

Survival of young black and white rhinoceroses in relation to rainfall

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Received 4 August 2023. To authors for revision 2 October 2023. Accepted 8 November 2023

Droughts have become more prevalent in recent years, causing problems for large herbivores such as the black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros, whose populations are influenced by variation in climatic conditions. This variation acts primarily through the effects of rainfall on forage availability but acts differently on browse or grass. Consequently, browsing black rhinos and grazing white rhinos might show differing responses to changes in rainfall. Moreover, young large herbivores have a more limited capacity to survive environmental stressors than do adult animals that are more resilient to environmental variation. Thus, our aim was to investigate the relationship between rainfall and the survival of young (<3 years old) black and white rhinos at Lapalala Wilderness Nature Reserve, South Africa. Using stratified Cox models, we found that both species had higher survival with more rain, but the effect was more similar than expected given the differences in diets. Moreover, there was evidence of an effect of age class for white rhinos but not for black rhinos. Additionally, most rhinos that died did so during the dry season when scarce forage and limited fat reserves likely constrained their ability to tolerate periodically low-quality diets. Despite the effect of rainfall operating through substantially different plant growth forms, young animals of both rhino species showed sensitivity to variation in rainfall that could ultimately affect population abundance and conservation status.

Keywords: *Ceratotherium simum*, climatic variation, *Diceros bicornis*, drought, Lapalala Wilderness Nature Reserve, resource variability.

INTRODUCTION

Recent changes in global weather patterns, particularly rainfall, are implicated in decreasing population abundance of wild herbivores such as the white (*Ceratotherium simum*) and black (*Diceros bicornis*) rhinoceros (Young, 1994; Ripple *et al.*, 2015; Abraham, Hempson & Staver, 2019) whose dynamics are a function of mortality and survival rates, fecundity and migration (Owen-Smith, Mason & Ogutu, 2005). These vital rates and their effects on abundance are driven primarily by food resources, which in turn, is the outcome of weather conditions, particularly precipitation (Caughley & Krebs, 1983; Andrewartha & Birch, 1984; Coulson, Milner-Gulland & Clutton-Brocks, 2000). Rain plays a central role in determining herbivore demographic rates and abundance through its effects on forage availability (Owen-Smith & Mason, 2005; Owen-Smith *et al.*, 2005). Those

effects depend on the species of herbivore and their diet and nutritional requirements, and on differential effects of rainfall on woody *versus* herbaceous forage plants (Coe, Cumming & Phillipson, 1976; Rutherford, 1980; Owen-Smith, 1990). Moreover, because young herbivores are more sensitive than adults to environmental stochasticity, survival of young herbivores could be a mechanism through which variation in rainfall and forage affect fluctuations in abundance (Gaillard, Festa-Bianchet & Yoccoz, 1998; Gaillard, Festa-Bianchet, Yoccoz, Loison, & Toigo, 2000).

Because white and black rhinos specialize on grass- and woody-dominated diets, respectively, each species' survival relationship with rainfall differs according to the dynamics and phenology of its preferred food type. Rain is a limiting factor for at least part of the year which affects the composition of both herbaceous and woody plants (Scholes & Archer, 1997; Sankaran *et al.*, 2005); however, reduced rainfall tends to affect herbaceous plants more immediately and severely

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(Vetter, 2009; Sankaran, Ratnam & Hanan, 2004). This difference is because trees can store nutrients and water, allowing for an earlier greening at the start of the wet season and longer retention of foliage at the end of the wet season. In contrast, grasses only become green a few days after the first rains of the wet season (Scholes & Archer, 1997; Do *et al.*, 2004; Shorrocks, 2007). As such, one would expect grazers feeding on herbaceous vegetation to be affected more during periods of low rainfall than browsers that feed on woody vegetation (Ferreira, le Roex & Greaver, 2019). Savannas are prone to highly variable precipitation, and because the phenology of semi-arid savannas is closely associated with the amount of annual rainfall, weather conditions should be the main factor acting on population dynamics of savanna herbivore populations (Smuts, 1978; Owen-Smith *et al.*, 2005; Shorrocks, 2007; Abraham *et al.*, 2019).

The effect of resource variability on herbivore survival depends on an individual's life stage (Owen-Smith & Mason, 2005). Survival of young animals is more sensitive to environmental conditions and population density, whilst adult survival is more resistant (Gaillard *et al.*, 1998, 2000). Density-dependent effects manifest first in juvenile survival, then age at first reproduction, adult fertility, and finally adult survival (Eberhardt, 1977, 2002). Variable survival in young animals is a consequence of resource allocation toward growth rather than storage; thus, they have smaller fat reserves, leaving them more susceptible to food shortages (Ballard & Whitman, 1987; Adams, 2003; Parker, 2003). Moreover, because young herbivores are more sensitive than adults to environmental stochasticity, in part because this is a period of initial independence from their mothers (Shrader & Owen-Smith, 2002), survival of young herbivores could be a mechanism through which variation in rainfall and forage affect fluctuations in abundance. Hence, population growth is dependent primarily on adult survival and fecundity, whereas changes in juvenile recruitment are more likely to cause year-to-year variation in population growth rates (Gaillard *et al.*, 2000; Wittemyer, Barner-Rasmussen & Douglas-Hamilton, 2007).

An increase in mortality of young rhinos over the last three decades has coincided with ongoing low-rainfall periods in South Africa (Ferreira *et al.*, 2019). Given the importance of rhino survival to population persistence, our objective was to investigate the relationships between rainfall and

survival of young (<3 years old) black and white rhinoceroses. We used historical rhino-monitoring and weather data from Lapalala Wilderness Nature Reserve (LWNR), South Africa, to investigate relationships between rainfall and survival. We tested the hypothesis that for white rhinos, whose forage is mainly rainfall-sensitive herbaceous plants, survival of young animals would show stronger relationships to rainfall than for black rhinos that depend on more rainfall-resistant woody browse. We demonstrate that, although forage types differ between species, survival for both is affected by rainfall, which in turn, could affect abundance and conservation efforts aimed at habitat or forage management.

METHODS

Study area

The reserve is a 48 000-ha private game reserve located in the Waterberg region, Limpopo Province, South Africa (23°44'–23°57'S, 28°09'–28°25'E; Fig. 1). It falls within the Central Bushveld Bioregion (Rutherford, Mucina & Powrie, 2006) and the common woody plants include *Combretum* spp., silver terminalia (*Terminalia sericea*), and Rhodesian rubber tree (*Diplorhynchus condylocarpon*). Common herbaceous plants include gum grass (*Eragrostis gummiflua*), threeawns (*Aristida* spp.), and common reed (*Phragmites* spp.) (<https://lapalala.com/wildlife/> accessed 1 August 2023). Soil quality varies spatially depending on whether the soil is derived from sandstone or basic norite intrusions. 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 precipitation. The range in annual rainfall is 400–600 mm (<https://www.lapalala.com/fast-facts/> accessed 1 August 2023) with most of that falling during the wet season (November – April). Mean monthly temperatures range from 30°C in the summer to 20°C in winter. Besides rhinos, other large herbivores include impalas (*Aepyceros melampus*), plains zebras (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), African elephants (*Loxodonta africana*), common eland (*Tragelaphus oryx*), giraffe (*Giraffa camelopardalis*) and roan antelope (*Hippotragus equinus*). Large carnivores include leopards (*Panthera pardus*), brown hyaenas (*Parahyaena brunnea*), and cheetahs (*Acinonyx jubatus*) (<https://lapalala.com/wildlife/> accessed 1 August 2023).

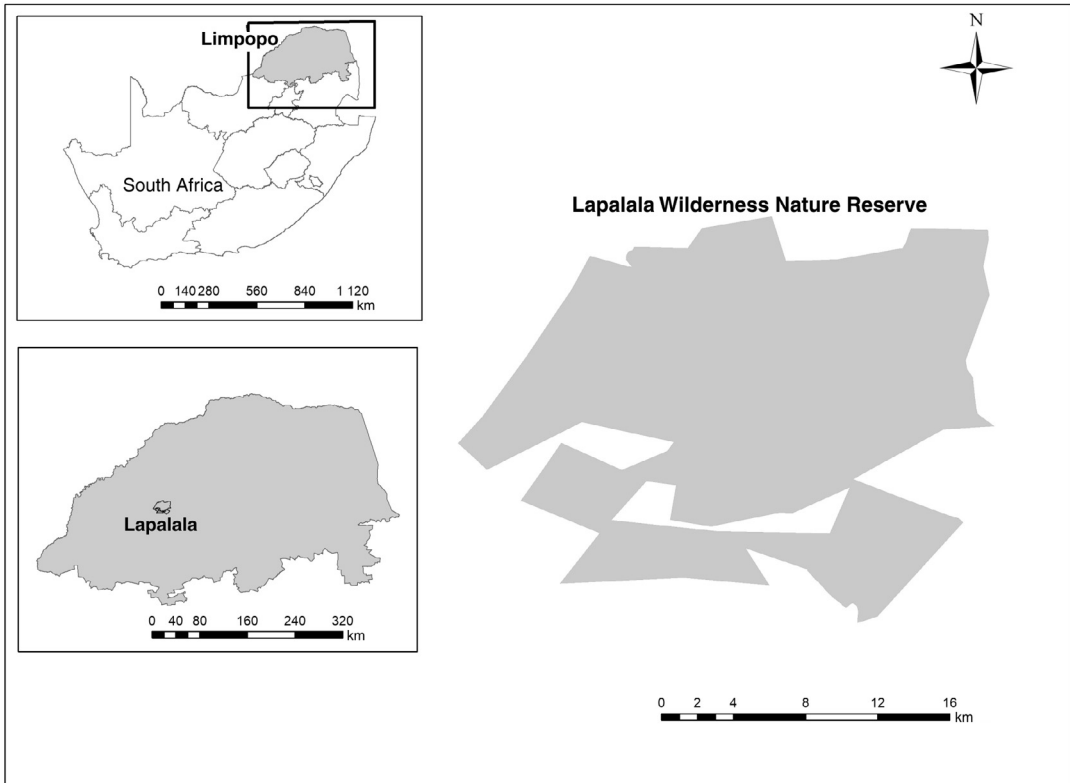


Fig. 1. Lapalala Wilderness Nature Reserve, Limpopo Province, South Africa.

Data collection

We used historical black and white rhino monitoring data, covering years 1994–2019 and focusing on animals up to the age of three years that were born at LWNR. A team of experienced rhino monitors tracked rhinos daily by following an individual's tracks on foot and by vehicle until the monitors could see the rhino. Mortalities were established with the discovery of a carcass, particularly for 2–3-year-old rhinos that were no longer associated with their mother; however, for younger calves dependent on their mothers, mortality was assumed when the calf was no longer seen with its mother. Because we focussed on survival responses to rainfall, we excluded records with causes of death that appeared independent of rainfall (e.g. fighting, accidental death, poaching).

We obtained historical rainfall data from the South African Weather Service for Mahwelereng, Ellisras-Pol and Marken weather stations (all <3 km from LWNR). To accommodate gaps in the rainfall records, we calculated monthly totals for each station, then we divided each monthly total by the station's monthly standard deviation. Finally, we

calculated monthly averages across stations, such that ≥ 1 station contributed to any monthly rainfall measurement. This approach produced a single continuous time series of standardized monthly rainfall measurements that correlated with rainfall in the reserve and that coincided with the period covered by the rhino monitoring data.

Data analyses

We analysed stage-specific survival with the Kaplan-Meier estimator (Pollock, Winterstein, Bunck & Curtis, 1989; Williams, Nichols & Conroy, 2002) and stratified Cox proportional hazard models (Therneau & Grambsch, 2000; Therneau, 2021), separately for black and white rhinos. The Kaplan-Meier procedure estimated temporal patterns of rhino survival in relation to their age. The proportional hazard model related time-to-mortality to time-dependent covariates (Conroy & Carroll, 2009; Weathers & Cutler, 2017), and we stratified by age category (calf: 0–1 year; juvenile: 1–3 years). The strata separated animals in the analysis according to whether they died as calves or juveniles, to compare relationships

between age classes. This separation recognizes the differences in life stage according to how dependent the rhino calves are on their mother and how rainfall conditions would affect them. In other words, calves which are mostly or entirely dependent on suckling would not experience resource limitations directly, whereas juveniles which have discontinued suckling would. We analysed a sample of 33 young black rhinos ($n=7$ calves; $n=26$ juveniles) spanning the period 1994–2019, of which 6 died by 1 year of age, 4 died between 1 and 3 years, and the remainder lived past 3 years or were alive at the end of the study period in 2019. By comparison, the sample of white rhinos over the same period analysed consisted of 73 animals ($n=22$ calves; $n=51$ juveniles), where 12 died by 1 year, 9 died between 1 and 3 years, and the remainder lived past 3 years or were alive at the end of the study.

For the Cox models, the response variable was time until a mortality occurred, and we defined several explanatory variables. Whether an animal was born in a drought year (binary) or died in a drought year (binary) were defined with the rainfall anomaly index (RAI; van Rooy, 1965; Keyantash & Dracup, 2002), which identifies drought periods by defining a threshold calculated from the 10 lowest values in a ranked rainfall dataset; negative values indicate drought conditions (Eshetu, Johansson & Garedew, 2016). Whether an animal died in an El Niño Southern Oscillation (ENSO) year (binary) was indexed with the Oceanic Niño Index (ONI; <https://ggweather.com/enso/oni.htm> accessed 1 August 2023), to test the effect of ENSO phase and associated drought on survival (Kruger, 1999; Ogutu & Owen-Smith, 2003). Nine derived rainfall variables were based on timing and totals across different time periods with respect to important phases in young rhino biology, to determine whether effects on survival were immediate or lagged (Erb, Boyce & Stenseth, 2001; Owen-Smith & Mills, 2006). The variables were lifetime both-season rainfall (total from birth to death or third birthday), lifetime wet-season rainfall (total from birth to death or third birthday), lifetime dry-season rainfall (total from birth to death or third birthday), total rainfall six months prior to rhino's birth, total rainfall one and two years prior to rhino's birth, total rainfall during the rhino's first year, total rainfall one month before rhino's birth, and rainfall the month after birth. In deriving these rainfall variables, we aimed to capture conditions directly before and after birth or death as well as conditions

the mother experienced while carrying a calf and nursing. Sex of first-year animals was difficult to establish and thus sex of animal was left out of the analysis.

We compared 22 models (Table S1) with Akaike's Information Criterion, adjusted for small sample size (AICc), and associated statistics. The model we used for inference was that with the highest AICc weight (w_i), differing by at least two AICc units from the other competing models having the fewest parameters (Burnham & Anderson, 2002). We used concordance to assess model goodness-of-fit, where values >0.55 suggest adequate fit between model and data and a better-than-chance ability to predict time to mortality (Therneau & Watson, 2015). All analyses were conducted in R with library 'survival' (R Core Team, 2021). Effects of variables were interpreted with hazard ratios (*i.e.* multiplicative change in odds of mortality with a change in the explanatory variable). Unless otherwise specified, we report 95% confidence intervals with all estimates.

RESULTS

For young rhinos before the first birthday, black rhinos showed noticeable drops in survival, particularly around their first and seventh months (Fig. 2), whereas white rhinos demonstrated more gradual decrease in survival to *c.* 8 months, when there was a noticeable drop (Fig. 2). By the first birthday, survival of both species became relatively constant. Black rhino survival remained so until just before the third birthday when there was another drop in survival. White rhinos, in contrast, showed a return to gradual decline from *c.* 19 months of age until the third birthday (Fig. 2). Survivorship estimates for black rhinos were 0.82 (0.70, 0.96) by age 1 year and 0.68 (0.53, 0.87) by age 3; for white rhinos estimates were 0.83 (0.74, 0.92) and 0.67 (0.56, 0.80).

For both species, top-ranking models included both-season and wet-season rainfall as explanatory variables (Table 1), which might be expected if most both-season rain falls during the wet season. Models that stratified by age had greater explanatory power for white than for black rhinos (Table 1). There was little evidence of an effect of variables based on ENSO or drought years on survival for either species (Table S1). There was also little evidence of an effect of rainfall during the prenatal period (Table S1) or dry-season rainfall, despite more than half the deaths occurring during the dry season (6 out of the 10 deaths for black rhinos and

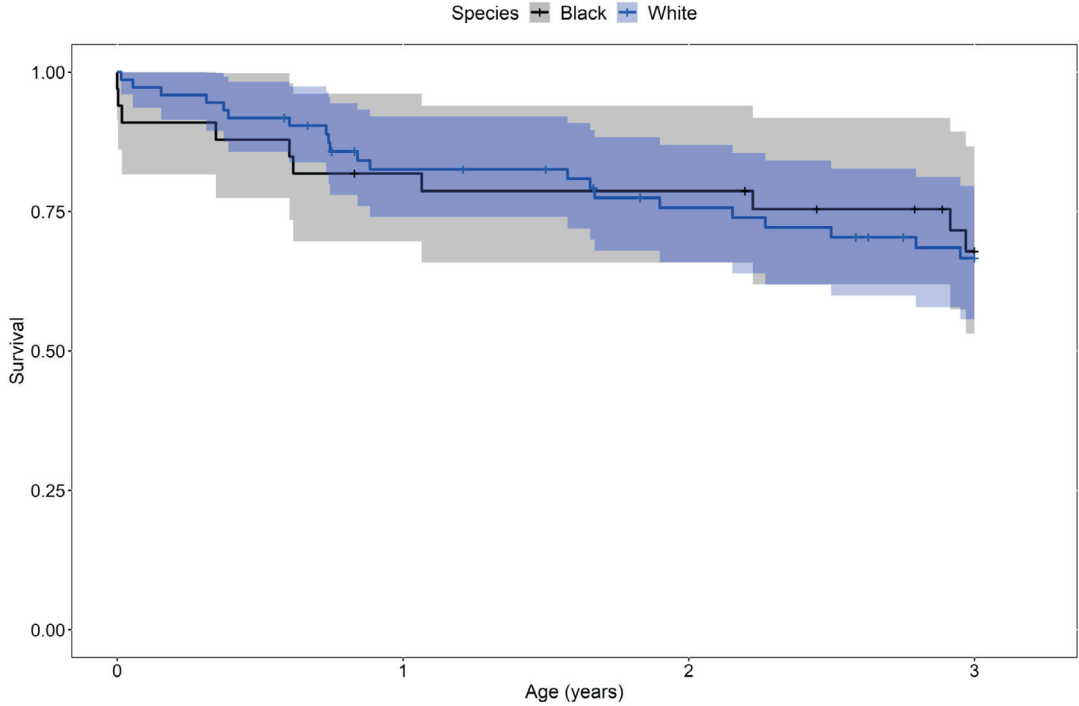


Fig. 2. Survival probability estimated for black and white rhinoceros, Lapalala Wilderness Nature Reserve, Limpopo Province, South Africa, 1994–2019. Presented are Kaplan-Meier survival estimates and 95% confidence intervals.

Table 1. Model selection: Cox proportional hazard models to analyse survival of young (0–3 years) black and white rhinoceroses, Lapalala Wilderness Nature Reserve, South Africa, 1994–2019. Presented are models for which $w_i \geq 0.001$. Models with interacting variables also contain the individual additive variables.

Model	AICc ^a	Δ AICc ^b	w_i^c	K^d	Concordance ^e
Black rhinos					
Wet-season rainfall	35.078	0.000	0.686	1	0.939 (0.026)
Both-season rainfall	36.650	1.572	0.142	1	0.914 (0.046)
Dry-season + wet-season rainfall	37.532	2.454	0.059	2	0.948 (0.020)
Age + wet-season rainfall	37.746	2.668	0.048	2	0.849 (0.062)
Age * wet-season rainfall	37.843	2.765	0.043	2	0.939 (0.026)
Age + both-season rainfall	39.374	4.296	0.009	2	0.788 (0.104)
Age * both-season rainfall	39.796	4.718	0.006	2	0.914 (0.046)
Age + dry-season rainfall	41.778	6.699	0.001	2	0.608 (0.128)
White rhinos					
Age + both-season rainfall	84.484	0.000	0.841	2	0.916 (0.030)
Age + wet-season rainfall	86.172	1.687	0.156	2	0.910 (0.031)
Wet-season rainfall	90.586	6.101	0.002	1	0.954 (0.015)

^aAICc = Akaike's Information Criterion, corrected for small sample size.

^b Δ AICc = AICc – min(AICc).

^c w_i = model probability.

^d K = no. of parameters.

^eStandard error in brackets.

Table 2. Model coefficients: Cox proportional hazard models to analyse survival of young (0–3 years) black and white rhinoceroses, Lapalala Wilderness Nature Reserve, South Africa, 1994–2019. Presented are models used for interpretation.

Model	Age	Estimate	S.E.	Hazard ratio	95% confidence intervals	
					Lower	Upper
Black rhinos						
Wet-season rainfall	Calf and juvenile	−0.403	0.129	0.669	0.518	0.862
Both-season rainfall	Calf and juvenile	−0.323	0.101	0.724	0.593	0.883
White rhinos						
Age + both-season rainfall	Calf	−0.941	0.298	0.390	0.218	0.700
	Juvenile	−0.377	0.101	0.686	0.563	0.837
Age + wet-season rainfall	Calf	−0.867	0.289	0.420	0.239	0.740
	Juvenile	−0.445	0.118	0.641	0.508	0.808

12 out of the 21 deaths for white rhinos) or before the first wet-season rains. The models we used for inference were wet-season rainfall ($w_i = 0.686$, concordance = 0.939) for black rhinos, and both-season rainfall stratified by age ($w_i = 0.841$, concordance = 0.916) for white rhinos (Table 1).

For both species and age groups the odds of mortality decreased with an increase in the rainfall explanatory variable (Table 2). For black rhinos, in which age groups were combined, odds of mortality decreased by a factor of 0.67 (0.52, 0.86) with each 1 S.D. increase in wet-season rainfall. By comparison, separate strata for white rhinos produced estimates where the odds of mortality differed substantially between calf and juvenile groups in relation to both-season rainfall (calf: 0.390 [0.218, 0.700]; juvenile: 0.686 [0.563, 0.837]). So as rainfall decreased, juvenile mortality increased at a rate approximately double that of calf mortality.

DISCUSSION

For both species, rainfall over an individual's life best explained survival of young rhinoceroses at LWNR. This effect was in the form of total wet-season or both-season rainfall experienced by an animal through its life. Models with both-season-based rainfall variables were better supported by the data than those with drought years based on RAI or ONI, or those with pre-natal rainfall. Moreover, there was evidence of a difference in survival between age classes for white rhinos but not for black rhinos.

Our findings emphasize how survival for young rhinos, like survival for other large herbivores, is affected by variation in precipitation and food (*e.g.* Owen-Smith, 1990; reviewed in Gaillard *et al.*,

1998; Coulson *et al.*, 2000; Shrader, Pimm & van Aarde, 2010). Both rhino species were exposed to variable rainfall and presumably forage conditions. The effect of rainfall for the combined age class in black rhinos was similar to that for juvenile white rhinos, suggesting a broadly similar effect of rainfall on both species. Thus, our hypothesis, that survival of white rhinos would show stronger relationships to rainfall because of their reliance on herbaceous forage, was not supported by our analysis.

Our finding of an age effect for white rhinos only was unexpected. This effect indicated a stronger relationship between rainfall and survival for calves than for juveniles, which would be expected if the maternal body resources and milk supply were buffering the effects of rainfall variation and fluctuating forage availability (Oftedal, 2000; Pettoelli *et al.*, 2007; Young & van Aarde, 2010; Ferreira, Greaver & Knight, 2011). As such, an age effect should have been evident for both species, or possibly more likely for black rhinos given the resilience of woody vegetation to variable rainfall making it easier for black rhino mothers to buffer variation in woody forage. With a larger sample of black rhinos in our analysis, however, an age effect might have been evident for that species as well.

Forage responses to rainfall

Although the role of rainfall on plant biomass is well established (Scholes & Walker, 1993; Scholes & Archer, 1997; February, Higgins, Bond, & Swemmer, 2013), the influence of rainfall on woody plants as a source of forage for browsing large herbivores remains a matter of debate (*e.g.* Shorrocks, 2007; Sankaran, Ratnam & Hanan, 2008; Augustine, 2010). Whereas woody plant

growth might be more resilient than herbaceous cover to the effect of rainfall variability, in semi-arid savannas leaf production and tree cover are still limited by mean annual precipitation (Birkett & Stevens-Woods, 2005; Sankaran *et al.*, 2005; Shorrocks, 2007). Woody plant growth is primarily determined by the previous season's rain as new shoots appear before the wet season (Rutherford, 1980). Even so, adequate rainfall is required to ensure that leafing events continue throughout the wet season and that shoots reach their full potential (Hughes, 2000; Barrett & Brown, 2021). Moreover, the period over which deciduous trees and shrubs retain leaves going into the dry season is also determined by the previous wet season (Owen-Smith, 1990). Thus, timing and amount of rainfall could affect short-term and long-term food supply for browsers, by decreasing both browse growth during the growing season and forage retention during the dormant season, particularly during the period when preferred plants are available (Mduma, Sinclair & Hilborn, 1999; Illius & O'Conner, 2000; Pettorelli, Pelletier, von Hardenberg, Festa-Bianchet & Côté, 2007; Thomson, 2009).

While many factors influence grass production, rainfall is a major determinant (Deshmukh, 1984). Drought periods decrease the production of herbaceous biomass available for the grazing as well as the time it will be available after the end of the wet season (Coe *et al.*, 1976; Mduma *et al.*, 1999). Unlike woody vegetation which can produce leaves some weeks before the start of the rainy season in response to photoperiod (Archibald & Scholes, 2007), grasses can take up to 10 days to start greening following the start of rains (Whitecross, Witkowski & Archibald, 2017). Despite the differences in responses to rainfall between these two plant growth forms, the effect of rainfall *via* plant growth might depend on longer-term cumulative acquisition of resources by young animals that might outweigh shorter-term differential responses of woody and herbaceous responses to rainfall.

Rhinoceros survival

In the present study, more than half of the young rhino deaths occurred during the dry season, coinciding with a time when available forage could have been low or depleted (Young, 1994). We hypothesize that although the difficult conditions of a dry season might have been the proximate cause of death, a lifetime of low rainfall and

resultant poor forage conditions could predispose young animals to higher mortality, perhaps operating through a reduction in the mother's body condition (*i.e.* as a result of reduced forage availability), influencing milk availability and quality (Lee & Moss, 1986) for suckling rhinos who are more dependent on mother for survival compared to juveniles. Young animals in general are more likely to be affected by food shortages than are adults because of the lower body reserves required to survive during harsh conditions (Ballard & Whitman, 1987; Adams, 2003; Parker, 2003). Their survival essentially depends on their mother's body condition, as access to enough forage benefits the calves by way of good or high-quality milk, and lesser forage 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). Moreover, selective foragers like rhinos have a limited capacity to adapt to forage scarcity, and they are less able to compensate for fluctuations in food quantity or quality as a strategy to limit decreases in body condition than are bulk grazers like zebras (Bell, 1971; Shrader, Owen-Smith & Ogutu, 2006). Whereas older rhinos might be able to compensate for lower dietary quality and seasonal fluctuations in food availability by eating more, building fat reserves (Owen-Smith, 1988; Landman, Schoeman & Kerley, 2013) and mobilizing those fat reserves, young rhinos do not have that luxury, and are thus more likely to require high-quality forage despite the season (*i.e.* during both wet and dry seasons) as they allocate resources to growth. Additionally, the most common grass species found within the study area have low nutritive values (Mokgakane, Mlambo, Ravuhali & Magoro, 2021) or tend to be avoided by white rhinos (Owen-Smith, 1988) again suggesting that young rhinos might not have been able to build adequate body reserves as a result of low-quality resources.

In addition to an effect of dry-season forage scarcity on small-bodied young rhinos, stress or adversity caused by separation between mother and calf could possibly contribute to young rhino mortality (Law *et al.*, 2013). Most of the juvenile deaths in our study occurred within the 2–3 years age group for both black and white rhinos. Young rhinos that leave their natal areas must establish their own home ranges and are faced with poor knowledge of a new environment, competitors for the same habitat and resources, and additional energetic expenditure as they search for food

sources in an unfamiliar landscape and adjust to a new social environment (Owen-Smith, 1988; Adcock, Hansen & Lindemann, 1998; Young & van Aarde, 2010). This situation is more likely to occur with the black rhinos because of their asocial nature (Owen-Smith, 1988; Law *et al.*, 2013; Pfannerstill *et al.*, 2022); whereas white rhinos tend to form relationships with conspecifics which aid in their dispersal (Shrader & Owen-Smith, 2002).

Interactions, either within or between species, over resources such as water, forage or habitat could influence how rhinos use space and thus what risks affect survival of young rhinos. For megaherbivores, density feedbacks *via* intra-specific competition typically affect individual growth and survival rates of the youngest age classes first (Eberhardt, 1977, 2002) and so effects of resource limitation might be intensified in fenced reserves with high herbivore densities. Both rhino species are selective feeders (Bell, 1971; Oloo, Brett & Young, 1994; Ganqa, Scogings & Raats, 2005; Shrader, Owen-Smith & Ogotu, 2006) that are subject to competition because of the patchy distribution of savanna resources (Young & van Aarde, 2010). These resource-related effects might increase because of competition, for example, between black rhinos and elephants, which switch to browsing during drought periods (Abraham *et al.*, 2019) and in doing so increase damage to woody vegetation (Codron *et al.*, 2007; Shrader *et al.*, 2010; Abraham *et al.*, 2019). Or similarly with white rhinos and other species such as buffalo (*Syncerus caffer*), wildebeest and impala, who switch to grazing on short grasses or the same species of grass during periods of food shortages or in areas of low food availability (Owen-Smith, 1988; Perrin & Brereton-Stiles, 1999)




Our findings suggest the importance of resource limitation, operating through rainfall variation, on the mortality of young black and white rhinos at LWNR. Although we did not detect a difference between species as we had predicted, it was clear for both species that rainfall experienced through life showed the strongest relationships with mortality. Changing climate is expected to increase rainfall variability (Pendergrass, Knutti, Lehner, Deser & Sanderson, 2017), leading to extreme events (Martinez-Villalobos & Neelin, 2023), and evapotranspiration caused by increasing temperature (Engelbrecht *et al.*, 2015). These changes will also affect plant productivity as a source of forage for large herbivores. Given the importance of these

changes for the survival of young rhinos and their subsequent effects on population abundance, management of nature reserves will need to accommodate increasing variability to maintain rhinoceros populations.

ACKNOWLEDGEMENTS

We thank field monitors at Lapalala Wilderness Nature Reserve for their contribution to this study, and the South African Weather Service for providing the rainfall data used in the study. Jacob Majakwara assisted with statistical analysis, and Francesca Parrini provided helpful comments on previous drafts. L.N. was supported by the University of the Witwatersrand Postgraduate Merit Award and the National Research Foundation (grant: 131288) during preparation of the manuscript.

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Supplementary material to:

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Survival of young black and white rhinoceroses in relation to rainfall
African Journal of Wildlife Research **53**: 196–205 (2023)

Table S1

Table S1. Model descriptions: Cox proportional hazard models to analyse survival of young (0–3 years) black and white rhinoceroses, Lapalala Wilderness Nature Reserve, South Africa, 1994–2019.

Model	Survival was affected by...
Age	or stratified by age (juvenile, subadult)
Lifetime rainfall	rainfall experienced through lifetime
Dry-season rainfall	dry-season rainfall experienced through lifetime
Wet-season rainfall	wet-season rainfall experienced through lifetime
Rainfall 6 months before birth	total rainfall the 6 months up to birth date
Rainfall 1 year before birth	total rainfall the 1 year up to birth date
Rainfall 2 years before birth	total rainfall the 2 years up to birth date
Annual rain during birth year	total rainfall in the birth year
Birth in drought year	being born in a drought year
Death in drought year	drought in year of death
ENSO year	El Niño-Southern Oscillation (ENSO) in year of death
Rainfall month before birth	total rainfall the months up to birth date
Rainfall month before death	total rainfall the month up to death date
Age * Lifetime rainfall	age and total rainfall experienced through lifetime
Age * dry-season rainfall	age and dry-season rainfall experienced through lifetime
Age * wet season rainfall	age and wet-season rainfall experienced through lifetime
Age + rainfall 1 year before birth	age and rainfall one year before birth
Annual rain + rain 1 year before birth + rain 2 years before birth	annual rain during birth year, rain one year before birth and rain two years before birth
Dry-season rainfall + wet-season rainfall	dry-season and wet-season rainfall experienced through lifetime (separate variables)
Age + lifetime rainfall	interaction between age and lifetime rainfall
Age + dry-season rainfall	interaction between age and lifetime dry-season rainfall
Age + wet-season rainfall	interaction between age and lifetime wet-season rainfall