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THE EFFECTS OF RESOURCE VARIABILITY ON THE DEMOGRAPHIC RATES OF BLACK AND WHITE RHINOCEROSES

by

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Dissertation

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in

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September 2023

DECLARATION

I declare that this dissertation is my own, unaided work. It is being submitted for the Degree of Master of Science at the University of the Witwatersrand, Johannesburg. It has not been submitted before for any degree or examination at any other University.



(Signature of candidate)

06 September 2023

ABSTRACT

Given the importance of rhino survival and reproduction to conservation goals, the aim of the study was to investigate the effects of resource variability on the demographic rates of black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinos at Lapalala Wilderness. I used historical rhino-monitoring, rainfall and vegetation greenness data to investigate the vital rates of two rhino populations. I investigated population demographics (mainly density, growth rates, age and sex structure) and survival using stratified Cox models. Black and white rhino density peaked at 0.06 rhinos/km^2 and 0.2 rhinos/km^2, respectively during the study period and was below the estimated maximum density for suitable rhino reserves. Average growth rate for the black rhinos was 4.784%, which was almost half of the white rhino's rate of 8.861%. The survival of both species was stage-specific, and rainfall effects were similar for both species and age groups as low amounts of rainfall, which likely represent decreased forage availability, were associated with increased mortality risk. Decreasing greenness was also associated with increased mortality except with white rhino calves, where mortality increased with greenness. I suggest that this case might have been caused by their nutritional requirements: most grasses lose nutritional value as the season progresses (i.e., represented as increases in greenness values and so reduced access to high quality forage might affect mom's body condition and her ability to produce nutritious milk, consequently resulting in increased mortality rates of calves. I also investigated the reproductive phenology (mainly conception and birth timing, age at primiparity and inter-calving intervals) and birth sex ratios in relation to sex allocation theories. White rhinos conceived and calved at an earlier age compared to the black rhinos; mean age at primiparity for white and black rhinos was 9.448 years (8.467, 10.43) and 11.724 years (10.52, 12.927), respectively. Conceptions for both species peaked during the wet season and were associated with periods of high forage availability; however, births were asynchronous and occurred

throughout the year. Effects of rainfall and greenness on age at first conception differed between species; the odds of having their first calf increased with rainfall, EVI and NDVI for white rhinos but decreased with EVI and NDVI for the black rhinos. Increases in wet-season integrated greenness during conception periods might indicate a shorter period of access to high quality forage for the black rhinos. Age at primiparity increased with density for both species because population density increases competition for resources, potentially making it difficult for females to accumulate the body mass and energy reserves needed to reproduce. Inter-calving intervals increased with rainfall, supporting the idea that excessive amounts of rainfall might result in lower forage quality, which then affects maternal body condition. In conclusion, vital rates of black and white rhinos are associated with resource availability as a function of environmental stochasticity and density, which in turn affects productivity and performance as climate change results in more variable conditions.

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CHAPTER 1: GENERAL INTRODUCTION

Broad Project aim

To investigate the effects of resource variability on the demographic rates of black and white rhinoceroses at Lapalala Wilderness Nature Reserve, and to compare resource effects between the two rhino species.

Problem statement and Motivation of study

A gradual loss of terrestrial biodiversity has been observed through the years, mostly due to anthropogenic land use changes (Sala et al., 2000; Lambin et al., 2001), overharvesting (i.e., excessive hunting) (Rosser & Manika, 2002) and the effects that climate change has both directly and indirectly on species (Sirami & Monadjem, 2012). These changes in weather patterns are resulting in increased mortality rates of endangered species by meddling with body functions (i.e., direct effects) and by altering their environments (i.e., indirect effects) (Sala et al., 2000). This is especially true in seasonal environments, such as savannas, which due to their rich biodiversity support a large number of different species, including the largest mammalian herbivores (DuToit & Cumming, 1999). Regardless of climate change, savannas are generally variable environments (Staver et al., 2011) whose composition of tree to grass ratios is largely determined by rainfall (Walter, 1970; Scholes & Archer, 1997; Sankaran et al., 2005). This in turn means that weather conditions in savanna environments play a large role in determining the population dynamics of large herbivores.

South Africa, which is home to some of the largest herbivores, is a water scarce country where rainfall has been predicted to decrease with an increase in global climate change (Roffe et al., 2019). Through numerous studies conducted on mostly temperate zone herbivores, it has been concluded that young and mature herbivores do not respond similarly to resource variability brought on by environmental stochasticity (Gaillard et al., 2000).

Monitoring the phenology of African savannas is therefore important for identifying future implications of changing climates on large herbivore population demographics (Pettorelli et al., 2011). Among the most recognizable of South African herbivores are the black rhinoceros (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*). Despite both species being herbivores, black rhinos are browsers and white rhinos are grazers, displaying the functional diversity found in African savannas. Therefore, one would expect them to react differently to environmental stochasticity and resource availability (Plotz, 2014). Assessing their demographic rates is of great importance, especially with regards to effective wildlife management (Duffy & Pettorelli, 2012) and in the face of population declines. For example, considering only the African continent, total rhino numbers declined from 2017 to 2021, with white rhinos declining at 3.1% per annum and black rhinos increasing by 3% per annum (Ferreira et al., 2022). However, for both species, South Africa's proportion and contribution, as part of the African range states, declined during the same period (Ferreira et al., 2022). Additionally, both black and white rhinos occurring within management models performed better than those within pure-state systems (Ferreira et al., 2022); with differences in population performances attributed to stochastic processes, social and ecological limitations (Lande et al., 2003; le Roex et al., 2018).

One such reserve that has dealt with rhino population declines is Lapalala Wilderness Nature Reserve (LWNR). The reserve is located in the Waterberg region of Limpopo, South Africa, falling in the bushveld bioregion, which is characterised by its semi-arid nature and varying degrees of canopy cover (Rutherford et al., 2006). As seasonality is a characteristic of this region, rainfall is a limiting factor for most of the year, falling predominantly during the summer season, suggesting fluctuations in resource availability for herbivores in the region (Scholes & Archer, 1997; Owen-Smith et al., 2005). Previously, declines in the rhino population at the reserve were thought to be caused by viruses, but this cause has been ruled

out (Muller, 2022 (unpublished source)). A number of studies have been conducted to determine the influence of resource availability (via proxy of climatic conditions and directly using vegetation greenness indices) on the demographics of large herbivores (Loe et al., 2005; Pettorelli et al., 2005; Pettorelli et al., 2007; Wittemyer et al., 2007; Young et al., 2009). In spite of that, few studies focusing on the rhinoceros species have been conducted. It has already been established that global climate change has resulted in an already water scarce South Africa becoming drought prone, meaning unexpected changes to rhino demographics (Ziervogel, 2014). However, the ability to predict future implications of climate change on resource variability, which affects herbivore species, may reduce declining species numbers. This study is important because rhinos are ecosystem engineers, that consume large quantities of vegetation, shaping the savanna landscape and creating habitats for other organisms (Waldram et al., 2008). The white rhino is near threatened (approximately 20 000 individuals worldwide) and the black rhino is critically endangered (approximately 5 000 individuals worldwide) mainly due to poaching, and so this study has conservation implications (last assessed in 2020- Emslie, 2020). As part of South Africa's 'Big Five', rhinos are quite the tourist attraction, contributing to ecotourism which generates a large sum of money for the economy. Lastly, if demographic parameters are influenced by resource availability, knowledge on this would go a long way for management teams in public and private reserves, which are strongholds for these two species.

Literature review

Population dynamics of large herbivores

Monitoring shifts in population health, as well as the extrinsic and intrinsic factors which affect population size, is essential to any species' conservation strategy (Gaillard et al., 1998; DeCesare et al., 2012). Keeping track of population demographics is an ideal way to infer

population dynamics of both rare and hard to observe species, as well as those that are much easier to observe and count (DeCesare et al., 2012). These population dynamics are defined as the end result of variations in survival or mortality, fecundity, and migration rates of a set population (Owen-Smith et al., 2005). The ability to identify which of these vital rates is more variable amongst populations (for example, between the different age classes) and which is the probable cause of fluctuating abundance is very useful for monitoring population dynamics (Caughley, 1977; Tuljapurkar & Caswell, 1997; Gaillard et al., 1998).

The population dynamics of large herbivores are influenced by both density-dependent and density-independent factors (Sæther, 1997). These factors mainly consist of food resources, predation, and weather; but also include inter/intraspecific competition, disease, habitat quality and human influence (Hairston et al., 1960; Caughley & Krebs, 1983; Andrewartha & Birch, 1984; Messier & Crete, 1985; Gaillard et al., 1998). Although there is still some disparity amongst ecologist as to how these factors act on the vital rates of most taxa, most concur that food resources, predation and weather conditions are the main factors acting on large savanna herbivores (Gaillard et al., 2000; Owen-Smith et al., 2005; Young, 1994; Shorrocks, 2007). This is because the savanna is a "climatically determined" biome, meaning that plant biomass is directly correlated with the amount of annual rainfall (Shorrocks, 2007). This also means that the unpredictability of savanna environments will be exacerbated with an intensification in climate change, ultimately affecting the dynamics of savanna herbivores (Pettorelli et al., 2007).

The different life history stages of large herbivores do not respond to environmental stochasticity in a similar manner. This is essentially because sensitivity to extreme climatic conditions differs among age classes (Bleu et al., 2015), primarily as a function of resource allocation towards growth and storage (i.e., fat reserves) (Adams, 2003; Parker, 2003). Juvenile survival rates, or survival during the first year of life, have been observed to be the

most sensitive among the age classes, being affected first by environmental variation and population density (Eberhardt, 1977; Gaillard et al., 1998; Eberhardt, 2002). Whilst prime-aged adults seem resistant to the effects of environmental variation and density on their survival (Gaillard et al., 1998; Gaillard et al., 2000; Gaillard & Yoccoz, 2003), senescent individuals may be just as vulnerable as juveniles (Bleu et al., 2015). Feedbacks from population density will then affect the age at first breeding, followed by the fertility rates of prime-aged females, and then only the survival of prime-aged adults (Eberhardt, 1997). However, it is important to take into account that these generalizations are based on studies focused mostly on temperate Northern hemisphere herbivores (i.e., mostly studies on different deer species; also predator free environments) (Owen-Smith and Mason, 2005). In his review on density-dependence in large herbivores, Fowler (1987) found that of 21 herbivore species, 15 showed that juvenile survival was affected, whilst effects on age at first reproduction were present in 12 and adult survival effects were present in only 9 species. Owen-Smith (1990) found that the survival of juvenile kudus (*Tragelaphus strepsiceros*) was correlated with both resource availability and population size; but was also the most important factor in determining population fluctuations. A study by Bleu et al. (2015), conducted on two chamois (*Rupicapra rupricapra*) populations, found that age at first breeding and the onset of senescence differed between the two due to environmental variation and timing of the warmer season. Young's (1994) study on the natural die-offs of 96 mammal species found that juveniles and yearlings were the most sensitive to resource limitations brought on by changes to their habitats. The parallels between these studies illustrate that population growth of large herbivores, which is at most times driven by juvenile recruitment and adult survival (Coulson et al., 2005), is most sensitive to changes in resource availability caused by environmental conditions.

Furthermore, because the reproduction of large herbivores is usually timed to coincide with nutritionally optimal periods, to support maternal demands (Gaillard et al., 1993; Langvatn et al., 2004; Wittemyer et al., 2007; Zerbe et al., 2012; Owen-Smith & Ogutu, 2013), evidence suggests that variations in resource availability possibly induce variations in offspring sex ratios (Clutton-Brock et al., 1984; Clutton-Brock & Iason, 1986; Post et al., 1999; Garroway & Broders, 2007). Because offspring viability is largely dependent on maternal investment (Clutton-Brock & Iason, 1986; Clutton-Brock, 1991; Post et al., 1999) adaptive theories suggest that offspring sex ratios will vary according to the costs and benefits associated with producing daughters and sons (Clutton-Brock & Iason, 1986; Trivers & Willard, 1973; Clark, 1978; Post et al., 1999; Cockburn et al., 2002). In sexually dimorphic and polygynous species (i.e., most large herbivores), sons are considered the more costly sex with higher fitness returns (Clutton-Brock et al., 1981; Gomendio et al., 1990; Cockburn et al., 2002) and so mothers in good condition should favour them over daughters (Trivers & Willard, 1973; Clutton-Brock et al., 1984; White et al., 2007). This forms the basis of one of three hypotheses used to explain offspring sex ratios in such species. The Trivers and Willard (1973) hypothesis (TWH) predicts that mothers in good condition (i.e., with more resources and energy/parental care) should produce more sons because their fitness returns are more variable than that of females. Alternatively, the local resource competition (Clark, 1978) hypothesis (LRC), which is based on sex-specific dispersal, predicts that mothers in poor condition should produce sons, the dispersing sex, who will emigrate from the mother's home range and not compete for resources (Silk, 1983; Weladji & Laflamme-Mayer, 2011). The final and most recent hypothesis, the extrinsic modification hypothesis (EMH), states that offspring sex ratios could be influenced by environmental conditions independently of any parental allocation strategies (Post et al., 1999). Several studies have revealed that environmental conditions, particularly in strongly seasonal environments might be more

influential than adaptive modification strategies in modifying herbivore sex ratios (e.g., Post et al., 1999; Weladji & Holland, 2003; Hrabar & Du Toit, 2005).

Spatio-temporal variability of South African savannas

Changes in environmental conditions, for example, temperature, CO_2 concentration, and precipitation, result in changes to vegetation dynamics (Keeling et al., 1996; Archibald & Scholes, 2007). This means that the environment is largely responsible for the phenology of plants and habitat composition (Gillespie, 1977; Loe et al., 2005). This is true for South African savannas, which coupled with being semi-arid are also unpredictable (Roffe et al., 2019; Staver et al., 2011; Abraham et al., 2019) and are characterized by a continuous grass layer with discontinuous tree cover (Frost et al., 1986). Thus, the interactions between grasses and trees are best observed in these habitats, although these interactions can be very complicated. Putting aside factors such as fire, nutrients, geology and herbivory; rainfall is considered the most important limiting factor to plant biomass in our savannas (Scholes & Archer, 1997; Whitecross et al., 2016). The amount of rainfall does not only determine biomass, it plays a role in plant green up or the flushing of new leaves, leaf retention time and timing of leaf fall (Scholes & Walker, 1993; Menzel, 2002; Archibald & Scholes, 2007). This means that the amount of rainfall will essentially determine the amount of biomass available to savanna herbivores, in turn affecting herbivore biomass (Shorrocks, 2007). However, droughts have become more frequent in South Africa's savannas as global climate change has increased (Roffe et al., 2019) posing a threat to these herbivores (Ripple et al., 2015).

Droughts are defined as periods of unusually low rainfall compared to the average rainfall expected in a certain area (McKee et al., 1993), however these droughts do not affect all herbivores equally. Abraham et al. (2019) found that browsers [steenbok (*Raphicerus campestris*), giraffe (*Giraffa camelopardalis*), kudu (*Tragelaphus strepsiceros*) and duiker

(*Sylvicapra grimmia*)] were not affected by drought periods in Kruger National Park, whereas grazers [waterbuck (*Kobus ellipsiprymnus*), buffalo (*Syncerus caffer*), wildebeest (*Connochaetes taurinus*), zebra (*Equus burchelli*) and warthog (*Phacochoerus africanus*)] experienced higher mortality rates and shifts in diets during these periods. The survival of white rhino calves was correlated with the annual rainfall from the two years prior to their birth (Ferreira et al., 2015) whereas there were no changes in the recruitment and survival of black rhinos during droughts (Ferreira et al., 2019). These differences between browsers and grazers come down to how rainfall affects vegetation composition; usually affecting herbaceous vegetation instantly and severely (Vetter, 2009). This is because woody plants can store water during the dry season, which allows for an earlier green-up and longer leaf retention period; contrasting herbaceous vegetation which only greens after the first rains of the wet season (Scholes & Archer, 1997; Shorrocks, 2007; Whitecross et al., 2016). This indicates how the composition and function of savanna vegetation is closely linked to seasonality (Archibald & Scholes, 2007), which allows us the ability to assess the bottom-up regulation of savanna herbivores (Rutherford, 1980; Pettorelli, 2011).

Remote-sensed vegetation indices

Understanding what drives savanna phenology is important for conservation strategies, and so multiple methods have been developed to predict savanna phenology (Archibald and Scholes, 2007; Pettorelli et al., 2011). Previous studies conducted on the effects of weather conditions on savanna phenology have made use of remote-sensed data, specifically the Normalized Difference Vegetation Index (NDVI) (Fuller, 1999; Chidumayo, 2001, Archibald & Scholes, 2007; Whitecross et al., 2016). Essentially, the NDVI provides an estimate of photosynthetically active radiation absorbed (Myneni & Williams, 1994) and near-infrared light that is reflected by vegetation (Pettorelli et al., 2011). NDVI is calculated using the formula:

$$\mathrm{NDVI} = \frac{(\mathrm{NIR} - \mathrm{RED})}{(\mathrm{NIR} + \mathrm{RED})}$$

Where NIR and RED correspond to the near-infrared and red light, respectively (Pettorelli et al., 2005). This has been shown to be associated with plant processes (for example, photosynthetic capacity and leaf area index (LAI)) allowing for the monitoring of disturbances (such as droughts) on wildlife, specifically large herbivores (Tucker et al., 1981; Pettorelli et al., 2005; 2011). Another commonly used vegetation index in such studies is the Enhanced Vegetation Index (EVI) (Huete et al., 2002). Similar to NDVI, EVI has been correlated with photosynthetic capacity and leaf thickness (LAI). Moreover, EVI is sensitive to saturations that may be caused by variations in canopy cover, correcting for atmospheric aerosol disturbance, and so may be a better index for areas with high biomass and canopy cover (Gao et al., 2000; Huete et al., 2002; Pettorelli et al., 2005; Fensholt et al., 2006). EVI is calculated using the formula:

$$\mathrm{NDVI} = \mathrm{G}\frac{\mathrm{NIR} - \mathrm{RED}}{\mathrm{NIR} + C_1 \times \mathrm{RED} + C_2 \times \mathrm{BLUE} + \mathrm{L}}$$

Where NIR, RED and BLUE correspond to the atmospheric-corrected surface reflectances; C_1 and C_2 are the aerosol resistance factors, L is the canopy background adjustment factor and G is a scaling factor (Huete et al., 1997; Huete et al., 2002; Fensholt et al., 2006; Didan et al., 2015). Using climatic data and NDVI to determine the influence of seasonality on breeding phenology of two red deer populations, Loe et al. (2005) found that the population experiencing the most seasonality in plant green-up rates exhibited high breeding synchrony. Wittemyer et al. (2007) found that the initiation of breeding in elephants was dependent on resource availability, and birth was also timed so that it occurred during periods of high resource availability; whereas, juvenile survival was not associated with resource availability. This illustrates the value of pairing rainfall data with remotely sensed data to monitor the demographics of large herbivores, allowing us a glimpse into their population dynamics.

Study site

Lapalala Wilderness Nature Reserve is a 480 km^2 private nature reserve located in the Waterberg region, Limpopo Province, South Africa (23°44'–23°57' S, 28°09'– 28°25' E; Figure 1.1). It was established in 1981 as a 360 km^2 reserve and has since seen two expansions (up to 480 km^2 by the end of 2022 (Muller, 2022 – unpublished source)). It falls within the savanna biome, and central bushveld bioregion, with eight land type communities (see Table 1.1 for the full list and Figures 1.2–3) having been identified according to the most dominant plant species found there— indicating heterogeneity and biodiversity. Common woody plants include *Combretum* spp., *Acacia* spp., silver terminalia (*Terminalia sericea*), and Rhodesian rubber tree (*Diplorhynchus condylocarpon*); and common herbaceous plants include gum grass (*Eragrostis gummiflua*), three-awns (*Aristida* spp.), and common reed (*Phragmites* spp.) (https://lapalala.com/wildlife/ accessed 14 December 2021). The reserve's soils are mostly nutrient poor and leached due to their sandstone composition but recently, more nutrient rich soils due to basic norite intrusions have been observed. The reserve is divided by the Palala River and Bloklands Spruit, which are fed by many other smaller streams, seeps and wetlands- whose water levels fluctuate in response to mean annual rainfall. The long-term mean annual rainfall is estimated at 500 mm (https://lapalala.com/about/ accessed 14 December 2021) with most of that falling during the wet season (November – April). Mean (minimum and maximum) monthly temperatures during the spring/summer period are 14°C and 30°C, and temperatures during the autumn/winter period are 20°C and 20°C. Besides rhinos, other large herbivores include impalas (*Aepyceros melampus*), plains zebras (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), African elephants (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), hippopotamus (*Hippopotamus amphibius*) and common eland (*Taurotragus oryx*). Large carnivores include leopards (*Panthera pardus*), brown hyenas (*Hyaena*

brunnea), and cheetahs (*Acinonyx jubatus*) (https://lapalala.com/wildlife/ accessed 14 December 2021).

Study species

The black rhinoceros (*Diceros bicornis*), also known as the hook-lipped rhino (Figure 1.4), is a browser (weight: 800–1100 kg). It feeds on leaves and twigs and requires the savanna habitat for food and shade (Shorrocks, 2007). Browsing predominantly on shrubs, the most commonly favoured plants in their diet include species from the genera *Acacia*, *Combretum*, *Croton*, *Dichrostachys*, *Grewia*, *Spirostachys* and *Terminalia* (Owen-Smith, 1988; Emslie, 1999). The white rhinoceros (*Ceratotherium simum*), also known as the square-lipped rhino (Figure 1.5), is a mega-grazer (weight: 1400–2300 kg). It feeds on short grasses but also requires the savanna habitat for shade (Shorrocks, 2007). Favoured species include those from genera *Panicum, Urochloa*, *Digitaria* and *Sporobolus* (Owen-Smith, 1988). Both species are perissodactyls (odd numbered toes), hind-gut fermenters (have simple stomachs and chew food once), and are dependent on surface water availability, with the black rhino observed to be slightly more water-dependent (Joubert, 1971; Owen-Smith, 1998; Emslie and Adcock, 2013). Both species' social groups consist of the mother and calf (which is dropped after a gestation period of 450–480 days, at 40kg), which remains with its mother for up to three (white rhino) or four (black rhino) years (Shorrocks, 2007). Feeding/suckling by young rhinos may last for 19 months in black rhinos and up to 12–18 months for white rhinos (Owen-Smith, 1988). The modal inter-calving interval for both species ranges between two- to two and a half years (Owen-Smith, 1988). Rhinos have no natural predators, but for humans who hunt and kill them for their horns (Emslie *et al*., 2016), with a few exceptions of calf injuries and deaths caused by hyenas (Owen-Smith, 1988). Black rhinos were first

introduced to the reserve in 1990 and white rhinos in 1982, and have since been tracked strictly, with all rhinos known individually.

Dissertation structure

The aim of this thesis is to investigate the relationships between resource variability, mainly via indirect proxy of rainfall and direct proxy of vegetation greenness indices, and demographic rates, mainly mortality and reproductive output, of black and white rhinos.

The dissertation has been separated into two data chapters, which are synthesized in the concluding chapter. The first chapter examines the relationship between rainfall, vegetation indices, density and survival of both black and white rhinos.

The main objectives were:

(1) To assess long-term variations in rainfall and greenness indices

(2) To compare population growth of black and white rhinos, and assess whether there was any evidence of density-dependence on their population growth

(3) To compare the survival of black and white rhinos in relation to rainfall, greenness, and density

The second research chapter investigates the reproductive phenology of black and white rhinos in response to variations in rainfall, vegetation greenness and density.

The main objectives were:

(1) To determine the influence of density on reproductive timing

(2) To compare the age at first calving of black and white rhinos in relation to rainfall, vegetation greenness and density

(3) To compare inter-calving intervals of black and white rhinos in relation to rainfall, vegetation greenness and density

(4) To investigate the skewed sex ratios of calves born at Lapalala in accordance with three theories (the influence of environmental conditions on sex allocation)

The fourth and final chapter synthesizes results from the two research chapters and makes use of those results to formulate recommendations on future conservation strategies based on the model outputs which provide a key starting point for monitoring the population dynamics of Lapalala rhinos.

The thesis is structured in a way that the first chapter entails an introduction to the study which provides relevant background information and the literature review, followed by the two data chapters, and concludes with the synthesis chapter. As both research chapters make use of historical rhino monitoring, rainfall, and vegetation greenness data, and occur at the same study site, some repetition (particularly in the methods section) is to be expected.

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Table 1.1. Classification of the identified land types and dominant vegetation communities of Lapalala Wilderness.

Community	Land type description	Vegetation community
1	Closed	*Diplorhynchus condylocarpon – Croton gratissiumus*
2	Open, Sandstone/conglomerate	*Diplorhynchus condylocarpon – Combretum apiculatum*
3	Open to closed, norite	*Acacia nigrescens – Combretum apiculatum*
4	Open to closed, norite	*Dichrostachys cinerea – Acacia tortilis*
5	Open to closed, Sandstone/conglomerate	*Terminalia sericea – Burkea africana*
6	Open, Vlei	*Terminalia sericea – Eragrostis gummiflua*
7	Closed	*Olea Europea – Pappea capensis – Combretum mole*
8	Open, Riverine on Palala	*Combretum erythrophyllum* – Phragmites spp.

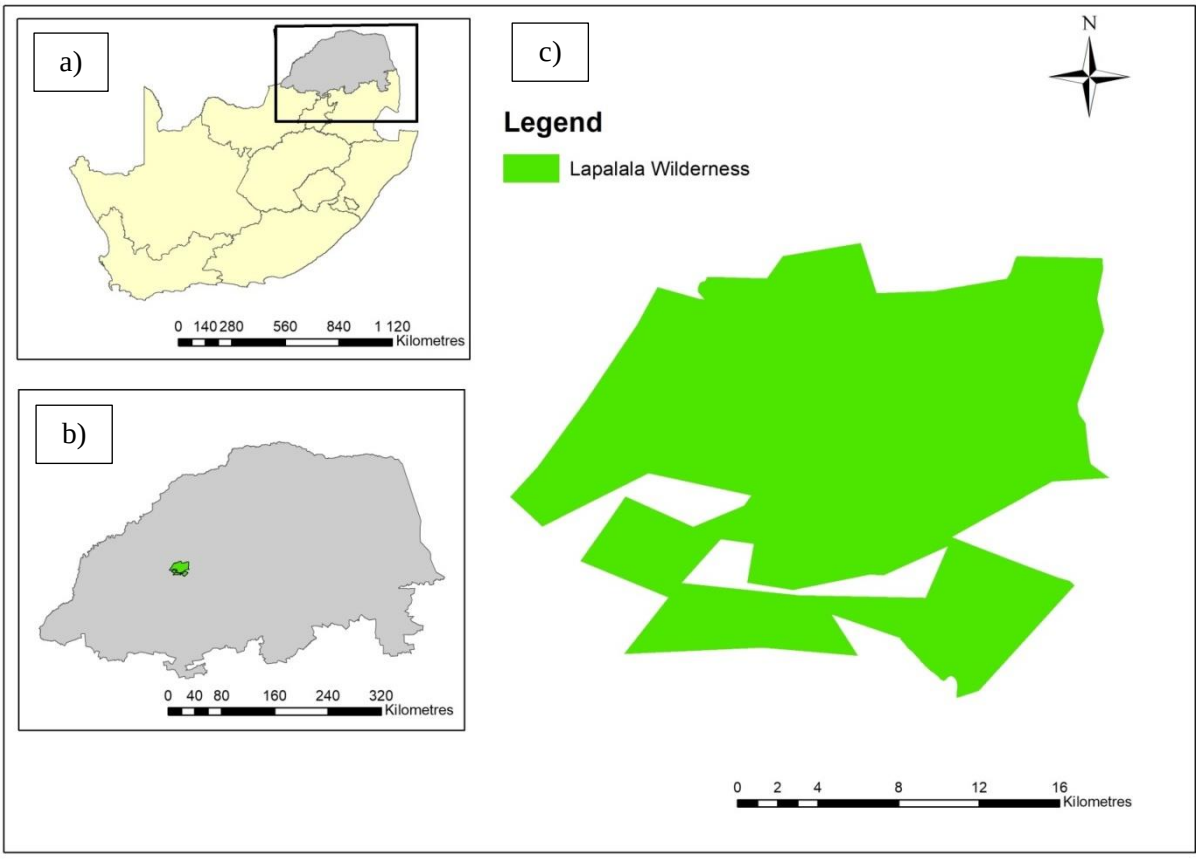


Figure 1.1. The study area in South Africa (a), and in the province of Limpopo (b), Lapalala Wilderness.



Figure 1.2. Photograph showing a section of the wilderness area, taken from the game drive route in June 2022. A white rhino mother and calf pair can be seen on the left side of the picture, along with some warthogs (*Phacochoerus africanus*).



Figure 1.3. Photograph showing a more open section of the wilderness area, taken from the game drive route in June 2022, with a solitary bull (white rhino) seen in the tall grass.



Figure 1.4. Black rhino (*Diceros bicornis*) in Lapalala Wilderness. (Photo from Lapalala Wilderness Nature Reserve).



Figure 1.5. White rhino (*Ceratotherium simum*) mother and calf pairing in Lapalala Wilderness. (This photograph was taken in June 2022 by Jason Marshal).

CHAPTER 2: SURVIVAL OF BLACK AND WHITE RHINOCEROSES IN RELATION TO RAINFALL, GREENNESS AND DENSITY

Abstract

The population dynamics and vital rates of large herbivores, such as the black and white rhinoceros, are influenced by both intrinsic and extrinsic factors. Among these factors, for savanna herbivores, environmental variation plays an important role as it directly affects resources, creating a ripple effect once density and age are considered. Given the differences in dietary guild between the two rhino species and differences in the relationship between rainfall and woody versus herbaceous plants, one would expect differences in their survival and other vital rates as a consequence of environmental stochasticity. I used historical rhino-monitoring, rainfall and vegetation greenness data to investigate rhino survival and other vital rates of two rhino populations at Lapalala Wilderness Nature Reserve. Black and white rhino density measured at 0.01 rhinos/km^2 during the first year of introductions and peaked at 0.06 rhinos/km^2 and 0.2 rhinos/km^2, respectively during the study. Population growth rates for both populations illustrated a weak but negative association with population density, and the average growth rate during the study period was 4.784% for black rhinos and 8.861% for white rhinos. Survivorship estimates for black rhinos were 0.870 by age 1, 0.774 by age 3, 0.591 by 7 and 0.241 by the end of the study period. And for white rhinos estimates were 0.911 by age 1, 0.830 by age 3, 0.711 by age 7 and 0.191 by the end of the study period. Model selection of Cox PH models showed that the survival of both species was stage-specific, and that survival increased with rainfall, likely indicating how low amounts of rainfall resulted in decreased resources. Greenness models showed similar results as survival increased with greenness for all stages except young white rhinos, which I suggest might have been a consequence of vegetation quality, which declines as the season progresses or as greenness increases. Additionally, for both species, mortalities occurred despite decreases in

density, indicating little evidence of density-dependence and leading me to believe that both populations might rather be resource limited. Therefore, I suggest that species-specific assessment of how environmental variation affects vital rates, might be necessary for effective conservation of these species in semi-arid regions.

Introduction

The survival of large herbivores, such as the black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros, is influenced by the interactions between intrinsic (age and sex) and extrinsic (habitat conditions, climate and predation) factors (Gaillard et al., 1998; Coulson et al., 2001). These factors regulate population dynamics and vital rates, particularly survival and mortality, as a result of their impacts on animal body condition (Mautz, 1978; Jorgenson et al., 1993; Simard et al., 2010). However, the timing and significance of these factors varies widely and depends on the species and its geographic range (Sæther, 1997). For animals found in tropical or sub-tropical environments, the timing of environmental conditions plays an important role as it directly affects resources, creating a ripple effect once density and age are considered (Owen-Smith et al., 2005). Additionally, in semi-arid environments, where the seasonal variation is extreme, vegetation growth and forage availability are directly linked to rainfall (Rutherford, 1980) and so effects to population demographics will differ according to the species of herbivore, their dietary requirements, interactions with density and age structure (Owen-Smith, 1988, 1990; Gaillard et al., 2000; Coulson et al., 2001; Owen-Smith & Mason, 2005; Owen-Smith et al., 2005; Bonenfant et al., 2009).

The effects of environmental stochasticity on herbivore survival tend to vary with age (Coulson et al., 2001; Simard et al., 2010). Juvenile survival has been shown to be the most variable, whilst adult survival tends to be more resistant to effects of environmental variability and density (Gaillard et al., 1998; Gaillard et al., 2000; Heppell et al., 2000). Senescent individuals, whose contributions to population structure and dynamics through reproduction are vital, also illustrate similar trends in survival as juveniles (Bleu et al., 2015). Prime-aged females also tend to have higher survival rates with low variability compared to similar aged males, especially during periods of poor environmental conditions (Loison et al.,

1999; Gaillard et al., 2000; Toïgo & Gaillard, 2003). The reasoning behind these differences is similar; age- and sex-specific sensitivity. Juvenile herbivores are sensitive to reduced resource availability as they do not have the means to sustain themselves during shortages (have little to no fat reserves), which is then also exacerbated by increased population densities (Ballard & Whitman, 1987; Adams, 2003; Parker, 2003; Festa-Bianchet et al., 2017). This is similar for senescent individuals whose declining body condition is worsened by food shortages (McDonald et al., 1996; Gaillard et al., 2000; Nussey et al., 2007a). Sex differences are attributed to male-male combat/competition and nutritional stress associated with a larger body size (Clutton-Brock et al., 1982; Toïgo et al., 2007). And so, three main age-specific stages can be recognised (Caughley, 1966), which is important because of their contributions to population growth, which is dependent on adult survivorship (and fecundity) but with changes in juvenile recruitment contributing to inconsistent growth rates (Gaillard et al., 1998; Gaillard et al., 2000; Wittemyer, 2007).

Because juvenile recruitment is sensitive to limiting factors induced by environmental stochasticity and density (Gaillard et al., 1998), it has been theorized that individuals who experience similar conditions during early life could meet the same predictable fate (Lindström, 1999). Cohort effects, which are variations in characteristics (e.g., survival and fertility) over time between individuals with some shared experience such as a year of birth or years of a specific exposure (Albon et al., 1987; Gaillard et al., 1998b; Gaillard et al., 2003), have also been identified as a source of variation in population dynamics (Beckerman et al., 2002; Pigeon et al., 2017). And so unfavourable conditions during early life could have negative effects on body condition, and in-turn on vital rates (Nussey et al., 2007b; Douhard et al., 2013); however, early life conditions could be over-turned by more favourable conditions experienced later on during adulthood (Pigeon et al., 2017). This has been referred to as ‘beneficially saturated conditions’ (Krist & Mundinger, 2015) and is the opposite of the

predictive adaptive response (PAR) hypothesis and silver-spoon effects, which predict that early life environment contributes to adaptation for adult conditions and that cohorts born during favourable conditions will have higher lifetime performance, respectively (Grafen, 1988; Gluckman et al., 2005). As cohort differences are frequently influenced by weather conditions, it is important to investigate the influence of climate on population dynamics especially in areas where climate change has been predicted to bring unfavourable conditions which may affect species vital rates unpredictably (Pigeon et al., 2017).

South Africa, which is abundant with large herbivores and is home to two of the rhinoceros species, is an already water-scarce country where more drought periods have been predicted because of climate change (Vogel, 1994; Vetter, 2009; Ripple et al., 2015). Generally, rainfall determines savanna composition; however, its effects on the plant types differs slightly (Scholes & Walker, 1993; Archibald & Scholes, 2007). Where the timing and (reduced) amount of rainfall affects herbaceous plants rapidly and severely because of their dependence on rain to start greening, woody plants can store nutrients and water to allow greening before the first wet season rains (Scholes & Archer, 1997; Do et al., 2004; Sankaran et al., 2004; Vetter, 2009). As such, one would expect that grazer species, such as the white rhino, would be affected more by decreasing amounts of rainfall compared to browser species, such as the black rhino (Ferreira et al., 2019). One climatic phenomenon that has garnered attention in the southern hemisphere is the El Niño-Southern Oscillation (ENSO) (e.g., Kruger, 1999; Ogutu & Owen-Smith, 2003; Ogutu et al., 2007) which causes irregularities in rainfall patterns (Ogallo, 1988; Ropelewski & Halpert, 1996) and in South Africa, is associated with drought periods or years with below average rainfall (van Heerden et al., 1988; Jury et al., 1994; Jury, 1996; Kruger, 1999; Ogutu et al., 2007). These dry spells are associated with low vegetation output during the wet season, and poor retention and

quality going into the dry season (Walker et al., 1987; Owen-Smith et al., 2005; Marshal et al., 2011) which could have major implications for herbivore population dynamics.

Studies on black and white rhinos have found differences in their survival because of the relationship between rainfall and their respective food types (e.g., Hrabar & du Toit, 2005; Ferreira et al., 2019; le Roex & Ferreira, 2020). But few studies have investigated the two proxies, rainfall and vegetation greenness, together and have been over a long period of time, with animals tracked extensively from birth to death. Where rainfall and NDVI represent both indirect and direct proxies of vegetation productivity, respectively, EVI is a more direct proxy of vegetation quality (Loarie et al., 2009; Tsalyuk et al., 2019) and so including both greenness indices could be valuable for integrating environmental features with population dynamics (Ryan et al., 2012). Given the importance of rhino survival to conservation goals, the aim of the study was to investigate the survival of black and white rhinos in relation to rainfall and vegetation greenness. I used historical rhino-monitoring, rainfall and vegetation greenness data to investigate rhino survival and other vital rates of two rhino populations. This study provides a starting point for population models of black and white rhinos at Lapalala Wilderness Nature Reserve (LWNR), primarily focused on the significance of climate change both at the individual level and population level. I hypothesized that (H_1) both species will experience high mortality rates of young and older individuals (senescent rhinos) during low rainfall periods (including El niño events), however rates may be higher for the white rhino population due to forage unavailability (Ferreira et al., 2019). As rainfall primarily determines vegetation biomass, I hypothesized that (H_2) high mortalities for both rhino species would be indicated by low NDVI and EVI values, particularly integrated greenness, which would indicate years of low productivity. Density effects and lagged effects may not be as evident (H_3) as large mammals tend to be affected less by density dependence if populations do not approach carrying capacity and are more

likely to be driven by environmental stochasticity (Sibly and Hone, 2002; Trimble et al., 2009).

Methods

Study site

Lapalala Wilderness Nature Reserve is a private nature reserve located in the Waterberg region, Limpopo Province, South Africa (Figure. 1.1). It was established in 1981 as a 360 km^2 reserve and grew to 480 km^2 by 2022 (https://lapalala.com/past/ accessed 14 December 2021). It falls within the savanna biome, and central bushveld bioregion (Rutherford et al., 2006). Common woody plants include Combretum spp., Acacia spp., silver terminalia (*Terminalia sericea*), and Rhodesian rubber tree (*Diplorhynchus condylocarpon*); and common herbaceous plants include gum grass (*Eragrostis gummiflua*), three-awns (*Aristida* spp.), and common reed (*Phragmites* spp.) (https://lapalala.com/wildlife/ accessed 14 December 2021). The long-term mean annual rainfall is 500 mm (https://lapalala.com/about/ accessed 14 December 2021) with most falling in November – April. Mean minimum and maximum monthly temperatures during spring and summer are 14°C and 30°C, and temperatures during autumn and winter are 20°C and 20°C. Besides rhinos, other large herbivores include impalas (*Aepyceros melampus*), plains zebras (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), African elephants (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), hippopotamus (*Hippopotamus amphibius*), roan antelope (*Hippotragus equines*) and common eland (*Taurotragus oryx*).

Rhino monitoring data

I used historical rhino monitoring data spanning 1982–2019. Five black rhinos were introduced to the reserve in 1990 and six white rhinos were introduced in 1982. Since then, additional rhinos have been introduced and a few have been removed or translocated to other

reserves. Black and white rhinos were tracked daily by an experienced team of rhino monitors at the reserve, who follow the rhino's tracks on foot and by vehicle (using a 4x4) until they see the rhinos. Recorded data include identity, health status, sex, reproductive status (e.g., whether they were seen with a calf or without their calf), group structure, broad location and any other remarks including cause of death, if it could be identified. Mortalities were established with the discovery of a carcass, specifically for older rhinos or non-dependent rhinos; however, for younger rhinos who were still dependent on their mother or immature rhinos that were still associated with their mother, mortality was presumed when the rhino was no longer seen with its mother. Both species are strictly monitored, and all rhinos are individually recognized, as they have been tracked from birth or upon arrival (i.e., translocated individuals). This study included all native and introduced (translocated) rhinos for most of the analyses to infer demographic parameters for the black and white populations; however, for the purpose of determining the influence of resource variability on their survival, only animals whose cause of death appeared to be resource related were used (i.e., animals with known causes of mortality, such as fighting and poaching, were excluded from the analyses because I focused on survival responses to rainfall, vegetation greenness and density).

Rainfall data

Historical rainfall data, spanning the period of the rhino data, was obtained from the South African Weather Service. This data was collected at the Ellisras-Pol, Marken and Mahwelereng weather stations which are all within 3 km to Lapalala Wilderness. At the three stations, data from the year 1967 (September) to the end of the study period was recorded inconsistently (i.e., some months had daily amounts, others had weekly amounts). To create a continuous rainfall record, monthly totals were standardized by dividing each station's

monthly total by its standard deviation. Monthly averages were then calculated across stations and were used to calculate rainfall variables used in the study.

Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) data

I indexed forage availability with Advanced Very High Resolution Radiometer (AVHRR) and Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI and EVI composites obtained from the NASA Land Processes Distributed Active Archive Centre (LPDAAC). MODIS products were established as a continuation index of AVHRR to allow for long-term monitoring, and the two products are comparable and complement each other (Huete et al., 1997, 2002; Didan et al., 2015). The AVHRR data spanned 1992–1996 (accessed from the Earth Resources Observation and Science (EROS) center via Earth Explorer https://earthexplorer.usgs.gov/) and had a 1.1 km spatial resolution and 10-day temporal resolution. The MODIS NDVI and EVI data spanned 2000–2019 (accessed from Oak Ridge National Laboratory (ORNL) DAAC via Earth Data https://daac.ornl.gov/) and had 250 m spatial resolution and 14-day temporal resolution. To work with both products, I rescaled the AVHRR data to the same spatial resolution of 250 m using the bilinear resampling method in ArcGIS 10.6, which is recommended for continuous data because it causes some smoothing of the resampled data without producing cell values outside of the range of the input raster (ArcGIS Desktop via https://desktop.arcgis.com/en/arcmap/). Greenness values were extracted for the 480 km^2 study area and mean values for each 10-day or 16-day image were calculated because I did not have GPS locations for the rhinos (du Plessis, 1999).

Data analyses

Population demographics

Following Owen-Smith's modelling conventions (see Owen-Smith & Mason, 2005; Owen-Smith et al., 2005; Owen-Smith & Mills, 2006) population size was estimated using the

number of individuals alive per year by the end of the annual year. Annual population growth rates (ΔN_t) were calculated using the formula:

$$\Delta N_t = log_e(N_{t+1}/N_t)$$

where N_t is the population size at the end of time *t*, and N_{t+1} is the population size at the end of time *t+1*. This formula considered not only births and deaths, but also rhinos which were introduced and removed from the population. To assess density dependence, the abundance level directly responsible for density feedbacks (N_{eff}) was calculated using the formula:

$$N_{eff} = 0.5N_t + 0.25N_{t+1} + 0.25N_{t-1}$$

This formula considers that for long-lived megaherbivores density effects possibly operate over a longer period than for most herbivores, from pre-conception up to post-birth (or time of annual counts in some cases). Chi-squared tests were used to test for differences in sex ratios (for individuals whose sex was known) for each species separately. Changes in age structure were monitored using summary statistics. Stage categories were defined from literature and based on the rhino's life history and functional life stages as: calf (less than a year old), juveniles (1–3 years), sub-adults (3–7 years), and adults (7+ years) (see Emslie et al., 1995; Law & Linklater, 2013; Balfour et al., 2019; le Roex & Ferreira, 2020; Muller, 2022 – unpublished source). However, to assess changes in age structure, calves, juveniles and sub-adults were combined to form one group, immature rhinos, and adults were left as they were (adapted from Greaver et al., 2014).

Density effects

In addition to assessing the effects of current abundance on rhino survival, prior population effects were also investigated because they can cause delayed effects on large herbivore populations and their vital rates, for example, through resource availability (Sinclair 1989, Turchin, 1995, Owen-Smith & Mills, 2006). High animal densities maintained for extended periods of time could impede vegetation recovery, lowering the availability of their food

sources (Owen-Smith & Mills, 2006). I calculated lagged rate correlations between population growth rates and previous density (as far as 10 years previous) to establish lagged density effects (Berryman & Turchin, 2001; Owen-Smith & Mills, 2006). I used a total of four indices to estimate the effect of prior density on rhino survival: an average of the population density over both a two-year and four-year block, excluding the year prior to the count which represents the direct feedback:

$$N_{den\ fac2} = \frac{N_{t-2}+N_{t-3}}{2} \ldots \text{(equation 1)} \ \& \ \ N_{den\ fac} = \frac{N_{t-2}+N_{t-3}+N_{t-4}+N_{t-5}}{4} \ldots \text{(equation 2)}$$

The third and fourth indices were calculated like the equations above except instead of using rhino abundance, I used the number of rhinos/km^2 (referred to as "conspecific density", over a two- and four-year block, as well as current density) because I was unable to calculate the ecological carrying capacity of the reserve as it is hard to estimate (Emslie et al., 2009). Where the first two indices estimate the periods over which impacts on herbaceous vegetation are expected to persist (Owen-Smith & Mills, 2006), the third and fourth estimate density-dependence in relation to reserve size, which can also limit resource sinks if conspecific density gets too high (i.e., spatial restrictions might indicate density-dependence, particularly for black rhinos) (Rachlow & Berger, 1998; Birkett, 2002; Linklater & Swaisgood, 2008; Sky et al., 2022). In total, 12 derived density variables were included for each species in the survival analysis (using the six indices mentioned, for the rhino's birth and death year).

Climatic variables: Rainfall

Rainfall indices: To evaluate whether the rainfall during a study year was a drought year I used the rainfall anomaly index (RAI). The RAI calculates annual precipitation anomalies by using a ranking system to allocate values to positive (higher than normal) and negative (lower than normal) rainfall amounts (van Rooy, 1965; Keyantash & Dracup, 2002) based on a threshold calculated from the rainfall amounts (Eshetu et al., 2016). More strongly positive values indicate wetter years; more strongly negative values indicate drier years (Eshetu *et al*.,

2016).

Cohorts: Data were insufficient to define each animal's born in year as separate cohorts. Using RAI, rhinos were assigned to cohorts based on the rainfall conditions in their year of birth, as wet, normal or dry, and I used this variable to assess cohort effects on survival. This was important as survival during the first year is especially important in dry savannas (Trimble et al., 2009).

El Niño Southern-Oscillation (ENSO): To test the effects of ENSO on rhino survival I used the Oceanic Niño Index (ONI) (https://ggweather.com/enso/oni.htm). The ONI is the primary index used by the National Oceanic and Atmospheric Administration (NOAA) to track ENSO events, ranking the severity of the events as weak, moderate and strong El Niño and La Niña phases (Glantz & Ramirez, 2020). For this study, moderate and strong El Niño phases were categorised as ENSO years and the rest as non-ENSO years and this index was implemented as a variable in the survival models.

Derived rainfall variables: Using the standardized rainfall from the three weather stations, rainfall variables were derived for animals used in the survival analysis. These variables were generated with respect to the rhino's life history, to capture both immediate and lagged responses. The variables were calculated specifically for each animal in the analysis and so there were some differences between native animals (those born at Lapalala) and those that were introduced, i.e., lifetime rainfall was not necessarily all the rainfall that transplants have been exposed to but was the amount of rainfall that they experienced in their time spent at Lapalala (this was also addressed by stratifying in the survival analysis). And so, the rainfall variables were: lifetime rainfall (total from birth to death, or total from arrival to death), lifetime dry-season (May–October) rainfall (total from birth/arrival to death), lifetime wet-season (November–April) rainfall (total from birth/arrival to death), rainfall six months prior to the rhino's birth/arrival, rainfall six months prior to the rhino's death, rainfall during the

rhino's first year (during the first 12 months), rainfall one month before birth/arrival, rainfall one month after birth/arrival, and rainfall one and two years before birth/arrival. Additionally, two variables, rainfall during the first year of "independence" (during the age 1–2 years) and rainfall during the juvenile stage (1–3 years), were derived to assess this vulnerable life stage and allow additional investigation into cohort effects.

Vegetation greenness indices: NDVI and EVI

I calculated monthly NDVI and EVI values using the 10- and 16-day mean values. I used these monthly values to derive nine greenness indices for NDVI and EVI separately: greenness in the month before birth/arrival, greenness in the month of birth/arrival, greenness one month before death, maximum greenness value in the year of birth/arrival, maximum greenness value in the year of death, wet-season integrated greenness (sum of monthly values during the wet season) during the birth year and in the year of death, and annually-integrated greenness (sum of monthly values during the twelve month period) in the birth year and in the year of death (Pettorelli et al., 2005; Rasmussen et al., 2006; Pettorelli et al., 2007). Although EVI is much more sensitive to saturations caused by canopy cover and is meant to complement NDVI in such studies, methods have been created to separate the tree and grass contributions to NDVI in savannas (Gao et al., 2000; Huete et al., 2002; Didan et al., 2015). Using methods shown by Chidumayo (2001) tree and grass components were extracted from NDVI values based on assumptions that trees will green before grasses do, i.e., increases in NDVI before the first rains are caused by the tree layer, and that increases in NDVI values after the first rains are due to the grass layer. Accordingly, the contribution of the tree layer was estimated using the equation:

$$NDVI_{tree\ component} = NDVI_{December} - NDVI_{August/September}$$

where $NDVI_{December}$ is the NDVI in December, which has been found to peak due to contributions of trees in African savannas (Dougill & Trodd, 1999) and

$NDVI_{August/September}$ is the lowest value observed towards the end of the dry season before NDVI increases. Likewise, the contribution of the grass layer was estimated using the equation:

$$NDVI_{grass\ component} = NDVI_{peak} - NDVI_{December}$$

where $NDVI_{peak}$ is the highest value recorded during or at the end of the wet season. These two variables, NDVI tree component and NDVI grass component in the year of death were included in the survival analysis.

Survival analysis

I analysed stage-specific survival using the Kaplan-Meier estimator (Pollock et al., 1989; Williams et al., 2002) and Cox proportional hazard models (Therneau & Grambsch, 2000; Therneau, 2021), separately for black and white rhinos. The Kaplan-Meier procedure estimated rhino survival over time, in relation to their age. It also allows for staggered entry, which was beneficial for this study as it occurred over a long period of time, meaning that individuals could enter the study at any given time and still be included in the analysis (Conroy & Carroll, 2009). The Cox proportional hazard (PH) model is a regression model which relates time-dependent covariates to time-to-mortality and allows stratification (Conroy & Carroll, 2009; Weathers & Cutler, 2017), and to measure the effect of the variables it uses the hazard rate, which is the risk of the event, or in this case death, occurring (Cox, 1972; Bradburn et al., 2003). I stratified using the stage categories mentioned previously (i.e., calf, juvenile, sub-adult and adult), origin (Lapalala native versus non-native or introduced rhinos [referred to as "external" in the analyses]) and for the cohort analysis I stratified using the rain level from the birth year (i.e., wet, normal, dry). Because the rhino's age was also the response variable (i.e., survival time) the stratified Cox model is useful to correct violations of PH assumptions and to allow groups to have different baseline hazards; for example, rainfall conditions in the month of birth (for natives) and arrival (transplants)

have different implications (Kleinbaum & Klein, 2012; Liu, 2012). To assess stage-specific survival, the strata separated the animals according to whether they died as calves, juveniles, sub-adults or adults. I used both models with and without interaction terms, and models violating PH assumptions were removed (Kleinbaum & Klein, 2005). I did not include sex in the models because preliminary analyses indicated no evidence of an effect on survival (see Results section, *Survival analysis*). To reiterate again, this portion of the analysis only included animals whose cause of death seemed to be resource related. The response variable was time/years until a mortality occurred and the explanatory variables (for each species) were the 12 derived density variables, whether an animal was born or died in a drought year (binary, determined with the RAI), born or died in an El Niño Southern Oscillation (ENSO) year (binary), 12 different derived rainfall variables (continuous) and the 10 derived greenness variables.

Model selection: Akaike's Information Criterion, adjusted for small sample size (AICc), and associated statistics, was used to compare the density, rainfall and greenness models (full list of all models can be found in Appendix A–D) separately (interactions between predictors were not considered because the number of variables would make the interpretation of results difficult and problematic). The model used for inference was that with the highest AICc weight (w_i), differing by at least two AICc units from the other competing models, also having the fewest parameters (Burnham & Anderson, 2002). Concordance values were used to assess the predictive ability of the model, where values >0.55 suggest adequate fit between model and data, values >0.7 indicate a good model, values >0.8 indicate a strong model and values close to 1 indicate models that perfectly predict outcomes (Therseau & Watson, 2015). All analyses were conducted in R with library "survival" (R Core Team, 2021).

Results

Population demographics

The black rhino population illustrated gradual increases in size since the first introductions in 1990 and reached its highest total in 2008 (n = 21) which was followed by a number of deaths and removals which declined the total, but again peaked in 2017 as a result of increased births in the population (Figure 2.1). Density measured at 0.01 rhinos/km^2 during the first year of introductions, peaked at 0.06 rhinos/km^2 before the reserve's expansion, and was at 0.05 rhinos/km^2 by the time of expansion and at the end of the study. In comparison, the white rhino population displayed a much slower increase in numbers since the first introductions in 1982. The population increased only from 1999, despite having no disturbance from removals in prior years, and illustrated increases that mimic exponential growth (peaked in 2019 with n = 87) that were largely due to births and introductions in later years. Density measured at 0.01 rhinos/km^2 during the first year of introductions and peaked at 0.2 rhinos/km^2 before and after the reserve's expansion, and by the end of the study.

Population growth rates for both populations illustrated a somewhat weak but negative association with population density (Figure 2.2). The effect was slightly stronger for the black rhino population ($F_{1,29}$ = 2.913, R^2 = 0.225, p = 0.099) and the average growth rate during the study period was 4.784% (95% C.I.: 4.710, 4.857). The negative association between white rhino growth rates and density was weak ($F_{1,37}$ = 0.237, R^2 = 0.0108, p = 0.629) and the average growth rate during the study period was 8.861% (95% C.I.: 8.765, 8.958). Further, the age structure of both populations demonstrated similar characteristics (Figure 2.3). The 'founding' members of the black rhino population consisted only of adults whereas the white rhinos consisted of a mix of adults and sub-adults. For most years, the black rhino population consisted of more adults than immature individuals (averaged 65%), except for years when there was more than one calf born. Contrastingly, the white rhino population always consisted of more adults (averaged 68%). For all but two years (1997 and

1998) the adult sex ratio favoured female black rhinos and averaged 68% during the study period. Whereas the sex ratio for adult white rhinos favoured male rhinos during the first few years, up until 1989 where females have since been favoured, and averaged 56% of the adult sex ratio during the study period.

There have been zero black rhinos lost to poaching in the population, however 18 rhinos (14 male, 4 female) have been removed from the population (Figure 2.4). There was one case of post-release related mortality and a few deaths by fighting (3 male, 2 female), and in one case, a juvenile black rhino male was killed by a white rhino. Most causes of death were independent from fighting, poaching and release stress, and these are the individuals which have been marked as 'resource related' mortalities and have been used in the Cox analyses. By comparison, 5 white rhinos (4 male, 1 female) were lost to poaching and one female rhino died of old age. None of the white rhinos died because of post-release related causes; however, there were 10 without a date of death, which were omitted from the survival analysis. Both social related mortalities were male rhinos that died from fighting, and 15 rhinos were removed (10 male, 5 female). Again, 52 white rhinos were used to infer resource related mortalities. Accidental deaths occurred when rhinos were wedged or fell off cliffs or struck by lightning; the 2 black rhinos included under euthanised/disease were because of respiratory related mortalities whereas the white rhinos were suspected to have died from Shuni virus.

Climatic variables

Although the oscillations indicate variable conditions throughout the study period, there were more years where rainfall was below average (drought conditions) compared to above normal conditions (Figure 2.5). The index also illustrated that during the first few years of introductions, rainfall anomalies were negative and founding populations might have experienced drier conditions. Additionally, most years categorized as negative anomaly years

were those identified as El Niño Southern Oscillation years or years with less than normal precipitation (El Niño years during the study period: 1982, 1983, 1986, 1987, 1988, 1991, 1992, 1994, 1995, 1997, 1998, 2002, 2003, 2009, 2010, 2015, 2016).

Similar trends in annually integrated values were displayed by the two vegetation indices, NDVI and EVI (Figure 2.6). The two greenness indices follow a similar trend to annual rainfall, as years with lower amounts of rainfall also had lower greenness values and years with higher rainfall amounts had higher greenness values. Using monthly values, I found that monthly NDVI was moderately correlated with monthly rainfall ($\rho = 0.619$, $p < 0.001$) and strongly correlated to rainfall with a 1-month lag ($\rho = 0.825$, $p < 0.001$). Monthly EVI values were strongly correlated with monthly rainfall ($\rho = 0.705$, $p < 0.001$) and had an even better association to rainfall with a 1-month lag ($\rho = 0.843$, $p < 0.001$). Annual rainfall averaged at 427.19 mm (Coefficient of Variation (CV): 29.33%), at the lower end of the reserve's estimated total.

Lagged effects: Density and resource conditions

The black rhino population showed negative lagged correlations between population growth rates and prior density; whereas, the white rhino population showed positive correlations (Figure 2.7a). For the black rhinos, the strongest correlations, albeit weak correlations ($\rho = -0.304$, $p = 0.091$), were within the one-to-four-year density lag (justifying the use of prior density variables with one-to-four-year lags in the survival analysis). The white rhino's positive correlation peaked ($\rho = 0.202$, $p = 0.216$) within the four-to-seven-year lag and illustrated the possibility that this population was not density-dependent. Lagged correlations between growth rates and prior rainfall peaked positively at the 2-year lag for black rhinos ($\rho = 0.078$, $p = 0.637$) and at the one-year lag for the white rhino population ($\rho = 0.314$, $p = 0.052$) (Figure 2.7b). For the black rhinos, all the other years showed negative correlations,

and the white rhino population followed the same trend after the three-year lag. This justified the use of a two-year rainfall variable in the survival analysis to account for previous resource conditions (or what Owen-Smith and Mills (2006) refer to as prior habitat conditions).

Survival analysis

I analysed a sample of 46 black rhinos spanning the period 1990–2019, of which 6 died by 1 year of age, 4 died between 1 and 3 years, 7 died between 3 and 4 years, and 8 died after their 7th birthday, and the remaining 21 were alive at the end of the study period in 2019. The sample was made up of 18 male, 22 female and 6 unsexed rhinos. By comparison, the sample of white rhinos spanning the period 1982–2019 consisted of 139 animals, where 12 died by 1 year, 10 died between 1 and 3 years, 13 died between 3 and 4 years, and 17 died after their 7th birthday and the remaining 87 were alive at the end of the study. The sample was made up of 49 male, 80 female and 10 unsexed rhinos.

Before the first birthday, black rhinos showed noticeable drops in survival, particularly around their first and seventh months whereas white rhinos demonstrated a more gradual decrease in survival until the 8th month, when there was a noticeable drop (Figure 2.8). By the first birthday, survival of both species became relatively constant. However, before the third year, there was another drop in survival of black rhinos. White rhinos, in contrast, showed another gradual decline from around 18 months of age until the third year. This pattern continued for both species, with another drop for the black rhinos before the seventh birthday whereas declines were generally gradual for white rhinos. The senescent stage is usually longer than the juvenile period and so the last few drops in survival (around the 20^{th} year) might be an indication of the beginning of that life stage. Survivorship estimates for black rhinos were 0.870 (0.777, 0.973) by age 1 year, 0.774 (0.660, 0.909) by age 3, 0.591 (0.457, 0.764) by 7 and 0.241 (0.113, 0.512) by the end of the study period; for white rhinos estimates were 0.911 (0.864, 0.960) by age 1, 0.830 (0.768, 0.898) by age 3,

0.711 (0.634, 0.798) by age 7 and 0.191 (0.045, 0.811) by the end of the study period. Additionally, there were no differences in survival between the sexes for both black ($\chi^2 = 2.6$, df = 1, p = 0.1) and white ($\chi^2 = 1$, df = 1, p = 0.3) rhino populations.

Rainfall models

Top ranking models differed between the species (Table 2.1). For black rhinos, top-ranking models included lifetime and wet-season rainfall as explanatory variables, which should be expected as most of the rainfall the rhinos experience during their life falls during the wet season. Whereas, for white rhinos, the sole ranking top model included the rainfall one month before their death. One similarity between the species; however, is that both species top models were those that stratified by age suggesting that survival was stage specific. And so, these top models, or rather the explanatory variables; wet-season rainfall ($w_i = 0.822$ and $w_i = 0.139$) for black rhinos and monthly rainfall ($w_i = 1.000$) for white rhinos, were used for inference. Models that stratified by origin had greater explanatory power for black than for white rhinos and there was little evidence of an effect of variables based on ENSO or drought years on survival for either species (Appendix A). Additionally, there was little evidence of cohort effects for both species (models with the variable "Rain-level").

For both species and age groups the odds of mortality decreased with an increase in the rainfall variable (Table 2.2). For black rhinos; as wet-season rainfall decreased, so did the odds of survival or rather, odds of mortality for black rhino calves decreased by a factor of 0.757 (0.492, 1.164) with each 1 SD increase in wet-season rainfall. The odds of mortality for juveniles, sub-adults and adults decreased by a factor of 0.663 (0.357, 1.233), 0.769 (0.613, 0.965) and 0.885 (0.786, 0.996), respectively. Although there was evidence of differences between the age classes, the only statistically significant estimates were those for sub-adults and adults, whose risk of mortality was higher compared to calves and juveniles during periods of low wet-season rainfall. Outputs from the second model illustrate similar results

except that it was stratified by origin, Lapalala born versus external rhinos. Odds of mortality were slightly higher for external rhinos [0.885 (0.786, 0.996)] compared to Lapalala born rhinos [0.731 (0.622, 0.859)] as wet-season rainfall decreased. By comparison, with the white rhinos (Table 2.), significant estimates were produced for all strata where the odds of mortality differed slightly between the age groups in relation to monthly rainfall. So as monthly rainfall decreased, so did the odds of survival, by a factor of 0.415 (0.199, 0.862) for calves, 0.162 (0.042, 0.633) for juveniles, 0.303 (0.113, 0.811) for sub-adults and 0.224 (0.128, 0.392) for adults. The odds of mortality were highest for individuals who had not reached their first birthday (almost double compared to juveniles and adults), as well as sub-adults.

NDVI models

For both species, top ranking models included the variable Annually Integrated NDVI (in the death year), with separate results for the age strata produced (Table 2.3). There was little evidence of an effect of shorter-term variables (such as monthly NDVI or maximum NDVI), and effects from conditions during early life (such as Annually Integrated NDVI during the birth year, or NDVI in the month of birth/arrival). The models used for inference were Annually Integrated NDVI stratified by age for both black (w_i = 1.000) and white rhinos (w_i = 1.000).

For all the black rhino age groups, odds of mortality decreased as annually integrated NDVI increased (Table 2.4). The odds of mortality decreased by a factor of 0.552 (0.203, 1.503) for calves, 0.258 (0.078, 0.852) for juveniles, 0.100 (0.024, 0.412) for sub-adults and 0.037 (0.007, 0.201) for adult rhinos with each 1 SD increase in integrated NDVI. So as greenness increased, risk of mortality significantly decreased for all groups, with the exception of calves. By comparison, separate strata for white rhino indicated that higher values of annually integrated NDVI resulted in increased mortalities of younger rhinos (calf

and juvenile age groups) but decreased mortalities for older rhinos (sub-adult and adult age group). The odds of mortality increased by a factor of 8.198 (2.009, 33.434) and 2.706 (0.917, 7.979) for calves and juveniles, respectively, with each 1 SD increase in integrated NDVI. Whereas the odds of mortality decreased by a factor of 0.821 (0.469, 1.438) and 0.050 (0.006, 0.404) for sub-adults and adults, respectively, with each 1 SD increase in integrated NDVI.

EVI models

The analysis with the secondary vegetation index, EVI, demonstrated similar results as both species top models included the Annually Integrated EVI variable (Table 2.5). Models that stratified by age had greater explanatory power for black rhinos than white rhinos. The models used for inference were integrated EVI stratified by age for the black rhinos (w_i = 0.709) and integrated EVI plus age (not stratified) for the white rhinos (w_i = 1.000).

For both species and age groups, the odds of mortality decreased as integrated EVI increased (Table 2.6). For black rhinos, odds of mortality decreased by a factor of 0.733 (0.037, 14.652), 0.289 (0.004, 18.826), 0.373 (0.040, 3.483) and 0.075 (0.000, 12.580) for the calves, juveniles, sub-adults and adults, respectively, with an increase in integrated EVI. For white rhinos, in which age was not stratified, odds of mortality decreased by a factor of 0.218 (0.079, 0.601) with each 1 SD increase in integrated EVI. The outputs for the models suggested that the EVI might be a better variable for the white rhinos than the black rhinos.

Density models

Although population growth rates and the relationship between growth rates, density and prior rainfall (resource availability) suggested little to no influence of density-dependence on the rhino populations, models with density variables were conducted. The top-ranking models for black rhinos included lagged density factors (prior density averaged over two and four

years), whilst the top-ranking model for white rhinos included current density as a variable (Table 2.7). For both species and age groups, mortalities occurred during periods of lower densities (negative beta coefficient) and so the odds of mortality increased despite lower conspecific density (Table 2.8).

Rainfall versus greenness models

When comparing between the rainfall models and greenness models, there was not a clear winner when assessing the black rhinos (Table 2.9). Although the EVI models had higher probabilities, the rainfall models had merit as well ($w_i > 0.001$). Although the evidence ratios suggest that empirical support for the EVI models was almost 6 times stronger than wet-season rainfall (EVI: $w_i = 0.835$, rainfall: $w_i = 0.143$, EVI was 5.839 times better), the rainfall models should still be considered and not completely cut-off (Anderson, 2008; Burnham et al., 2011). By comparison, the greenness indices proved to be much better predictors for the white rhinos (Table 2.9), as all the top NDVI and EVI models ranked higher than the rainfall models. Again, most of the top models had age included as variable, further supporting the hypothesis that survival might be age specific.

Discussion

One of the main objectives of this study was to build predictive models to assess the survival of black and white rhinos at LWNR, considering both climatic (direct and indirect) and non-climatic influences. My findings illustrate the importance of resources, as a consequence of climatic variation, on the population dynamics of African savanna ungulates (Rutherford, 1980; Owen-Smith, 1990). I found support that survival in both black and white rhino populations was stage-specific and found less support for density-dependence. Both rainfall and the vegetation greenness were strong predictors for survival, although greenness proved to be the better predictor for white rhinos. There was little support for cohort effects for both

species assessed using rainfall conditions. Although both populations are increasing, the white rhino population is increasing at double the rate of the black rhino population. No differences between the sexes were found in the survival analysis (resource effects) and both species' age structure favoured older individuals (adults 15+ years).

Population demographics

By investigating long-term at Lapalala Wilderness, it is clear that the white rhino population is increasing rapidly whereas the black rhino population has shown a much slower yet steady increase (Figure 2.1). Rapid population surges are common in large herbivore populations, especially in populations that have been introduced into unoccupied lands or re-introduced into areas that they historically occupied (Leader-Williams, 1980; Rachlow & Berger, 1998). Although life histories may be the most important factor in explaining these differences, it is worth noting that the black rhino population experienced more disturbances in the form of removals, or these disturbances were exacerbated by the smaller population size. These disturbances are also visible in the much more unstable age structure (Figure 2.3) compared to the white rhinos where the number of immature versus mature individuals remained somewhat similar during the study period. This phenomenon of changing or unstable age structures due to disturbances is referred to as transient dynamics (Stott, 2016; Capdevila et al., 2020; Guldemond et al., 2022) and are likely to occur in unpredictable environments such as savannas (Ogutu & Owen-Smith, 2003). Guldemond et al. (2022) found that disturbances caused by removals, and intensified by droughts, impeded population growth and size of elephants in a protected area. Additionally, for black rhinos, most of the years when the proportion of adults was much higher coincided with removals (Figure 2.1–3). Although the removal of individuals, and the introduction of new individuals, may generate genetic diversity (Emslie et al., 2009), these short-term disturbances may be slowing down an already slow growing population. Despite that, both black and white rhino's age structure was

characteristic of stable populations (Owen-Smith, 1988), which might be caused by more deaths occurring within the younger stages or more individuals moving into the adult life stage (Festa-Bianchet et al., 2003; Owen-Smith & Mason, 2005). Additionally, the adult sex ratios for both species favoured females despite what has been observed in literature (black rhinos tend to favour males and white rhinos tend to have even sex ratios (Owen-Smith, 1988)).

The difference between the two species is also evident in their growth rates (Figure 2.2). The white rhino growth rate was typical of growing rhino populations at about 9% per annum (Owen-Smith, 1988; Conway & Goodman, 1989; Smith et al., 1993; Rachlow & Berger, 1998); whereas the black rhino growth rate was comparatively low at less than 5%, which is the target growth rate proposed by the South African Black Rhino Management Plan (Knight et al., 2013), with weak support for a density-dependent effect. Greaver et al. (2014) found similar results for the black rhino population in Ithala Game Reserve and attributed the low growth rates to density-dependence acting through increased social interactions, i.e., increased mortalities attributed to fighting. However, I do not believe that this was the case for the Lapalala population as only a small percentage of mortalities were caused by fighting compared to the number of deaths believed to be resource related (Figure 2.4). Densities or Ecological carrying Capacities (ECC) have also remained far below any of the estimates for black rhino (0.08–0.8 rhino/km^2) throughout the study period (Emslie et al., 2009), leading me to believe that the black rhino population may only be approaching density-dependence and that the mechanism of density-dependence might act through a number of factors, including the poor nutrient status of the reserve, the impact of frost on browse and competition with other browsers (Adcock et al., 1998; Hrabar & du Toit, 2005).

Survival: Rainfall models

The importance of rainfall on large herbivore population dynamics has been reiterated in literature, and its influence on savanna herbivores should be investigated first before other factors are to be considered (Ogutu et al., 2008). This is largely due to the role of rainfall on savanna structure (Frost et al., 1986), which in turn limits large herbivore populations primarily through vegetation availability (Coe et al., 1976). Unsurprisingly, the black rhino population exhibited rainfall related consequences, particularly with longer term variables such as wet-season rainfall and lifetime rainfall. Despite their browsing diet their survival appeared to be influenced by rainfall, acting through resource limitations. Woody cover and composition of semi-arid savannas is constrained by annual precipitation (Sankaran et al., 2005). Tree growth, although slightly more resilient than herbaceous cover to rainfall variability, is also limited by the amount of rainfall (Birkett & Stevens-Woods, 2005). Leaf production and tree cover increase linearly with precipitation in semi-arid savannas with mean annual precipitation (MAP) that is less than 650 mm (Sankaran et al., 2005; Shorrocks, 2007), such as Lapalala Wilderness. Although the start of growth (or greening) is primarily determined by the dry season because new shoots appear before the wet season (Rutherford, 1980), the interval at which deciduous trees and shrubs will retain leaves going into the dry season is determined by the previous wet season (Owen-Smith, 1990). This not only indicates the importance of quantity of rainfall, but the timing as well, as this will determine the amount of available browse and length of availability, going into the dry season. Most deaths (almost two thirds) occurred during the dry season, suggesting that food reserves may have been low or depleted and deaths might occur because of starvation or decreased body condition (Young, 1994). Sub-adults and adults were more likely to be affected by decreased rainfall, although this may have been the consequence of a smaller sample size within the calf and juvenile age groups (whose results were not significant). Additionally, calves rely mostly on their mother for feeding and juveniles may also feed on both milk and browse until they

leave their mothers and so that may explain their weak relationship with rainfall (Owen-Smith, 1988).

In comparison, the white rhinos' grazing diet suggested that rainfall would affect their survival and I found evidence that all age categories were negatively affected by decreased monthly rainfall. As it has been established previously, decreased amounts of rainfall will affect the herbaceous layer almost immediately (Rutherford, 1980; Vetter, 2009), and although multiple factors influence grass production, rainfall is the major determinant as growth increases linearly with rainfall (Deshmukh, 1984). Periods of decreased rainfall do not only decrease the amount of herbaceous biomass available for grazers to consume, but also decrease the time it will be available for consumption by the end of the wet season (Coe et al., 1976; Mduma et al., 1999; Ogutu & Owen-Smith, 2003). Additionally, grasses do not start greening before the first wet-season rains (Archibald & Scholes, 2007; Whitecross et al., 2017), further complicating matters for white rhinos as dry-season forage has been found to have stronger impacts on population dynamics (Mduma et al., 1999; Ogutu & Owen-Smith, 2003). Just as the black rhinos, most deaths occurred during the dry season and at the start of the wet season, indicating how food shortages as a result of rainfall affected their survival. Being selective grazers, white rhinos do not compensate for seasonal changes in food quantity or quality as their body condition typically decreases at a slower rate (Bell, 1971; Shrader et al., 2006). However, this only applies to adult rhinos who are typically able to survive for longer periods because of substantial fat and other body reserves, whilst calves, juveniles and sub-adults have little to none (Ballard, 1987; Parker, 2003), leaving them much more susceptible to food shortages. This potentially explains why adult survival was almost double the survival measured for white rhino calves.

There was no evidence of cohort effects detected, indexed using rainfall. Despite being born in years with normal or higher precipitation, decreased rainfall negatively affected

survival and this goes for individuals who were born during the drought and non-drought years, including El Niño years. Again, this may have been a consequence of a small sample size or there may just be no cohort effects for both populations, supporting neither the predictive adaptive response (PAR) or silver-spoon effects hypotheses but slightly supporting the 'beneficially saturated conditions' hypothesis as good conditions (increased rainfall) could overturn early life conditions (Krist & Mundinger, 2015). Pigeon et al. (2017) argued that any cohort effects detected in their bighorn ewes (*Ovis canadensis*) population was due to long-term density-dependent effects (lagged effects). Lagged density effects can act as the mechanism through which cohort effects will be present in populations (Beckerman et al., 2002; Forchhammer et al., 2001); however, both rhino populations showed no evidence of any lagged effects (using density and rainfall) and so this may not be the case for these populations. So rather than cohort effects, there is a general effect of decreased rainfall for both populations. In a similar manner with ENSO, their population dynamics are influenced by local weather conditions and not large-scale climatic events.

Survival: NDVI and EVI models

The use of vegetation indices, NDVI and EVI, to assess vegetation productivity and quality, has been shown to correlate with herbivore biomass and population dynamics (e.g., Pettorelli et al., 2011; Duffy & Pettorelli, 2012). As such, it was expected that integrated NDVI would be a strong predictor for black and white rhino survival, suggesting a similar broad effect of integrated NDVI on their survival, with some differences between the age categories. For the black rhinos, survival decreased with greenness, suggesting that increased primary productivity and browse availability increased their odds of survival. Increased greenness or increased vegetation productivity could allow individuals to increase body condition and add to fat reserves, enabling higher rates of survival throughout the years (Davis et al., 2016). In addition to giving a more direct estimation of an area's vegetation output, NDVI provides a

glimpse into the temporal variation in primary productivity (Goward & Prince, 1995; Scanlon et al., 2002; Rasmussen et al., 2006). This is especially true with integrated greenness, which allow us to compare productivity between the years and relate that to the vital rates of resource limited herbivores (Rasmussen et al., 2006; Yan et al., 2022). Lower NDVI values decreased survival for all age groups; however, the small sample size for the calves and the indirect dependence on vegetation may have been the reason why I was not able to detect a clear effect of the variable. Their survival essentially depends on their mother's body condition, as access to enough browse benefits the calves (good or high-quality milk) and lesser browse would be detrimental to both mother and calf but would affect the calf severely as they have no body reserves to rely on (Pettorelli et al., 2007). Similar results were found when using the secondary index (EVI), with survival for all age groups decreasing with integrated EVI. Again, increased greenness translates into increased biomass which increases body condition, in-turn increasing the survival probability of the rhinos.

With the white rhinos, the sub-adult and adult categories illustrated what would be expected as their survival also decreased with NDVI, suggesting that increased primary productivity and browse availability increased their odds of survival. Calf and juvenile survival, however, decreased with an increase in vegetation greenness. I suggest that these cases may be caused by their nutritional requirements or energy reserves, which vary from that of sub-adults and adults, who for the most part rely on quantity over quality to meet their requirements. Although high NDVI values may indicate high biomass quantities, most grasses lose their nutritional quality as greenness increases, or as they grow and so high vegetation productivity (high integrated values) might not equal high resource availability (Van Soest, 1994; Hebblewhite et al., 2008; Pettorelli et al., 2011). Reduced access to high quality forage may affect mom's body condition and her ability to produce nutritious milk (high quality), consequently resulting in increased mortality rates of calves and juveniles.

Additionally, most of the juveniles died before their third birthday, which is usually the time they are driven off by their mothers to find their own territories (because of the birth of a new calf or their age) and so their deaths may be a consequence of stress, the inability to successfully establish and nutritional stress (e.g., choosing to eat grasses with reduced digestibility) (Owen-Smith, 1988; Muller, 2022 (unpublished source)). Using the secondary index (EVI), there were no differences between the age groups, as survival probability increased with greenness, suggesting that increased biomass might be a good indicator for white rhino survival.

Surprisingly, when comparing the performance of the rainfall and vegetation indices as predictors, the greenness models outperformed rainfall for the white rhinos, whereas for the black rhinos, both rainfall and the greenness were strong predictors. Despite the challenge of having missing vegetation data, the greenness indices proved to be good predictors, especially EVI, which was developed to be used in conjunction with NDVI as it is corrected for atmospheric disturbances and canopy background making it a useful tool in South African savannas (Huete et al., 1997; Huete et al., 2002; Jamali et al., 2011). Additionally, rainfall and greenness were strongly correlated (Davenport & Nicholson, 1993; Richard & Poccard, 1998; Jamali et al., 2011), suggesting further that rainfall is the limiting factor for vegetation growth in this savanna (Huntley & Walker, 1982; Frost et al., 1986; Shorrocks, 2007). This likely demonstrates the potential usefulness in pairing both rainfall and greenness indices when assessing consequences of environmental variation on species survival and other vital rates (e.g., Rasmussen et al., 2006; Davis et al., 2016). It would have been beneficial to include full models with both rainfall and greenness variables however because of missing data and the different strata (age, cohort, origin) this would have made it difficult to interpret the data.

In summary, findings provide a starting point for models of population dynamics of rhinos at Lapalala Wilderness. Models provided evidence that survival is stage specific, regardless of species or dietary differences, and that population dynamics are governed by fluctuating resources as indexed by rainfall and vegetation greenness. Where rainfall acts as an indirect proxy, NDVI and EVI provide a measurable index of vegetation quality, biomass and photosynthetic activity. Evidence suggested a stronger stage-specific response with the white rhinos compared to the black rhinos, as I hypothesized. However, this may have been the consequence of a smaller black rhino sample size. Despite the differing dietary guilds, there was weak evidence for cohort effects for both species, or mortalities brought on by ENSO periods or drought years. Integrated greenness variables had more explanatory power than short-term greenness variables, suggesting that environmental variability through the years is a top factor in both species' survival. Density effects (both immediate and lagged) were somewhat trivial for both populations as the populations seem to be resource limited (density-dependence has not been detected). In conclusion, population growth, which is a function of juvenile recruitment and adult survival, of large herbivores is most sensitive to changes in resource availability caused by environmental conditions. Therefore, species-specific assessment of how environmental variation affects survival might be necessary for effective conservation of these species in semi-arid regions.

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Table 2.1. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to rainfall, Lapalala Wilderness, South Africa, 1982–2019.

Species	#	Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos	23	Age + wet-season rainfall	56.046	0.000	0.822	4	0.910 (0.035)
	28	Origin + wet-season rainfall	57.827	1.781	0.139	2	0.958 (0.013)
	21	Age + lifetime rainfall	59.117	3.071	0.038	4	0.898 (0.039)
	24	Origin + lifetime rainfall	62.948	6.902	0.001	2	0.953 (0.014)
White rhinos	36	Age + rainfall one month before death	210.490	0.000	1.000	4	0.850 (0.029)

[a] AICc = Akaike's Information Criterion, corrected for small sample size, [b] ΔAICc = AICc – min(AICc), [c] w_i = model probability, [d] K = number of parameters, [e] Standard error in parentheses.

Table 2.2. Model coefficients: Cox proportional hazard models used to analyse survival of black and white rhinoceroses, Lapalala Wilderness, South Africa, 1982–2019. Presented are the rainfall models used for interpretation.

					95% confidence intervals	
Model	Stratum (Age/Origin)	Estimate	*SE*	Hazard ratio	Lower	Upper
Black rhinos						
Age + wet-season rainfall	Calf	-0.279	0.219	0.757	0.492	1.164
	Juvenile	-0.411	0.316	0.663	0.357	1.233
	Sub-adult	**-0.263**	0.116	**0.769**	0.613	0.965
	Adult	**-0.122**	0.060	**0.885**	0.786	0.996
Origin + wet-season rainfall	Lapalala	**-0.313**	0.082	**0.731**	0.622	0.859
	External	**-0.122**	0.060	**0.885**	0.786	0.996
White rhinos						
Age + rainfall one month before death	Calf	**-0.879**	0.373	**0.415**	0.199	0.862
	Juvenile	**-1.819**	0.695	**0.162**	0.042	0.633
	Sub-adult	**-1.194**	0.503	**0.303**	0.113	0.811
	Adult	**-1.499**	0.286	**0.224**	0.128	0.392

*Estimates and Hazard Ratios (HR) of predictors with standard errors excluding 1.000 are in bold.

Table 2.3. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to the vegetation index, NDVI, Lapalala Wilderness, South Africa, 1982–2019.

Species	#	Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos	10	Age × Annually Integrated NDVI during death year	57.985	0.000	1.000	4	0.931 (0.023)
White rhinos	10	Age × Annually Integrated NDVI during death year	155.246	0.000	1.000	4	0.954 (0.009)

[a] AICc = Akaike's Information Criterion, corrected for small sample size, [b] ΔAICc = AICc – min(AICc), [c] w_i = model probability, [d] K = number of parameters, [e] Standard error in parentheses.

Table 2.4. Model coefficients: Cox proportional hazard models used to analyse survival of black and white rhinoceroses, Lapalala Wilderness, South Africa, 1982–2019. Presented are the NDVI models used for interpretation.

					95% confidence intervals	
Model	Stratum (Age/Origin)	Estimate	*SE*	Hazard ratio	Lower	Upper
Black rhinos						
Age × Annually Integrated NDVI during death year	Calf	-0.593	0.511	0.552	0.203	1.503
	Juvenile	**-1.353**	0.609	**0.258**	0.078	0.852
	Sub-adult	**-2.303**	0.722	**0.100**	0.024	0.412
	Adult	**-3.301**	0.865	**0.037**	0.007	0.201
White rhinos						
Age × Annually Integrated NDVI during death year	Calf	**2.104**	0.717	**8.198**	2.009	33.434
	Juvenile	0.995	0.552	2.706	0.917	7.979
	Sub-adult	-0.197	0.286	0.821	0.469	1.438
	Adult	**-2.989**	1.063	**0.050**	0.006	0.404

*Estimates and Hazard Ratios (HR) of predictors with standard errors excluding 1.000 are in bold.

Table 2.5. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to the vegetation index, EVI, Lapalala Wilderness, South Africa, 1982–2019.

Species	#	Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos	6	Age + Annually Integrated EVI during death year	54.467	0.000	0.709	4	0.731 (0.097)
	5	Age × Annually Integrated EVI during death year	55.359	0.892	0.291	4	0.945 (0.018)
White rhinos	6	Annually Integrated EVI during death year	118.434	0.000	1.000	1	0.677 (0.081)

[a] AICc = Akaike's Information Criterion, corrected for small sample size, [b] ΔAICc = AICc – min(AICc), [c] w_i = model probability, [d] K = number of parameters, [e] Standard error in parentheses.

Table 2.6. Model coefficients: Cox proportional hazard models used to analyse survival of black and white rhinoceroses, Lapalala Wilderness, South Africa, 1982–2019. Presented are the EVI models used for interpretation.

					95% confidence intervals	
Model	Stratum (Age/Origin)	Estimate	*SE*	Hazard ratio	Lower	Upper
Black rhinos						
Age + Annually Integrated EVI during death year	Calf	-0.311	1.528	0.733	0.037	14.652
	Juvenile	-1.241	2.131	0.289	0.004	18.826
	Sub-adult	-0.985	1.139	0.373	0.040	3.483
	Adult	-2.587	2.612	0.075	0.000	12.580
White rhinos						
Annually Integrated EVI	All rhinos	**-1.523**	0.518	**0.218**	0.079	0.601

*Estimates and Hazard Ratios (HR) of predictors with standard errors excluding 1.000 are in bold.

Table 2.7. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to density, Lapalala Wilderness, South Africa, 1982–2019.

Species	#	Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos	29	Age + prior density F2 during death year	83.940	0.000	0.710	4	0.722 (0.067)
	27	Age + prior density during death year	84.838	0.897	0.290	4	0.691 (0.093)
White rhinos	25	Age + density during death year	198.995	0.000	0.953	4	0.869 (0.027)
	27	Age + prior density during death year	202.249	3.254	0.037	4	0.881 (0.028)
	29	Age + prior density F2 during death year	203.490	4.496	0.011	4	0.854 (0.026)

[a] AICc = Akaike's Information Criterion, corrected for small sample size, [b] ΔAICc = AICc – min(AICc), [c] w_i = model probability, [d] K = number of parameters, [e] Standard error in parentheses.

Table 2.8. Model coefficients: Cox proportional hazard models used to analyse survival of black and white rhinoceroses, Lapalala Wilderness, South Africa, 1982–2019. Presented are the density models used for interpretation.

					95% confidence intervals	
Model	Stratum (Age/Origin)	Estimate	*SE*	Hazard ratio	Lower	Upper
Black rhinos						
Age + prior density F2 during death year	Calf	-0.232	0.169	0.793	0.569	1.105
	Juvenile	-0.557	0.355	0.573	0.286	1.149
	Sub-adult	-0.139	0.130	0.870	0.675	1.123
	Adult	-0.240	0.085	0.787	0.666	0.929
White rhinos						
Age + density during death year	Calf	-0.005	0.002	0.995	0.991	0.999
	Juvenile	-0.004	0.002	0.996	0.992	1.000
	Sub-adult	-0.018	0.018	0.982	0.947	1.018
	Adult	-0.019	0.015	0.980	0.952	1.001

*Estimates and Hazard Ratios (HR) of predictors with standard errors excluding 1.000 are in bold.

Table 2.9. Model comparison: Rainfall, NDVI and EVI models used to analyse the survival of black and white rhinoceroses, Lapalala Wilderness, South Africa, 1982–2019.

Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos					
Age + Annually Integrated EVI during death year	54.467	0.000	0.592	4	0.731 (0.097)
Age × Annually Integrated EVI during death year	55.359	0.892	0.243	4	0.945 (0.018)
Age + wet-season rainfall	56.046	1.579	0.122	4	0.910 (0.035)
Origin + wet-season rainfall	57.827	3.359	0.021	2	0.958 (0.013)
Age × Annually Integrated NDVI	57.985	3.518	0.018	4	0.931 (0.023)
Age + lifetime rainfall	59.117	4.650	0.006	4	0.898 (0.039)
Origin + lifetime rainfall	62.948	8.481	0.000	2	0.953 (0.014)
Age × Wet-season Integrated NDVI	66.454	11.987	0.000	4	0.895 (0.026)
White rhinos					
Annually Integrated EVI	118.434	0.000	1.000	1	0.677 (0.081)
Age × Annually Integrated NDVI during death year	155.246	36.812	0.000	4	0.954 (0.009)
Age + Wet-season Integrated NDVI during death year	164.949	46.515	0.000	1	0.584 (0.092)
Origin + Annually Integrated EVI during death year	200.855	82.421	0.000	2	0.694 (0.073)
Age + rainfall one month before death	210.490	92.057	0.000	4	0.850 (0.029)
Age + lifetime rainfall	231.674	113.240	0.000	4	0.866 (0.027)

[a] AICc = Akaike's Information Criterion, corrected for small sample size, [b] ΔAICc = AICc – min(AICc), [c] w_i = model probability, [d] K = number of parameters, [e] Standard error in parentheses.

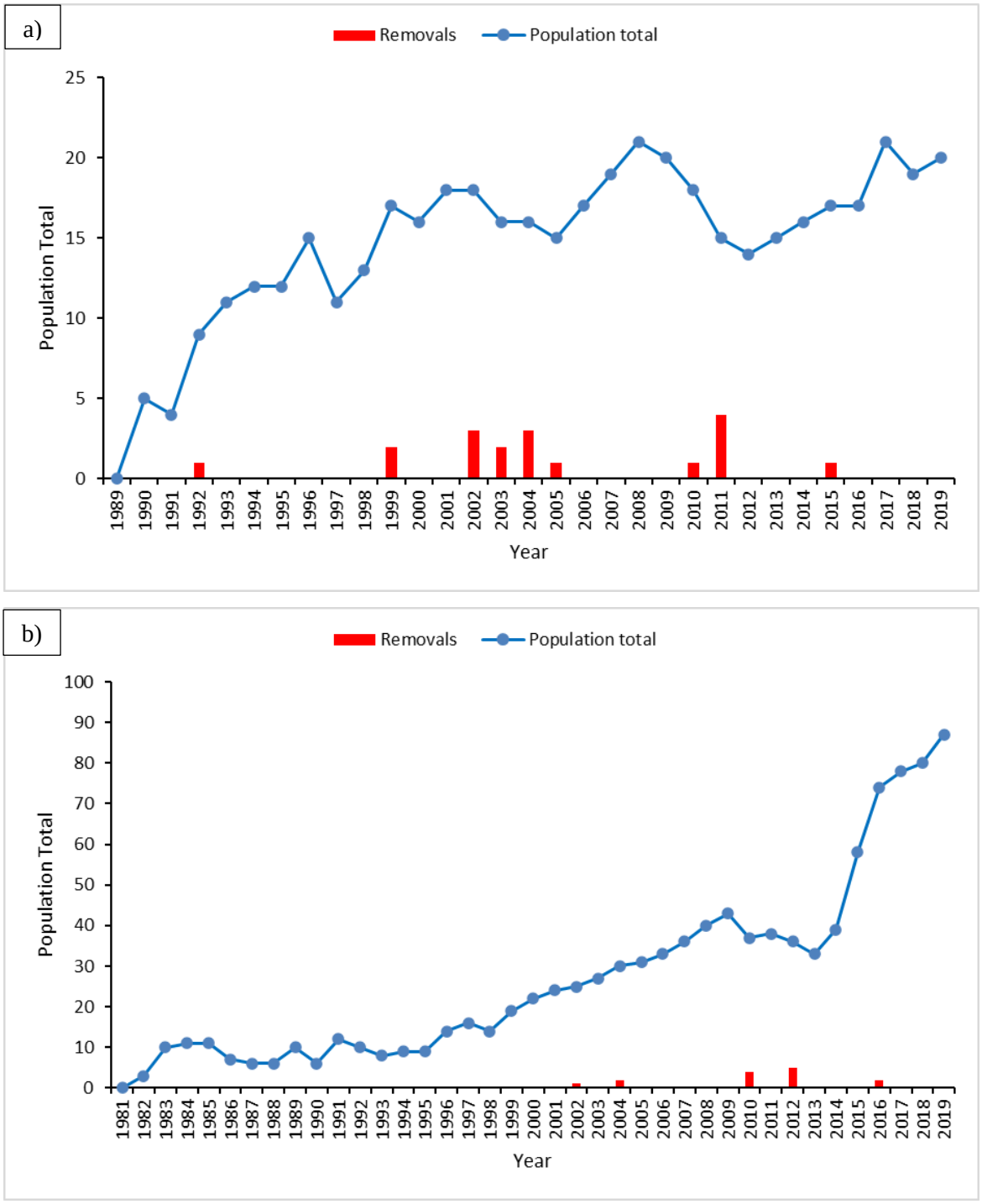


Figure 2.1. Black rhino (a) and white rhino (b) population totals, since the first introductions in Lapalala Wilderness in 1990 and 1982, with removals shown.

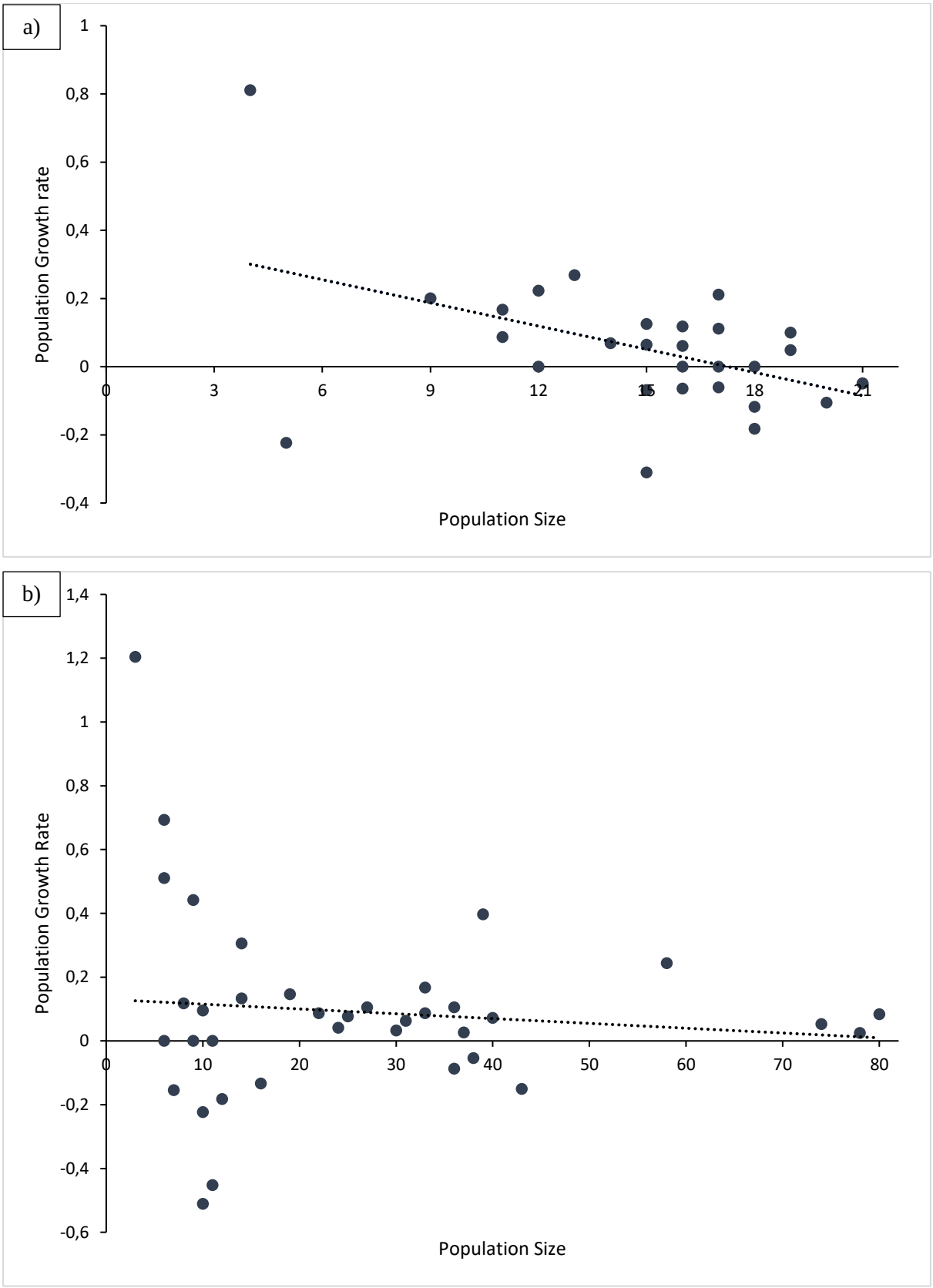


Figure 2.2. Black rhino (a) and white rhino (b) population growth rates, from 1990 to 2019 for the black rhinos and 1982 to 2019 for the white rhinos.

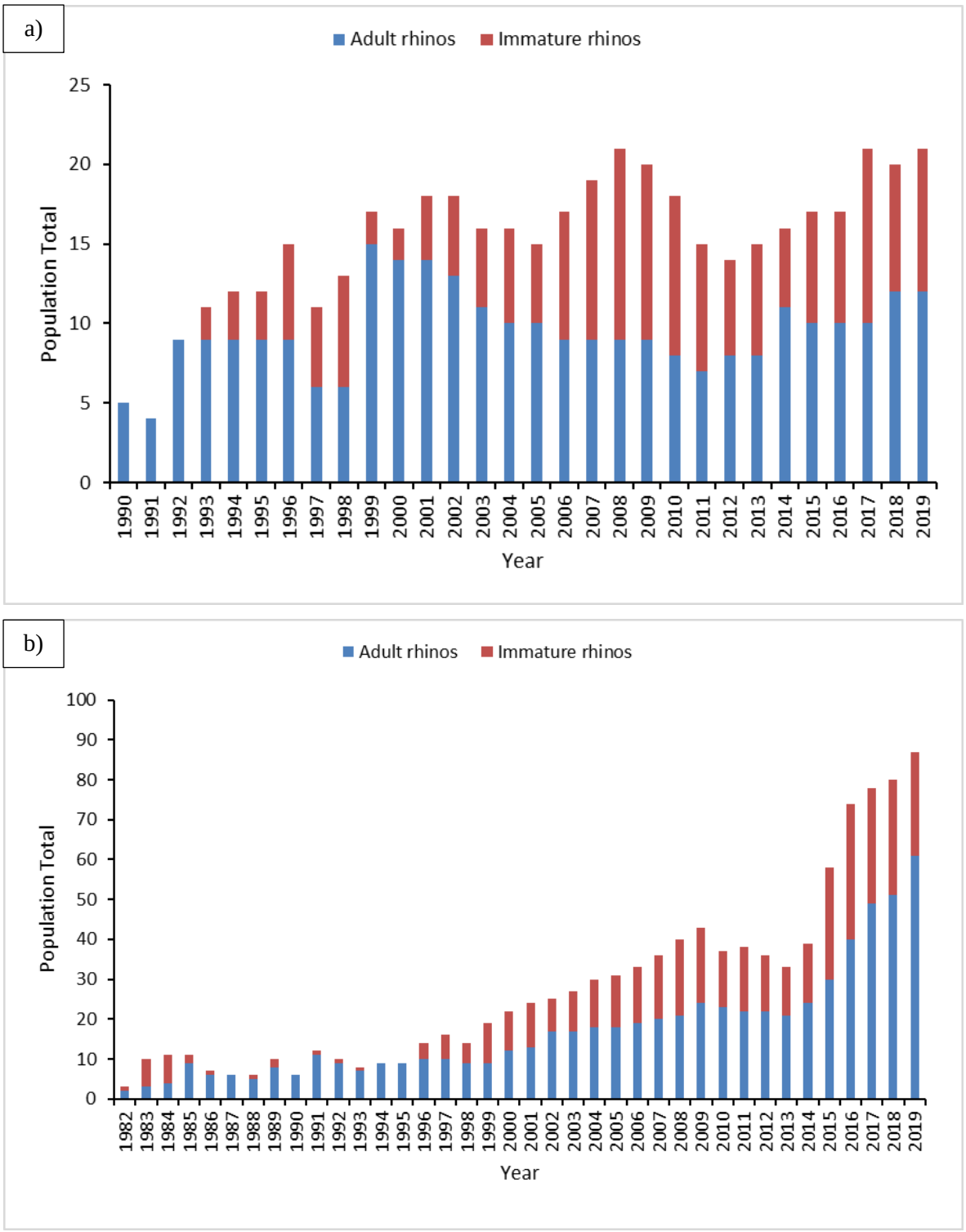


Figure 2.3. The number of adult (sexually mature) and immature black rhinos (a) from 1990 to 2019, and white rhinos (b), from 1982 to 2019.

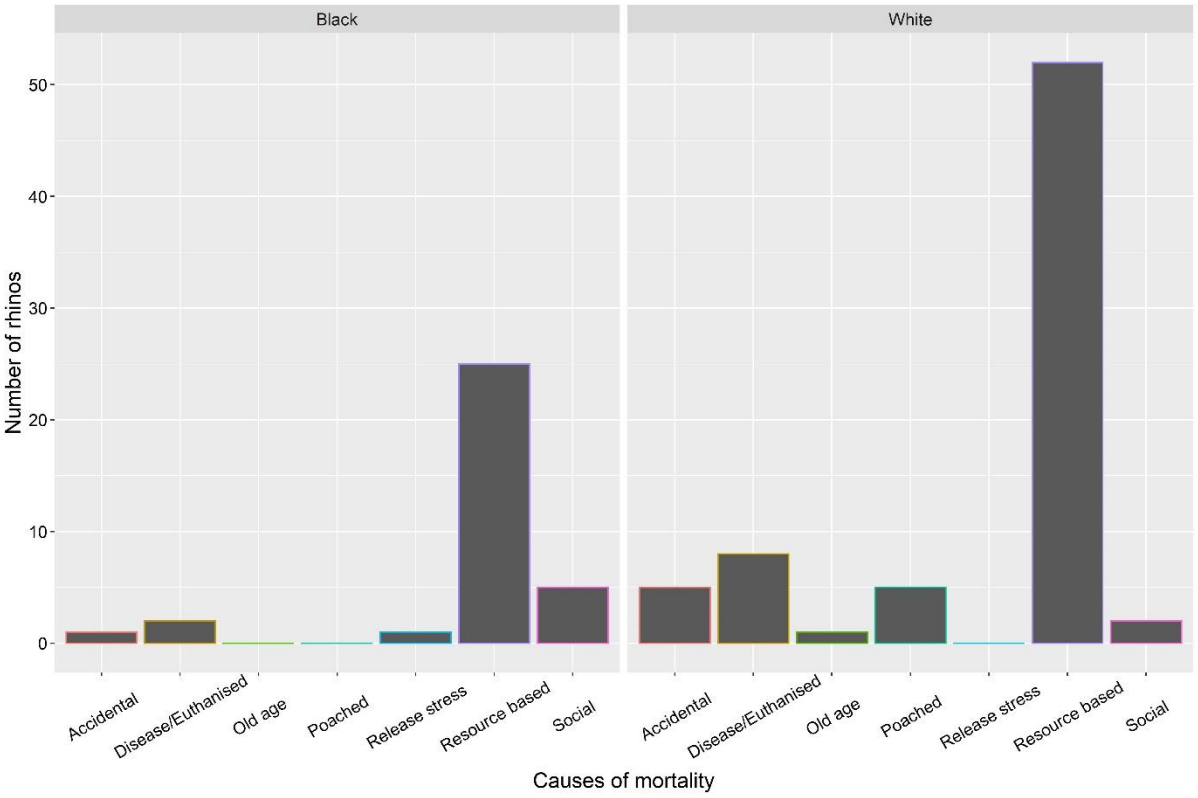


Figure 2.4. The number and causes of mortality for black and white rhinos in Lapalala Wilderness, recorded from 1982 to 2019. The resource based category includes individuals whose deaths were recorded as unknown and were included in the survival analyses.

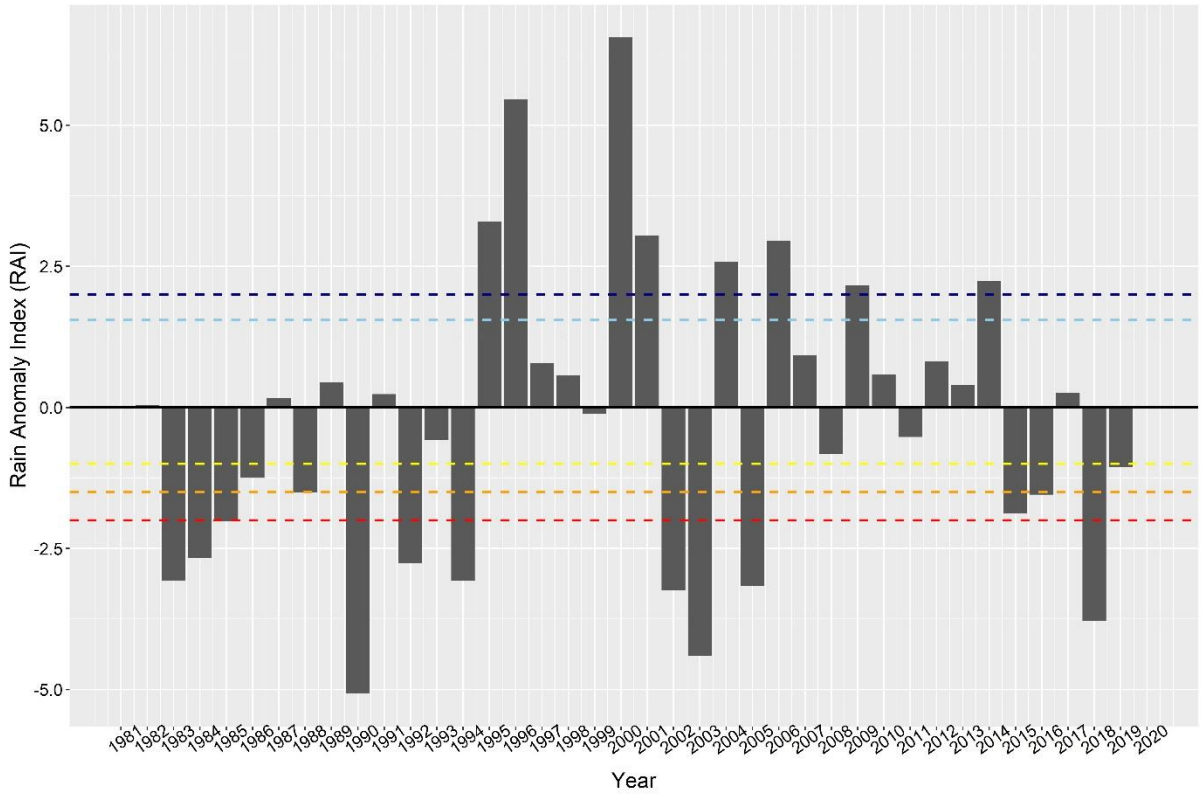


Figure 2.5. Time series of the annual rainfall anomalies during the 37-year study period, obtained using the standardised annual precipitation from the Ellisras-Pol. Marken and Mahwelereng weather stations. Positive values indicate normal and positive anomalies, whereas negative values indicate negative anomalies. More accurately; values above zero (or the solid black line) indicate normal precipitation, values above the light blue line indicate severely wet years and values above the dark blue line indicate extremely wet years. Values below the black line indicate mild droughts, values below the yellow line indicate moderate drought years, values below the orange line indicate severe drought years and values below the red line indicate extreme drought years (Eshetu et al., 2016).

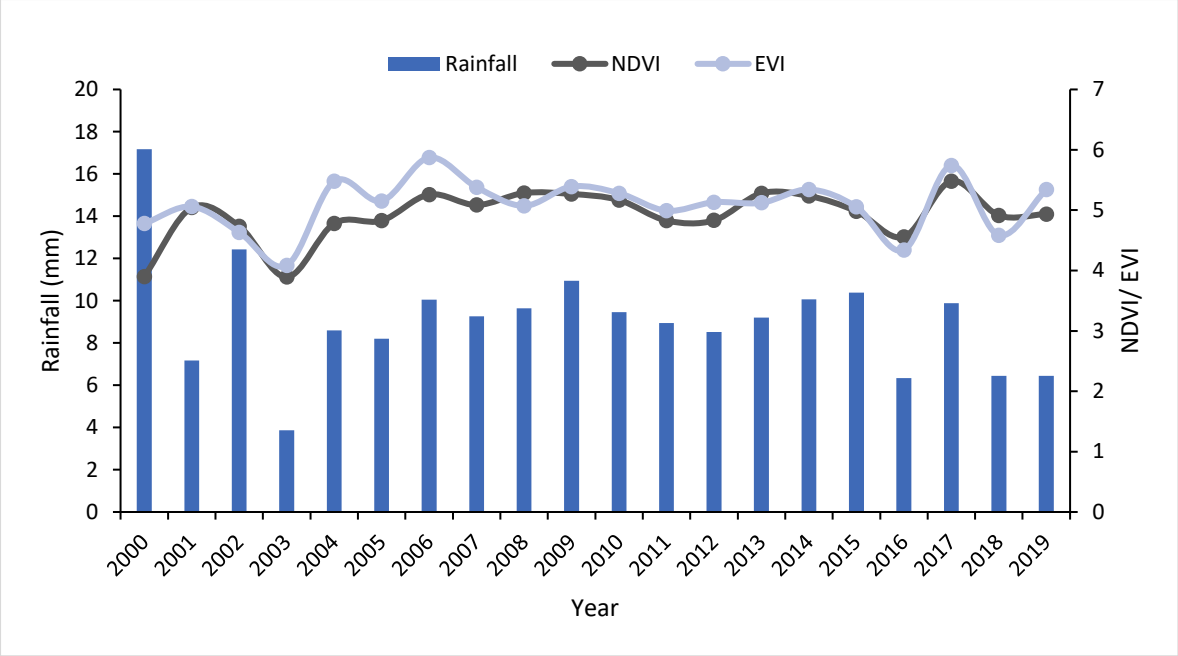


Figure 2.6. Time series of standardised annual rainfall, annually integrated NDVI and annually integrated EVI from 2000 to 2019 (November–October).

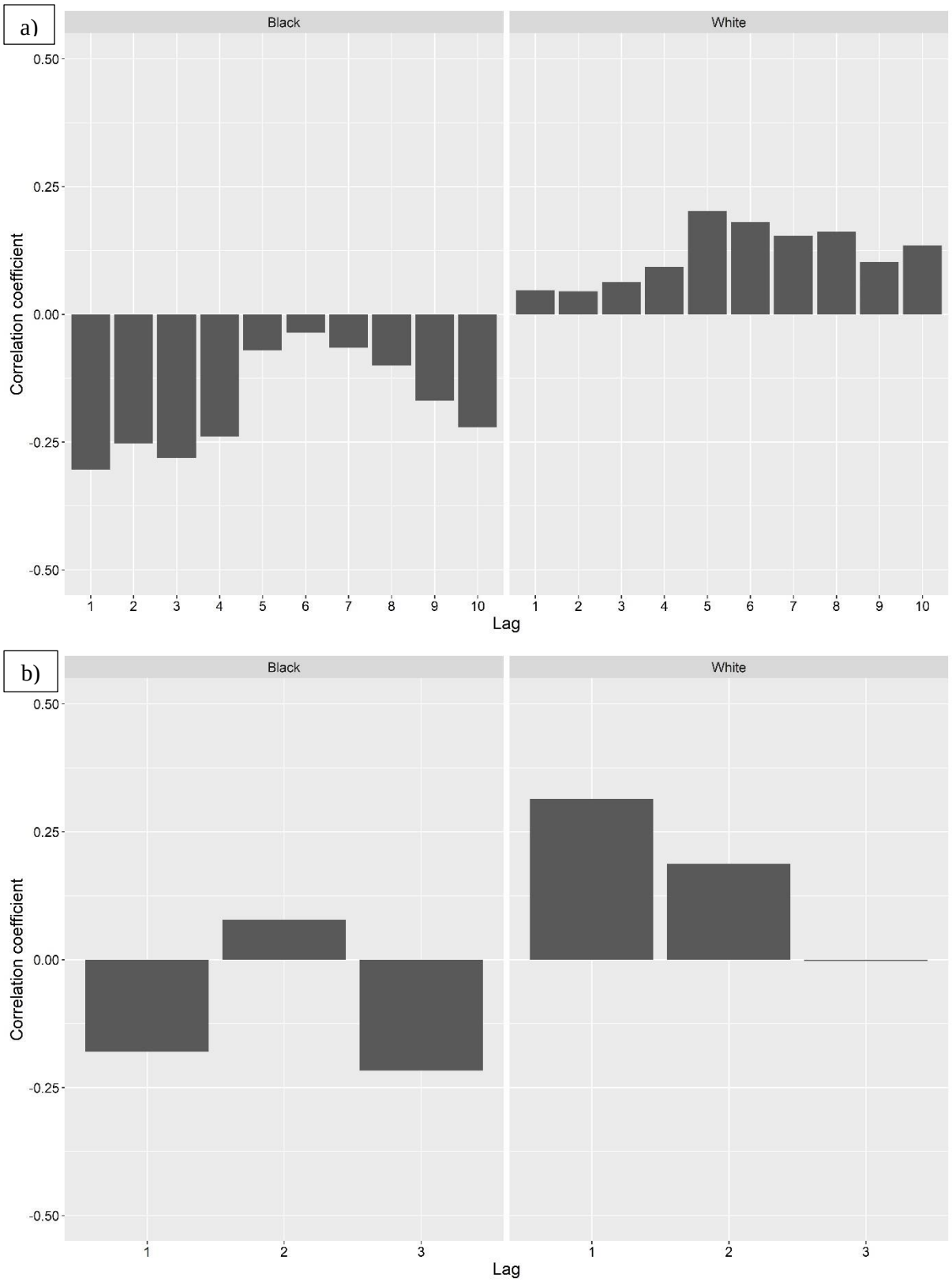


Figure 2.7. Correlations between annual population growth and prior density (a) at increasing annual time lags(1–10) and correlations between annual population growth and prior rainfall (b) at increasing time lags (1–3), for black and white rhinos in Lapalala Wilderness.

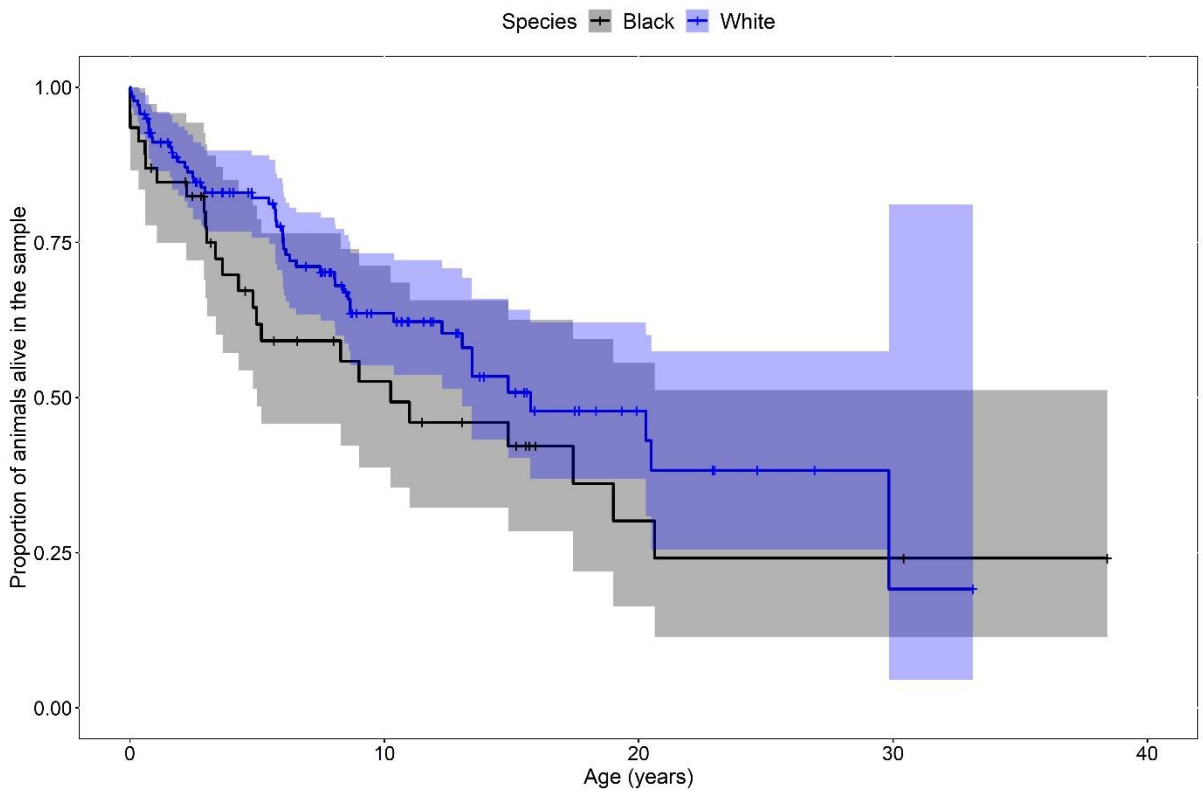


Figure 2.8. Survival probability estimated for black (black curve) and white (blue curve) rhinos, Lapalala Wilderness, 1982–2020. Presented are Kaplan-Meyer survival estimates and 95% confidence intervals.

Appendices

Appendix A: Rainfall models that were used to summarize the data set, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	Survival was affected by age
2	Survival was affected by rainfall experienced throughout their lifetime
3	Survival was affected by dry-season rainfall experienced throughout their lifetime
4	Survival was affected by wet-season rainfall experienced throughout their lifetime
5	Survival was affected by rainfall from six months before birth
6	Survival was affected by rainfall from six months before death
7	Survival was affected by rainfall from the year prior to birth or arrival
8	Survival was affected by rain falling two years prior to birth or arrival
9	Survival was affected by annual rainfall in the birth or arrival year
10	Survival was affected by a drought year (born in a drought year)
11	Survival was affected by a drought year (died in a drought year) (
12	Survival was affected by El niño-Southern Oscillation years (Death in ENSO year)
13	Survival was affected by the rainfall from the month prior to birth or arrival
14	Survival was affected by the rainfall from the month prior to death
15	Survival was affected by the interaction between age and lifetime rainfall
16	Survival was affected by the interaction between age and lifetime dry-season rainfall
17	Survival was affected by the interaction between age and lifetime wet-season rainfall
18	Survival was affected by the interaction between origin and lifetime rainfall
19	Survival was affected by annual rainfall after birth/arrival and rainfall six months before death
20	Survival was affected by lifetime dry-season and wet-season rainfall
21	Survival was affected by the interaction between age (stratified) and lifetime rainfall

22	Survival was affected by the interaction between age (stratified) and lifetime dry-season rainfall
23	Survival was affected by the interaction between age (stratified) and lifetime wet-season rainfall
24	Survival was affected by the interaction between origin (stratified) and lifetime rainfall
25	Survival was affected by the interaction between origin and lifetime dry-season rainfall
26	Survival was affected by the interaction between origin and lifetime wet-season rainfall
27	Survival was affected by the interaction between origin (stratified) and lifetime dry-season rainfall
28	Survival was affected by the interaction between origin and (stratified) lifetime wet-season rainfall
29	Survival was affected by El niño-Southern Oscillation years (Birth/arrival in ENSO year)
30	Survival was affected by the rainfall twelve months prior to death
31	Survival was affected by the interaction between age and the rainfall twelve months prior to death
32	Survival was affected by the interaction between age (stratified) and the rainfall twelve months prior to death
33	Survival was affected by the interaction between origin and the rainfall twelve months prior to death
34	Survival was affected by the interaction between origin (stratified) and the rainfall twelve months prior to death
35	Survival was affected by the interaction between age and the rainfall one month prior to death
36	Survival was affected by the interaction between age (stratified) and the rainfall one month prior to death
37	Survival was affected by the interaction between origin and the rainfall one month prior to death
38	Survival was affected by the interaction between origin (stratified) and the rainfall one month prior to death

39	Survival was affected by El niño-Southern Oscillation years and the rainfall twelve months prior to death
40	Survival was affected by El niño-Southern Oscillation years and the rainfall one month prior to death
41	Survival was affected by the rain-level during birth/arrival (cohort effects)
42	Survival was affected by the rainfall during the first year of ‘independence’ (between 1–2 years) or rainfall after first year since arrival
43	Survival was affected by the rainfall during juvenile years (1–3 years) or rainfall after first year since arrival
44	Survival was affected by the interaction between rain-level (stratified) and lifetime rainfall
45	Survival was affected by the interaction between rain-level (stratified) and the rainfall one month prior to death
46	Survival was affected by the interaction between rain-level and lifetime rainfall
47	Survival was affected by the interaction between rain-level and the rainfall one month prior to death

Appendix B. NDVI models that were used to summarize the data set, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	Survival was affected by NDVI one month before birth/arrival
2	Survival was affected by NDVI during birth/arrival month
3	Survival was affected by NDVI one month prior to death
4	Survival was affected by Annually Integrated NDVI during birth/arrival year
5	Survival was affected by Annually Integrated NDVI during death year
6	Survival was affected by maximum wet-season NDVI during birth/arrival year
7	Survival was affected by maximum wet-season NDVI during death year
8	Survival was affected by Wet-season Integrated NDVI during birth/arrival year
9	Survival was affected by Wet-season Integrated NDVI during death year
10	Survival was affected by the interaction between age and Annually Integrated NDVI during death year
11	Survival was affected by the interaction between age and Wet-season Integrated NDVI during death year
12	Survival was affected by the interaction between origin and Annually Integrated NDVI during death year
13	Survival was affected by the interaction between origin (stratified) and Annually Integrated NDVI during death year
14	Survival was affected by the interaction between origin and Wet-season Integrated NDVI during death year
15	Survival was affected by the interaction between origin (stratified) and Wet-season Integrated NDVI during death year
16	Survival was affected by $NDVI_{tree/grass\ component}$ during birth/arrival year
17	Survival was affected by $NDVI_{tree/grass\ component}$ during death year

Appendix C. The EVI models that were used to summarize the data set, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	Survival was affected by Annually Integrated EVI during birth/arrival year
2	Survival was affected by Annually Integrated EVI during death year
3	Survival was affected by Wet-season Integrated EVI during birth/arrival year
4	Survival was affected by Wet-season Integrated EVI during death year
5	Survival was affected by the interaction between age and Annually Integrated EVI during death year
6	Survival was affected by the interaction between age (stratified) and Annually Integrated EVI during death year
7	Survival was affected by the interaction between origin and Annually Integrated EVI during death year
8	Survival was affected by the interaction between origin (stratified) and Annually Integrated EVI during death year
9	Survival was affected by the interaction between origin and Wet-season Integrated EVI during death year

Appendix D. The density models that were used to summarize the data set, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	Survival was affected by density during birth/arrival year
2	Survival was affected by density during death year
3	Survival was affected by prior density during birth/arrival year
4	Survival was affected by prior density during death year
5	Survival was affected by prior density (F2) during birth/arrival year
6	Survival was affected by prior density (F2) during death year
7	Survival was affected by the interaction between origin and density during birth/arrival year
8	Survival was affected by the interaction between origin and density during death year
9	Survival was affected by the interaction between origin and prior density during birth/arrival year
10	Survival was affected by the interaction between origin and prior density during death year
11	Survival was affected by the interaction between origin and prior density (F2) during birth/arrival year
12	Survival was affected by the interaction between origin and prior density (F2) during death year
13	Survival was affected by the interaction between origin (stratified) and density during birth/arrival year
14	Survival was affected by the interaction between origin (stratified) and density during death year
15	Survival was affected by the interaction between origin (stratified) and prior density during birth/arrival year
16	Survival was affected by the interaction between origin (stratified) and prior density during death year
17	Survival was affected by the interaction between origin (stratified) and prior density (F2) during birth/arrival year
18	Survival was affected by the interaction between origin (stratified) and prior density (F2) during death year

19	Survival was affected by the interaction between age and density during birth/arrival year
20	Survival was affected by the interaction between age and density during death year
21	Survival was affected by the interaction between age and conspecific density (F2) during birth/arrival year
22	Survival was affected by the interaction between age and prior density during death year
23	Survival was affected by the interaction between age and prior density (F2) during death year
24	Survival was affected by the interaction between age (stratified) and density during birth/arrival year
25	Survival was affected by the interaction between age (stratified) and density during death year
26	Survival was affected by the interaction between age (stratified) and prior density during birth/arrival year
27	Survival was affected by the interaction between age (stratified) and prior density during death year
28	Survival was affected by the interaction between age (stratified) and prior density (F2) during birth/arrival year
29	Survival was affected by the interaction between age (stratified) and prior density (F2) during death year

CHAPTER 3: REPRODUCTIVE PHENOLOGY OF BLACK AND WHITE RHINOCEROSES IN RELATION TO RAINFALL, GREENNESS AND DENSITY

Abstract

For species like the black and white rhinoceros, which live in seasonal environments, changing global and local climate might result in reproduction becoming desynchronized with periods of favourable conditions. This is important because energy costs of reproduction and reproductive success depend on the timing of reproduction with favourable environmental conditions. Additionally, variations in environmental conditions have also been implicated in influencing calf sex ratios and so the aim of this study was to investigate the reproductive life histories of black and white rhinos at Lapalala Wilderness Nature Reserve, in response to variation in rainfall, vegetation greenness and density. I used detailed historical rhino-monitoring data to investigate reproductive parameters such as age at primiparity, inter-calving intervals (ICIs), timing of conceptions/births and offspring sex ratios. Twelve black rhino females calved during the study period and mean age at first conception and calving was 10.473 and 11.724 years, respectively. Whereas 38 white rhino females calved during the study period and the mean age at first conception and calving was 8.12 and 9.448 years, respectively. White rhino ICIs were slightly longer than black rhino ICIs and averaged 37.64 and 33.04 months, respectively. Conceptions for both species peaked during the wet season and were associated with periods of high forage availability. Effects of rainfall and greenness on age at primiparity differed between species; the odds of calving increased with rainfall and greenness for white rhinos but decreased with greenness for the black rhinos. I suggest that increases in greenness during conception periods might indicate increased production of vegetation that the black rhinos may not have access to; whereas for white rhinos, they were more likely to reproduce when resource availability was high. I found a positive relationship between ICIs and rainfall for both species, supporting the

idea that normal and high, but not excessive amounts of rainfall increase the odds of conception. Lastly, the birth sex ratios remained male biased for both species; however, there was little evidence from modelling for a strong influence of environmental conditions on calf sex. However, I found evidence that the reproduction of both species was influenced by environmental factors and so it is possible that maternal condition may affect sex allocation because male fitness for polygynous mammals is related to their growth and maternal investment. In conclusion, findings provide evidence that the reproductive phenology of black and white rhinos is associated with resource availability and that reduced access to resources because of environmental stochasticity may further alter population dynamics and vital rates of these growing populations.

Introduction

Recent changes in global weather patterns are implicated in altering biological systems (Inouye et al. 2000; Hughes, 2000; Hulme, 2005), and the life history strategies of many organisms (Post & Stenseth, 1999; Pettorelli et al., 2007). Such changes become especially important for species living in seasonal environments such as semi-arid savannas, where environmental variation influences resource availability and consequently population dynamics and vital rates (Sæther, 1997; Gaillard et al., 1998; Illius & O'Connor, 2000; Owen-Smith et al., 2005). Thus, critical periods, such as reproductive timing, for individuals living in variable systems should correspond with the best environmental conditions (Pettorelli et al., 2007). For large herbivores, such as the black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*), the effects of environmental variation on their vital rates vary with age and sex (Gaillard et al., 2000; Coulson et al., 2001). For example, juvenile survival, age at primiparity, reproductive timing and fecundity are the first to respond to limiting factors (Eberhardt, 1977; Gaillard et al., 1998). Additionally, for large herbivores density-dependence will first affect recruitment (juvenile survival and the number of females breeding) and then age at first reproduction which are two vital rates that influence population size (Eberhardt, 1977, 2002; Gaillard et al., 1998). However, with changing global and local climate, reproduction could become desynchronised or out of phase with periods of favourable conditions (Thomas et al., 2001; Berteaux et al., 2004; Pettorelli et al., 2007) resulting in poor population performance and recruitment, which depend on body condition (Albon et al., 1987), of already vulnerable species. Therefore, resource availability, as a consequence of environmental stochasticity, should drive variations in reproductive timing, rates and success (Trimble et al., 2009).

Energy costs of reproduction and reproductive success depend on the timing of reproduction with favourable environmental conditions (Pianka, 1976; Kennish, 1997;

Wittemyer et al., 2007; Fynn & Provenza, 2023). Late pregnancy and early lactation are the most nutritionally taxing stages of herbivore reproduction (Oftedal, 1985; Clutton-Brock et al., 1989). Females who match this period of demand to peak resource availability or alternatively, with high quality fecundity resources, have higher fitness (Festa-Bianchet. 1988; Loe et al., 2005; Fynn & Provenza, 2003). For most Northern temperate herbivores, birth peaks correlate with increasing spring temperatures (Bronson, 1985; Festa-Bianchet, 1988; Gaillard et al., 1993; Moyes et al., 2011), during which vegetation quality is highest before digestibility decreases (Crawley, 1983). Whereas photoperiod is the immediate cue affecting breeding phenology and synchrony of temperate herbivores (Bronson, 1985; Bradshaw & Holzapfel, 2007), in subtropical savannas, rainfall plays this synchronising role (Rutherford, 1980; Deshmukh, 1984). Thus, for rainfall-driven savanna herbivores, births should coincide with early wet season peaks in vegetation quality and digestibility (Ogutu et al., 2014).

In savanna environments, rainfall is an important determinant of vegetation growth and availability because it is a limiting factor for at least part of the year (Rutherford, 1980; Deshmukh, 1984; Scholes & Archer, 1997), influencing herbivore body condition and energy expenditure through its effects on forage availability (Sæther, 1997; Illius & O'Connor, 2000; Parker et al., 2009). Seasonal variability in rainfall modifies the quantity and quality of vegetation available, determining the period during which herbivores achieve the most nutritional gains (Owen-Smith & Ogutu, 2013). However, some differences can occur between browsing and grazing herbivores depending on the differential effects of rainfall on their preferred forage (Ogutu et al., 2013; Owen-Smith & Ogutu, 2013). For example, trees flush with new growth before the first wet season rains and declines in quality are slower than grasses; whereas grasses green after the first wet season rains (Pellow, 1983; Owen-Smith, 1994, 2008; Scholes & Archer, 1997; Do et al., 2005; Shorrocks, 2007). Despite these

differences, births for browsers and grazers should coincide with early wet season for savanna herbivores (Ogutu et al., 2014).

Rather than timing seasonal pulses in births to coincide with favourable conditions, the season of parturition depends on the timing of mating, conception and gestation length (Owen-Smith & Ogutu, 2013). Mating must occur sufficiently in advance of favourable environmental conditions for reproductive success to follow (Sadleir, 1969; Zerbe et al., 2012). For black and white rhinos' gestation can span 15–16 months, meaning that nutritional conditions experienced during the conception period are unlikely to match conditions during birth (Owen-Smith & Ogutu, 2013). Birth pulses are thus more likely to be spread out through the year (i.e., continuous, and not seasonal) or peak during the dry season because conceptions are concentrated in the wet season (Hall-Martin et al., 1975; Owen-Smith, 1988; Ogutu et al., 2014, 2015). Hence fertility depends on the female herbivores' condition during conception, which depends on the nutritional quality of the forage available at the same time (Owen-Smith, 1988; Cook et al., 2001; Ogutu et al., 2013, 2015; Owen-Smith & Ogutu, 2013).

The age at first calving, a function of female condition and fertility, is also influenced by rainfall variability and depends on resource availability (Thomas, 1982; Jorgenson et al., 1993; Ogutu et al., 2014). Early reproduction should be selected for as it increases lifetime reproduction (McGraw & Caswell, 1996; Oli et al., 2002; Martin & Festa-Bianchet, 2012); however, pregnancy requires sufficient energy and body condition, so much so that fertility will be delayed if those conditions are not met (du Plessis, 1972; Grimsdell, 1973; Stearns, 1992; Prins, 1996; Ryan et al., 2007). Early reproduction might also be delayed in favour of survival in long-lived species because lifetime reproductive success varies with breeding longevity (Reid et al., 2003), which depends on sufficient energy and body reserves being

available for survival and recruitment (Clutton-Brock et al., 1988; Owen-Smith, 1988; Fay et al., 2016). And because rhinos, and all megaherbivores are considered capital breeders, they can suppress reproduction as a response to unfavourable conditions (Hall-Martin et al., 1975; Owen-Smith, 1988; Andersen et al., 2000). In other words, oestrous cycling and ovulation can be delayed if optimal nutritional status and accumulated body reserves do not exceed the threshold required for successful pregnancy (Thomas, 1982; Owen-Smith, 1988; Jorgenson et al., 1993; Loe et al., 2005). Variations in environmental conditions therefore affect reproductive success and age of primiparity by way of resource variability, which affects body condition, oestrous and mating (Moe et al., 2007; Ogutu et al., 2010; Ogutu et al., 2015).

Variations in environmental conditions have also been implicated in influencing herbivore birth sex ratios (Clutton-Brock & Iason, 1986; Post et al., 1999). For sexually dimorphic and polygynous species, such as the black and white rhino, sons are regarded as more costly to produce than daughters (Clutton-Brock et al., 1981,1983; Gomendio et al., 1990) and more likely to survive when produced by healthier mothers (Clutton-Brock et al., 1984, 1986). Three hypotheses have been proposed to explain the variation in offspring sex ratios, with the main mechanism through which they function being maternal condition (Clutton-Brock & Iason, 1986) which is affected by environmental conditions (Kruuk et al., 1999). The Trivers and Willard (1973) hypothesis (TWH) argues that females in good physiological condition are more likely to produce sons over daughters; females in poor condition tend to produce daughters because less-fit daughters would outperform a son born in the same condition (i.e., fitness benefits of mothers in good condition translates into advantages for sons in male-male competition) (Trivers & Willard, 1973; Clark, 1978; Silk, 1983; Cameron & Linklater, 2007). The local resource competition (Clark, 1978) hypothesis (LRC), based on sex-specific dispersal (Clark, 1978), proposes that females in poor condition

produce sons, because they are the dispersing sex, whilst daughters remain within their mothers' home ranges and compete with for resources (Mech, 1975; Verme, 1983; Johnson, 1988; Weladji & Laflamme-Mayer, 2011). The third hypothesis, extrinsic modification hypothesis (EMH), proposes that extrinsic factors affecting maternal condition also influence sex ratio beyond adaptive modification of maternal investment (Post et al., 1999). Studies of red deer (*Cervus elaphus*, Kruuk et al., 1999; Post et al., 1999; Mysterud et al., 2000), reindeer (*Rangifer tarandus*, Weladji & Holand, 2003) and black rhino (Hrabar & Du Toit, 2005; Berkeley & Linklater, 2010; Weladji & Laflamme-Mayer, 2011), found that birth sex ratios are influenced by local environmental conditions in support of EMH (Post et al., 1999; Weladji & Laflamme-Mayer, 2011).

Vital rates associated with reproduction, such as age at first calving (or age at sexual maturity), sex ratios and inter-calving intervals (ICI) impact population growth, age structure and sex structure, turnover times, and lifetime reproduction success (Owen-Smith, 1988; Gaillard et al., 1998; Gaillard et al., 2000; Mysterud & Ostbye, 2006). Considering the influence of environmental variability on reproduction, population abundance and conservation status, my aim was to investigate the reproductive phenology of black and white rhinos at Lapalala Wilderness Nature Reserve (LWNR), in response to variation in rainfall, vegetation greenness and density. I hypothesized that (H_1) births would occur throughout the year but peaks for both species would not be during the wet season because of their long gestation times; however, conceptions should be correlated with periods of high resource availability (high rainfall and greenness) because this affects body condition. There would be little influence of density on the reproduction of both rhino species, contrary to Eberhardt's (2002) prediction that density-dependence would affect fecundity because both species' abundances are relatively small compared to other rhino populations where density-dependence has been observed (H_2) (see Rachlow & Berger, 1998; Hrabar & du Toit, 2005;

Law et al., 2013; Greaver et al., 2014) and for large herbivores, density-dependence is usually observed as populations approach carrying capacity (Sibly & Hone, 2002). The age at primiparity and inter-calving intervals would increase (H_3) with decreasing rainfall conditions, drought conditions (including El Niño Southern Oscillation years) and low vegetation greenness values because this would affect female body condition. I also predicted that (H_4) resource availability assessed using rainfall and greenness, would affect the sex ratios of both species and that the probability for mothers to have a male calf would increase with rainfall and vegetation greenness if the TW and EM hypotheses hold; but decrease with increasing rainfall and vegetation greenness if the LRC hypothesis holds.

Methods

Study site

Lapalala Wilderness Nature Reserve is a private nature reserve located in the Waterberg region, Limpopo Province, South Africa (Figure. 1.1). It was established in 1981 as a 360 km^2 reserve and grew to 480 km^2 by 2022 (https://lapalala.com/past/ accessed 14 December 2021). It falls within the savanna biome, and central bushveld bioregion (Rutherford et al., 2006). Common woody plants include Combretum spp., Acacia spp., silver terminalia (*Terminalia sericea*), and Rhodesian rubber tree (*Diplorhynchus condylocarpon*); and common herbaceous plants include gum grass (*Eragrostis gummiflua*), three-awns (*Aristida* spp.), and common reed (*Phragmites* spp.) (https://lapalala.com/wildlife/ accessed 14 December 2021). The long-term mean annual rainfall is 500 mm (https://lapalala.com/about/ accessed 14 December 2021) with most falling in November – April. Mean minimum and maximum monthly temperatures during spring and summer are 14°C and 30°C, and temperatures during autumn and winter are 20°C and 20°C. Besides rhinos, other large

herbivores include impalas (*Aepyceros melampus*), plains zebras (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), African elephants (*Loxodonta africana*), giraffe (*Giraffa camelopardalis*), hippopotamus (*Hippopotamus amphibius*), roan antelope (*Hippotragus equines*) and common eland (*Taurotragus oryx*).

Rhino monitoring data

I used historical rhino monitoring data spanning 1982–2019. Black and white rhinos were tracked daily by an experienced team of rhino monitors at the reserve, who follow the rhino's tracks on foot and by vehicle (using a 4x4) until they see the rhinos. Recorded data include identity, health status, sex, group structure, broad location and remarks such as cause of death. For female rhinos, reproductive status (e.g., whether they were seen with a calf) was recorded along with estimated birth date and sex of the calf. Both species are individually recognized and have been tracked from birth or since they have been translocated, with their Dams noted. This study included all native and transplanted female rhinos with calving records and covered only their reproduction at Lapalala Wilderness.

Rainfall data

Historical rainfall data, spanning the period of the rhino data, was obtained from the South African Weather Service. This data was collected at the Ellisras-Pol, Marken and Mahwelereng weather stations which are all within 3 km to Lapalala Wilderness. At the three stations, data from the year 1967 (September) to the end of the study period was recorded inconsistently (i.e., some months had daily amounts, others had weekly amounts). To create a continuous rainfall record, monthly totals were standardized by dividing each station's monthly total by its standard deviation. Monthly averages were then calculated across stations and were used to calculate rainfall variables used in the study.

Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI) data

I used Advanced Very High Resolution Radiometer (AVHRR) and Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI and EVI composites obtained from the NASA Land Processes Distributed Active Archive Centre (LPDAAC) to index forage availability. MODIS products were established as a continuation index of AVHRR to allow for long-term monitoring, and the two products are comparable and complement each other (Huete et al., 1997, 2002; Didan et al., 2015). The AVHRR data spanned 1992–1996 (accessed from the Earth Resources Observation and Science (EROS) center via Earth Explorer https://earthexplorer.usgs.gov/) and had a 1.1 km spatial resolution and 10-day temporal resolution. The MODIS NDVI and EVI data spanned 2000–2019 (accessed from Oak Ridge National Laboratory (ORNL) DAAC via Earth Data https://daac.ornl.gov/) and had 250 m spatial resolution and 14-day temporal resolution. To work with both products, I rescaled the AVHRR data to the same spatial resolution of 250 m using the bilinear resampling method in ArcGIS 10.6, which is recommended for continuous data because it causes some smoothing of the resampled data without producing cell values outside of the range of the input raster (ArcGIS Desktop via https://desktop.arcgis.com/en/arcmap/). Greenness values were extracted for the 480 km^2 study area and mean values for each 10-day or 16-day image were calculated because GPS locations were inconsistently available.

Data analyses

Demographic parameters

Variables used in all analyses focused primarily on conditions experienced by females during conception and less on conditions experienced during and after birth. I estimated the dates of conception for all calves using the recorded birth dates (Skinner & Smithers, 1990), and ICIs as the time between the birth of the previous calf and successive calf for each female (with >1 calf). The average age at conception and calving, and mean ICIs were calculated separately

for black and white rhinos. The monthly and seasonal timing of conceptions and births was assessed to determine whether either species exhibited any patterns with their reproductive timing; for example, conception peaks could correlate with early wet season as (forage) nutritional conditions peak. The birth rate or proportion of females calving was calculated as the number of births in the year divided by the number of adult females (i.e., ≥7 years old) that were alive during any part of that year (Law & Fike, 2018). To assess the potential influence of environmental conditions on calf sex allocation, I used records of all sexed individuals born at Lapalala Wilderness. Female body condition data was not available; however, the relationship between body condition and resource variability is well established (Albon et al, 1987; Jönsson, 1997; Parker et al., 2007; Simard et al., 2014) and so rainfall, greenness and density variables were used as proxies to assess the influence of environmental conditions on birth sex ratios.

Density effects

In addition to assessing the effects of current abundance on rhino reproduction, prior population effects were also investigated because they can cause delayed effects on large herbivore populations and their vital rates, for example, through resource availability (Sinclair 1989, Turchin, 1995, Owen-Smith & Mills, 2006). High animal densities maintained for extended periods of time could impede vegetation recovery, lowering the availability of their food sources (Owen-Smith & Mills, 2006). In addition to calculating the abundance level responsible for direct density feedback, I used four indices to estimate the effect of prior density on reproductive timing: an average of the population density over both a two-year and four-year block (i.e., density factor), excluding the year prior to the count which represents the direct feedback:

$$N_{den\ fac2} = \frac{N_{t-2}+N_{t-3}}{2} \ldots \text{(equation 1)} \quad \& \quad N_{den\ fac} = \frac{N_{t-2}+N_{t-3}+N_{t-4}+N_{t-5}}{4} \ldots \text{(equation 2)}$$

The third and fourth indices were calculated like the equations above except instead of using rhino abundance, I used the number of rhinos/km^2 (referred to as "conspecific density", over a two- and four-year block, as well as current density) to estimate density-dependence as a function of reserve size (Emslie et al., 2009). Where the first two indices estimate the periods over which impacts on herbaceous vegetation are expected to persist (Owen-Smith & Mills, 2006), the third and fourth estimate density-dependence in relation to reserve size, which can also limit resource sinks if conspecific density gets too high (i.e., spatial restrictions might indicate density-dependence, particularly for black rhinos) (Rachlow & Berger, 1998; Birkett, 2002; Linklater & Swaisgood, 2008; Sky et al., 2022). In total, six derived density variables were included for each species in the analyses.

Climatic variables: Rainfall

Rainfall indices: To evaluate whether the rainfall during a study year was a drought year I used the rainfall anomaly index (RAI). The RAI calculates annual precipitation anomalies by using a ranking system to allocate values to positive (higher than normal) and negative (lower than normal) rainfall amounts (van Rooy, 1965; Keyantash & Dracup, 2002) based on a threshold calculated from the rainfall amounts (Eshetu et al., 2016). More strongly positive values indicate wetter years; more strongly negative values indicate drier years (Eshetu *et al*., 2016).

El Niño Southern-Oscillation (ENSO): To test the effects of ENSO on rhino reproduction I used the Oceanic Niño Index (ONI) (https://ggweather.com/enso/oni.htm). The ONI is the primary index used by the National Oceanic and Atmospheric Administration (NOAA) to track ENSO events, ranking the severity of the events as weak, moderate and strong El Niño and La Niña phases (Glantz & Ramirez, 2020). For this study, moderate and strong El Niño phases were categorised as ENSO years and the rest as non-ENSO years and this index was implemented as a variable in the models.

Derived rainfall variables: I calculated rainfall variables using the standardized values from the three weather stations. These variables were generated with respect to the rhino's life history, to capture both immediate and lagged responses. I calculated variables specifically for each animal in the analyses and for each reproductive event: rainfall one, six, twelve and twenty-four months before conception, wet-season rainfall in the year prior to conception, rainfall during the gestation period, and rainfall one and two years ending in the calf's birth.

Vegetation greenness indices: NDVI and EVI

I calculated monthly NDVI and EVI values using the 10- and 16-day mean values. I used these monthly values to derive seven greenness indices for NDVI and EVI separately: greenness in the month of conception and birth, maximum greenness value in the year of conception, wet-season integrated greenness during the conception year and in the birth year, and annually-integrated greenness in the conception year and in the year of birth (Pettorelli et al., 2005; Rasmussen et al., 2006; Pettorelli et al., 2007).

Statistical analyses

I analysed the timing of primiparity using the Kaplan-Meier estimator and Cox proportional hazard models (Van Noord-Zaadstra et al., 1991; Therneau & Grambsch, 2000; Mitchell et al., 2016; Kunnuji et al., 2018; Therneau, 2021), separately for black and white rhinos. I used these models as an alternative to binary outcomes of birthing events because I was interested in testing the time to the event (calving) (Van Noord-Zaadstra et al., 1991; Rahman & Hoque, 2015; Mitchell et al., 2016; Kunnuji et al., 2018) and the Cox proportional hazard model is a regression model which relates time-dependent covariates to time-to-events and allows stratification (Conroy & Carroll, 2009; Weathers & Cutler, 2017). To measure the effect of the variables it uses the hazard rate, which is the risk of the event, or in this case calving, occurring (Cox, 1972; Bradburn et al., 2003). For females who had more than one calving

event, I used generalised linear models (GLM) and generalised linear mixed models (GLMM) with an identity-link function to investigate the effects of the predictor variables on calving events and ICIs (also time-to-event data), with Dam identity as a random effect. For the analysis relating age at primiparity to the predictor variables I stratified using the females' origin (Lapalala native or external). The response variable was time to calving or time between the previous calving and the next conception, and the explanatory variables were the six derived density variables, whether an animal was conceived in a drought or wet year (binary, estimated with the RAI), conceived during an El Niño Southern Oscillation (ENSO) year (binary), eight different derived rainfall variables (continuous) and the seven derived greenness variables (continuous).

Calf sex

I analysed the probability of a female giving birth to a male calf and the influence of rainfall, greenness and density on the event, using GLMs and GLMMs) with a logit-link function (Weladji & Laflamme-Mayer, 2011). I ran separate models for each set of predictor variables and for the GLMMs I used Dam identity as a random effect (Weladji & Leflamme-Mayer, 2011). The response variable was calf sex, and the explanatory variables were the six derived density variables, whether an animal was conceived in a drought or wet year (binary, estimated with the RAI), whether an animal was conceived during an El Niño Southern Oscillation (ENSO) year (binary), eight different derived rainfall variables (continuous) and the seven derived greenness variables (continuous).

Model selection: I used Akaike's Information Criterion, adjusted for small sample size (AICc), and associated statistics, to compare the rainfall, greenness and density models separately for each analysis (see Appendix A–D for full lists of models), after which the top-ranking rainfall, greenness and density models were compared (i.e., a two-step selection process). The model used for inference was that with the highest AICc weight (w_i), differing

by at least two AICc units from the other competing models, also having the fewest parameters (Burnham & Anderson, 2002). Estimates for some competing models are also presented (i.e., top rainfall, greenness and density models are presented to examine their influence on rhino reproduction). All estimates are presented as Hazard or Odds ratios. Concordance values were used to assess the predictive ability of the Cox model, where values >0.55 suggest adequate fit between model and data, values >0.7 indicate a good model, values >0.8 indicate a strong model and values close to 1 indicate models that perfectly predict outcomes (Therseau & Watson, 2015). All analyses were conducted in R with library "survival", "lme4" and "nlme" (R Core Team, 2021).

Results

By the end of the study a total of 46 black and 92 white rhinos were born at Lapalala. Of these 46 black rhinos, 16 were female, 24 were male and 6 were unsexed; whereas, of the 92 white rhinos, 39 were female, 44 were male and 9 were unsexed. Twelve black rhino females calved between 1992–2019 and defining three maternal age classes as young (< 10 years), prime-aged (10–24 years) and old births (≥ 25 years) (Law et al., 2014), 6.522% of the births were young, 78.261% were prime-aged and 15.217% were defined as old-aged. By comparison, 38 white rhino females calved between 1990–2019 and the distribution of maternal age class births were 30.435% young, 65.217% prime and 4.348% old-aged. White rhinos conceived and calved at an earlier age compared to the black rhinos; mean age at first conception and calving was 8.12 (7.134, 9.097) and 9.448 years (8.467, 10.43) for white and 10.473 (9.27, 11.677) and 11.724 years (10.52, 12.927) for black rhinos (Figure 3.1). White rhino ICIs were also longer than black rhino ICIs (Figure 3.2) and averaged 37.64 (34.79–40.49) and 33.04 months (28.89–37.19), respectively. White rhinos exhibited more of a

pattern in terms of the seasonality of conception and births, with conceptions and births peaking during the early wet season and late wet season, respectively; whereas, the black rhinos did not exhibit as clear a pattern, their conceptions and births did peak at the end of the dry season and mid wet season (Figure 3.3).

Birth rate

The black rhino birth rate or fertility rate was highest in 1996 and 1998 when all the adult females in the population gave birth, but there were also seven years of 0 births during the study period (Figure 3.4). By comparison, the white rhino birth rate was highest in 1999 (80%) and lowest in 1991, '92, '94 and '98 when it was 0% (Figure 3.4). The birth rates over the study period averaged at 26.78% and 22.82% for black and white rhinos, respectively.

Effects of rainfall, greenness and density on the age at first conception

Top ranking models differed between the species (Table 3.1). Model selection of rainfall, greenness and density models showed that greenness models, and in particular EVI models, had greater explanatory power for age at primiparity for both species. For black rhinos, the top model included wet-season integrated EVI during the year of conception; whereas, for white rhinos, annually integrated EVI during the year of conception was the top variable. Both species' bottom ranking models included density variables. These top variables, wet-season integrated EVI (w_i = 0.901) for black rhinos and annually integrated EVI (w_i = 0.906) for white rhinos, were used for inference. However, because all the models included in Table 3.1 were top models in the separate analyses, I also interpreted any significant variables (i.e., the other models with significant hazard ratios). There was little evidence of an effect of variables based on ENSO or drought years on fertility for either species (Appendix A1).

For the black rhino population, I was not able to detect a clear effect of the EVI variable on age at first calving (Table 3.2). However, model output suggested that the odds of

calving decreased with a factor of 0.624 (0.232, 1.676) with each unit increase in wet-season integrated EVI, suggesting that black rhinos were more likely to conceive their first calf as vegetation greenness decreased. Contrary to the black rhinos, the odds of calving increased with the EVI variable for the white rhino population (Table 3.2). The odds of calving increased by a factor of 3.907 (1.755, 8.70) with each unit increase in annually integrated EVI, and so white rhinos were more likely to successfully conceive their first calf as vegetation greenness increased.

NDVI & density (black rhinos): Although there was no clear evidence for an effect of EVI on the black rhino population, the top NDVI variable suggested that the odds of calving decreased by a factor of 0.00007 (0, 0.452) with each unit increase in wet-season maximum NDVI (Table 3.2). Regarding density, for both native and external black rhinos, odds of having their first calf decreased as density increased (Table 3.2). Estimates between native and external black rhinos were similar as the odds of calving decreased by a factor of 0.937 (0.841, 1.044) and 0.876 (0.767, 0.999) with each unit increase in density, respectively, suggesting that age at first calving increased with density, particularly for external rhinos.

Rainfall & density (white rhinos): Similarly for white rhinos, there was a clearer effect of the rainfall variable on the age at primiparity for external-born rhinos compared to Lapalala rhinos (Table 3.2). The odds of calving for native and external rhinos increased by a factor of 1.857 (0.854, 4.040), and 2.069 (1.356, 3.157), respectively, with each 1 SD increase in monthly rainfall. This suggests that the age at primiparity decreased with increased rainfall, particularly for external white rhinos. Regarding density, odds of having their first calf decreased as density increased for both external and native white rhinos (Table 3.2). Odds of calving decreased by a factor of 0.942 (0.907, 0.979) with each unit increase in prior density, also suggesting an increase in age at primiparity with density, like the black rhinos.

Effects of rainfall, greenness and density on ICIs

Both species' top models were the same and the order of variables was the same except for the density variables (Table 3.3). Model ranking rainfall, greenness and density variables showed that rainfall had greater explanatory power and was the most important variable in explaining ICIs. The variable I used for inference was rainfall between the previous calving and conception of the next calf (w_i = 1.000 and w_i = 1.000) for both black and white rhinos.

For both species, ICIs increased with rainfall (Figure 3.5). The odds of successfully conceiving their next calf soon increased with a decrease in rainfall for black and white rhinos. For black rhinos, ICIs increased by a factor of 1.097 (1.088, 1.106) for each 1 SD increase in rainfall. For white rhinos, ICIs increased by a factor of 1.103 (1.092, 1.115) for each 1 SD increase in rainfall. Both species' ICIs were strongly correlated with rainfall (black: $\rho = 0.888$, $p < 0.001$; white: $\rho = 0.926$, $p < 0.001$).

Effects of rainfall, greenness and density on calf sex

By the end of the study period the birth sex ratio (BSR) of both black and white rhinos was male biased but did not differ significantly from an equal ratio ($\chi^2 = 0.3$, df = 1, $p = 0.6$ for black rhinos and $\chi^2 = 3.2$, df = 1, $p = 0.07$ for white rhinos). However, the black rhino ratio did not remain similar throughout, as there were more females born during dry years and more males born during normal and wet years ($\chi^2 = 7.759$, df = 2, $p = 0.021$) but there were no differences in sex ratios for white rhinos ($\chi^2 = 3.028$, df = 2, $p = 0.220$).

Additionally, top ranking models differed between species (Table 3.4). Model ranking rainfall, greenness and density models showed that greenness variables had greater explanatory power for both species. Current density had greater explanatory power for black rhinos compared to white rhinos and rainfall had greater explanatory power for the white rhinos compared to black rhinos. There was little evidence of an effect of dam identity for

both species. In addition to presenting the top variables, wet-season integrated EVI (w_i = 0.971) for black rhinos and annually integrated EVI (w_i = 0.649) for white rhinos, rainfall and density variables are presented to illustrate their influence on rhino birth sex ratios.

For black rhinos, the probability of conceiving and birthing a male calf decreased as EVI increased (Figure 3.6). The odds of having a male calf decreased by a factor of 0.121 (0.005, 0.785) with each unit increase in integrated EVI during the year of conception. Although I was not able to detect a clear effect for the white rhinos, analyses suggested that the probability of conceiving and birthing a male white rhino calf increased with EVI (Figure 3.7). The odds of having a male calf increased by a factor of 2.391 (0.889, 6.945) with each unit increase in integrated EVI.

Rainfall: For black rhinos, analyses suggested that the probability that a conception during a wet year (compared to normal and dry years) resulted in the birth of a male calf was low compared to a female birth (Figure 3.8a, the odds of conceiving a male decreased by a factor of 0.440 [0.091, 1.989]). The second model suggested that the probability that a male calf was birthed was positively influenced by rainfall twelve months prior (Figure 3.8b, the odds of conceiving a male increased by a factor of 1.133 [0.906, 1.490]). For the white rhinos, the probability of conceiving and birthing a male calf increased with monthly rainfall (Figure 3.9a, the odds of having a male calf increased by 1.475 [0.925, 2.455]). Although BSR was not affected by ENSO, results suggested that conceptions during ENSO years were more likely to result in the birth of female calves (Figure 3.9b, the odds of having a male calf decreased by 0.593 [0.246, 1.411]).

Density: For both species, the probability of having a male calf decreased as density increased (Figures 3.10–11). The odds of having a male calf decreased by a factor of 0.951 (0.765, 1.147) and 0.902 (0.164, 4.711) with each unit increase in density during the

conception year for black and white rhinos, respectively. Although not significant, the effect of density on sex allocation was clearer with the black rhinos compared to white rhinos.

There was a tendency for black rhino females that had three or more calves to produce more males than females (83% of the females, n = 6). The two females that had the highest number of calves (seven and eight) both had one or two female calves, and the females with one calf each only had female calves. Similarly for the white rhinos, females with three or more calves (57% of the females, n = 14) produced more males than females, whilst the rest either produced more females or had an equal number of males and females. Of the three females with the highest number of calves (six and seven) only one produced more females and had one male calf. Additionally, one white rhino female exclusively produced male calves (n = 3). The occurrence of successive same-sex calves versus alternating sexes was more common for black than for white rhinos (16 versus 12 and 20 versus 25, respectively).

Discussion

The main aim of this study was to assess the timing of reproductive events in black and white rhino populations and to assess the influence of environmental variation on the population's reproductive parameters. Although white rhinos were more likely to conceive and calve at an earlier age than the black rhinos, both species reproductive events were not strictly seasonal; conception and births occurred throughout the year, which makes sense considering their 15–16 month gestation periods. There were some differences between rhinos born at Lapalala and external rhinos for both species regarding the conditions in which they reproduced, which I liken to a 'demographic heterogeneity' effect (i.e., variation at the individual level associated with differences in early life and access to resources [Kendall et al., 2011; Stover et al, 2012; Sky et al., 2022]) because conditions experienced throughout their life prior to

Lapalala possibly influenced their nutritional gains and consequently, their body condition. Surprisingly, shorter periods between the previous birth and next calving (ICIs) were associated with lower amounts of rainfall for both species, which could be a locality situation seeing that for most years, rainfall was lower than average. One difference between the species, however, was how greenness, particularly EVI, affected birth sex ratios. Increased greenness was associated with a lower probability of conceiving a male black rhino, whereas increased greenness was associated with a higher probability of conceiving a male white rhino.

Reproductive timing: Seasonal distribution of births & conceptions

Both species reproduced and calved throughout the year, despite environmental conditions; however, both had their conception peaks at times when conditions would be most favourable, supporting my first hypothesis. For megaherbivores, such as the black and white rhino, because gestation exceeds 12 months, births tend to be spread throughout the year because there is less selective pressure favouring critical periods to coincide with nutritionally optimal periods during the year (Owen-Smith, 1988; Owen-Smith & Ogutu, 2013). Instead, fertility or rather oestrous cycling depends strongly on female condition so much so that it becomes the overriding factor so that conception peaks will coincide with nutritionally optimal periods (Owen-Smith, 1988; Cook et al., 2001; Owen-Smith & Ogutu, 2013). For Southern African savannas, rainfall primarily influences plant growth, forage availability and quality (Rutherford, 1980; Deshmukh, 1984) meaning that forage quality and digestibility change with rainfall seasonality (Boutton et al., 1988a; Ogutu et al., 2014). For black rhinos, conceptions peaked before the wet season and secondarily during the wet season (Figure 3.3a). Whereas conceptions peaked during the early wet season for white rhinos (Figure 3.3b). Most woody plants will put on leaves and green before the first wet season rains (Rutherford, 1980) and decline in nutritional quality at a slower rate than grasses

(Pellew, 1983; Owen-Smith, 1994, 2008), suggesting that black rhinos would take advantage of this period to reproduce. On the other hand, herbaceous plants reach their nutritional peaks shortly after the first wet season rains (Boutton et al., 1988a, 1988b; Owen-Smith, 2008) again suggesting that their reproduction would be associated with the period at which grass quality increases.

The black rhino population in the Hluhluwe/Corridor/Umfolozi Game Reserve Complex also reproduced throughout the year, with two conception peaks in October and November and another between April and July (Hitchins & Anderson, 1983). The first peak which occurs in spring was associated with an improved nutritional state; however, the second peak in autumn was suggested to be associated with photoperiod (Hitchins & Anderson, 1983). The bimodal pattern in conceptions for white rhinos in the same reserve, peaked in November and again in February, and was associated with the bimodal pattern in spring/summer rainfall (Owen-Smith, 1973). Because white rhino conception peaks were associated more with periods of optimal forage availability, black rhino conception was concluded to be cued by light (Anderson, 1979; Hitchins & Anderson, 1983). Most megaherbivores in rainfall-driven savannas, excluding elephants, show conception peaks in spring/summer when conditions are optimal, and birth peaks during the dry season (Owen-Smith & Ogutu, 2013).

Relating age at first calving to rainfall, greenness and density

The relationship between reproduction and greenness indices should be similar to that reported for reproduction and rainfall as greenness indices offer a direct measure of vegetation production (Goward & Prince, 1995; Huete et al., 2002). Surprisingly however, the age at which black rhinos conceived their first calf increased with EVI and NDVI (Table 3.2). Although the EVI model was not significant, I suggest that increases in wet-season integrated EVI and maximum NDVI during conception periods might indicate a shorter

period of access to high quality forage (Pettorelli et al., 2007) or increased production of vegetation that the black rhinos may not have access to (i.e., vegetation that they do not consume, increased grass production). By comparison, the age at which white rhinos had their first calf decreased as EVI increased (Table 3.2). This suggests that they were more likely to reproduce when vegetation productivity was high (Rasmussen et al., 2006), which would support body condition and allow for the onset of oestrous. Additionally, most conceptions occurred at the beginning of the wet season suggesting that females might take advantage of high quality forage as greenness increases to build up body reserves and maintain the physical condition necessary to successfully conceive their first calf (Ryan et al., 2007; Pettorelli et al., 2007; Therrien et al., 2007).

Age at sexual maturity (ASM, primiparity) decreased as rainfall increased for both species, in support of my third hypothesis. For black rhinos, although not significant, the rainfall six months prior to conception had some influence on both Lapalala and external born rhinos. The rainfall one month prior to conception had a positive influence on both Lapalala and external born white rhinos and was a significant predictor variable for the external rhinos. The age at sexual maturity is influenced by female body condition, which for savanna herbivores is largely influenced by rainfall conditions (Owen-Smith, 1988; Owen-Smith & Ogutu, 2013). In savannas where mean annual precipitation is less than 800 mm, vegetation production and thus forage availability is directly correlated with rainfall (Coe et al., 1976; Rutherford, 1980). High amounts of rainfall and forage support body condition and the accumulation of fat reserves which allow for the onset of puberty and oestrous (du Plessis, 1972; Hamilton & Blaxter, 1980; Prins 1996; Gaillard et al., 2000).

Lastly, both species had a similar response to density, as ASM decreased with density despite what I had hypothesized (H_2). After juvenile survival, density-dependence should reduce fertility (Eberhardt, 2002) and increase ASM (Sæther, 1997). This is because

population density increases competition for resources, potentially making it difficult for females to accumulate the body mass and fat reserves needed to reproduce (Hamilton & Blaxter, 1980). However, it is important to recognise that the determination of age at sexual maturity in this study depended on the birth of the first known calf. Therefore, increased ASM might have been influenced by the consequences of environmental conditions on female body condition, but also on pregnancies that were not carried to full-term, abortions and a combination of all three (Nhleko et al., 2017).

Through modelling the effects of rainfall and density on the ASM of the black rhino population at the Great Fish River Reserve (GFRR), the only evidence of any effects was that ASM increased with density (Law et al., 2013). Both the Lapalala and GFRR populations are similar in abundance and reserve size and so it is not surprising that successful reproduction could be hindered by increasing density. Similarly, ASM increased with density for the Hluhluwe/Corridor/Umfolozi Game Reserve Complex (Hitchins & Anderson, 1983) and Pilanesburg (Hrabar & du Toit, 2005) black rhino populations. No effect of rainfall on ASM was detected in the Pilanesburg population; however, density-dependence on ASM was reduced during high rainfall years (Hrabar & du Toit, 2005). Contrary to my results, ASM for a game-ranched white rhino population did not increase with density (Ververs et al., 2017) but ASM increased with density for the Matobo National Park white rhino population (Rachlow & Berger, 1998). This is important because ASM for rhinos is sensitive to population density (Rachlow & Berger, 1998) and so if rhinos are provided with supplementary resources during periods of low vegetation availability and increased density, much like the game-ranched population (Ververs et al., 2017), this suggests that their reproduction might not be delayed. Although few studies have been conducted to access the influence of rainfall and greenness on rhino ASM, results suggest that rhinos in poor habitats,

and in most cases, with increased competition (i.e., density-dependence) might have delayed reproduction because of poor body condition (Gaillard et al., 2000; Patton et al., 2008)

Relating ICIs to rainfall, greenness and density

Rainfall was the most important variable in explaining the ICIs for both rhino species (Table 3.3). I found a positive relationship between ICIs and rainfall (Figure 3.5) which again supports the idea that normal and high, but not excessive amounts of rainfall increase the odds of conception for both species, also disputing my third hypothesis. Inter-calving intervals vary amongst populations and individuals but are influenced by female age and forage availability and quality (du Toit, 2006). Both species were strongly influenced by cumulative rainfall (since the birth of the previous calf to the conception of the next) compared to immediate rainfall (monthly rainfall) suggesting that they were building up reserves and improving body condition during that time. After parturition female body condition needs time to improve and build up reserves again because most of their energy was spent on late gestation, lactation and weaning (Dunham & Murray, 1982; Sims et al., 2007; Therrien et al., 2007; Ogutu et al., 2014). And so, when wet season rains are sufficient female rhinos might be able to consume enough and highly nutritious food to recover body condition for the next conception (du Plessis, 1972; Georgiadis & McNaughton, 1990); whereas, oestrous and fertility could be suppressed because of deteriorating food quality as rainfall increases (Owen-Smith, 1988; Owen-Smith & Ogutu, 2013). This is also supported by the conception peaks that occur during the early wet season when forage quality is highest (Georgiadis & McNaughton, 1990; Ogutu et al., 2014).

Contrary to both populations at Lapalala, the black rhino population at Pilanesburg had shorter ICIs when rainfall increased (Hrabar & du Toit), which was linked to the relationship between rainfall and forage availability. Conceptions for the Lapalala populations were associated with lower amounts of rainfall but never drought conditions

(measured using RAI) or ENSO conditions. I suggest that this could allude to the fact that increased rainfall increases forage availability, but lower amounts of rainfall may prolong periods of access to high quality forage (Georgiadis & McNaughton, 1990), possibly allowing the accumulation of fat reserves and peak body condition for the Lapalala rhinos (du Plessis, 1972; Hamilton & Blaxter, 1980; Prins 1996; Gaillard et al., 2000). There was no influence of rainfall or density on ICIs detected for the GFFR black rhino population, but Law et al. (2013) reported that the population was still young at the time and that future work might detect some sort of influence. I did not detect any influences of current and prior density on both species' ICIs, which could also be improved or later detected, as the populations, particularly the black rhinos, grow.

Relating calf sex (BSR) to rainfall, greenness and density

Although the birth sex ratios remained male biased by the end of the study period for both species, there was little evidence from the logistic regression models for a strong influence of environmental conditions on calf sex. The probability of black rhinos conceiving a male calf decreased as EVI increased, in support of the LRC hypothesis. In polygynous mammals, males are the dispersing sex and so rhinos in resource limited environments and in poor condition should produce more sons (Clark, 1978) and produce more females when resources are abundant. In support of my fourth hypothesis and the TW and EM hypotheses, there was little evidence that females from both species were more likely to conceive males as rainfall increased. Additionally, results suggested that white rhinos were more likely to favour female calves during ENSO years again supporting the idea that females in good condition, with enough resources will produce more sons (Trivers & Willard, 1973; Hrabar & du Toit, 2005). Also, in support of the TWH and EMH, both species favoured male calves as population density decreased. This again supports the idea that rainfall affects vegetation production and that females in good condition are more likely to produce male calves (Hrabar & du toit,

2005; Ogutu & Owen-Smith, 2005; Cameron & Linklater, 2007). Although most results were not significant, I suggest that both populations may show evidence in support of the EMH in future as the population grows. I found evidence that the reproduction of both species was influenced by environmental factors and so it is possible that maternal conditions may affect sex allocation because male fitness (polygynous mammals) is related to their growth and maternal investment (Clutton-Brock et al., 1986; Clutton-Brock, 1988).

Rainfall during pregnancy had a positive influence on the probability of black rhino mothers having sons at the Mkuze Game Reserve (Weladji & Leflamme-Mayer, 2011), but there was no influence of rainfall experienced prior to conception. Similar to the black rhinos at Lapalala, calf sex was not influenced by ENSO during pregnancy or in the year prior to conception (Weladji & Leflamme-Mayer, 2011). Berkeley and Linklater (2010) reported that black rhinos in Hluhluwe-iMfolozi were more likely to conceive males during wet years compared to dry years. There were more female black rhinos conceived during years with below average rainfall at Pilanesburg (Hrabar & du Toit, 2005), and more males conceived during years with above average rainfall. There was no influence of rainfall detected on sex ratios for a population of game-ranged white rhinos, like the Lapalala rhinos. The results of modelling maternal condition via rainfall and calf sex are mixed and so I suggest that greenness might be a better proxy because it is a direct measure of primary productivity and was the only strong evidence for any effect of maternal condition on calf sex at Lapalala.

This study supports the notion that the reproductive phenology of megaherbivores is not based on anticipated conditions during births but rather conditions during conception (see Owen-Smith, 1988; Cook et al., 2001; Owen-Smith & Ogutu, 2013). Conception peaks for both species correlated with periods of high forage availability and quality (H_1) supporting the strong associations and ideas that environmental conditions drive the population performance of large herbivores. Both populations show some evidence in support of

Eberhardt's (2002) prediction that after juvenile recruitment, density will then affect the age at primiparity, whilst effects on adult fertility remained trivial, disputing my second hypothesis (H_2). The other predictor variables, rainfall and greenness, had a positive influence on earlier reproduction for both species' first calving events (H_2) in support of the association between environmental conditions and female body condition. Inter-calving intervals increased with rainfall, contradicting what is known in literature (see Hrabar & du Toit, 2005) but supporting the idea that excessive amounts of rainfall might result in lower forage quality, which then affects maternal body condition. Birth sex ratios indicate little support for the TWH and EMH as results were not significantly associated with rainfall and density (H_4), however this may be improved over time with a larger sample. Findings provide evidence that the reproductive timing of black and white rhinos, especially the age at parturition, is associated with resource availability as a result of environmental stochasticity and density. This is important for management to achieve maximum productivity and assess the performance of these rhino populations as climate change will result in more variable conditions, and to make informed decisions based on population performance (such as removals) whilst keeping a balanced sex ratio.

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Table 3.1. Model selection: Cox proportional hazard models to analyse age at first calving of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness, South Africa, 1990–2019.

Species	Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos	Wet-season Integrated EVI during conception year	24.187	0.000	0.901	1	0.697 (0.118)
	Origin × Wet-season Integrated EVI during conception year	26.452	2.264	0.094	2	0.758 (0.100)
	Wet-season max NDVI during conception year	29.356	5.169	0.005	1	0.750 (0.067)
	Origin + rainfall six months before conception	40.549	16.362	0.000	2	0.656 (0.087)
	Origin + rainfall twelve months before conception	43.974	19.787	0.000	2	0.590 (0.081)
	Density (factor) during conception year	53.729	29.541	0.000	1	0.570 (0.112)
	Origin × density (factor) during conception year	54.758	30.570	0.000	2	0.737 (0.069)
White rhinos	Annually Integrated EVI during conception year	196.498	0.000	0.906	1	0.673 (0.056)
	Origin × Annually Integrated EVI during conception year	198.768	2.270	0.094	2	0.677 (0.055)
	Origin + rainfall one month before conception	210.276	13.777	0.000	2	0.690 (0.053)
	Annually Integrated NDVI during conception year	213.821	17.323	0.000	1	0.651 (0.057)
	Origin + rainfall twelve months before conception	216.355	19.857	0.000	2	0.639 (0.060)
	Prior conspecific density during conception year	237.615	41.117	0.000	1	0.575 (0.057)
	Conspecific density during conception year	240.518	44.019	0.000	1	0.593 (0.056)

[a] AICc = Akaike's Information Criterion, corrected for small sample size, [b] ΔAICc = AICc – min(AICc), [c] w_i = model probability, [d] K = number of parameters, [e] Standard error in parentheses.

Table 3.2. Model coefficients: Cox proportional hazard models used to analyse age at first calving of black and white rhinoceroses, Lapalala Wilderness, South Africa, 1990–2019. Presented are the rainfall, greenness and density models used for interpretation.

					95% confidence intervals	
Model	Stratum (Origin)	Estimate	*SE*	Hazard ratio	Lower	Upper
Black rhinos						
Wet-season Integrated EVI during conception year	All	-0.472	0.504	0.624	0.232	1.676
Wet-season max NDVI during conception year	All	**-1.177**	0.560	**0.000007**	0.000	0.452
Origin × Density factor during conception year	Lapalala	-0.065	0.055	0.937	0.841	1.044
	External	**-0.133**	0.067	**0.876**	0.767	0.999
White rhinos						
Annually Integrated EVI during conception year	All	**1.363**	0.408	**3.907**	1.755	8.700
Origin + rainfall one month before conception	Lapalala	0.619	0.397	1.857	0.854	4.040
	External	**0.727**	0.216	**2.069**	1.356	3.157
Prior conspecific density during conception year	All	**-0.059**	0.194	**0.942**	0.907	0.979

*Estimates and Hazard Ratios (HR) of predictors with standard errors excluding 1.000 are in bold.

Table 3.3. Model selection: Rainfall, greenness and density models used to analyse the ICIs of black and white rhinoceroses, Lapalala Wilderness, South Africa, 1990–2019.

Species	#	Model	AICc[a]	ΔAICc[b]	w_i[c]
Black rhinos	1	Rainfall between previous calving and conception	7.360	0.000	1.000
	4	Wet-season Integrated EVI during conception year	88.522	81.162	0.000
	3	Annually Integrated EVI during conception year	89.031	81.671	0.000
	2	Annually Integrated NDVI during conception year	90.300	82.940	0.000
	5	Conspecific density during conception year + Dam ID	97.365	90.005	0.000
	6	Prior conspecific density during conception year + Dam ID	97.469	90.109	0.000
White rhinos	1	Rainfall between previous calving and conception	32.995	0.000	1.000
	4	Wet-season Integrated EVI during conception year	124.710	91.716	0.000
	3	Annually Integrated EVI during conception year	125.904	92.909	0.000
	2	Annually Integrated NDVI during conception year	128.413	95.418	0.000
	6	Prior conspecific density during conception year + Dam ID	138.317	105.322	0.000
	5	Conspecific density during conception year + Dam ID	142.809	109.815	0.000

[a] AICc = Akaike's Information Criterion, corrected for small sample size, [b] ΔAICc = AICc – min(AICc), [c] w_i = model probability.

Table 3.4. Model selection: Regression models used to analyse birth sex ratios of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness, South Africa, 1990–2019.

Species	Model	AICc[a]	ΔAICc[b]	w_i[c]
Black rhinos	Wet-season Integrated EVI during conception year	40.257	0.000	0.971
	Wet-season Integrated NDVI during conception year	43.783	3.525	0.029
	Conspecific density during conception year	56.522	16.264	0.000
	Conception during wet year	57.014	16.756	0.000
	Rainfall twelve months before conception	57.022	16.765	0.000
	Rainfall two years before conception	57.312	17.055	0.000
	Density (factor) during conception year	57.903	17.646	0.000
White rhinos	Annually Integrated EVI during conception year	100.789	0.000	0.649
	Wet-season Integrated EVI during conception year	101.417	0.628	0.346
	Annually Integrated NDVI during conception year	105.679	4.889	0.005
	Rainfall one month before conception	116.267	15.477	0.000
	Rainfall two years before conception	116.997	16.207	0.000
	Conception during ENSO year	117.519	16.729	0.000
	Conspecific density during conception year	118.892	18.102	0.000
	Prior density factor during conception year	118.892	18.102	0.000

[a] AICc = Akaike's Information Criterion, corrected for small sample size, [b] ΔAICc = AICc – min(AICc), [c] w_i = model probability.

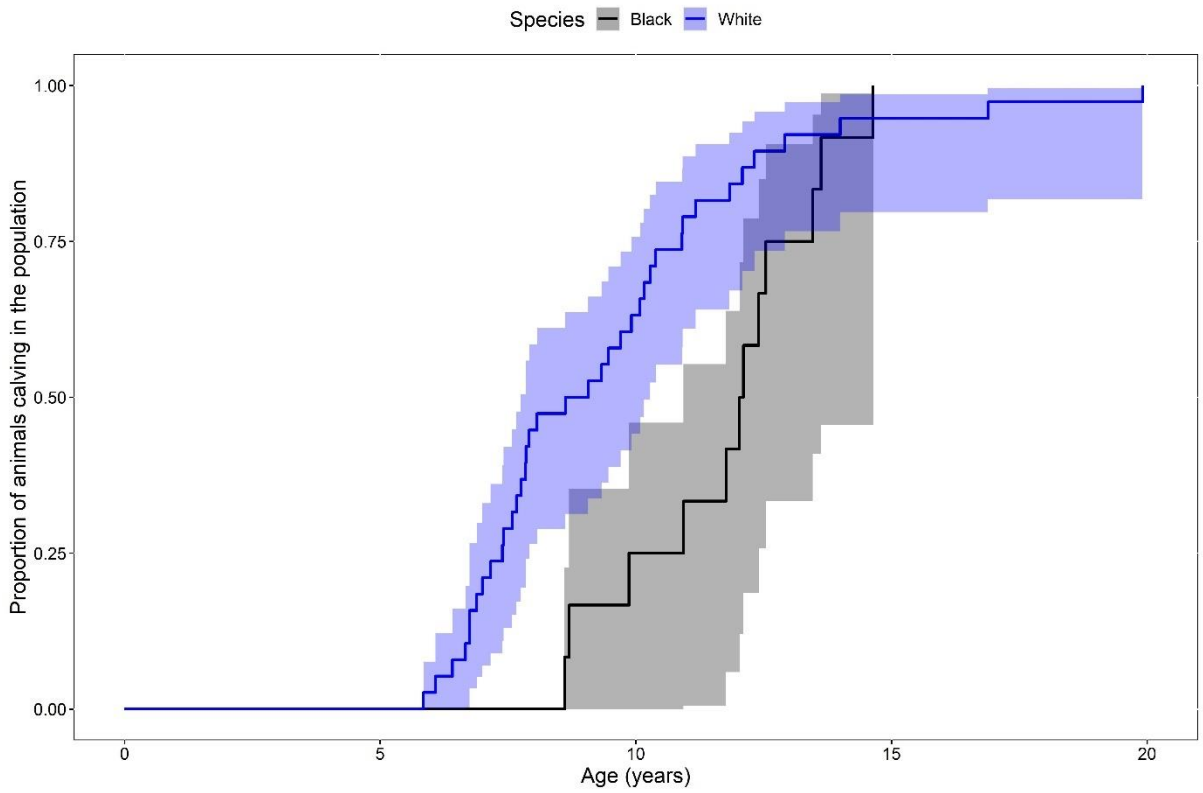


Figure 3.1. Age at first calving estimated for black (black curve) and white (blue curve) rhinos, Lapalala Wilderness, 1990–2019. Presented are Kaplan-Meyer time-to-event estimates and 95% confidence intervals.

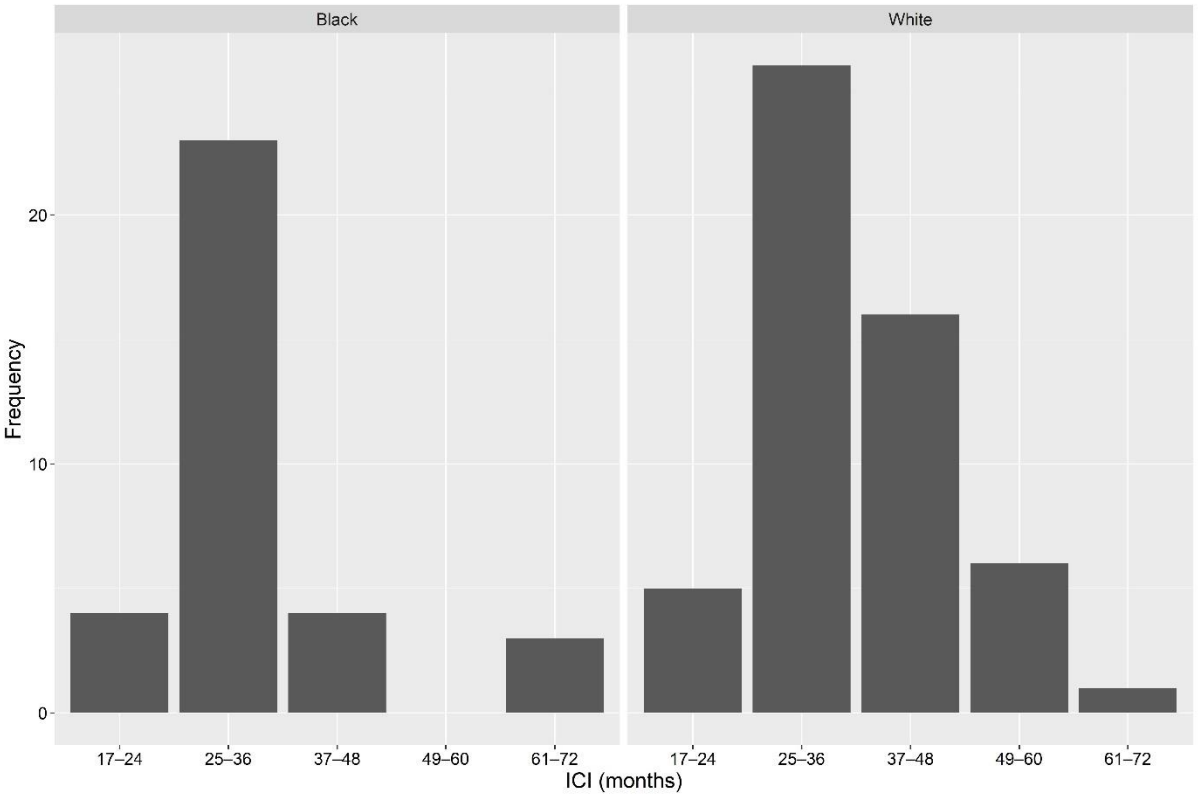


Figure 3.2. Frequency distribution of inter-calving intervals (ICIs) for black and white rhinos, Lapalala Wilderness, 1990–2019. A total of 10 black rhino females and 21 white rhino females had more than one calving event.

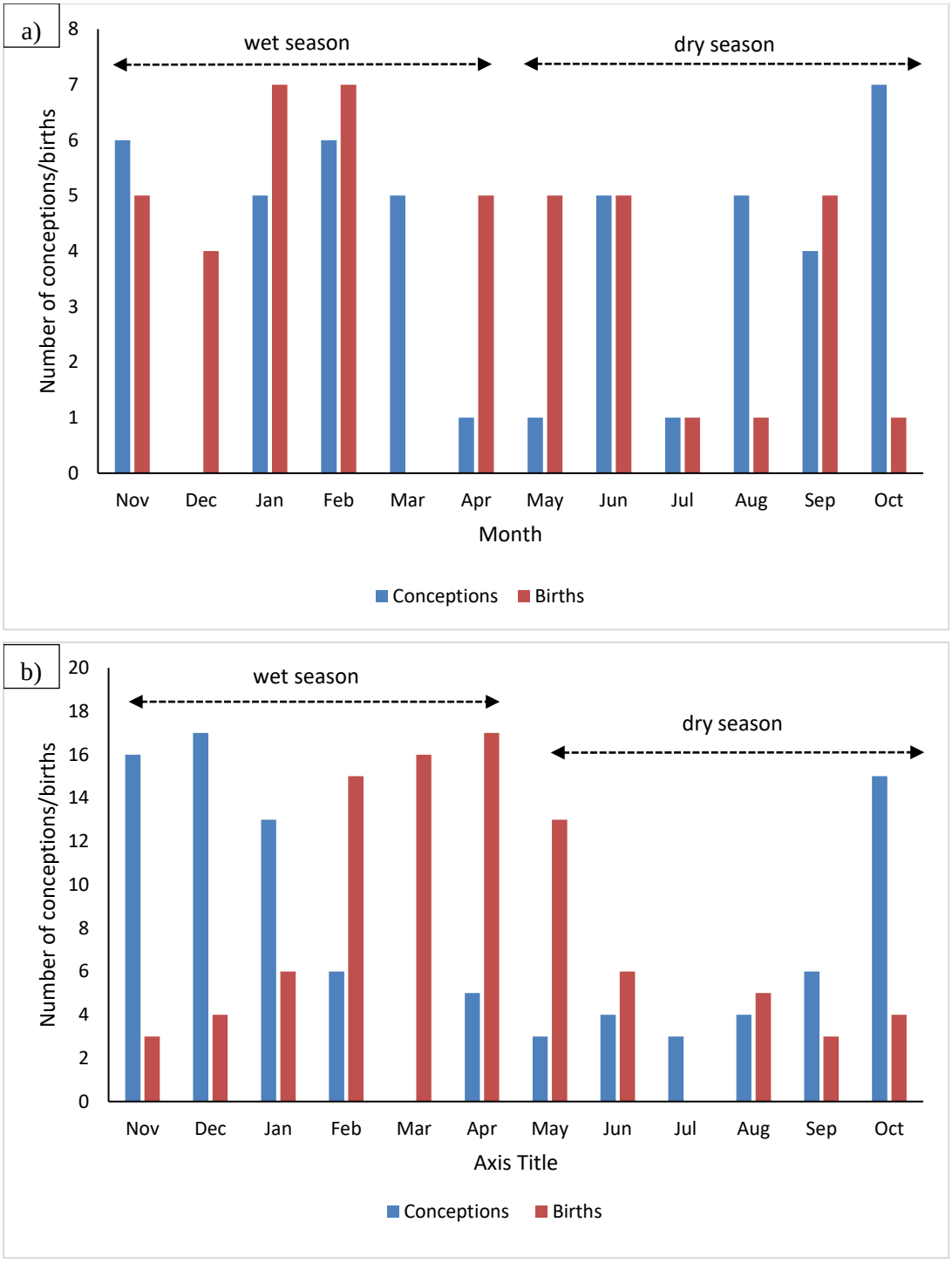


Figure 3.3. Seasonal distribution of all conception and birthing events for (a) black and (b) white rhinos, Lapalala Wilderness, 1990–2019.

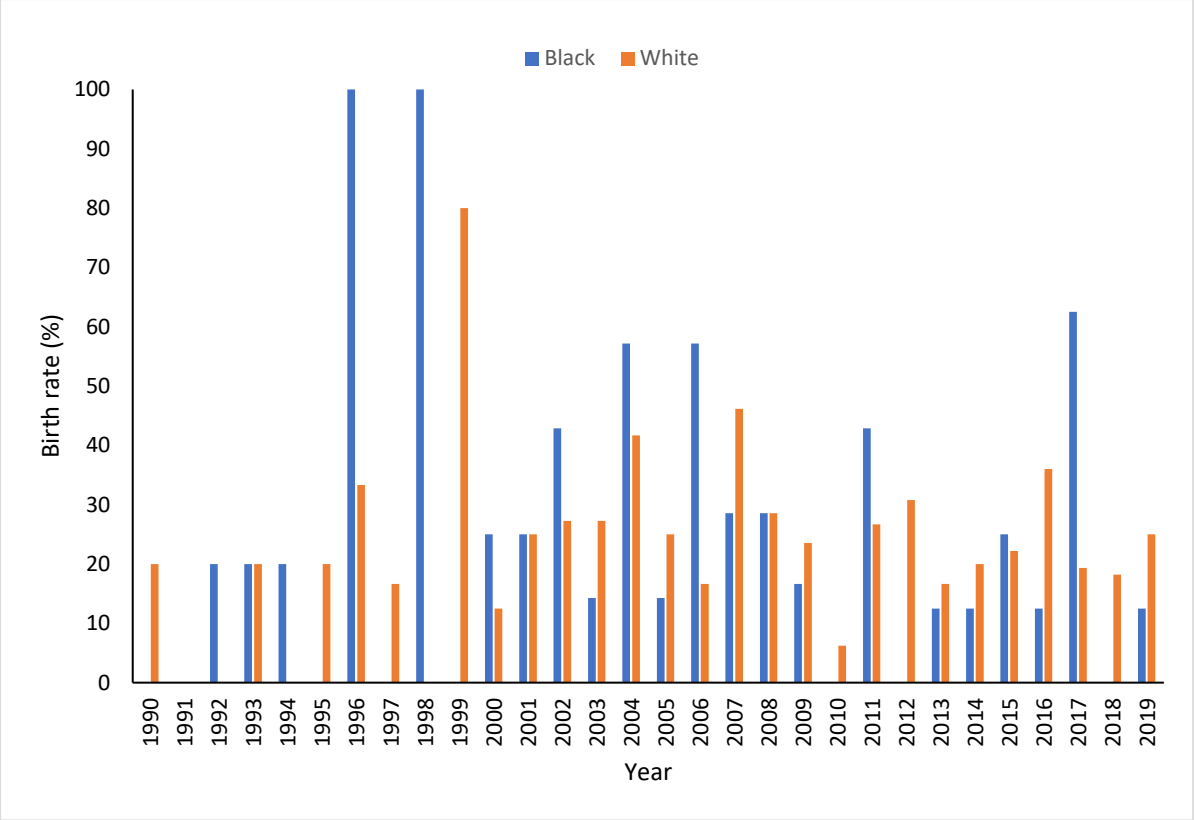


Figure 3.4. The birth/fertility rate for black and white rhino populations, Lapalala Wilderness, 1990–2019. Years where the percentage of birth rate was 100% indicate a year where all adult females in the population successfully calved.

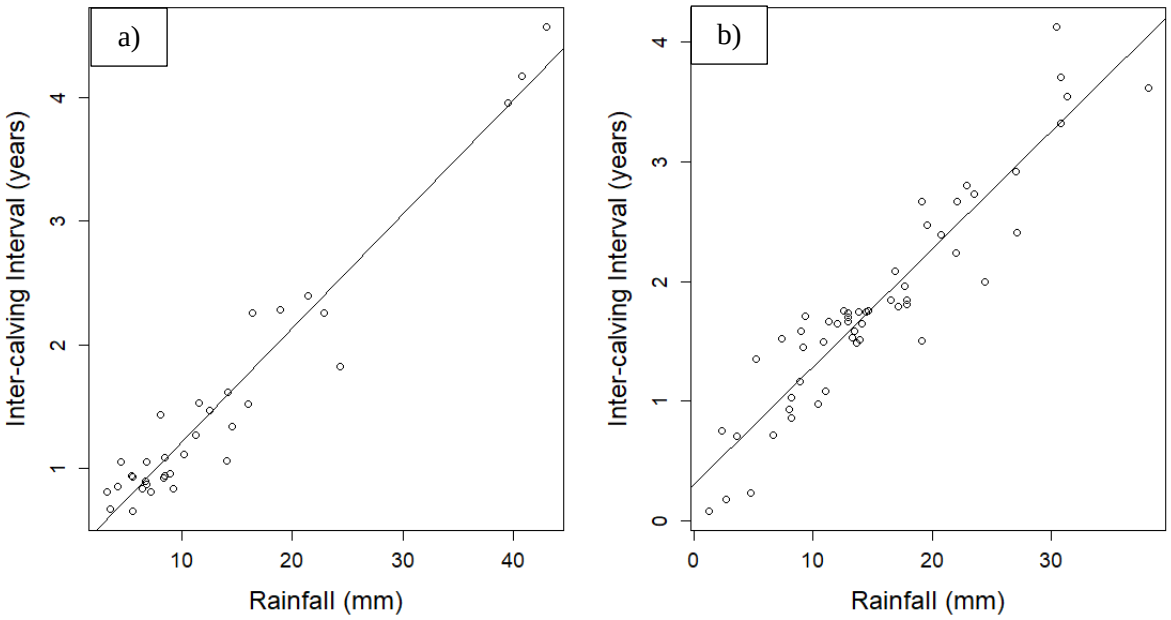


Figure 3.5. Relationship between rainfall and inter-calving intervals for (a) black and (b) white rhinos, Lapalala Wilderness, 1990–2019. This portion of the study only included females that had more than one calf, and so the amount of rainfall (i.e., rainfall between the birth and estimated conception date of the next calf) in between the dropping of calves was calculated specifically for each female.

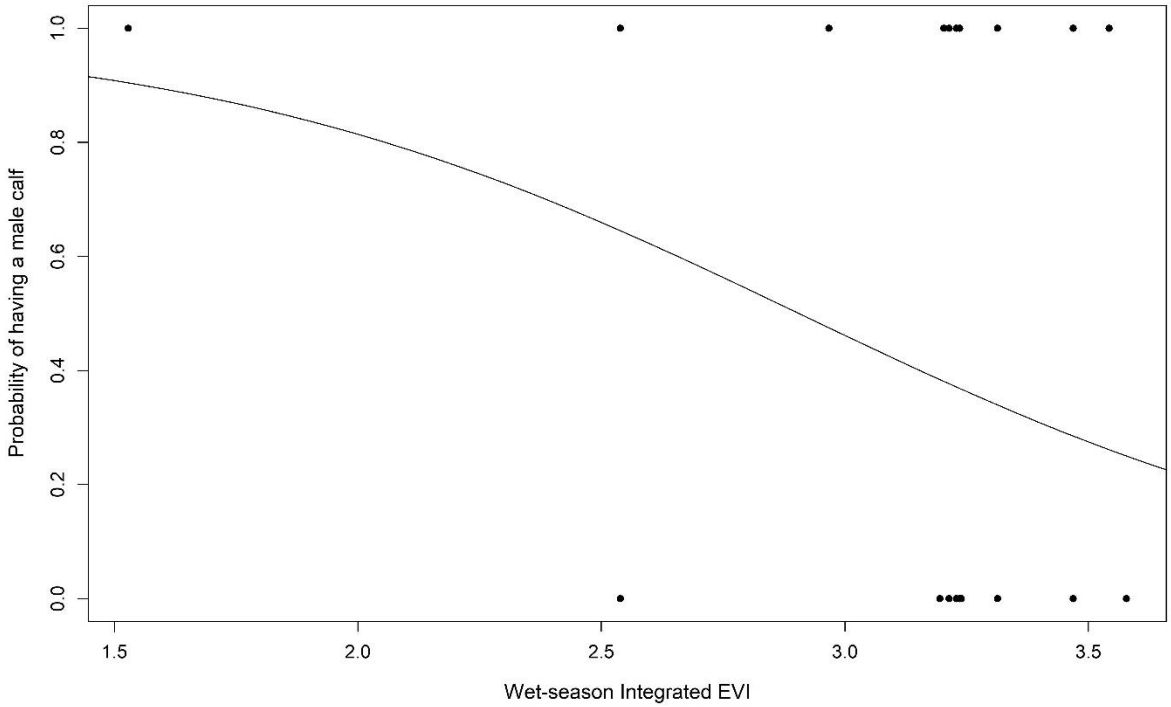


Figure 3.6. Logistic regression curve representing the effect of EVI on the probability of conceiving a male black rhino calf, Lapalala Wilderness, 1990–2019.

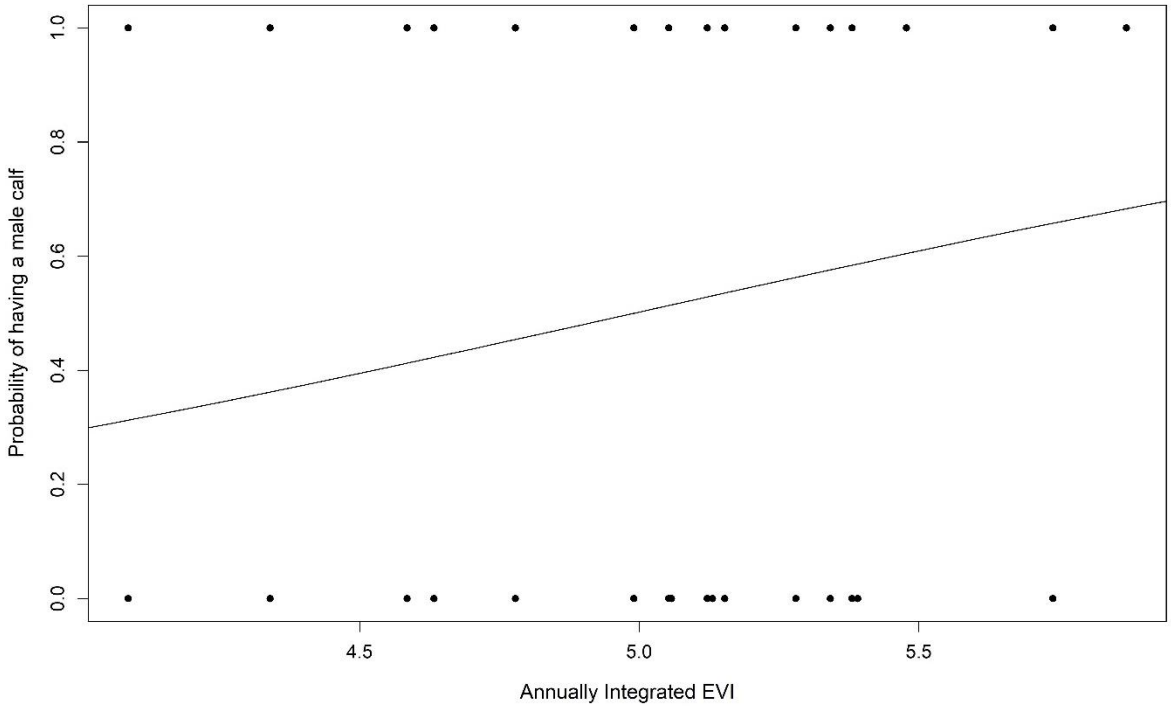


Figure 3.7. Logistic regression curve representing the effect of EVI on the probability of conceiving a male white rhino calf, Lapalala Wilderness, 1990–2019.

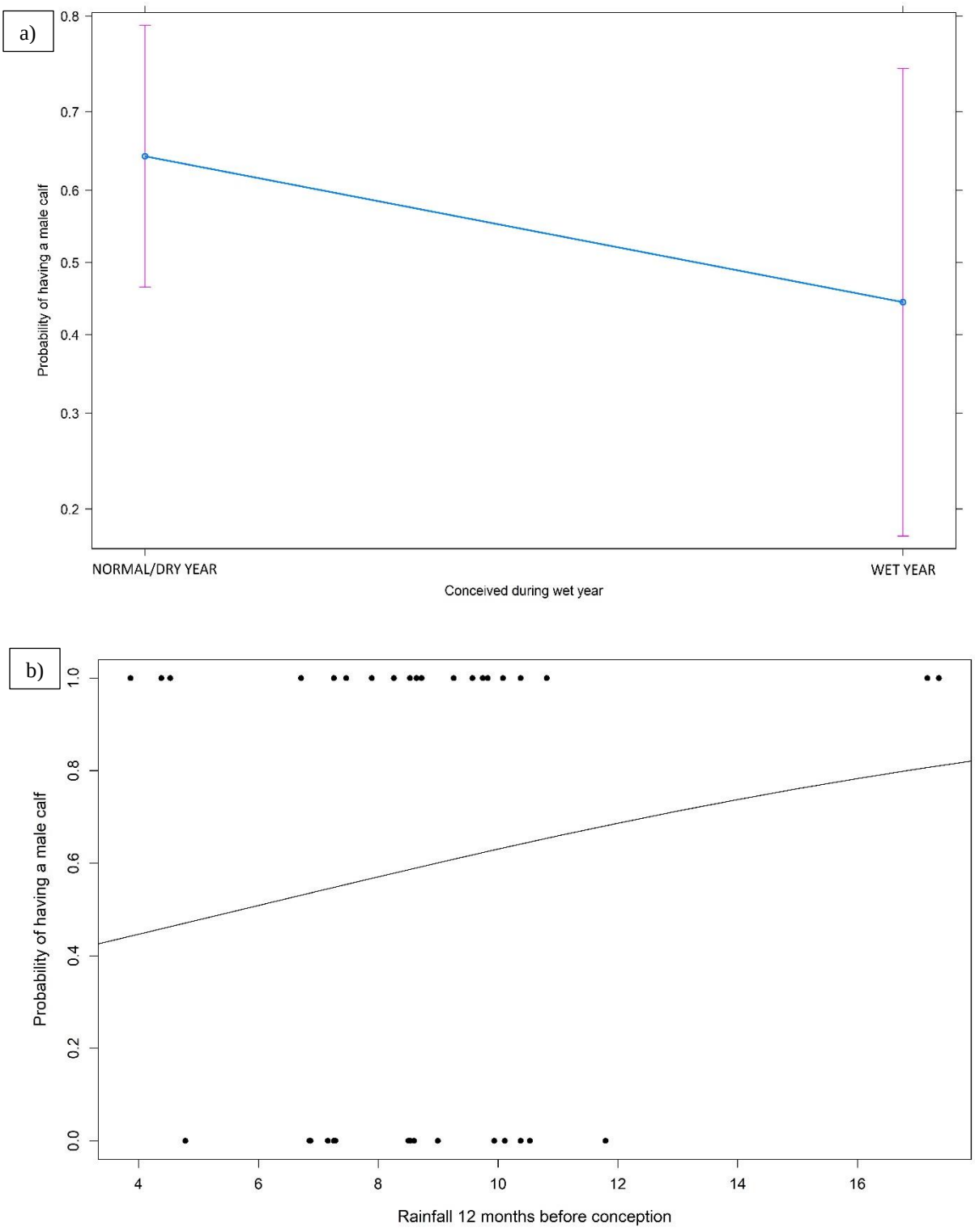


Figure 3.8. Logistic regression curve representing the effect of (a) wet years and (b) rainfall on the probability of conceiving a male black rhino calf, Lapalala Wilderness, 1990–2019.

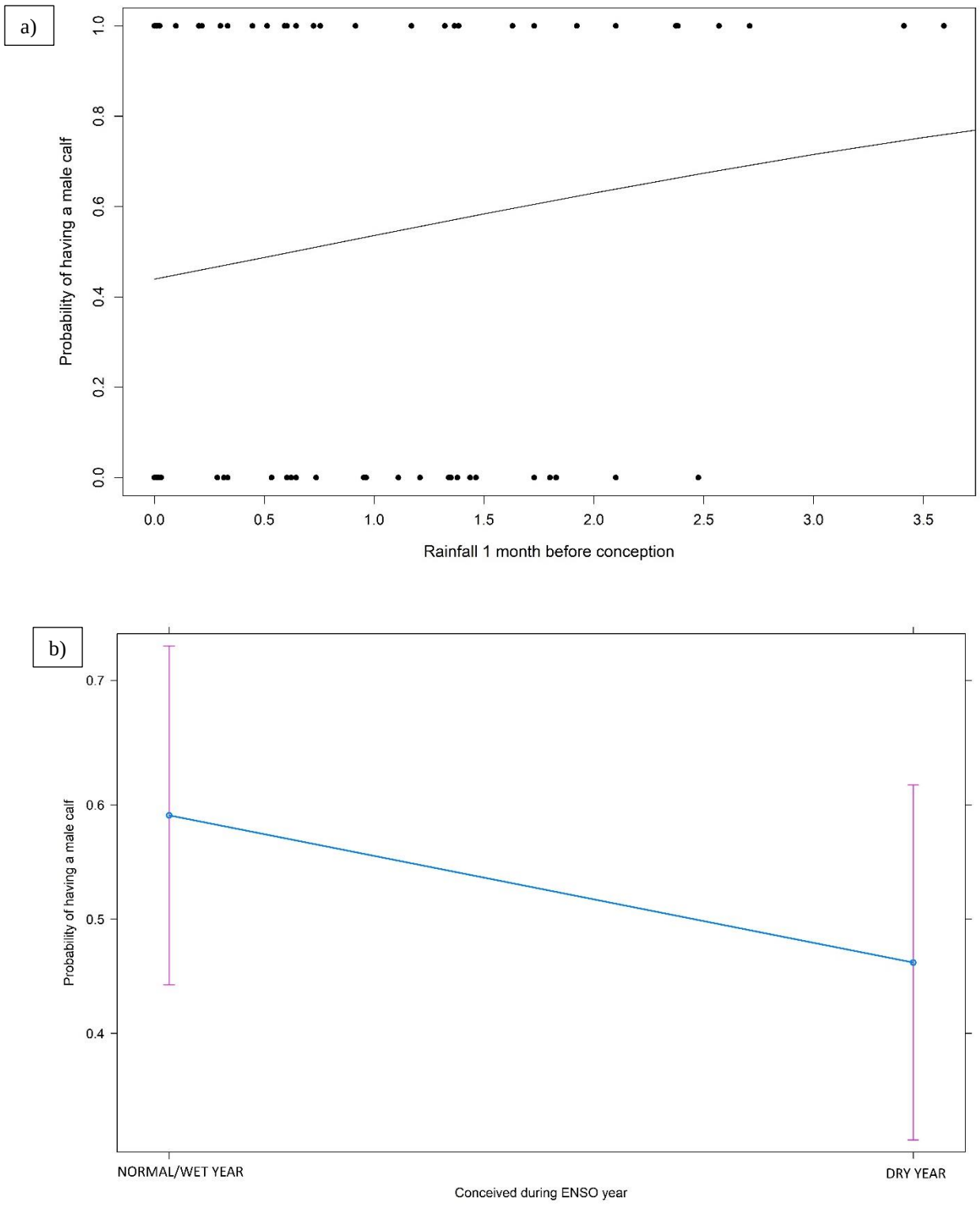


Figure 3.9. Logistic regression curve representing the effect of (a) rainfall and (b) ENSO on the probability of conceiving a male white rhino calf, Lapalala Wilderness, 1990–2019.

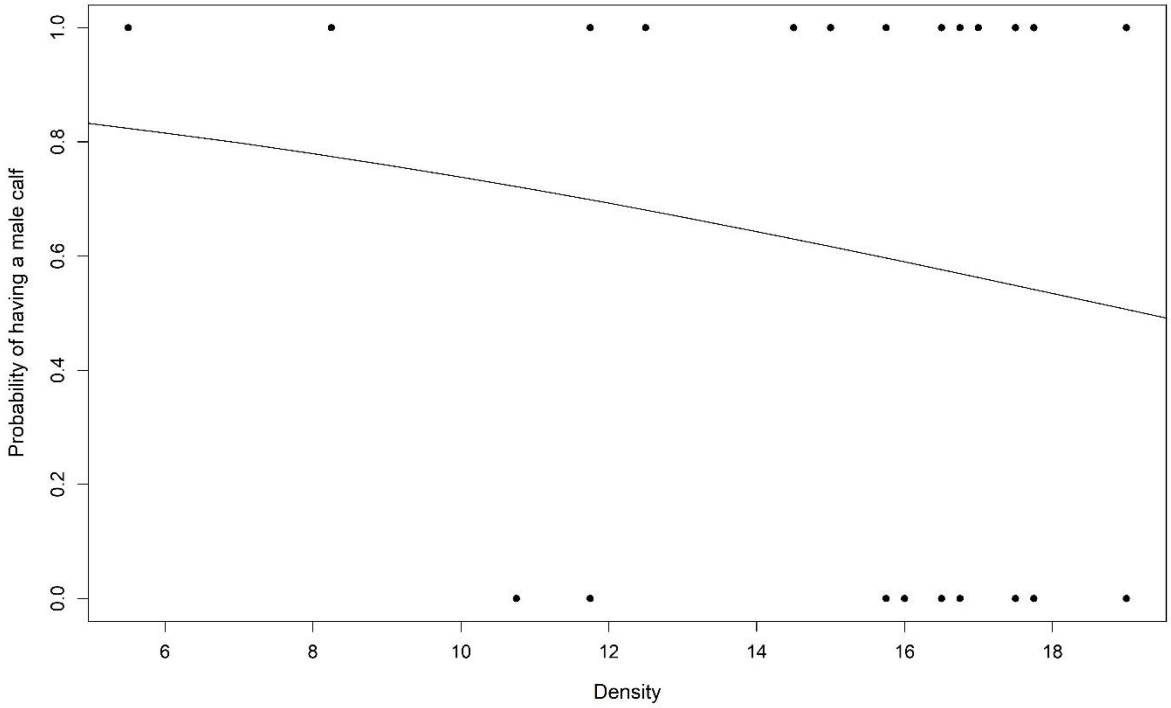


Figure 3.10. Logistic regression curve representing the effect of density on the probability of conceiving a male black rhino calf, Lapalala Wilderness, 1990–2019.

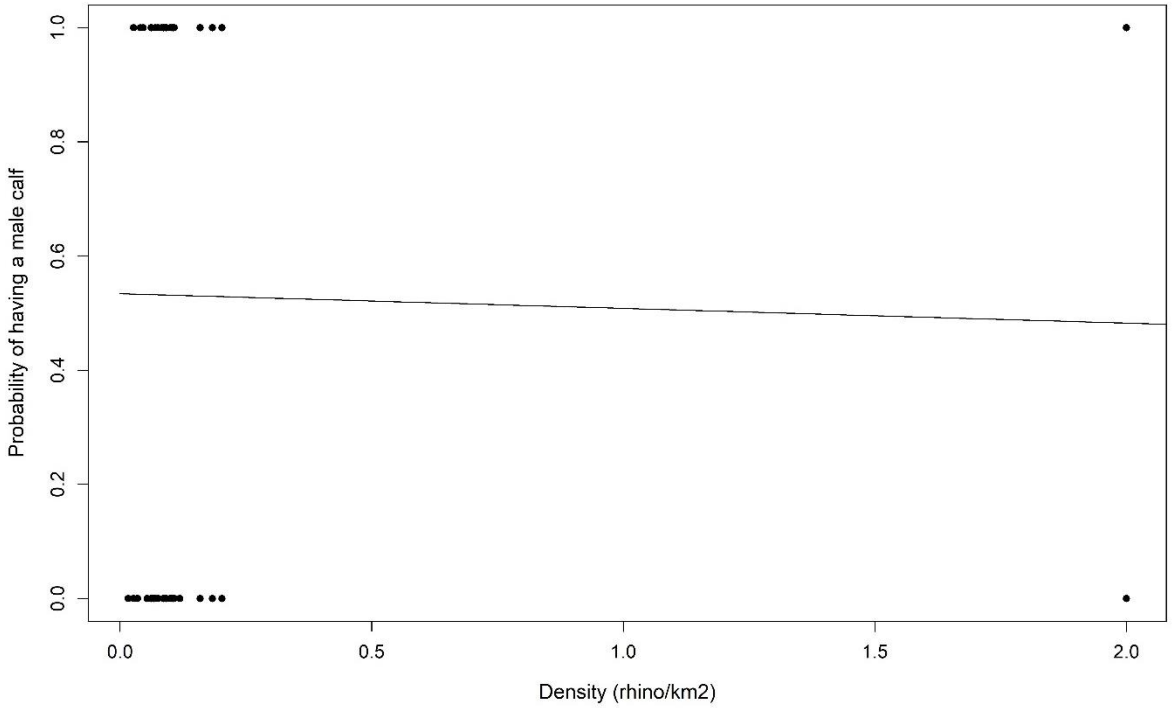


Figure 3.11. Logistic regression curve representing the effect of density on the probability of conceiving a male white rhino calf, Lapalala Wilderness, 1990–2019.

Appendices

Appendix A1: Rainfall models that were used to summarize the age at sexual maturity (ASM) data set, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	ASM was affected by rainfall 12 months before conception
2	ASM was affected by rainfall 24 months before conception
3	ASM was affected by a drought year (conception in drought year)
4	ASM was affected by a wet year (conception in wet year)
5	ASM was affected by El niño-Southern Oscillation years (conception in ENSO year)
6	ASM was affected by rainfall six months before conception
7	ASM was affected by wet-season rainfall in the year prior to conception
8	ASM was affected by rainfall one month before conception
9	ASM was affected by rainfall during the gestation period
10	ASM was affected by rainfall 12 months before birth
11	ASM was affected by rainfall 24 months before birth
12	ASM was affected by the rain-level during year of conception
13	ASM was affected by the interaction between Dam origin and wet-season rainfall in the year prior to conception
14	ASM was affected by the interaction between Dam origin (stratified) and wet-season rainfall in the year prior to conception
15	ASM was affected by the interaction between Dam origin and the rainfall six months before conception
16	ASM was affected by the interaction between Dam origin (stratified) and the rainfall six months before conception
17	ASM was affected by the interaction between Dam origin and the rainfall 12 months before conception
18	ASM was affected by the interaction between Dam origin (stratified) and the rainfall 12 months before conception
19	ASM was affected by the interaction between Dam origin and the rainfall 24 months before conception

20	ASM was affected by the interaction between Dam origin (stratified) and the rainfall 24 months before conception
21	ASM was affected by the interaction between Dam origin and the rainfall one month before conception
22	ASM was affected by the interaction between Dam origin (stratified) and the rainfall one month before conception

Appendix A2: Rainfall models that were used to summarize ICIs, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	ICI was affected by rainfall 12 months before conception
2	ICI was affected by rainfall between previous calving and conception
3	ICI was affected by a drought year (conception in drought year)
4	ICI was affected by a wet year (conception in wet year)
5	ICI was affected by El niño-Southern Oscillation years (conception in ENSO year)
6	ICI was affected by rainfall six months before conception
7	ICI was affected by wet-season rainfall in the year prior to conception
8	ICI was affected by dry-season rainfall between previous calving and conception
9	ICI was affected by wet-season rainfall between previous calving and conception
10	ICI was affected by wet-season rainfall in the year prior to conception + Dam identity
11	ICI was affected by rainfall six months before conception + Dam identity
12	ICI was affected by rainfall 12 months before conception + Dam identity
13	ICI was affected by rainfall between previous calving and conception + Dam identity
14	ICI was affected by dry-season rainfall between previous calving and conception + Dam identity
15	ICI was affected by wet-season rainfall between previous calving and conception + Dam identity

Appendix A3: Rainfall models that were used to summarize calf sex, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	Sex was affected by rainfall twelve months before conception
2	Sex was affected by rainfall two years before conception
3	Sex was affected by a drought year (conception during drought year)
4	Sex was affected by a wet year (conception during a wet year)
5	Sex was affected by El niño-Southern Oscillation years (conception in ENSO year)
6	Sex was affected by rainfall six months before conception
7	Sex was affected by wet-season rainfall the year before conception
8	Sex was affected by rainfall one month before conception
9	Sex was affected by rainfall during gestation
10	Sex was affected by the rain-level during conception year
11	Sex was affected by the interaction between Dam identity and rainfall 12 months before conception
12	Sex was affected by the interaction between Dam identity and rainfall 24 months before conception
13	Sex was affected by the interaction between Dam identity and rainfall six months before conception
14	Sex was affected by the interaction between Dam identity and wet-season rainfall the year before conception
15	Sex was affected by the interaction between Dam identity and rainfall one month before conception
16	Sex was affected by the interaction between Dam identity and rainfall during gestation

Appendix B1. Greenness models that were used to summarize the ASM data set, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	ASM was affected by Annually Integrated NDVI during conception year
2	ASM was affected by maximum wet-season NDVI during conception year
3	ASM was affected by Wet-season Integrated NDVI during conception year
4	ASM was affected by NDVI during birth month
5	ASM was affected by Annually Integrated NDVI during calf birth year
6	ASM was affected by Wet-season Integrated NDVI during calf birth year
7	ASM was affected by the interaction between origin and Annually Integrated NDVI during conception year
8	ASM was affected by the interaction between origin and Wet-season Integrated NDVI during conception year
9	ASM was affected by Wet-season Integrated EVI during conception year
10	ASM was affected by Wet-season Integrated EVI during calf birth year
11	ASM was affected by the interaction between origin and Wet-season Integrated EVI during conception year
12	ASM was affected by Annually Integrated EVI during conception year
13	ASM was affected by the interaction between origin and Annually Integrated EVI during conception

Appendix B2. Greenness models that were used to summarize ICIs, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	ICI was affected by Annually Integrated NDVI during conception year
2	ICI was affected by Wet-season Integrated NDVI during conception year
3	ICI was affected by Annually Integrated EVI during conception year
4	ICI was affected by Wet-season Integrated EVI during conception year
5	ICI was affected by Annually Integrated NDVI during conception year + Dam identity
6	ICI was affected by Wet-season Integrated NDVI during conception year + Dam identity
7	ICI was affected by Annually Integrated EVI during conception year + Dam identity
8	ICI was affected by Wet-season Integrated EVI during conception year + Dam identity

Appendix B3. Greenness models that were used to summarize calf sex, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	Sex was affected by Annually Integrated NDVI during conception year
2	Sex was affected by wet-season max NDVI during conception year
3	Sex was affected by Wet-season Integrated NDVI during conception year
4	Sex was affected by Wet-season Integrated EVI during conception year
5	Sex was affected by Annually Integrated EVI during conception year
6	Sex was affected by the interaction between Dam identity and Annually Integrated NDVI during conception year
7	Sex was affected by the interaction between Dam identity and wet-season max NDVI during conception year
8	Sex was affected by the interaction between Dam identity and Wet-season Integrated NDVI during conception year
9	Sex was affected by the interaction between Dam identity and Wet-season Integrated EVI during conception year
10	Sex was affected by the interaction between Dam identity and Annually Integrated EVI during conception year

Appendix C1. Density models that were used to summarize the data set, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	ASM was affected by density during conception year
2	ASM was affected by prior density during conception year
3	ASM was affected by prior density (F2) density during conception year
4	ASM was affected by the interaction between origin and the density during conception year
5	ASM was affected by the interaction between origin and prior density during conception year
6	ASM was affected by the interaction between origin and prior density (F2) density during conception year
7	ASM was affected by conspecific density during conception year
8	ASM was affected by prior conspecific density during conception year
9	ASM was affected by prior conspecific density (F2) during conception year

Appendix C2. Density models that were used to summarize ICIs, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	ICI was affected by density during conception year
2	ICI was affected by conspecific density during conception
3	ICI was affected by prior density F2 during conception year
4	ICI was affected by prior conspecific density F2 during conception
5	ICI was affected by density during conception year + Dam identity
6	ICI was affected by conspecific density during conception + Dam identity
7	ICI was affected by prior density F2 during conception year + Dam identity
8	ICI was affected by prior conspecific density F2 during conception + Dam identity

Appendix C3. Density models that were used to summarize calf sex, computed using R Studio, Lapalala Wilderness, South Africa, 1982–2019.

Model no.	Model explanation
1	Sex was affected by density during conception year
2	Sex was affected by prior density during conception year
3	Sex was affected by prior density factor 2 during conception year
4	Sex was affected by conspecific density during conception year
5	Sex was affected by prior conspecific density during conception year
6	Sex was affected by prior conspecific density 2 during conception year
7	Sex was affected by the interaction between Dam origin and density during conception year
8	Sex was affected by the interaction between Dam identity and density during conception year
9	Sex was affected by the interaction between Dam identity and prior density during conception year
10	Sex was affected by the interaction between Dam identity and prior density factor 2 during conception year
11	Sex was affected by the interaction between Dam identity and conspecific density during conception year
12	Sex was affected by the interaction between Dam identity and prior conspecific density during conception year
13	Sex was affected by the interaction between Dam identity and prior conspecific density 2 during conception year

CHAPTER 4: CONCLUSION & SYNOPSIS

The main aim of my research was to investigate the effects of climatic variation on two demographic parameters, survival and reproduction, of two growing populations of black and white rhino. Population dynamics and demography are driven by both intrinsic (age and sex) and extrinsic (climate and habitat conditions) factors (Gaillard, 1998; Coulson et al., 2001) which operate on individuals directly through physiological effects and indirectly through resource availability (Mautz, 1978; Jorgenson et al., 1993; Grenfell et al., 1998; Post & Stenseth, 1999; Simard et al., 2010). For large savanna herbivores, food resources and local climate are the main factors acting on their vital rates (Gaillard et al., 2000; Owen-Smith et al., 2005; Young, 1994; Shorrocks, 2007), and this is because savanna environments are "climatically determined" meaning that the vegetation, and hence resource availability is directly correlated with the amount and seasonality of rainfall (Rutherford, 1980; Huntley, 1982; Deshmukh, 1984; Frost et al., 1986; Illius & O'Connor, 2000; Shorrocks, 2007). However, with droughts expected to be a more common occurrence in an already variable system (Vogel, 1994; Vetter, 2009; Abraham et al., 2019; Roffe et al., 2019), it is important to monitor species' responses especially in the context of conservation because the black rhino is critically endangered and the white rhino is near threatened (last assessed in 2020, (Emslie, 2020)). Using long-term monitoring data, I investigated both intrinsic and extrinsic factors that could influence the demographic rates of black and white rhinos at Lapalala Wilderness Nature Reserve. I assessed direct and delayed influences of density and proxy measures on the vital rates and population performance indicators of two rhino populations. A graphical summary (conceptual diagram) of the main findings of the study is provided in Figure 4.1.

Integration of findings and future implications

The ability to identify factors affecting population demographics, and how those factors might affect vital rates and cause fluctuations in abundance is an ideal way to infer population dynamics, especially in the context of any species' conservation strategy (Tuljapurkar & Caswell, 1997; Gaillard et al., 1998). Small populations, such as the black and white rhinos at Lapalala Wilderness Nature Reserve, are especially vulnerable to the possibility of dying out (Caughley, 1994) because effects of environmental and demographic stochasticity (Lande et al., 2003), and density-dependence are exacerbated as population size decreases (Sky et al., 2022). And so, as the populations decrease, individual variance or demographic heterogeneity can have a large influence on the population's demographics, resulting in the fluctuation of vital rates over time (Schleuning & Matthies, 2009). This was best observed with the black rhinos, which for some years had high birth peaks, including 100% birth rates, reflecting some stochastic effects characteristic of small populations. Additionally, environmental stochasticity could exacerbate the risks of extinction for small populations (Lande et al., 2003). Both rhino species at Lapalala exhibit slower life history traits and vital rates compared to other populations of similar sizes and this could be attributed to the low productivity of the region or lack of suitable habitats available for the rhinos. Both species are selective feeders and so if their preferred habitat is declining (in both quantity and quality) due to climate change and Lapalala's potentially dystrophic nature, we would expect that their survival would be shorter and reproduction would be slower (Laws et al., 1975; Chamaillé-Jammes et al., 2008). As such, the vital rates (i.e., mortality and reproduction) of Lapalala rhinos should change as a result of climate, food resources and density (Fowler, 1987; Gaillard, 1998; 2000; Eberhardt, 2002).

Despite both species having "founder" populations of similar size (i.e., the first individuals introduced in the reserve) and gestation periods similar in length, the black rhino population has failed to reach population numbers similar or close to the white rhino

population. Average annual population growth rate for the black rhinos was half that of the white rhinos despite similarities in age structure, as both populations are regarded as stable because of the higher adult to sexually immature individuals' ratio (Owen-Smith, 1988). The black rhino population at Ithala, which is similar in size to the Lapalala population also had growth rates < 5% but this was suggested to be density-dependence limiting conceptions (Greaver et al., 2014). The much larger black rhino population at Hluhluwe-iMfolozi also had low growth rates and a higher proportion (> 60%) of adult rhinos, also suggesting a stable population (Nhleko et al., 2017). By comparison, an increasing rhino population at the Great Fish River Nature Reserve comprised of 44% adults (Fike, 2011; Law et al., 2013). The lack of correlation between density and growth rates suggests that the black rhinos may be experiencing inverse density-dependence (i.e., Allee effects) (Allee, 1931; Møller & Legendre, 2001). Sexual selection has been proposed as an important force leading to Allee effects (Møller & Legendre, 2001) acting particularly through poor reproductive performance caused by the inability to find suitable mates (Møller & Legendre, 2001). For example, the unsuccessful breeding of mammals in captivity or in forced breeding programmes has been reported for giant pandas (*Ailuropoda melanoleuca*; Kleinman, 1994), tigers (*Panthera tigris*; van Bemmel, 1968) and even black (Smith & Read, 1992) and white rhinos (Lindemann, 1982). A large selection pool of suitable mates (i.e., males) and male-male competition is necessary to increase the probability of reproduction and reproductive success (Lindemann, 1982; Owen-Smith, 1988; Møller & Legendre, 2001). This leads me to suggest that the lack of suitable mates might be the cause of low population growth for the Lapalala black rhinos. For most years, the adult sex ratio remained female biased whilst the birth sex ratio was male biased (i.e., suggesting that for many years there were more sexually immature males compared to mature males), thus suitable mates might have been in shortage. Additionally, populations with adult sex ratios in favour of females, under favourable conditions, should

demonstrate high growth rates (Owen-Smith, 1988; Emslie, 1999; Okita-Ouma, 2009). However, if black rhino females cannot exert some type of selection or are isolated from suitable mates (Franklin, 1980; Lindemann, 1982; Conway & Goodman, 1989) the effective population size and reproductive rates will remain low and population growth will be minimal. I suggest that management could increase the number of adult males by increasing sub-adult males translocated into the reserve, and because it is not unusual for black rhino populations to remain somewhat isolated (Walpole et al., 2001), management could include strategies to monitor rhino distribution as poor dispersal in the reserve might result in imbalanced social structures (Adcock et al., 2001; Reid et al., 2007), which reduce the chances for any reproductive activity (Reid et al., 2007).

Another point which leads me to believe that the black rhino population has not reached density dependence, along with the white rhino population, is that there was no clear evidence of density-dependent mortalities. The influence of density on the vital rates of large herbivores follows a sequence: an increase in juvenile mortalities, followed by an increase in age at first reproduction, a decrease in female reproductive rate and lastly, an increase in adult mortalities (Eberhardt, 1977, 2002; Gaillard et al., 2000). For both species and all age groups, mortalities occurred despite increases in rhino density. The age at first reproduction was higher for the black rhino population, but again I believe that this was because of a lack of suitable mates [i.e., females and males not meeting, as female movement is restricted by water, forage and cover availability (Goddard, 1967; Berger & Cunningham, 1995)] or demographic stochasticity and not density-dependence. Additionally, there were two instances where the black rhino fertility/birth rate was 100%, and this coincided with years when the adult female to male ratio was almost equal or skewed towards males. There was also more evidence that the white rhinos' age at primiparity increased with density; however, this might just be a characteristic of Lapalala rhinos because age at primiparity differs

amongst populations (Bronson, 1989). The age at first calving was 6.5 years for a low-density black rhino population (0.1 rhinos/km^2) at Umfolozi Reserve and 12 years for a high-density population (0.7 rhinos/km^2) at the neighbouring Hluhluwe Reserve (Hitchins & Anderson, 1983); whereas age at first calving was 7.4 years for a low-density white rhino population and 10.1 years for their high-density counterparts at Matobo National Park (Rachlow & Berger, 1998). Both Lapalala black and white rhino population densities are comparable to the low-density populations however age at first calving was similar to the high-density population, and because greenness and rainfall had the largest influence on their age at primiparity and ICIs I believe that both populations are more likely to be resource limited (i.e., not density limited but rather limited by the quality of their environment). A threshold mass or optimal body condition must be attained before large herbivores attain sexual maturity and so reproduction can be suppressed as a result of resource variability caused by environmental conditions (Hall-Martin et al., 1975; Owen-Smith, 1988; Andersen et al., 2000; Gaillard et al., 2000). Lapalala might possibly be lower in productivity and nutrient status compared to other reserves, and so stochastic environmental events might further limit vegetation quantity and quality for the rhinos (McNaughton et al., 1988). Thus, Lapalala rhinos could possibly attain sexual maturity at a later stage compared to other rhinos which are not resource limited (i.e., possibly occupying better habitats).

High rates of post-release rhino deaths, and deaths in general, have been attributed to high conspecific densities in small reserves (Adcock et al, 1998; Brett, 1998; Emslie & du Toit, 2006; Linklater & Swaisgood, 2008); however, at Lapalala there were very few cases of fighting-related deaths and one case where a black rhino died from post-release stress. This again supports the idea that the rhinos are not limited by density, particularly in a socially driven manner (Law et al., 2013). Rather, the effects of density might be acting through resource limitation (Law et al., 2013), which can be seen by the high support for greenness

and rainfall models for both species. The lack of evidence for any effect of density on rhino mortalities, but support for effects of density on rhino reproduction corroborates Owen-Smith's prediction (1988) that density will affect megaherbivores primarily through fecundity and not mortality. Results from my analyses suggest that rainfall and greenness, two proxies for resource availability, influence mortality for both species, despite the black rhino's browsing diet (see Ferreira et al., 2019 for an example where no influence of rainfall on black rhino mortality was detected). Black rhinos are selective feeders (Goddard, 1968; Muya & Oguge, 2000; Ganqa et al., 2005) and seasonal variation of food (i.e., plant availability) has an important effect on their demography. If their preferred plant species are not available, as a consequence of low rainfall and indexed as low greenness values, and they cannot migrate (i.e., dispersal) and look for alternatives to evade the food shortage then they are more likely to starve (Owen-Smith, 1988). Similarly, white rhinos are selective grazers which do not compensate for seasonal changes in forage availability and quality (Bell, 1971; Shrader et al., 2006), thus without the chance to disperse and look for alternative food sources, they might succumb to starvation. Elephant populations located in reserves where they have access to water all-year round (i.e., water provision through artificial boreholes) still experienced mortalities during low rainfall years (Shrader et al., 2010; Smit et al., 2020); however, populations in unfenced reserves were better off as they could find alternative food sources by leaving (Shrader et al., 2010). Similar to my study Shrader et al. (2010) concluded that major events such as droughts were not required to impact elephant survival because minor decreases in rainfall were enough to impact food sources and consequently, population demographics.

Climatic variations, particularly during early life, commonly result in cohort effects or differences amongst individuals in vital rates such as survival and fecundity (Post et al., 1997; Lindström, 1999). My results from the survival analysis suggested that rainfall during the

first year of life was important for white rhinos but was inconclusive for the black rhinos. The black rhino sample was smaller and that might have contributed to the results; additionally, I could not model cohort survival using birth years for either species because data was insufficient (i.e., most years had less than five births). However, there were no differences in survival between individuals born during low, normal and high rainfall years because decreased rainfall and greenness affected their survival either way. In a similar manner, where environmental conditions influence maternal condition and birth sex ratios (Clutton-Brock & Iason, 1986; Post et al., 1999), there was inconclusive evidence for support of mothers having more sons during periods of favourable conditions. I could not however test for cohort effects amongst mothers or use long-term variables because most of them were translocated from differing reserves. As such, environmental stochasticity and density can result in reproductive skews (Sky et al., 2022) for both female and male rhinos, and increase demographic heterogeneity (i.e., individual variation) which will consequently destabilize population dynamics (Lindström & Kokko, 2002). Thus, the long-term monitoring of rhinos from birth might be the key to mitigating low population performance, especially for the black rhinos, whose demographics also seem to be influenced by environmental conditions.

Future recommendations and conclusions

Lapalala Wilderness is situated in the Waterberg region and the reserve's location relative to other reserves in the area (for example Marakele National Park and The Waterberg Biosphere Reserve) make it a suitable candidate for collaboration. This study was focused on one white and black rhino population; however, future studies could compare between populations that are exposed to similar situations (i.e., rhino populations that are similar in size, in similar sized reserves and experience similar climatic conditions) so that conclusions could be applied to black and white rhinos in general, and even other megaherbivores. Seasonality is a

characteristic of the Waterberg region so rainfall is a limiting factor for most of the year, and drought periods are likely to be a commonality (Ziervogel, 2014); however, because droughts are usually not spatially homogenous, neighbouring reserves could act as "refugia" (Smit et al., 2020). And so rhinos could mitigate resource limitation by migrating to areas where they are more likely to survive than remain in the reserve as resource pools are drained.

I believe that the addition of field work or measurements would greatly improve associations between the two proxies (i.e., rainfall and greenness) and vital rates of the rhinos, especially because my study does suggest that the rhinos are resource limited. The reserve has eight land type communities which have been identified according to the most dominant plant species found there and so there is some heterogeneity, which is important considering that both species are selective feeders. A behavioural study would be beneficial in determining habitat use and diet selection, which are also affected by accessibility of an area (Ganqa et al., 2005) and will assist management in determining which parts of the reserve are used by the rhinos and to what degree (Kotze & Zacharias, 1993). Another behavioural aspect that could be investigated, particularly for the black rhinos, is their social behaviour. As I mentioned previously, the low population growth rates might be the result of unsuitable mates or imbalanced social structures in some parts of the park (i.e., rhinos not meeting or not enough males). Additionally, because puberty in males usually occurs a few years after it does in females (Owen-Smith, 1988), males might be driving the reproductive rates (i.e., high age at primiparity) and population growth; and so tracking male reproduction might be a feature of interest in rhino demography.

My study failed to find conclusive evidence on the association between maternal condition and investment on birth sex ratios; however, behavioural studies on maternal investment might better support the relevance of the Trivers-Willard (TWH), local resource competition (LRC) and extrinsic modification (EMH) hypotheses to Lapalala rhinos. Thus, if

studies could compare the reproductive success of female versus male rhinos and associations between maternal condition, there would be more support for sex allocation theory. However, successful female and male rhinos might not exhibit differences in lifetime fitness (Owen-Smith, 1988) and so facultative sex allocation might not be relevant for rhino demography. Future work could use a better index for maternal body condition (i.e., better than rainfall and greenness), although the only model that had merit was a greenness model. It would be difficult to get mass measurements and so "non-invasive" methods such as assessing body fat and muscle mass gains of pregnant females, and comparing differences between lactating and non-lactating females would give better results (Rachlow & Berger, 1998).

Similarly, future studies could assess the effects of resource variability on vital rates by using direct measures of body condition. For example, using carcass mass (long-term index) to investigate seasonal variation of body condition and resources across years, sex and age groups (Marshal et al., 2012). Lastly, future studies could incorporate interspecific interactions seeing as the reserve supports a large number of herbivores, and species interactions, water, food availability and species density influence how rhinos use their space. For example, elephants tend to exclusively feed on browse during periods of low rainfall and resource availability (Abraham et al., 2019; Smit et al., 2020) and could possibly directly compete with black rhinos and other browsers, effectively reducing the resources available to strictly browsing populations.

Findings from my study provide a starting point for models of population dynamics of rhinos at Lapalala Wilderness. Models provided evidence that survival is stage specific, regardless of species or dietary differences, and that prior and current density had little influence on rhino survival. There was little support for cohort effects for both species, or mortalities brought on by ENSO periods or drought years, rather mortalities were associated with low amounts of rainfall (i.e., as opposed to large scale events). Conception peaks for

both species correlated with periods of high forage availability and quality, and age at primiparity was positively influenced by increased rainfall and greenness. However, density effects on primiparity were not trivial as age at first calving increased with density. Birth sex ratios for both species favoured males by the end of the study; however, there was little support for sex allocation hypotheses and maternal condition. In conclusion, the population dynamics of both black and white rhinos are governed by fluctuating resources as indexed by rainfall, vegetation greenness and to some degree, density. Thus, the ability to identify fluctuating population dynamics of these two rhino species, that are important for South Africa's economy, ecosystems and whose numbers are declining in the face of climate change is especially important for populations who are not challenged with poaching but rather whose demographics are influenced by environmental conditions, intrinsic factors and the interaction between both.

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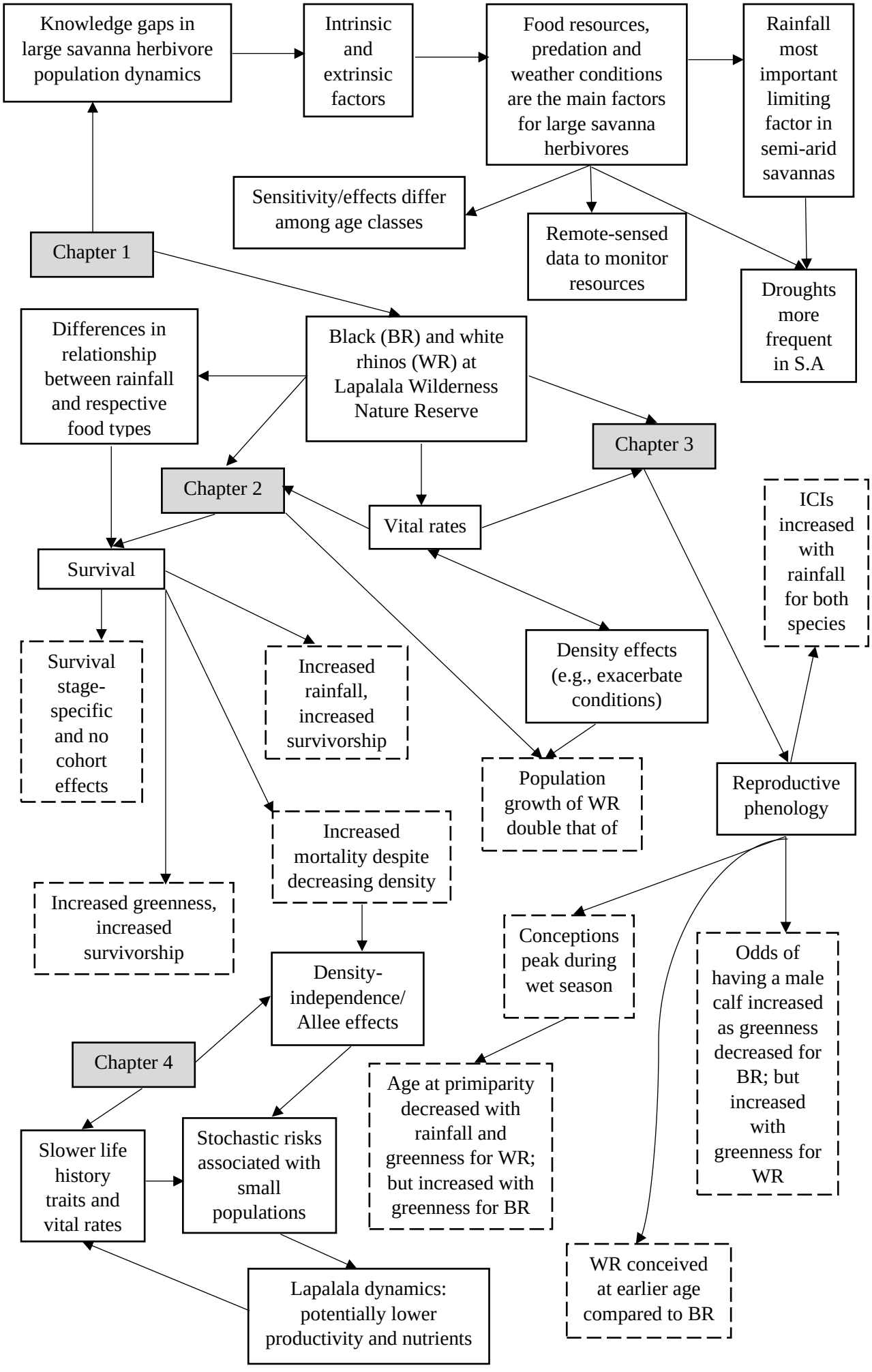

Knowledge gaps in large savanna herbivore population dynamics
Intrinsic and extrinsic factors
Food resources, predation and weather conditions are the main factors for large savanna herbivores
Rainfall most important limiting factor in semi-arid savannas
Sensitivity/effects differ among age classes
Remote-sensed data to monitor resources
Droughts more frequent in S.A
Chapter 1
Differences in relationship between rainfall and respective food types
Black (BR) and white rhinos (WR) at Lapalala Wilderness Nature Reserve
Chapter 3
Chapter 2
Vital rates
ICIs increased with rainfall for both species
Survival
Survival stage-specific and no cohort effects
Increased rainfall, increased survivorship
Density effects (e.g., exacerbate conditions)
Population growth of WR double that of
Reproductive phenology
Increased mortality despite decreasing density
Increased greenness, increased survivorship
Conceptions peak during wet season
Odds of having a male calf increased as greenness decreased for BR; but increased with greenness for WR
Density-independence/ Allee effects
Chapter 4
Age at primiparity decreased with rainfall and greenness for WR; but increased with greenness for BR
Slower life history traits and vital rates
Stochastic risks associated with small populations
WR conceived at earlier age compared to BR
Lapalala dynamics: potentially lower productivity and nutrients

Figure 4.1. Conceptual diagram with the main concepts and findings from the study. The concepts and focus topics of the study are represented by the full boxes and the main findings are represented by dashed boxes.