, only four animals in my study were related; male B was the calf of female A while male D was the calf of female C.

Goddard (1967) found home ranges as small as 2.6 km^2 in the Ngorongoro Crater, Tanzania, while in the Ndumo Game Reserve, KwaZulu-Natal, South Africa, seven black rhinos were found to share a home range of 4.3 km^2 situated in a moist woodland (Conway and Goodman, 1989). By contrast, black rhino home range sizes in the drier parts of the Serengeti, Tanzania, can be as large as 70 – 100 km^2 (Frame, 1980; Tatman *et al.,* 2000). As variable as home range sizes can be, most studies have found that black rhino home ranges generally fall between the two extremes found in the Ngorongoro Crater, Tanzania (Goddard,1967) and the Serengeti, Tanzania (Frame, 1980, Tatman *et al.,* 2000). For example, in the Masai Mara Game Reserve, Kenya, black rhino home range sizes were between 3.6 and 90.7 km^2 and between 15.0 and 90.7 km^2 at the Laikipia Plateau in Kenya (Tatman *et al.,* 2000). Home ranges in a Kenyan rhino sanctuary were found to range between 2.25 km^2 and 7.65 km^2 (Tatman *et al.,* 2000). It was concluded that the small home range sizes found at the Kenyan rhino sanctuary meant that the habitat at the sanctuary was highly suitable for black rhinos (Tatman *et al.,* 2000). The crude home range estimates for my study were between 1.2 and 37.3 km^2. Male black rhino home ranges in the Serengeti, Tanzania, tended to be larger than those of females; black rhino adult males had ranges of between 88 and 133 km^2 while females had ranges between 70 and 99 km^2 (Frame, 1980).

Home ranges of both male and female black rhinos in the Serengeti, Tanzania, had some degree of overlap, indicating that these males did not show any territoriality (Frame, 1980). However, Hitchins (1971) found that black rhino males at HiP held territories while the females had home ranges. In addition, there was little overlap in the territories of males (Hitchins, 1971). In the 1970 study at HiP, the male territories (3.93 – 4.66 km^2) were smaller than the home ranges of females (5.83 – 7.69 km^2) (Hitchins, 1971), hinting at the added energetic cost of defending a territory (Börger *et al.*, 2008). The overlapping of male home ranges in my study may mean that there is probably no territoriality amongst the males, and this may have allowed the males in the park to occupy much bigger areas than they would have if they were defending territories (Börger *et al.*, 2008).

Black rhinos are known to restrict their movements during hot periods (Owen-Smith, 1988). Thick shrub and bushland habitats seem to be optimal for black rhinos (Tatman *et al.,* 2000). This could be due to the availability of cover, which black rhinos use for shade during hot parts of the day (Mukinya, 1973). These habitats also contain the preferred black rhino browse species (Tatman *et al*., 2000) and are known to support high black rhino densities; 1.4 rhino/km^2 (Goddard, 1970); 1.6 rhino/km^2 (Conway and Goodman, 1989). Clearly, black rhinos inhabiting these habitats are able to fulfil their nutritional requirements in the smallest of home ranges (Goddard, 1967; Tatman *et al.,* 2000). Significantly, black rhinos can change the location and size of their home range depending on environmental conditions and the individual's nutritional state (Börger *et al*., 2008). During the summer months, black rhinos at HiP preferred to rest and feed in habitats on the hills and ridges (Hitchins, 1971; Joubert and Eloff, 1971). By contrast, black rhinos were found in more open grassland areas during the wet season to take advantage of the vegetation growth that occurs after rains (Shaw, 2011). My study covered both the wet and dry seasons and the MCP home range size estimates cited include sightings from both seasons.

Black rhino home ranges in the Serengeti, Tanzania, were not evenly distributed across the landscape (Frame, 1980). Instead, black rhinos avoided areas with short to medium grasslands that occurred 3 km away from wooded grasslands or drainage lines (Frame, 1980). Black rhinos were found in drainage lines even when there was no cover, suggesting that the availability of water and food, and not the presence of cover, determined the distribution of black rhino home ranges (Schenkel and Schenkel-Hulliger, 1969; Frame, 1980). However, the location of black rhino sightings in my study could be due to observer bias and the method use to find rhinos. The black rhinos were generally found close to water sources, and this may highlight the importance of water for black rhinos. Both male and female black rhinos in my study preferred low-lying areas, the males occupied steeper slopes than the females but these were generally low-lying areas.

Conclusion

The number of sightings per rhino and the method used to estimate the home range sizes in my study means that the estimates are crude estimates. However, I hope that the limitations of this study will better inform future research planning to ensure that a study of this nature will yield enough data to be appropriately analyzed. By closely studying the habitat selection of selected individuals in specific age classes, any seasonal changes in habitat use patterns can be detected (Shaw, 2011). Dry season habitat use patterns are an important component of habitat quality (Owen-Smith, 2002) and habitat use patterns in black rhinos during the dry season could give an indication of whether the population is approaching carrying capacity (Shaw, 2011). This is because these habitat use patterns give information on the alternative plant species that black rhinos use once their important dry season plant species are depleted (Shaw, 2011). Thus, by knowing the persistence of these alternative plant species in the park, management would be able to asses how suitable the habitat is for black rhinos (Owen-Smith, 2002). Even crude estimates of a species' home range gives insight into mating patterns, reproduction, social organization and interactions (Powell, 2000; Monterroso *et al.,* 2013). Home range also gives information on the species' foraging and food choices, the resources which may limit population growth and the important components of its habitat (Powell, 2000). All this allows reserve managers to better manage the species and is especially important for endangered species such as the black rhino (Monterroso *et al*., 2013).

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CHAPTER FIVE

SUMMARY & MANAGEMENT IMPLICATIONS

This study was initiated to determine the factors that may be affecting the reproductive performance of the black rhino population at HiP. Since this population is a primary source of black rhinos for the Black Rhino Range Expansion Programme (BRREP), it is important to understand why the population may not be performing as expected.

As reported in Chapter 3, the population growth rate of the HiP black rhino population was 6.3%; this was a slight decrease from the growth rate in the previous year. However, the 2012 population growth rate was above the 5% minimum growth rate target set by the Rhino Management Group. The mean age at sexual maturity (ASM) was delayed from the average 7.5 years found in most poor performing black rhino populations (du Toit, 2006) to 12 years. In addition, the current black rhino population has an ASM that is twice what it was at HiP in 1983. The intercalving interval was three years and nine months; this is slightly longer than the three years and four months which is found in populations with poor fecundity (du Toit, 2006). The black rhino population had a slight female bias but had a 21% fertility rate. The population comprised 60% adults, 36% sub-adults and 13% juveniles, and this is indicative of populations that are close to reaching carrying capacity (Couslon *et al.*, 2004). All these parameters; the delayed ASM, the longer ICI, the low fertility rates and high adult component point to a population that may be suffering from density dependent impacts. The black rhino population at HiP seems to be experiencing density dependent effects (Hrabar and du Toit, 2005).

The reason for the relatively poor performance of the black rhinos at HiP could also be due, in part, to the removals done as part of BRREP. Removals are known to disrupt the social structures of ungulate populations (Patton *et al*., 2008). Disruptions in social structure can lead to home range shifts and reduce the productivity of black rhino populations (Patton *et al*., 2008). Poor habitat quality and thus poor nutrition could also be causing the delayed ASM, longer ICI and thus lower fertility rates. Poor nutrition leads to the delayed attainment of sexual maturity; underweight black rhino females do not ovulate and thus cannot reproduce (Patton *et al*., 2008). Significantly, black rhinos are known to lengthen their ICI during periods of food scarcity (Owen-Smith, 1988).

In order to promote increased reproductive success amongst HiP black rhinos, I believe there are several management options which the park should consider. Firstly, levels of bush encroachment could be assessed and reduced if necessary (Conway and Goodman, 1989; Emslie, 1999). By reducing bush encroachment, the growth of the plant species preferred by black rhinos may be enhanced (Emslie, 1999; Patton *et al*., 2008). The plant diversity in the reserve will also be increased (Ward, 2005). This may result in an increase in the carrying capacity for black rhino in the park (Ward, 2005). The enhanced food availability will likely promote better nutrition in HiP black rhinos, which may lead to females gaining the body weight required for reproduction earlier (Gaillard *et al.,* 2000). The females might then attain sexual maturity earlier than the current 12 years seen at HiP and thus the lifetime reproductivity will be longer and the population should increase (Owen-Smith, 1988). However, a reduction in bush encroachment will also result in the loss of potential shelter and shade which black rhinos use to rest under after feeding and wallowing during the day (Mukinya, 1973; Emslie and Adcock, 1994). It may also negatively impact other browsing species, such as the elephant, that may be feeding on the plant species that occur in these woody habitats (Emslie, 1999). Secondly, as part of the annual removals, the HiP management may wish to target older black rhino individuals. Those older than at least 20 years and have already contributed at least three to four calves to the population (Patton *et al*., 2008). Those females still have the potential to give birth to at least another two calves at a new site (Fike, 2011). Currently, HiP does not prescribe how many calves a female should produce before it is considered suitable for removal (Druce, 2012; pers comm.). The removal of older black rhinos may allow younger females to attain sexual maturity earlier, due to a lack of competition for food with older females (Bronson, 1989; Gaillard *et al.,* 2000). In addition, juvenile recruitment may increase if the adult component is reduced (Owen-Smith, 1988; Coulson *et al*, 2004). An increase in the number of young females attaining sexual maturity will result in an increase in fecundity, this will result in increased births, increased population growth rates and increased population numbers.

The removal of older, and possibly dominant black rhino bulls, may also allow younger subordinate black rhino males to gain access to females unhindered by the dominant males and this could increase productivity as more males will be mating with females (Owen-Smith, 1988). However, removing older black rhino females might disrupt their breeding performance and so they may not breed in the new site, rendering the translocation exercise a waste of resources (Patton *et al*., 2008). Removing older individuals might also create a skew in the population dynamics and disrupt the social structure so that the remaining individuals take longer to re-establish themselves and to start mating (Patton *et al*., 2008). In addition, complications related to translocations increase with the animal's age, thus removing older animals may also increase translocation-related deaths (Patton *et al*., 2008). Finally, and perhaps most importantly, park management may want to consider a moratorium on black rhino removals in order to allow the population to increase to ~75% of the calculated carrying capacity (Adcock, 2001) before removing further individuals. This may result in accelerated population growth rates (> 5%) while avoiding density-dependent effects (Adcock, 2001; Hrabar and du Toit, 2005; du Toit, 2006). The negative side of not removing any animals would be the increase in older black rhinos in the population, which may eventually lead to the decline in the population as there will be less juvenile recruitment (Borner *et al*., 1987). The increase in black rhino population densities may also lead to an increase in density-dependent effects such as even longer intercalving intervals (ICI), lower fecundity and fertility rates (Hrabar and du Toit, 2005). High black rhino densities will also result in food resource limitations; these will result in increased susceptibility to diseases, reduced infant survival, slow population growth rates and the delayed attainment of sexual maturity (Skogland, 1985; Rachlow and Berger, 1998; Hrabar and du Toit, 2005).

Reducing bush encroachment may be the most viable management option. However, the reduction of bush encroachment is an ongoing management intervention that requires follow-up treatments to avoid the rapid development of the woody species (Emslie, 1999).

In chapter 4, I presented the broad characteristics of home range and habitat use of the black rhino population at HiP. The number of sightings per individual black rhino was low and this made an in-depth analysis of how space use influences reproductive success problematic. I was, however, able to tentatively map some black rhino home ranges. The proximity of permanent water sources appeared to influence the location of black rhino home ranges at HiP. Both the male and female black rhinos had home ranges closer to rivers than expected. In addition, the majority of the black rhino sightings were located in the Zululand Lowveld habitat type. This is a habitat characterized by plants such as *Acacia nilotica, A. burkei, A. gerrardii* and *Dichrostachys cinerea.* Moreover, forests of *A. robusta* are most often found close to rivers (Mucina and Rutherford, 2006). These *Acacia* plants make up at least 46% of the black rhino diet in the Mfolozi part of HiP and 34% of the diet of black rhinos in the Hluhluwe section of HiP (Emslie and Adcock, 1994). The fact that the black rhino home ranges in this study occurred in this habitat type where these plant species occur suggests that these plant species are important for the survival of the population. It is possible that these plant species do not occur uniformly throughout the park which is why the black rhinos had overlapping home ranges in these areas so as to utilize the food resources available in these areas (Conway and Goodman, 1989). If these plant species occurred more abundantly in the park, then black rhino nutrition may be improved. An improvement of the black rhino nutrition will result in more healthy black rhinos; this may result in increased fecundity and fertility rates (Gaillard *et al.,* 2000). All of this will result in great reproductive success for the black rhino population at HiP (Gaillard *et al.,* 2000).

To better understand the home range and habitat use of black rhinos at HiP I would suggest that future studies consider using tracking equipment such as GPS collars to track the movements of individual black rhinos (Hitchins, 1971; Morgan, 2010). The terrain and vegetation at HiP makes finding black rhinos by random searching very difficult (Hitchins, 1971). Also, the random search method does not ensure regular re-sightings of individual as the data in my study highlight. It has been suggested that at least 30 to 40 sightings per individual black rhino per year is required to adequately estimate home ranges (Tatman *et al*., 2000). By using tracking equipment, the number of sightings per individual black rhino will be significantly increased and this will allow for a more comprehensive assessment of space use. Further, GPS satellite collars will also allow for the collection of nocturnal spatial data for black rhinos (Hitchins, 1971; Morgan, 2010). These data cannot be accurately quantified using the current method (Morgan, 2010).

Two broad conclusions can be drawn from my study; that the annual black rhino removals may be disrupting the social structure of black rhinos at HiP, and that this, in turn, could be negatively affecting the reproductive performance of the population. Secondly, the habitat quality, particularly the occurrence of bush encroachment, seems to be negatively impacting on the black rhino population and may have reduced the carrying capacity for black rhinos in the park. The poor nutrition resulting from the bush encroachment is likely affecting the reproductive success of the population. However, further research and increased monitoring efforts are required to provide a better overall picture of the ecology of the black rhino population at HiP.

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Appendix A: Description of the Rhino Management approved age classes for aging black rhino in the field (Hitchins, 1970; Emslie *et al*., 1993).