RESEARCH ARTICLE

Resource variability and survival of black and white rhinoceroses at Lapalala Wilderness Nature Reserve

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Population dynamics and vital rates of savanna large herbivores, such as the black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*), are influenced by intrinsic and extrinsic factors, among which environmental fluctuations play an important role as they affect food resources. Given the differences in diets between the two rhino species and the differences in relationships between rainfall and woody *versus* herbaceous plants, there should also be differences in their survival and other vital rates in response to environmental stochasticity. We 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. Mean population growth rates during the study were 4.8% for black rhinos and 8.9% for white rhinos, and both populations illustrated no evidence of density-dependence. Cox proportional hazard models showed that survival of both species was stage-specific and increased with rainfall. Vegetation greenness models similarly showed that survival increased with integrated annual greenness for all stages and proved to be the better proxy for white rhino survival. Additionally, density effects were somewhat trivial for both black and white rhinos as the populations seem to be rather resource limited. With droughts expected to be more common in an already variable system, species-specific assessment of how environmental stochasticity affects vital rates will be necessary for effective conservation of species in semi-arid regions.

Keywords: *Ceratotherium simum*, climatic variation, density, *Diceros bicornis*, mortality, population demographics, rainfall, vegetation greenness.

INTRODUCTION

Survival of large herbivores, such as the black (*Diceros bicornis*) and white (*Ceratotherium simum*) rhinoceros, is influenced by the interactions between intrinsic factors, such as age and sex, and extrinsic factors, such as habitat conditions, climate and predation (Gaillard, Festa-Bianchet & Yoccoz, 1998; Coulson *et al.*, 2001). These factors influence population dynamics and vital rates, particularly survival, through their relationship with animal body condition (Simard, Coulson, Gingras & Côté, 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 subtropical environments, the timing of environmental conditions plays an important role as it directly affects resources, and consequently vital rates, particularly when density-dependent feedbacks and age structure are considered (Owen-Smith, Mason & Ogutu, 2005). Additionally, in semi-arid environments with strong seasonality, vegetation growth and forage availability are directly linked to rainfall (Rutherford, 1980). However, because rainfall affects herbaceous and woody plant forms differently, effects of rainfall on herbivore population demographics will differ according to the species of herbivore, their dietary requirements, density and age structure (Owen-Smith, 1988; Gaillard, Festa-Bianchet, Yoccoz, Loison & Toïgo, 2000; Coulson *et al.*, 2001; Owen-Smith & Mason, 2005).

The effects of environmental stochasticity (*e.g.* changes in weather conditions and food availability)

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on herbivore survival tend to vary with age (Coulson *et al*., 2001; Simard *et al*., 2010). This is particularly because sensitivity to climatic conditions differs among age classes (Bleu *et al*., 2015) as a function of resource allocation towards growth and storage (*i.e*. fat reserves) (Adams, 2003; Parker, 2003). Juvenile survival is the most variable, whilst adult survival is more resistant to effects of environmental variability and density (Gaillard *et al*., 1998; Gaillard *et al*., 2000). Juvenile herbivores are sensitive to resource variability and density-dependent effects having little fat reserves to sustain themselves during shortages (Adams, 2003; Parker, 2003; Festa-Bianchet, Douhard, Gaillard & Pelletier, 2017). This is similar for senescent individuals whose declining body condition is worsened by food shortages (Gaillard *et al*., 2000). Thus, three age-related demographic parameters should respond to environmental stochasticity and density-dependence in the order of their sensitivity: juvenile survival, followed by reproductive rates, and lastly adult survival (Eberhardt 2002). However, adult large herbivores living in semi-arid savannas might nonetheless be susceptible to resource variability and density-dependent effects despite their age. This is not only due to the large quantity of food that they need to sustain themselves compared to smaller herbivores but also because these savannas are variable, seasonal systems, where plant biomass correlates with the amount of annual rainfall (Shorrocks, 2007). Moreover, changing climate could exacerbate the unpredictability of savanna environments, ultimately affecting the dynamics of savanna herbivores (Pettorelli, Pelletier, von Hardenberg, Festa-Bianchet & Côté, 2007).

South Africa is a water-scarce country where drought periods are predicted to increase due to climate change (Vogel, 1994; Vetter, 2009). Although rainfall determines savanna plant productivity, its effect on growth depends on the plant functional form (Scholes & Walker, 1993; Archibald & Scholes, 2007). Whereas growth and die-back of herbaceous plants depend on timing and amount of rainfall, woody plants can store nutrients and water to allow greening outside of the growing season (Scholes & Archer, 1997; Do *et al*., 2004). Given this difference, grazers such as white rhino might be affected more by changes in rainfall than a browser like black rhino (Ferreira, le Roex & Greaver, 2019). However, years with poor rainfall and plant growth lead to poor foliage retention and quality going into the dry season, (Owen-Smith *et al*., 2005) which could have implications for herbivore population dynamics irrespective of diet.

Because of differences in the relationship between rainfall and herbaceous and woody plant growth, and the potentially different consequences for survival between black and white rhinos (*e.g*. Ferreira *et al*., 2019; Le Roex & Ferreira, 2020) our aim was to investigate effects of rainfall, vegetation greenness (an index for estimating vegetation productivity based on photosynthetic activity; Huete *et al*., 2002) and population density on survival of the two rhino species. We use historical monitoring data to assess the population dynamics of both black and white rhinos, and we compare the usefulness of rainfall and greenness proxies (measured with Normalized Difference Vegetation Index (NDVI) and Enhanced Vegetation Index (EVI)) as predictors of rhino survival. We predicted that (1) both species would experience high mortality rates of young and senescent individuals during low rainfall periods; however, rates might be higher for white rhinos because of larger effects on herbaceous forage (Ferreira *et al*., 2019). Also, we expected that (2) high mortalities for both rhino species would be associated with low NDVI and EVI values, particularly integrated greenness or cumulative vegetation greenness (*i.e*. the sum of monthly NDVI/EVI values during a 12-month period or over a specific time period, respectively), which would indicate years of low productivity. Finally, we expected that (3) density effects would not be evident if populations are below equilibrium density and are driven more by environmental stochasticity (Sibly & Hone, 2002; Trimble, Ferreira & van Aarde, 2009).

METHODS

Study area

Lapalala Wilderness Nature Reserve (Lapalala, from this point forward) is a 480 km^2 private nature reserve (https://lapalala.com/lapalala-wilderness/ accessed 26 March 2025) situated in the savanna biome and central bushveld bioregion (Rutherford, Mucina & Powrie, 2006) of the Waterberg Biosphere, Limpopo Province, South Africa (Fig. 1). Since its establishment in 1981, the reserve's area has increased from 360 km^2 to 480 km^2. Ten vegetation communities have been identified according to the most dominant plant species found there, demonstrating the heterogeneity and biodiversity of the reserve. These include *Combretum*

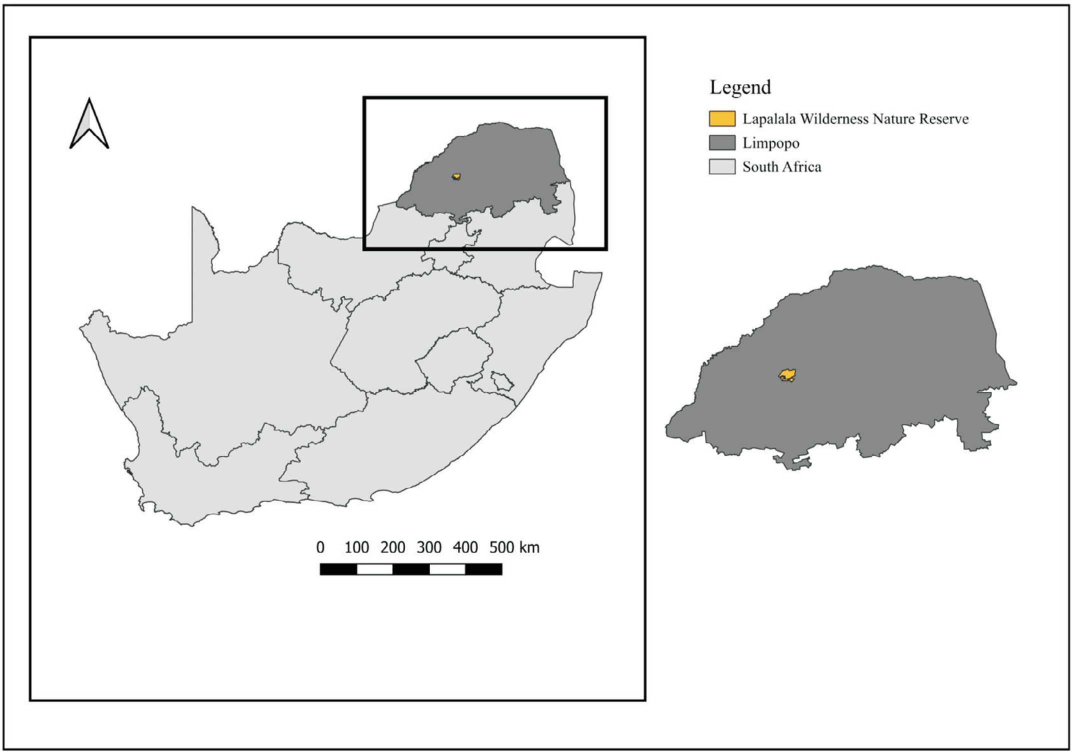


Fig. 1. Lapalala Wilderness Nature Reserve, Limpopo Province, South Africa.

molle–*Schmidtia pappophoroides* woodland, *Terminalia sericea*–*Aristida diffusa* woodland and *Andropogon eucomus*–*Eragrostis heteromera* grassland (Womack, 2021). Soil quality also varies spatially with the majority of the soil deriving from acidic sandstone and the central part of the reserve deriving from basic norite. Common woody plants include *Combretum* spp., *Senegalia* spp., Rhodesian rubber tree (*Diplorhynchus condylocarpon*), silver terminalia (*Terminalia sericea*), and wild syringa (*Burkea africana*); the last two species are commonly avoided by large herbivores or consumed during restricted periods only (Owen-Smith & Cooper, 1987; Cooper, Owen-Smith & Bryant, 1988). Common herbaceous plants include gum grass (*Eragrostis gummiflua*), three-awns (*Aristida* spp.), and common reed (*Phragmites* spp.), which are considered low-quality grazing grasses (Owen-Smith, 1988; Shrader, 2003). Other grasses found on the reserve and considered to be of average or high grazing quality include curly leaf grass (*Eragrostis rigidior*), spear grass (*Heteropogon contortus*) and Guinea grass (*Panicum maximum*) (Shrader, 2003; Womack, 2021). The climate is semi-arid and the area receives *c*. 500 mm of rainfall with most of that falling during the wet season (November–April). Mean monthly temperatures are 14–30°C during spring and summer, and 8–20°C during autumn and winter. The reserve hosts *c*. 60 mammalian species including large herbivores such as African elephant (*Loxodonta africana*), blue wildebeest (*Connochaetes taurinus*), common eland (*Tragelaphus oryx*), giraffe (*Giraffa giraffa*), hippopotamus (*Hippopotamus amphibius*), impala (*Aepyceros melampus*), plains zebra (*Equus quagga*) and roan antelope (*Hippotragus equinus*), among others.

Data sources

We used historical rhino monitoring data spanning 1982–2019. Five black rhinos were introduced to the reserve in 1990 and six white rhinos in 1982. Of the five black rhinos introduced, three were female adults aged 8–9 years and the remaining two were adult males aged 10 and 14. The six white rhinos included three females: one 14-year-old adult and two 5.5-year-old subadults, and three males: one 14-year-old adult and two 5.5-year-old subadults. Since then, additional rhinos have been introduced, and some have been translocated to other reserves. Black and white rhinos were tracked daily by an experienced team of rhino monitors. Mortalities were established with the discovery of a carcass for non-dependent rhinos; for younger rhinos who were still associated with their mother, mortality was presumed when the rhino was no longer seen with its mother. All rhinos were individually recognized using ear notches. This study included data on native-born and introduced rhinos to estimate survival; however, only animals whose cause of death appeared to be resource-related (*i.e.* not causes such as fighting and poaching; see Fig. S1 in Supplementary material) were used to assess the influence of resource variability on survival. Data for 46 black and 139 white rhinos were used for the survival analysis.

We obtained historical rainfall data, spanning the same period as the rhino data, from the South African Weather Service. Daily rainfall measurements were collected at the Ellisras-Pol, Marken and Mahwelereng weather stations, which were all within 3 km of Lapalala. The data were recorded inconsistently (*i.e.* some months only had weekly and not daily recordings) and so to create a continuous rainfall record we standardized monthly totals by dividing each station's monthly total by its standard deviation. Finally, we calculated monthly means across the stations and used these values to calculate rainfall variables used in the study.

Forage availability was assessed with NDVI and EVI data obtained from the NASA Land Processes Distributed Active Archive Centre. These two indices, NDVI and EVI, reliably represent variation in plant productivity (Fuller, Prince & Astle, 1997; Tucker & Yager, 2011; Huete *et al.*, 2002) and have been used in monitoring habitat for large herbivores (Pettorelli *et al.*, 2005; 2011). These indices are measures of vegetation greenness and have been shown to correlate with annual net primary productivity, leaf area and leaf biomass (Goward & Prince, 1995; Myneni, Hall, Sellers & Marshak, 1995; Huete *et al.*, 2002; Fensholt *et al.*, 2012). For the period 1992–1996 we used Advanced Very High Resolution Radiometer (AVHRR) NDVI composites (https://earthexplorer.usgs.gov/ accessed 26 March 2025) which had a 1.1 km spatial resolution and 10-day temporal resolution. For the period 2000–2019 we used Moderate Resolution Imaging Spectroradiometer (MODIS) NDVI and EVI composites (https://daac.ornl.gov/ accessed 26 March 2025) which had a 250 m spatial resolution and 14-day temporal resolution. MODIS products were established as a continuation index of AVHRR, and the two products are comparable (Huete *et al.*, 2002; Didan, Munoz, Solano & Huete, 2015). We were able to work with both products by rescaling 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 produces a smoother output from the resampled data without producing cell values outside of the range of the input raster (ArcGIS Desktop *via* https://desktop.arcgis.com/en/arcmap/ accessed 26 March 2025). Finally, we extracted greenness values for the 480 km^2 study area and mean values for each 10-day or 14-day image were calculated and used as a proxy for forage availability.

Data analyses

Our analysis follows Owen-Smith *et al.* (2005) and Owen-Smith & Mills (2006). We calculated population size using the number of individuals alive per year by the end of the annual year. Annual population growth rates were calculated using: $\Delta N_t = \log_e(N_{t+1}/N_t)$, 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 (*i.e.* $N_{t+1} = N(t) + B(t) - D(t) + I(t) + R(t)$. This eqaution incorporated births (B), deaths (D), introductions (I) and removals (R). To assess density dependence, the abundance level directly responsible for density feedbacks was calculated using $N_{eff} = 0.5N_t + 0.25N_{t+1} + 0.25N_{t-1}$. This eqaution considers that for long-lived animals density effects could operate over multiple years. We used Chi-square tests and summary statistics to assess differences in sex ratios and age structure for each species separately (*i.e.* log-rank tests to determine if there were differences between their survival curves/an association between sex/age-stage and survival). Age-stage categories were defined from literature and based on rhino functional life stages: calf (<1 year), juvenile (1–3 years), subadult (3–7 years), and adults (>7 years) (Emslie, Adcock & Hansen, 1995; Law & Linklater, 2014; Balfour *et al.*, 2019; le Roex & Ferreira, 2020).

In addition to investigating the role of current density on rhino survival, we evaluated the role of prior density because of potential delayed effects on large herbivore populations and their vital rates, for example, through resource availability (Turchin, 1995, Owen-Smith & Mills, 2006). We used four indices to estimate the effect of prior density on rhino survival: mean population size (*i.e.* number of individuals) over a (i) two-year and (ii) four-year block, and mean population density (*i.e.* individuals per km^2) over a (iii) two-year and (iv) four-year block. The year prior to the count represents direct density feedback and was therefore excluded. Indices (i) and (ii) estimate the periods over which impacts on vegetation are expected to persist (Owen-Smith & Mills, 2006), and indices (iii) and (iv) estimate density-dependence in relation to reserve size, which can affect access to resource patches if conspecific density gets too high (Rachlow & Berger, 1998; Linklater & Swaisgood, 2008; Sky *et al.*, 2022). In total, 12 derived density variables were calculated for each individual rhino and included in the survival analysis: indices (i)–(iv) for each rhino's birth and death year (*i.e.* prior density during the rhino's birth year), rhino population size during the rhino's birth and death year, and rhino density during the rhino's birth and death year.

We assessed whether a particular year was a drought year with the rainfall anomaly index (RAI), which calculates annual precipitation anomalies by using a ranking system to allocate values to positive and negative rainfall amounts (van Rooy, 1965; Keyantash & Dracup, 2002) based on a threshold calculated from the rainfall data (Eshetu, Johansson & Garedew, 2016). To test the effects of the El Niño-Southern Oscillation (ENSO) and associated rainfall irregularities on rhino survival (Kruger, 1999; Ogutu & Owen-Smith, 2003) we used the Oceanic Niño Index (https://ggweather.com/enso/oni.htm accessed 26 March 2025). We assessed cohort effects on survival (Beckerman, Benton, Ranta, Kaitala & Lundberg, 2002; Pigeon, Festa-Bianchet & Pelletier, 2017) by using RAI to assign rhinos to rainfall cohorts based on the rainfall conditions in their year of birth (*i.e.* wet, normal, dry) (*e.g.* Lee, Bond & Bolger, 2017).

Using the standardized rainfall from the three weather stations, we calculated rainfall variables to assess immediate and lagged relationships between rainfall and survival. The rainfall variables were: lifetime rainfall, lifetime dry-season rainfall, lifetime wet-season rainfall, rainfall six months prior to the rhino's death, rainfall during the rhino's first year, rainfall one month after birth, and rainfall one month prior to death. Additionally, we calculated two variables, rainfall during the first year of independence/post-weaning (age 1–2 years) and rainfall during the juvenile stage (age 1–3 years), to assess this vulnerable life stage and allow additional investigation into any cohort effects. For older animals that were introduced to Lapalala, we treated date of arrival as their date of birth and stratified native-born and introduced animals in subsequent analyses. We did this only for the rainfall variables that did not depend on an accurate birth date (total, dry- and wet-season rainfall experienced at Lapalala, rainfall six months prior to the rhino's death, and rainfall one month prior to death); the rest were removed for these rhinos.

We calculated monthly NDVI and EVI values using the 10- and 14-day composite greenness values. We used these monthly values to derive eight greenness indices for NDVI and EVI separately: greenness in the month of birth, greenness one month before death, maximum greenness value in the year of birth, maximum greenness value in the year of death, wet-season integrated greenness as the sum of monthly values for the wet season during the birth and death year, and annually-integrated greenness as the sum of monthly values for a 12-month period during the birth and death year (Pettorelli *et al.*, 2005; Rasmussen, Wittemyer & Douglas-Hamilton, 2006; Pettorelli *et al.*, 2007).

We analysed age-stage specific survival using the Kaplan-Meier estimator (Pollock, Winterstein, Bunck & Curtis 1989; Williams, Nichols & Conroy, 2002) and Cox proportional hazard (PH) model (Therneau & Grambsch, 2000; Therneau, 2021), separately for black and white rhinos. The Kaplan-Meier procedure estimates changes in survival as individuals age (Conroy & Carroll, 2009). The Cox PH model relates time-dependent covariates to time-to-mortality, and it allows for stratification of groups in the data set (Conroy & Carroll, 2009; Weathers & Cutler, 2017). To measure the effect of the variables it uses the hazard ratio, which is the risk probability of death occurring (Cox, 1972; Bradburn, Clark, Love & Altman, 2003). We stratified by age class (calf, juvenile, subadult, adult) to assess stage-specific survival and by origin (Lapalala, introduced). We analysed a sample of 46 black rhinos spanning the period 1990–2019 where 18 were male, 22 were female and 6 were unsexed. The sample of white rhinos spanned the period 1982–2019, contained 139 animals and was made up of 49 male, 80 female and 10 unsexed rhinos. Models violating PH assumptions were removed (Kleinbaum & Klein, 2005). We did not include sex of animal in the models because preliminary analyses indicated no evidence of an effect on survival. The response variable was years until a mortality occurred and the explanatory variables were the 12 density variables, the binary rainfall variables (RAI and ENSO), nine rainfall variables and the eight greenness variables as described above.

We used multi-model inference, based on small-sample Akaike's Information Criterion (AICc), in a two-step process to find the models best supported by our data. The first step compared models for density, rainfall and greenness, each as separate candidate sets (*i.e*. density, rainfall and greenness models were compared separately, Burnham & Anderson, 2002). The second step was to compare the top-ranking rainfall, greenness and density models between sets. If more than one model fell within two AICc units of the best-ranked model, we used the model having the fewest parameters for inference (Burnham & Anderson, 2002). Further, we used evidence ratios to compare the relative likelihood of the different models and to measure the difference in importance between the model sets (Anderson, 2008; Burnham, Anderson & Huyvaert, 2011). Evidence ratios are a formal measure of model strength (*i.e*. comparison of evidence) where higher evidence ratios indicate stronger support for the model/s (Burnham *et al*., 2011). Concordance values assessed the predictive ability of the model, where possible values ranged from 0.50 (no better than random) to 1 (perfect prediction) (Therneau & Watson, 2015). Effects of variables were interpreted with hazard ratios and all estimates were reported with 95% confidence intervals (C.I.). All analyses were conducted in *R ver. 4.0.5* (R Core Team, 2021) with library 'survival' (Therneau, 2021) .

RESULTS

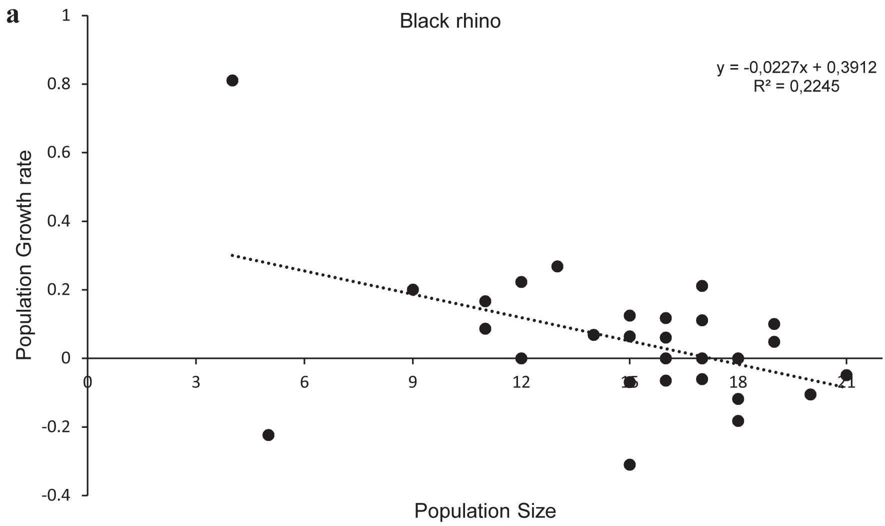
Black rhino density was 0.01 rhinos/km^2 during the first year of introductions, peaked at 0.06 rhinos/km^2 before the reserve's expansion in 2017, and remained 0.05 rhinos/km^2 thereafter. White rhino density was 0.01 rhinos/km^2 around the first introductions, grew to 0.2 rhinos/km^2 at expansion, where it remained thereafter. For black rhinos, there was no evidence of a relationship between population growth and population size ($F_{1,29}$ = 2.913, R^2 = 0.225, P = 0.10; Fig. 2a), and mean growth rate during the study period was 4.8% (C.I.: 4.7, 4.9). For white rhinos, there was no evidence of a relationship between population growth and size ($F_{1,37}$ = 0.237, R^2 = 0.0108, P = 0.629; Fig. 2a), but the mean growth rate during the study was higher than for black rhinos (8.9%; C.I.: 8.8, 9.0).

Age structure of both populations demonstrated similar characteristics (Fig. 3). For most years, the black rhino population consisted of more reproductively mature adults, averaging 66% during the study period, except for years when there was more than one calf born. By contrast, the white rhino adult population varied more over the years, averaging 59%. For all years but 1997 and 1998, the adult sex ratio favoured female black rhinos and averaged 68% during the study period. The sex ratio for adult white rhinos favoured male rhinos between 1982–1989, after which females have been favoured and averaged 56% of the adult sex ratio. By the end of the study period the male: female ratio was 1:1.5 and 1:1.74 for black and white rhinos, respectively.

From the sample of 46 black rhinos included in the survival analysis, 25 were dead and 21 were alive at the end of the study (Table 1). By comparison, from the sample of 139 white rhinos 52 were dead and the remaining 87 were alive at the end of the study (Table 1). Most of the deaths (18 of 25: 4 calves, 2 juveniles, 6 subadults and 6 adults) occurred during the dry season for the black rhinos and just over half (27 of 52: 7 calves, 4 juveniles, 7 subadults, 9 adults) occurred during the dry season for the white rhinos.

For most of the study, black and white rhinos had similar survival trends (Fig. 4). Both species had several steep drops in survival: the highest for black rhinos were during the calf stage and for white rhinos during the juvenile stage. The steep drop in survival for white rhinos around the age of 30 resulted in lower survivorship estimates by the end of the study compared to black rhinos. Survivorship estimates for black rhinos were 0.870 (C.I.: 0.777, 0.973) by age 1 and 0.241 (C.I.: 0.113, 0.512) by the end of the study period; for white rhinos estimates were 0.911 (C.I.: 0.864, 0.960) by age 1 and 0.191 (C.I.: 0.045, 0.811) by the end of the study period. Additionally, survival did not appear different between the sexes for black (χ^2 = 2.6, d.f. = 1, P = 0.1) or white (χ^2 = 1, d.f. = 1, P = 0.3) rhino populations.

Top-ranking models for both species included greenness variables, particularly integrated EVI during the death year (Table 2). Rainfall models had greater explanatory power for the black rhinos and there was little evidence for effects of cohort



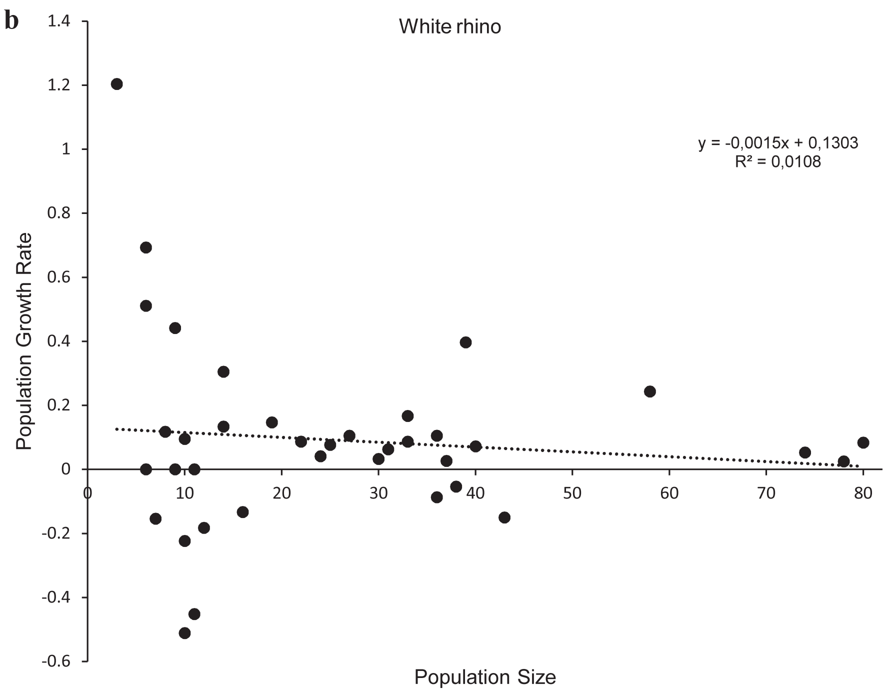
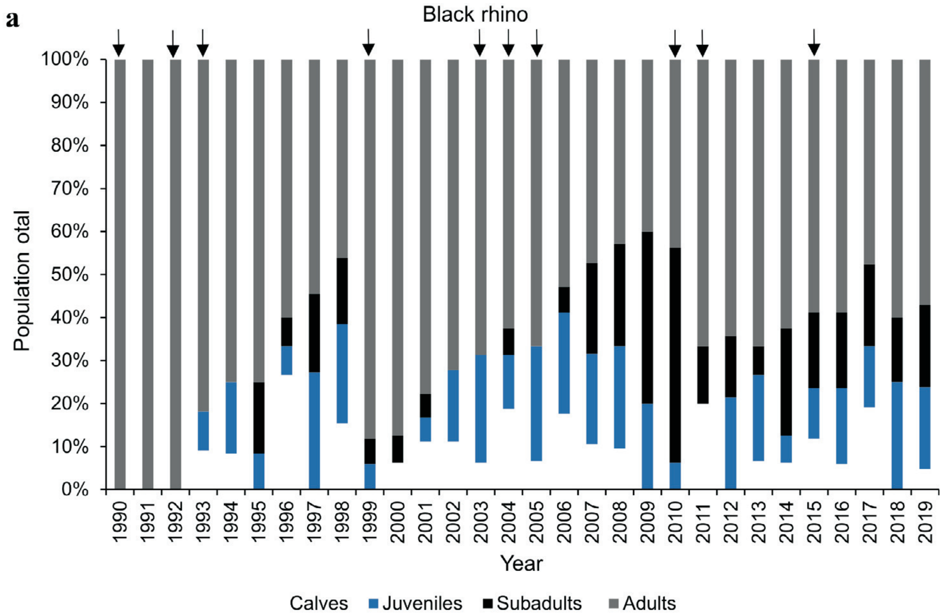


Fig. 2. Black rhino (**a**) and white rhino (**b**) population growth rates, from 1990 to 2019 for the black rhinos and 1982 to 2019 for the white rhinos. Population growth rates for both populations illustrated a weak negative correlation with population density.

effects, ENSO or density for both species (Tables S1–4 in Supplementary material). For both species, models with cohort and ENSO variables ranked lower than models that included longer-term variables such as lifetime rainfall and wet-season rainfall. The only exception was monthly rainfall which was the best-ranked rainfall model for white rhinos (Table S1). Additionally, there was little evidence of an effect of shorter-term greenness variables or resource conditions during early life (Table S2). For the black rhino population, the best-ranked model had EVI in year of death, but the confidence intervals overlapped 1, indicating no statistically significant effect of EVI on mortality



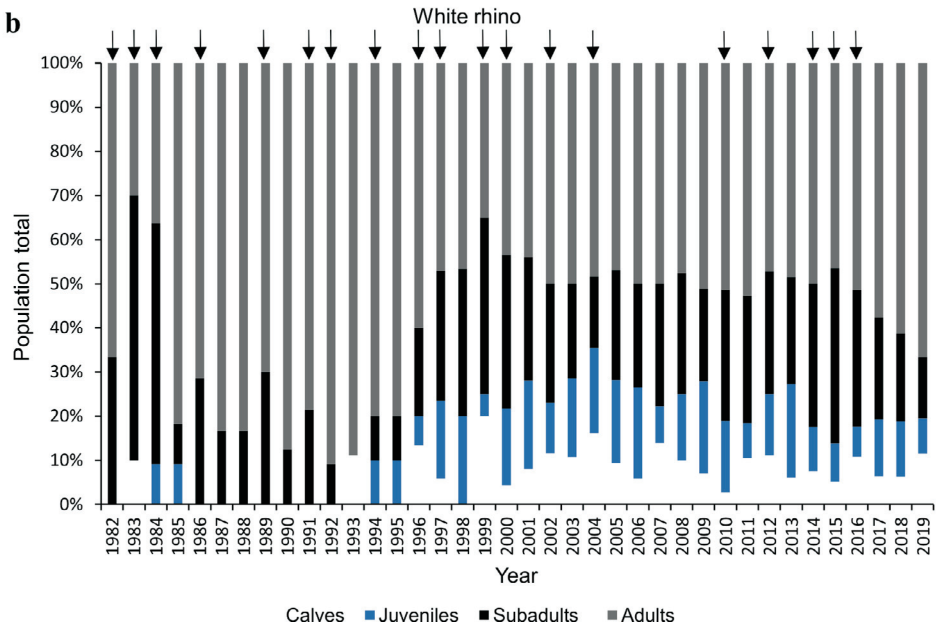


Fig. 3. Proportion of sexually mature and immature black rhinos (**a**) from 1990 to 2019, and white rhinos (**b**), from 1982 to 2019. Immature rhinos include calves, juveniles and subadults. The years in which translocations (additions and removals) occurred are indicated with arrows.

risk. A closely-ranked second model contained wet-season rainfall, had higher concordance, and indicated that the odds of mortality for black rhinos tended to decrease with increasing wet-season rainfall (Table 3) by a factor of 0.769 (C.I.: 0.613, 0.965) and 0.885 (C.I.: 0.786, 0.996) for subadults and adults, respectively. There was also no evidence of a relationship for calves and juveniles (0.757 (C.I.: 0.492, 1.164) and 0.663 (C.I.: 0.357, 1.233), respectively). For white rhinos, the odds of mortality for all ages combined decreased by a factor of 0.218 (C.I.: 0.079, 0.601) with each unit

Table 1. Summary of Kaplan-Meier results: number of black and white rhinos dead and alive within each age-stage by the end of the study, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019.

	Black rhino		White rhino	
Age-stage	Dead	Alive	Dead	Alive
Calf (<1 year)	6	1	12	10
Juvenile (1–3 years)	4	4	10	7
Subadult (3–7 years)	7	4	13	12
Adult (>7 years)	8	12	17	58

increase in integrated EVI (Table 3). The best-ranked rainfall model suggested that white rhino survival decreased with monthly rainfall by a factor of 0.415 (C.I.: 0.199, 0.862) for calves, 0.162 (C.I.: 0.042, 0.633) for juveniles, 0.303 (C.I.: 0.113, 0.811) for subadults and 0.224 (C.I.: 0.128, 0.392) for adults. Furthermore, for both species and all age-stages, there was little evidence of a relationship between survival and rhino densities; however, adult black rhino mortality decreased by a factor of 0.787 (C.I.: 0.666, 0.929) with each unit increase in prior rhino density.

When comparing between the rainfall models and greenness models, neither was better supported for black rhinos. Although the EVI models had higher probabilities (Akaike weight), the rainfall models had some support as well (w_i > 0.001). Evidence ratios suggest that models containing EVI for black rhino had almost five times more support than those with rainfall (EVI: w_i = 0.781, *versus* wet-season rainfall: w_i = 0.161). By comparison, the greenness indices proved to be much better predictors for the white rhinos, as all the top NDVI and EVI models ranked higher than the rainfall models (evidence ratio >1000, EVI: w_i = 1.000, *versus* rainfall: w_i <0.001).

DISCUSSION

Our findings support an important role of resource variability on the survival of black and white rhinos at Lapalala, as has been generally found for the population dynamics of African savanna large herbivores (Rutherford, 1980; Owen-Smith, 1990). Survival in black and white rhinos was age stage-specific, but as predicted, we found little support for density-dependence. As we expected, both rainfall and vegetation greenness were strong predictors for survival, with greenness being a better predictor for white rhinos. Neither species showed evidence that conditions during year of birth influenced survival later in life and both species' age structures favoured older individuals. Both populations were increasing, but the white rhino population increased at double the rate of the black rhino population.

Table 2. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to rainfall, vegetation greenness and density, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019. Presented are models for which $w_i \geq 0.001$ and/or top-ranking rainfall, NDVI, EVI and density models for each species. Models with interacting variables also contain the individual additive variables. Models were stratified by age or origin, unless stated otherwise.

Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos					
strata(age)* + Annually Integrated EVI during death year	54.467	0.000	0.781	4	0.731 (0.097)
strata(age) + wet-season rainfall	56.046	1.579	0.161	4	0.910 (0.035)
strata(age) × Annually Integrated NDVI during death year	57.985	3.518	0.023	4	0.931 (0.023)
strata(age) + lifetime rainfall	59.117	4.650	0.007	4	0.898 (0.039)
strata(age) + prior density during death year	83.940	29.474	0.000	4	0.722 (0.067)
White rhinos					
Annually Integrated EVI during death year	118.434	0.000	1.000	1	0.677 (0.081)
strata(age) × Annually Integrated NDVI during death year	155.246	36.812	0.000	4	0.954 (0.009)
strata(age) + density during death year	198.995	80.561	0.000	4	0.869 (0.027)
strata(age) + rainfall one month before death	210.490	92.057	0.000	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 = no. parameters (*i.e.* no. regression coefficients).
[e]Standard error in brackets.
*'strata' refers to the division of the rhinos into subgroups (age-stage classes).

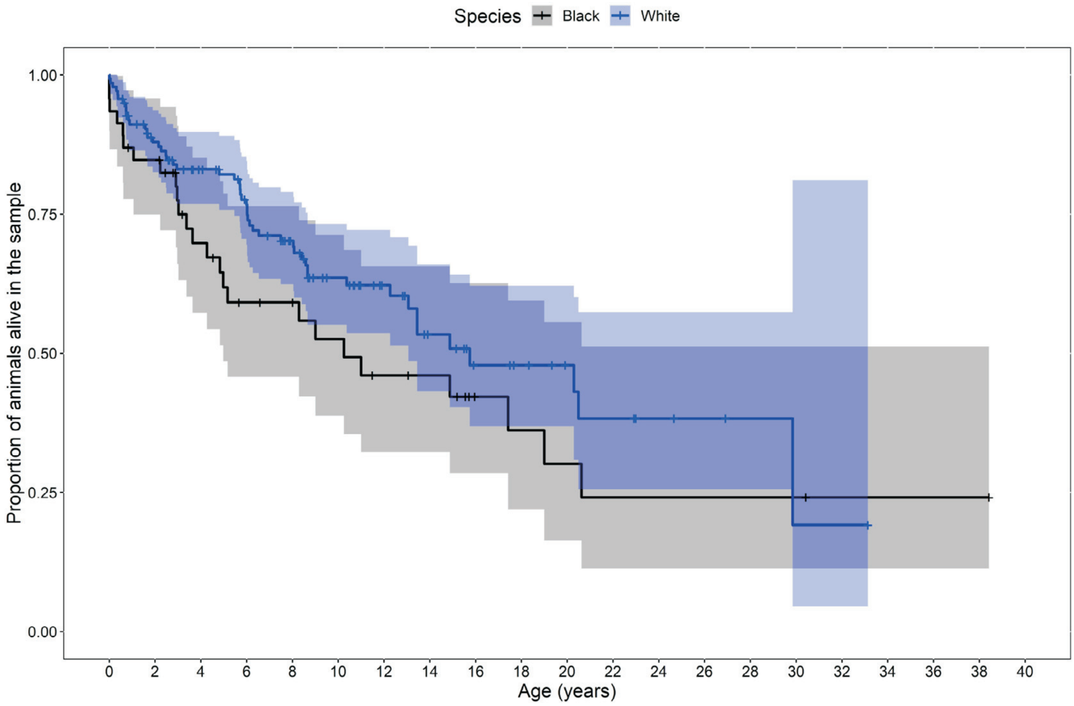


Fig. 4. Survival probability estimated for black and white rhinoceros, Lapalala Wilderness Nature Reserve, Limpopo Province, South Africa, 1982–2019. Presented are Kaplan-Meier survival estimates and 95% confidence intervals. The curve dips or steps down over time (*i.e.* years) as deaths in the population occur. Surviving rhinos were censored (right-censoring) and this is represented by the crosses (+) on the curve. The survival analysis allows for staggered entry, which means that despite an individual's date of birth or entry into the study it will be presented as though they all began the study at the same time.

Population dynamics

Eruptions are common in large herbivore populations, especially where populations have been introduced into unoccupied lands or re-introduced into areas that they historically occupied (Leader-Williams, 1980; Rachlow & Berger, 1998). Although differences in life histories might explain differences in population growth, the black rhino population experienced more disturbances in the form of removals, whose effects were likely exacerbated by the smaller population size. Those consequences were also visible in the more variable age structure; proportions of sexually immature *versus* mature individuals varied year-to--year showing no particular trend through the last 19 years of the study period. Changes in age structure because of disturbances (*i.e.* transient dynamics; Stott, 2016; Guldemond, Louw, Maré, Nørgaard & van Aarde, 2022) is common in variable environments such as savannas (Ogutu & Owen-Smith, 2003). For example, disturbances caused by removals and droughts impeded population growth of elephants in Addo National Park, South Africa (Guldemond *et al*., 2022). Although translocation of individuals may facilitate gene flow (Emslie, Amin & Kock, 2009), the cost could be slowing down an already slow-growing population by increasing recovery time of disruptions, particularly once environmental conditions are considered. Translocation can influence reproductive output physiologically and behaviourally by elevating rhino stress levels, which impairs reproduction, and by disrupting previously established relationships between breeding-age rhinos, resulting in delayed conceptions (Brett, 1998; Facka *et al*., 2016). Because the black rhino population is small, failure to disperse after translocations and the inability to find suitable mates might result in reduced mating opportunities and ultimately stunt population growth (le Roex & Ferreira, 2020). For example, the mean age at calving was 11.7 (C.I.: 10.5, 12.9) and 9.4 (C.I.: 8.5, 10.4) years for black and white rhinos at Lapalala, respectively (Ndlovu, Marshal, van der Goot & Müller, 2025). For most years, the black rhino adult sex ratio remained female biased (male: female

Table 3. Model coefficients: Cox proportional hazard models to analyse survival of black and white rhinoceroses, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019. Presented are the rainfall, vegetation greenness and density models used for interpretation.

Model	Stratum	Estimate*	S.E.	Hazard ratio*	95% confidence intervals	
					Lower	Upper
Black rhinos						
strata(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
	Subadult	–0.985	1.139	0.373	0.040	3.483
	Adult	–2.587	2.612	0.075	0.000	12.580
strata(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
	Subadult	**–0.263**	0.116	**0.769**	0.613	0.965
	Adult	**–0.122**	0.060	**0.885**	0.786	0.996
strata(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
	Subadult	**–2.303**	0.722	**0.100**	0.024	0.412
	Adult	**–3.301**	0.865	**0.037**	0.007	0.201
strata(age) + lifetime rainfall	Calf	–0.294	0.218	0.745	0.486	1.142
	Juvenile	–0.271	0.227	0.763	0.489	1.190
	Subadult	**–0.163**	0.076	**0.849**	0.733	0.986
	Adult	**–0.106**	0.053	**0.899**	0.811	0.997
strata(age) + prior density 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
	Subadult	–0.139	0.130	0.870	0.675	1.123
	Adult	**–0.240**	0.085	**0.787**	0.666	0.929
White rhinos						
Annually Integrated EVI during death year	All stages	**–1.523**	0.518	**0.218**	0.079	0.601
strata(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
	Subadult	–0.197	0.286	0.821	0.469	1.438
	Adult	**–2.989**	1.063	**0.050**	0.006	0.404
strata(age) + density during death year	Calf	–0.005	0.002	0.995	0.991	1.000
	Juvenile	–0.004	0.002	0.996	0.992	1.000
	Subadult	–0.018	0.018	0.982	0.947	1.018
	Adult	–0.019	0.015	0.980	0.952	1.001
strata(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
	Subadult	**–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.

ratio was 1:1.5) whilst the birth sex ratio was male biased (Ndlovu *et al.*, 2025), thus suitable mates might have been in shortage, which leads us to suggest that the lack of suitable mates might be the cause of low population growth for the black rhinos. Furthermore, both species' age structures appeared fairly stable towards the end of the study, possibly a result of deaths in the younger stages or more individuals moving into the adult life stage (Festa-Bianchet, Gaillard & Coté, 2003; Owen-Smith & Mason, 2005). Additionally, the adult sex ratios for both species favoured females, which under favourable conditions should improve growth rates and increase population numbers (Okita-Ouma, Amin, Van Langevelde & Leader-Willians, 2009).

Growth rate of white rhinos was typical of growing rhino populations at about 9% per annum

(Owen-Smith, 1988; Rachlow & Berger, 1998); whereas the black rhino growth rate was comparatively low at 4.8% (*i.e.* below 5%, the target proposed by the South African Black Rhino Management Plan; Knight, Balfour & Emslie, 2013). Population growth of black rhinos at Ithala Game Reserve was 4.9% (Greaver, Ferreira & Slotow, 2014), and slow growth was attributed to density-dependence acting through increased mortalities associated with fighting. This effect was unlikely at Lapalala because only a small percentage of mortalities were attributed to fighting compared to a larger number believed to be resource-related (Fig. S1); however, increasing densities in small reserves often result in increased social interactions which might result in mortalities directly (*i.e.* fighting) and indirectly from stress associated with rhino social structure (Greaver *et al.*, 2014). Throughout the study period, black rhino densities at Lapalala were below that at which the effects of competition were expected to occur (0.5–2 rhinos/km^2; Emslie *et al.*, 2009) and white rhino densities remained below densities where resource competition becomes evident (0.08–0.8 rhino/km^2; Emslie *et al.*, 2009). If density-dependent effects begin to emerge, it could be expected that they would operate through several mechanisms, including the availability of soil nutrients, the quantity and quality of forage, and competition with other browsers (Adcock, Hansen & Linderman, 1998; Hrabar & du Toit, 2005).

Effect of rainfall

Rainfall in savannas limits large herbivore populations through vegetation affecting forage or habitat (Coe, Cumming & Phillipson, 1976; Frost *et al.*, 1986). Black rhinos exhibited evidence of relationships between survival and longer-term rainfall variables (*e.g.* wet-season rainfall, lifetime rainfall), which we expected given the longer-term relationship between rainfall and woody savanna vegetation (Ryan, Williams, Grace, Woollen & Lehmann, 2016). Although tree growth is more resilient than herbaceous cover to rainfall variability (Rutherford, 1980; Scholes & Archer, 1997), it is also restricted by the amount of rainfall (Birkett & Stevens-Woods, 2005). Because green-up for woody plants begins before the wet-season (Rutherford, 1980), growth of green browse depends on rainfall during the previous wet season as well as what little rain falls during the dry season (Owen-Smith, 1990). Thus, quantity and timing of rainfall determine the growth of browse and persistence through the dry season. Almost 75% (18/25) of black rhino deaths at Lapalala occurred during the dry season, and they corresponded with low rainfall from the previous wet season (Table 3). Subadults and adults are more likely to be affected by decreased rainfall compared to calves and juveniles, possibly because calves mostly nurse and juveniles feed on both milk and browse until they leave their mothers and so they might be buffered from direct effects of rainfall on their forage (Owen-Smith, 1988).

By comparison, we expected the white rhinos' grazing diet to link their survival more directly with rainfall, and we found evidence that all age categories were negatively affected by low monthly rainfall. Because rainfall is a primary determinant of grass production, decreased rainfall should affect the herbaceous layer with a much shorter lag (Rutherford, 1980; Deshmukh, 1984; Vetter, 2009). Periods of decreased rainfall not only can decrease the amount of forage available for grazers but also can decrease its persistence into the dry season (Coe *et al.*, 1976; Mduma, Sinclair & Hilborn, 1999; Ogutu & Owen-Smith, 2003). Similar to black rhinos, most deaths (58%) occurred during the dry season, demonstrating how likely food shortages because of rainfall affected their survival. All stages were affected by decreased rainfall despite adult body condition typically decreasing at a rate slower than that of young animals (Bell, 1971; Shrader, Owen-Smith & Ogutu, 2006) and that adults typically survive for longer periods because of greater body reserves (Ballard, 1987; Parker, 2003). This difference in body reserves could explain why calf mortality increased at a rate approximately double that of adult mortality as rainfall decreased (Table 3). In addition to dealing with decreasing forage availability, mortality in the subadult group could be intensified by stress caused by separating from their mother and adversity associated with translocation (*i.e.* new additions to Lapalala) (Brett, 1998; Law, Fike & Lent, 2013). These young rhinos are faced with establishing their own home ranges whilst dealing with a new environment, competition for resources and environmental stressors such as decreasing rainfall and low forage availability during the dry season (Owen-Smith, 1988; Brett, 1998).

In contrast to our results, there was no influence of rainfall on mortality detected for black rhinos at Kruger National Park (KNP). White rhinos, however, exhibited drought-related mortalities, which were attributed to their grazing diet (Ferreira *et al.*, 2019). Ferreira *et al.* (2019) concluded that the primary cause of black rhino deaths is density-related responses and poaching, but there was no mention of whether survival varied amongst age classes. However, it is worth noting that KNP's larger size (19 485 km^2) might allow for better rhino survival because rhinos can range further to look for alternative food sources whereas rhinos in smaller reserves cannot (Shrader, Pimm & van Aarde, 2010). Mortalities of young black rhinos at Pilanesburg National Park, South Africa, were most common during low rainfall years (Hraber & Du Toit, 2005) and increases in calf mortalities for white rhinos at Ithala Game Reserve, South Africa, are associated with low rainfall and long dry seasons (De Lange, Bonnet & Shrader, 2024). Although our greenness and rainfall models had similar support, they demonstrate the important role of rainfall in influencing survival of browsers and grazers across life stages likely through availability of forage for both species.

Effect of vegetation greenness

The use of NDVI and EVI to assess vegetation productivity correlates with herbivore biomass and population dynamics (Pettorelli *et al.*, 2011; Duffy & Pettorelli, 2012). As such, it was expected that integrated greenness would be a strong predictor of survival. For the black rhinos, survival increased with greenness for all age-classes, suggesting better survival with greater primary productivity and browse availability. Survival also increased with integrated NDVI with no evidence of differences between age-classes. Increased forage availability as indicated by increased greenness allows individuals to increase body condition and add to body reserves, enabling higher rates of survival throughout the years (Davis, Stephens & Kjellander, 2016). With the white rhinos, there was no evidence of age stage-specific relationships between survival and EVI. Increased greenness translates into increased forage availability which results in improved body condition for juveniles, subadults and adults directly, and indirectly for calves through nursing (Pettorelli *et al.*, 2011). Because forage availability peaks during the wet season, rhinos likely take advantage of this period to bulk up; however, if forage availability is low as a result of rainfall and as indicated by vegetation greenness, rhino survival decreases because of starvation (Wato *et al.*, 2016).

Similar to our results, survival for elephants in the Tsavo Protected Area, Kenya, decreased with rainfall and vegetation greenness and was likely due to starvation as a result of prolonged drought periods (Wato *et al.*, 2016). For the giraffe (*Giraffa tippelskirchi*) population at Tanzania's Tarangire National Park, low adult survival was associated with higher than normal vegetation greenness; however, the lack of correlation for the juvenile giraffes led them to conclude that despite the reduced browse quality, giraffe mothers were able to provide the necessary nutrients to their nursing calves, at the expense of their own declining health (Bond, Ozgul & Lee, 2023). Variation in body mass and condition of blue wildebeest, red hartebeest (*Alcelaphus buselaphus*) and greater kudu (*Tragelaphus strepsiceros*) was positively related to vegetation availability (assessed with NDVI; Fuentes-Allende, Stephens, MacTavish, MacTavish & Willis, 2023). The correlation between body condition and vegetation greenness was stronger for the two grazer species compared to the browser (Fuentes-Allende *et al.*, 2023), which was similar to our results as the relationship between survival and greenness was stronger for the white rhinos. These differences might be a consequence of the relationship between the vegetation types and rainfall (Fuentes-Allende *et al.*, 2023) because grass quality, quantity and persistence throughout the dry season decline as a direct consequence of seasonal rainfall variations, thus leading to the stronger response in body condition and survival shown by the grazer species.

Effect of density

Small populations, such as those of black and white rhinos at Lapalala, are especially vulnerable (Caughley, 1994) because of increased susceptibility to environmental and demographic stochasticity (Lande, Engen & Sæther, 2003; Sky *et al.*, 2022). Thus, as populations decrease individual variance or demographic heterogeneity can have a larger influence on the population's demographics, resulting in the fluctuation of vital rates over time (Schleuning & Matthies, 2009). The trend between density and mortality was similar for both species and all age groups, but the only significant hazard ratio was from the adult black rhinos (*i.e.* adult black rhino odds of mortality decreased as density increased).

For animals (including both rhino species) taken from a high-density reserve and translocated, those animals tend to suffer higher post-release mortality in their new environments (*i.e.* consequences of post-release dispersal and associated social interactions) (Adcock *et al*, 1998; Linklater & Swaisgood, 2008). At Lapalala, there were few cases of fighting-related deaths (five black rhinos and two white rhinos) and one case where a black rhino died from post-release stress (Fig. S1). There was no evidence of correlation between density and growth rates, and there was no clear evidence of density-dependent mortalities, all supporting the idea that the rhinos were not experiencing negative density-dependence (Law, Fike & Lent, 2013). Similarly, black rhinos in Pilanesberg (Hrabar & Du Toit, 2005) and white rhinos in Matobo National Park (Rachlow & Berger, 1998), showed no evidence of density-related mortality, but they rather demonstrated density relationships with their reproductive performance where age at primiparity and inter-calving intervals increased with population density.

Our results suggest that rainfall and greenness influence mortality for both species, despite their differences in diet. Both rhino species are selective feeders (Shrader *et al.*, 2006; Muya & Oguge, 2000; Ganqa, Scogings & Raats, 2005). If preferred plant species are not available during the dry season and they cannot rely on less preferred species or move to look for alternatives, they are more likely to starve (Owen-Smith, 1988). Lapalala's location relative to other reserves in the area (*e.g.* Marakele National Park, Waterberg Biosphere Reserve) make it a suitable candidate for collaboration and to identify potential drought refugia to assist with rhino resilience as climate change is expected to increase rainfall variability (Pendergrass, Knutti, Lehner, Deser & Sanderson, 2017). Elephant populations located in reserves where they had access to water year-round (*i.e.* water provision through artificial boreholes) still experienced mortalities during low rainfall years (Shrader *et al.*, 2010; Smit, Peel, Ferreira, Greaver & Pienaar, 2020); however, populations in unfenced reserves were better off as they could find alternative food sources by leaving (Shrader *et al.*, 2010). Similar to our 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.

Our findings provide evidence that for black and white rhinos at Lapalala, survival is affected by fluctuations in food resources, as indexed by rainfall and vegetation greenness. We found evidence that both species experienced high mortality rates during low rainfall periods; however, the effect was stronger for all age classes within the white rhino population. As we predicted, high mortalities for both rhino species were associated with low integrated NDVI and EVI (*i.e.* low productivity) and density effects were not evident for white rhinos, whereas a decrease in adult black rhino mortality was observed as density increased. Density effects on rhino survival and population growth remain to be seen for both species and could become an important factor contributing to long-term population viability (Rachlow & Berger, 1998), particularly for the black rhinos which demonstrated lower population growth compared to white rhinos. As climatic changes are occurring at a faster rate than expected in southern Africa (Solomon *et al.*, 2007), extreme weather events such as heatwaves, floods and droughts are becoming more common (Kupika, Gandiwa, Kativu & Nhamo, 2018). Moreover, because seasonality is a characteristic of semi-arid savannas, altered rainfall patterns will result in fluctuations in resource availability for herbivores in the region (Scholes & Archer, 1997; Owen-Smith *et al.*, 2005). Sensitivity to extreme climatic conditions tends to differ among age classes (Bleu *et al.*, 2015) and diet specialization (Abraham, Hempson & Staver, 2019); however, we found that resource variability affected the survival of all life-stages, even more so with the grazing species. Although younger herbivores are more vulnerable to fluctuating resources, adult herbivores might be just as defenceless, particularly if they cannot mitigate the impacts of varying rainfall patterns by finding alternative food sources or by moving to drought refugia (Abraham *et al.*, 2019). Ultimately, our study highlights the importance of fluctuating resources on rhino survival, and we demonstrate that the population dynamics of both species depend on extrinsic factors. Thus, ongoing monitoring will continue to provide important information for managing black and white rhinos in the face of strongly seasonal rainfall, differences in diet, and effects of density and age structure in semi-arid environments.

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Supplementary material to:

Population performance and survival of black and white rhinoceroses in relation to rainfall, greenness and density

Latoya Ndlovu, Jason P. Marshal, Annemieke C. van der Goot & Hermann P. Müller

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Table S1. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to rainfall, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019. Presented are models for which $w_i \geq 0.001$ and/or top-ranking models for each species.

Table S2. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to productivity, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019. Presented are models for which $w_i \geq 0.001$ and/or top-ranking models for each species.

Table S3. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to density, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019. Presented are models for which $w_i \geq 0.001$ and/or top-ranking models for each species.

Table S4. Variable descriptions: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to rainfall, productivity and density Lapalala Wilderness Nature Reserve, South Africa, 1982–2019.

Fig. S1. The number and causes of mortality for black and white rhinos in Lapalala Wilderness Nature Reserve, recorded from 1982 to 2019. The resource-based category includes individuals whose deaths were recorded as unknown/resource-related and were included in the survival analyses. When a post mortem was performed the cause of death was attributed to a resource-related or natural death when (1) there were no signs of fighting or injuries found on the body, (2) there was little to no milk in the stomach and/or a lot of grass in the stomach of calves (*i.e.* mismothering was suspected) and (3) very little fat reserves were found in the body. Lastly, some deaths were labelled as nutritional stress/resource related when all other causes of death (*i.e.* accidental, disease, old-age, poaching or social) were ruled out.

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Table S1. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to rainfall, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019. Presented are models for which w_i ≥ 0.001 and/or top-ranking models for each species.

Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos					
strata(age) + wet-season rainfall	56.046	0.000	0.955	4	0.910 (0.035)
strata(age) + lifetime rainfall	59.117	3.071	0.044	4	0.898 (0.039)
strata(origin) + lifetime rainfall	62.948	6.902	0.001	2	0.953 (0.014)
strata(age) + dry-season rainfall	64.796	8.750	0.000	4	0.787 (0.086)
White rhinos					
strata(age) + rainfall one month before death	210.490	0.000	1.000	4	0.850 (0.029)
strata(age) + lifetime rainfall	231.674	21.184	0.000	4	0.866 (0.027)
strata(age) + wet-season rainfall	233.142	22.652	0.000	4	0.867 (0.027)
strata(origin) + wet-season rainfall	238.229	27.739	0.000	2	0.953 (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 = no. parameters.
[e]Standard error in brackets.

Table S2. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to productivity, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019. Presented are models for which w_i ≥ 0.001 and/or top-ranking models for each species.

Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos					
strata(age) + Annually Integrated EVI during death year	54.467	0.000	0.971	4	0.731 (0.097)
strata(age) × Annually Integrated NDVI during death year	57.985	3.518	0.029	4	0.931 (0.023)
strata(age) + wet-season integrated NDVI during death year	66.454	11.987	0.000	4	0.895 (0.026)
strata(origin) + Annually Integrated EVI during death year	81.776	27.309	0.000	2	0.564 (0.116)
White rhinos					
Annually Integrated EVI during death year	118.434	0.000	1.000	1	0.677 (0.081)
strata(age) × Annually Integrated NDVI during death year	155.246	36.812	0.000	4	0.954 (0.009)
strata(origin) + Annually Integrated EVI during death year	198.995	80.561	0.000	4	0.694 (0.073)
strata(origin) + wet-season Integrated EVI during death year	210.490	92.057	0.000	4	0.802 (0.043)

[a]AICc = Akaike's Information Criterion, corrected for small sample size.
[b]ΔAICc = AICc – min(AICc).
[c]w_i = model probability.
[d]K = no. parameters.
[e]Standard error in brackets.

Table S3. Model selection: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to density, Lapalala Wilderness Nature Reserve, South Africa, 1982–2019. Presented are models for which $w_i \geq 0.001$ and/or top-ranking models for each species.

Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
Black rhinos					
strata(age) + prior density during death year (F4)	83.940	0.000	0.710	4	0.722 (0.067)
strata(age) + prior density during death year (F2)	84.838	0.897	0.290	4	0.691 (0.093)
strata(age) + prior density during birth year	92.560	8.619	0.000	4	0.645 (0.086)
strata(age) + prior density during birth year (F4)	93.847	9.907	0.000	4	0.605 (0.087)
White rhinos					
strata(age) + density during death year	198.995	0.000	0.953	4	0.869 (0.027)
strata(age) + prior density during death year (F2)	202.249	3.254	0.037	4	0.954 (0.009)
strata(age) + prior density during death year (F4)	203.490	4.496	0.011	4	0.869 (0.027)
strata(age) + prior density during birth year	222.979	23.985	0.000	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 = no. parameters.
[e]Standard error in brackets.
The 'F2' and 'F4' refer to the density calculated over a two-year and four-year block, respectively.

Table S4. Variable descriptions: Cox proportional hazard models to analyse survival of black and white rhinoceroses in relation to rainfall, productivity and density Lapalala Wilderness Nature Reserve, South Africa, 1982–2019.

Model	Survival was affected by…
Age	or stratified by age (calf, juvenile, subadult, adult)
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 death	total rainfall the 6 months up to death date
Annual rain during birth/arrival year	total rainfall in the birth/arrival 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 1 month before death	total rainfall during the month up to death date
Rainfall 1 year before death	total rainfall 12 months up to death date
RainNlevel (cohorts)	rain-level during birth/arrival (cohort effects)
Rainfall during 1st year of independence	rainfall during the 1st year of independence
Rainfall during juvenile years	rainfall during juvenile years (1–3 years)
NDVI during birth/arrival month	NDVI during the month of birth/arrival
NDVI 1 month before death	NDVI one month prior to death
Annually Integrated NDVI (AINDVI) during birth/arrival	annually integrated NDVI during the birth/arrival year
AINDVI during death	annually integrated NDVI during the death year
Maximum wet-season NDVI during birth/arrival	maximum wet-season NDVI reached during birth/arrival year
Maximum wet-season NDVI during death	maximum wet-season NDVI reached during death year
Wet-season Integrated NDVI during birth/arrival	wet-season integrated NDVI during the birth/arrival year
Wet-season Integrated NDVI during death	wet-season integrated NDVI during the death year
Annually Integrated EVI (AIEVI) during birth/arrival	annually integrated EVI during the birth/arrival year
AIEVI during death	annually integrated EVI during the death year
Wet-season Integrated EVI during birth/arrival	maximum wet-season EVI reached during birth/arrival year
Wet-season Integrated EVI during death	maximum wet-season EVI reached during death year
Density during birth year	density during birth/arrival year
Density during death year	density during death year
Prior density during birth year	prior density during birth/arrival year, calculated over a two-year block
Prior density during death year	prior density during death year, calculated over a two-year block
Prior density (F4) during birth year	prior density during birth/arrival year, calculated over a four-year block
Prior density (F4) during death year	prior density during death year, calculated over a four-year block

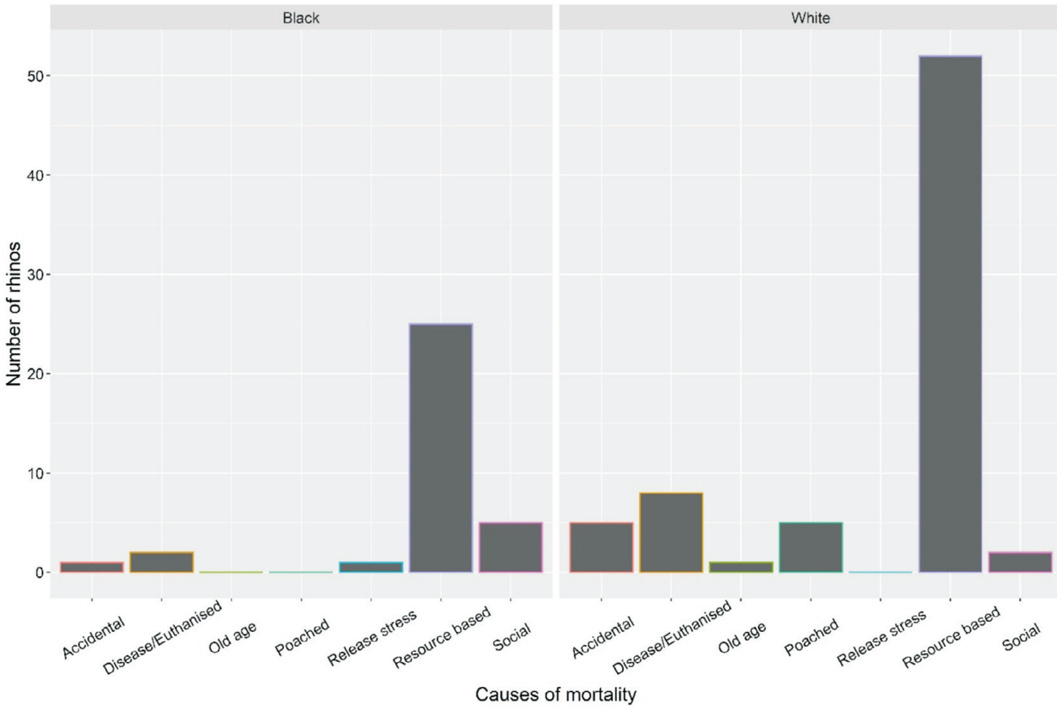

Fig. S1. The number and causes of mortality for black and white rhinos in Lapalala Wilderness Nature Reserve, recorded from 1982 to 2019. The resource-based category includes individuals whose deaths were recorded as unknown/resource-related and were included in the survival analyses. When a postmortem was performed the cause of death was attributed to a resource-related or natural death when (1) there were no signs of fighting or injuries found on the body, (2) there was little to no milk in the stomach and/or a lot of grass in the stomach of calves (*i.e.* mis-mothering was suspected) and (3) very little fat reserves were found in the body. Lastly, some deaths were labelled as nutritional stress/resource related when all other causes of death (*i.e.* accidental, disease, old-age, poaching or social) were ruled out.