RESEARCH ARTICLE

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

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Costs of reproduction and reproductive success depend on the timing of reproduction with favourable environmental conditions. For species like the black and white rhinoceros, which live in seasonal environments, changing climate might desynchronize reproduction and periods of favourable conditions. Additionally, fluctuations in environmental conditions can affect calf sex ratios. We thus investigated the reproductive life histories of black and white rhinoceroses at Lapalala Wilderness Nature Reserve, and their response to variations in rainfall, vegetation greenness and population density. We used historical rhino-monitoring data to assess age at primiparity, inter-calving intervals and offspring sex ratios. White rhinos had their first calf earlier than black rhinos (9.4 *versus* 11.7 years, respectively) but the inter-calving intervals of white rhino were longer than those of black rhino, averaging 38 and 33 months, respectively. Conceptions for both species peaked during the wet season and were associated with periods of high forage availability. Effects of greenness on age at primiparity differed between species, being positive for white rhinos and negative for black rhinos. We suggest that increases in greenness during conception periods might indicate increased grass production which the black rhinos do not have access to and might not consume. The birth sex ratio was male-biased for both species; however, there was evidence for an environmental effect on calf sex allocation. In particular, black rhinos favoured male calves during periods of decreased vegetation greenness. Although reproduction for both species appears to be related to resources, observed differences are possibly influenced at least in part by differences in the dynamics of plant growth forms that each consumes and the responses of each rhino to those dynamics.

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

INTRODUCTION

Shifts in global climate are implicated in altering biological systems (Inouye, Barr, Armitage & Inouye, 2000; Hughes, 2000; Hulme, 2005), and consequently, life history strategies of large herbivores (Post & Stenseth, 1999; Pettorelli, Pelletier, von Hardenberg, Festa-Bianchet & Côté, 2007). These changes are especially important in seasonal environments, where environmental variation influences resource availability, vital rates and population dynamics (Sæther, 1997; Gaillard, Festa-Bianchet & Yoccoz, 1998; Owen-Smith, Mason & Ogutu, 2005). Reproductive timing for individuals living in variable systems should correspond with peak seasonal conditions (Pettorelli *et al*., 2007). Additionally, for large herbivores, the effects of environmental variation on vital rates vary with age, sex and density (Gaillard, Festa-Bianchet, Yoccoz, Loison & Toïgo, 2000; Coulson, Milner-Gulland & Clutton-Brock, 2001). For example, age at primiparity and reproductive timing are some of the first vital rates to respond to limiting factors (Eberhardt, 1977; Gaillard *et al*., 1998). However, with changing climate, reproduction could become desynchronized with periods of favourable conditions (Pettorelli *et al*., 2007) resulting in poor body condition, recruitment and population performance (Albon, Clutton-Brock & Guinness, 1987).

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Resource availability, a product of environmental stochasticity, should therefore drive reproductive timing, rates and success (Trimble, Ferreira & van Aarde, 2009).

Reproductive success depends on the timing of reproduction with favourable conditions (Pianka, 1976; Wittemyer, Barner-Rasmussen & Douglas-Hamilton, 2007; Fynn & Provenza, 2023). Because late pregnancy and early lactation are the most nutritionally taxing stages of herbivore reproduction (Oftedal, 1985; Clutton-Brock, Albon & Guinness, 1989), females who match this period of demand to peak resource availability or quality should have higher fitness (Festa-Bianchet, 1988; Loe *et al.*, 2005; Fynn & Provenza, 2003). For most northern temperate herbivores, birth peaks correlate with increasing spring temperatures (Festa-Bianchet, 1988; Gaillard, Delorme, Jullien & Tatin, 1993; Moyes *et al.*, 2011), during which time vegetation quality is high (Crawley, 1983). Whereas photoperiod is the immediate cue affecting breeding phenology of temperate herbivores (Bronson, 1985), in subtropical savannas, rainfall plays this synchronizing role (Rutherford, 1980; Deshmukh, 1984). Thus, for rainfall-driven savanna herbivore populations, births should coincide with early wet-season peaks in vegetation quality and digestibility (Ogutu, Piepho & Dublin, 2014).

When gestation length is >1 year, an effective strategy is to time conception rather than birth to the rainy season, because conditions influencing oestrus and female condition during conception are the overriding factor that determines their capability to meet maternal demands associated with late pregnancy and early lactation (Owen-Smith, 1988). In other words, for capital breeders or most large herbivores, maternal nutrition affecting stored body reserves and oestrus cycling, is the proximate cue for mating (Owen-Smith, 1988; Parker, Barboza & Gillingham, 2009; Ogutu *et al.*, 2014). While mating should occur sufficiently in advance of favourable environmental conditions to optimize reproductive success (Sadleir, 1969; Zerbe *et al.*, 2012), gestation length for black and white rhinos spans 15–16 months, meaning that nutritional conditions experienced during the conception period are unlikely to match conditions during birth (Owen-Smith & Ogutu, 2013). Birth pulses are thus more likely to be spread through the year or peak during the dry season because conceptions are concentrated in the wet season (Hall-Martin, Skinner & Van Dyk, 1975; Owen-Smith, 1988; Ogutu *et al.*, 2014; Ogutu, Owen-Smith, Piepho & Dublin, 2015). Hence fertility depends on the female herbivores' condition during conception, which depends on the nutritional quality of the forage available at the same time (Owen-Smith, 1988; Cook, Murray, Cook, Zager & Monfort, 2001; Ogutu *et al.*, 2013, 2015; Owen-Smith & Ogutu, 2013).

Furthermore, timing and fluctuations in resource availability could influence offspring sex ratios (Clutton-Brock, Albon & Guinness, 1984; Clutton-Brock & Iason, 1986; Post, Forchhammer, Stenseth & Langvatn, 1999). Because offspring viability is largely dependent on maternal investment (Clutton-Brock & Iason, 1986; Clutton-Brock, 1991; Post *et al.*, 1999) adaptive theories suggest that offspring sex ratios will vary according to the costs and benefits associated with producing daughters and sons (Clutton-Brock & Iason, 1986; Trivers & Willard, 1973; Clark, 1978). For sexually dimorphic and polygynous species, sons are more costly to produce than daughters (Clutton-Brock *et al.*, 1981, 1983, 1986; Gomendio, Clutton-Brock, Albon, Guinness & Simpson, 1990) and more likely to survive when produced by healthier mothers (Clutton-Brock *et al.*, 1984).

Three hypotheses have been proposed to explain offspring sex ratios as a function of maternal condition. The hypothesis of Trivers and Willard (1973) (TWH) argues that mothers in poor condition should produce daughters because they would outperform sons born in the same condition; whereas, mothers in good condition (*i.e.* with more resources and parental care or investment) translates into advantages for sons in male–male competition (Trivers & Willard, 1973; Clark, 1978; Silk, 1983). The local resource competition hypothesis (LRCH), which is based on sex-specific dispersal, proposes that mothers in poor condition produce sons, because males are the dispersing sex, whilst daughters remain within their mothers' home ranges and benefit from sharing mother's resources (Clark, 1978; Verme, 1983; Weladji & Laflamme-Mayer, 2011). The third hypothesis, the extrinsic modification hypothesis (EMH), proposes that extrinsic factors, such as local environmental conditions and density, also influence birth sex ratios directly or in interaction with maternal condition (Post *et al.*, 1999; Mysterud, Yoccoz, Stenseth & Langvatn, 2000; Weladji & Holand, 2003; Berkeley & Linklater, 2010; Weladji & Laflamme-Mayer, 2011). This hypothesis proposes that mothers exposed to limited resources during conception and gestation should produce daughters, because male offspring tend to be heavier and more energetically expensive (Post *et al.*, 1999; Weladji & Holand, 2003).

Considering the importance of environmental variability on reproduction, population abundance and conservation status, our aim was to investigate the reproductive phenology of the black (*Diceros bicornis*) and white rhinoceros (*Ceratotherium simum*) at Lapalala Wilderness Nature Reserve (Lapalala, from this point forward), in response to variation in rainfall, vegetation greenness and population density. We used historical rhino-monitoring data to assess the reproductive parameters of a growing black and white rhino population and to investigate the relationship between reproductive performance, resource variability and population density. We expected that reproduction events would be influenced by environmental conditions, and we made the following predictions. First, conceptions rather than births would correlate with periods of high resource availability because of the long gestation time in rhinos. Second, age at primiparity would increase with decreasing rainfall and vegetation greenness because of their effect on body condition. Third, the proportion of male calves would increase with rainfall and vegetation greenness if the Trivers and Willard and extrinsic modification hypotheses are true, but decrease with rainfall and greenness if the local resource competition hypothesis is true. Because we lacked data on body condition, we did not try to distinguish between TWH and EMH. Our final prediction was that there would be little influence of population density on the reproduction of both species because both populations are relatively small (Emslie, Amin & Kock, 2009) and density-dependence is usually observed as populations approach carrying capacity (Sibly & Hone, 2002).

METHODS

Study area

Lapalala Wilderness Nature Reserve is a private nature reserve located in the Waterberg region, Limpopo Province, South Africa (Fig. 1). It was established in 1981 as a 360 km^2 reserve and grew to 480 km^2 by 2022 (https://lapalala.com/lapalala-

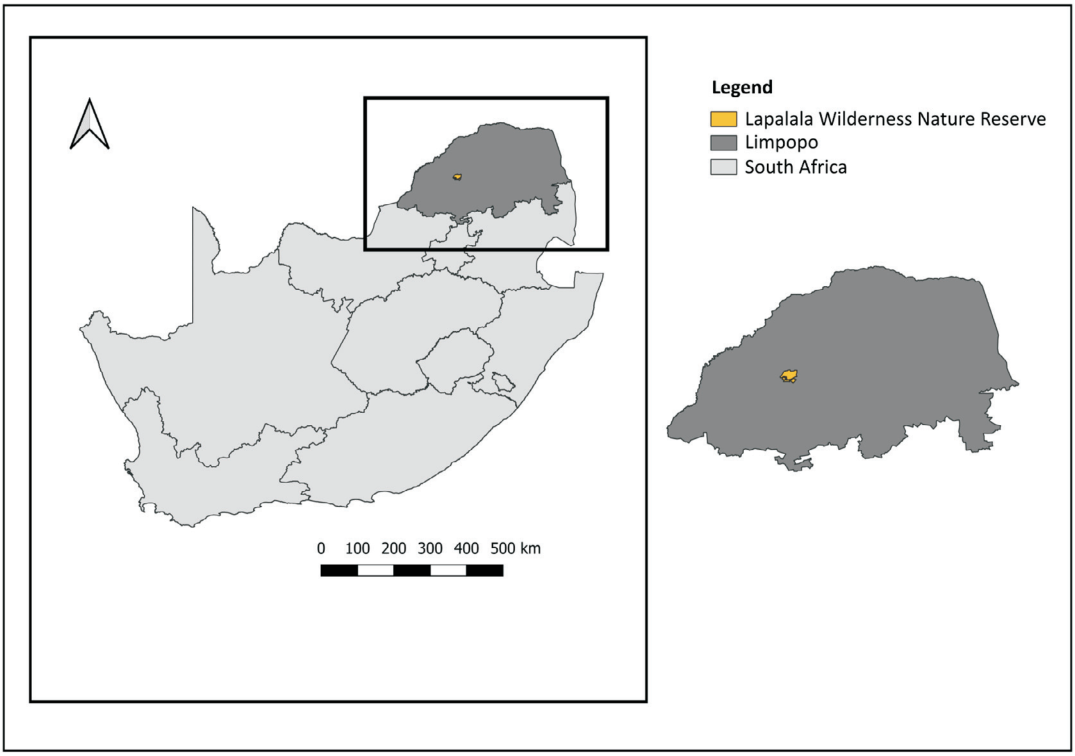

Fig. 1. Lapalala Wilderness Nature Reserve, Limpopo Province, South Africa.

wilderness/ – accessed 4 September 2024). It falls within the savanna biome, and central bushveld bioregion (Rutherford, Mucina & Powrie 2006). 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 (i.e. unpalatable to 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) (https://lapalala.com/lapalala-wilderness/ – accessed 4 September 2024). The long-term mean annual rainfall is 500 mm (https://lapalala.com/lapalala-wilderness/ – accessed 4 September 2024) with most falling during the wet season (November–April). Mean minimum and maximum monthly temperatures during spring and summer are 14°C and 30°C, and temperatures during autumn and winter are 20°C and 20°C. Besides rhinos, other large herbivores include impalas (*Aepyceros melampus*), plains zebras (*Equus quagga*), blue wildebeest (*Connochaetes taurinus*), African elephants (*Loxodonta africana*), giraffe (*Giraffa giraffa*), hippopotamus (*Hippopotamus amphibius*), roan antelope (*Hippotragus equinus*) and common eland (*Tragelaphus oryx*), among others.

Data collection

We used historical rhino monitoring data spanning 1982–2019. Black and white rhinos were tracked daily by an experienced team of rhino monitors at the reserve, who followed the rhino's tracks on foot and by vehicle (using a 4×4) until they saw the rhinos. Recorded data included identity, health status, sex, group structure, broad location and cause of death if applicable and known. For female rhinos, reproductive status (*i.e.* whether they were seen with a calf) was recorded along with estimated birth date and sex of the calf. Both species were individually recognized and have been tracked from birth or since they were translocated, with their mother's identity noted. This study included all native and translocated female rhinos with calving records, and it covered only their reproduction at Lapalala.

Historical rainfall data, spanning the same period as the rhino data, were obtained from the South African Weather Service. These data were collected at the Ellisras-Pol, Marken and Mahwelereng weather stations which are all within 3 km of Lapalala Wilderness. At the three stations, data from the year 1967 (September) to the end of the study period was recorded inconsistently, such that some stations had gaps in their records. To create a continuous rainfall record, monthly totals were standardized by dividing each station's monthly total by its standard deviation. We then calculated monthly means across the stations and used these values to calculate the rainfall variables used in the study.

We used Advanced Very High Resolution Radiometer (AVHRR) and Moderate Resolution Imaging Spectroradiometer (MODIS) normalized difference vegetation index (NDVI) and enhanced vegetation index (EVI) composites obtained from the NASA Land Processes Distributed Active Archive Centre to index forage availability. MODIS products were established as a continuation index of AVHRR to allow for long-term monitoring, and the two products are comparable and complement each other (Huete, Liu, Batchily & Van Leeuwen, 1997; Huete *et al*., 2002; Didan, Munoz, Solano & Huete, 2015). The AVHRR data spanned 1992–1996 (accessed from the Earth Resources Observation and Science centre *via* Earth Explorer https://earthexplorer.usgs.gov/ – accessed 4 September 2024) and had a 1.1 km spatial resolution and 10-day temporal resolution. The MODIS NDVI and EVI data spanned 2000–2019 (accessed from Oak Ridge National Laboratory DAAC *via* Earth Data https://daac.ornl.gov/ –accessed 4 September 2024) and had 250 m spatial resolution and 14-day temporal resolution. To work with both products, we rescaled the AVHRR data to the same spatial resolution of 250 m using the bilinear resampling method in ArcGIS 10.6, which is recommended for continuous data because it allows for some smoothing of the resampled data without producing cell values outside of the range of the input raster (ArcGIS Desktop *via* https://desktop.arcgis.com/en/arcmap/ – accessed 4 September 2024). We calculated a mean greenness value for the 480-km^2 study area for each 10-day or 14-day image.

Data analyses

Reproductive parameters

Variables for all analyses focused primarily on conditions experienced by females during conception and gestation, partly because fertility is influenced by conditions experienced prior to conception and partly because parturition might be modified by conditions experienced during gestation (Hrabar & Du Toit, 2005; Ogutu *et al.*, 2014, 2015). We estimated the dates of conception for all calves by subtracting 15 and 16 months from the recorded birth dates and inter-calving intervals as the time between the birth of the previous calf and successive calf for each multiparous female. The mean age at conception and calving, and mean inter-calving interval, were calculated separately for black and white rhinos. The monthly and seasonal timing of conceptions and births was assessed to determine whether either species exhibited any patterns with their reproductive timing; for example, conception peaks could correlate with early wet season as nutritional conditions peak. The birth rate or proportion of females calving was calculated as the number of births in the year divided by the number of adult females (*i.e.* ≥7 years old) that were alive during any part of that year (Law & Fike, 2018). To assess the potential influence of environmental conditions on calf sex allocation, we used records of all sexed individuals born at Lapalala. Female body condition data were not available, but the relationship between body condition of large herbivores and resource variability is well established (Albon *et al*, 1987; Jönsson, 1997; Parker *et al.*, 2009). Therefore, rainfall, greenness and density variables were used to directly assess the influence of environmental conditions on birth sex ratios.

Density effects

In addition to assessing the effects of current abundance on rhino reproduction, prior population effects were also evaluated because there can be delayed effects between abundance and vital rates, for example through changes in resource availability (Sinclair 1989, Turchin, 1995, Owen-Smith & Mills, 2006). High animal densities maintained for extended periods of time could impede vegetation recovery, lowering the availability of their food sources (Owen-Smith & Mills, 2006). In addition to calculating the abundance level responsible for direct density-dependence, we used four indices to estimate the effect of prior density on reproductive timing: the mean population size over a two-year and four-year block (*i.e.* abundance), and mean population density over a two-year and four-year block calculated using the number of rhinos present per square kilometre (*i.e.* conspecific density). Where the first two indices estimate the periods over which impacts on herbaceous vegetation are expected to persist (Owen-Smith & Mills, 2006), the third and fourth estimate density-dependence in relation to reserve size, which can also limit resource sinks if conspecific density gets too high (*i.e.* spatial restrictions might indicate density-dependence, particularly for black rhinos) (Rachlow & Berger, 1998; Linklater & Swaisgood, 2008; Sky *et al.*, 2022). In addition to the density analyses, we investigated the potential impact of competitor species by assessing relationships with density of other large browsers, herbivores and mixed feeders. In total, six derived density variables were included for each species in the analyses: density during the year of conception, prior density over a two-year period and prior density over a four-year period; conspecific density during the year of conception, prior conspecific density over a two-year period and prior conspecific density over a four-year period.

Rainfall and vegetation greenness (NDVI and EVI)

To evaluate whether a study year was a drought year we used the rainfall anomaly index, which calculates annual precipitation anomalies by using a ranking system to define thresholds that identify higher-than-normal rainfall and lower-than-normal rainfall (van Rooy, 1965; Keyantash & Dracup, 2002; Eshetu, Johansson & Garedew, 2016). Anomaly values that were below the negative thresholds were identified as drought years (Eshetu *et al.*, 2016). To assess the effects of El Niño-Southern Oscillation (El Niño) phenomena and associated drought on rhino reproduction we used the Oceanic Niño Index (https://ggweather.com/enso/oni.htm – accessed 4 September 2024) to categorize moderate and strong El Niño phases as El Niño years. Lastly, we calculated eight derived rainfall variables using the standardized values from the three weather stations specifically for each animal in the analyses and for each reproductive event. These variables were generated with respect to the rhino's life history, to capture both immediate and lagged responses. The variables were rainfall one, six, twelve and twenty-four months before conception, wet-season rainfall in the year prior to conception, rainfall during the gestation period, and rainfall one and two years prior, ending in the calf's birth.

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

Statistical analyses

We assessed the factors influencing the timing of primiparity using the Kaplan-Meier estimator and Cox proportional hazard models (Van Noord-Zaadstra *et al.*, 1991; Therneau & Grambsch, 2000; Rahman & Hoque, 2015; Therneau, 2021). To estimate the effect of the variables it uses the hazard rate, *i.e.* the risk of the event occurring (Cox, 1972; Bradburn, Clark, Love & Altman, 2003). We included origin of the female (Lapalala native or external) as a stratifying variable in the Cox model. The response variable was time to calving. The explanatory variables, included no more than two at a time in the models, were: the six derived density variables, whether an animal was conceived in a drought or wet year (binary), conceived during an El Niño year (binary), the eight derived rainfall variables (continuous) and the seven derived greenness variables (continuous).

We analysed the probability of a female giving birth to a male calf and the influence of rainfall, greenness and population density on the event, using generalized linear mixed models with a logit-link function and female identity as a random effect (Weladji & Leflamme-Mayer, 2011). The response variable was calf sex, and the explanatory variables included the same density, rainfall and greenness variables as described previously. All models were conducted separately for black and white rhinos.

Separately for each analysis, we used multi-model inference to rank candidate models in two steps. In step 1, we used small-sample Akaike's Information Criterion (AICc) and associated statistics, to compare the rainfall, greenness and density models separately within three candidate sets (Tables S1 & S2 in Supplementary material). In step 2, we compared top-ranking rainfall, greenness and density models between the three sets. The selected model was that with the highest AICc weight (w_i), as long as it differed by at least two AICc units from the other competing models. For models with less than two AICc units difference the selected model was that with fewest parameters (Burnham & Anderson, 2002). Estimates for top competing models are also presented as hazard or odds ratios. Concordance values were used to assess the predictive ability of the Cox model, where values >0.55 suggest adequate fit between model and data, values >0.7 indicate a good model, values >0.8 indicate a strong model and values close to 1 indicate models that perfectly predict outcomes (Therneau & Watson, 2015). All analyses were conducted in *R ver. 4.0.5* (R Core Team, 2021) with libraries 'survival' (Therneau, 2021), 'lme4' (Bates, Maechler, Bolker & Walker, 2015) and 'nlme' (Pinheiro, Bates, DebRoy, Sarkar & R Core Team, 2021). Estimates are presented with 95% confidence intervals.

RESULTS

By the end of the study a total of 46 black and 92 white rhinos had been born at Lapalala. Of the black rhinos, 16 were female, 24 were male and 6 were unsexed. Of the white rhinos, 39 were female, 44 were male and 9 were unsexed.

Twelve black rhino females and 38 white rhino females calved during 1992–2019 and the mean age at first conception was 10.5 (9.3, 11.6) and 8.1 years (7.1, 9.1), respectively. The resulting age at first calving was 11.7 years (10.5, 12.9) for black rhinos and 9.4 years (8.5, 10.4) for white rhinos. White rhino inter-calving intervals were longer than those of black rhino's (Fig. 2) and the mean was 38 (35, 41) and 33 (29, 37) months, respectively. White rhino conceptions peaked during the early-wet season and births peaked in late-wet season. In contrast, black rhino conceptions peaked at the end of the dry season and births peaked in the mid-wet season (Fig. 3). The black rhino birth rate was highest in 1996 and 1998 when all the adult females in the population gave birth, but there were also seven years of 0 births during the study period (Fig. 4). By comparison, the white rhino birth rate was highest at 80% in 1999 and 0% in 1991, 1992, 1994 and 1998 (Fig. 4). Mean annual birth rates over the study period were 26.8% and 22.8% for black and white rhinos, respectively.

Top ranking models for age at first conception differed somewhat between the species (Table 1). For both species, greenness models, and particularly EVI models, had greater explanatory power than the rainfall and density models. For black rhinos, however, the top model included wet-

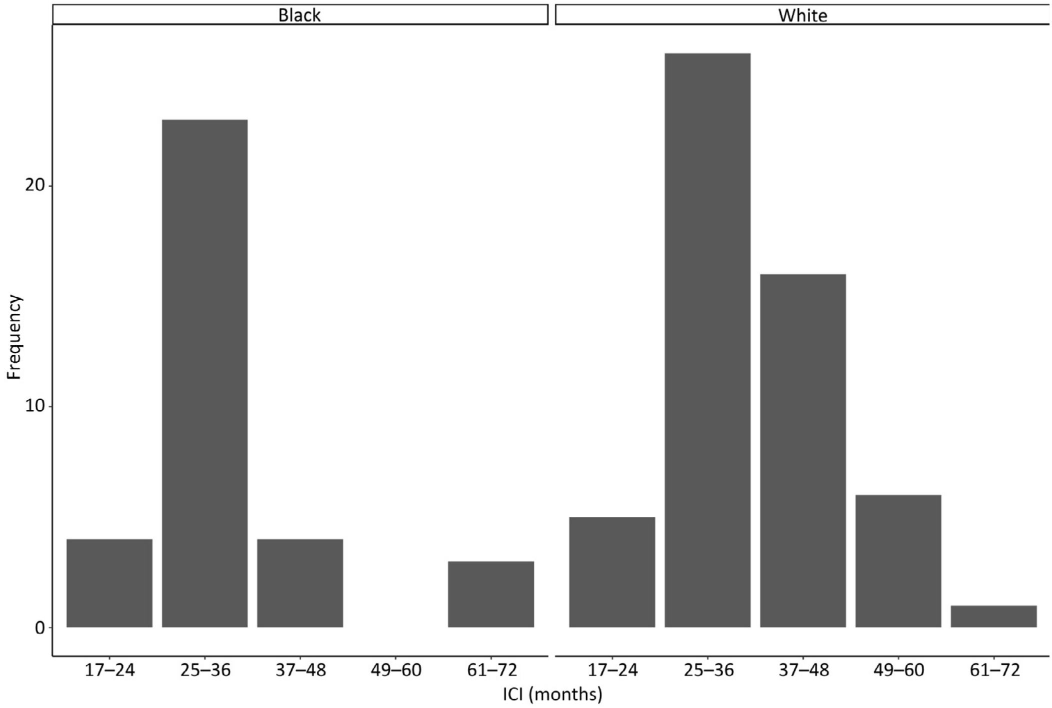

Fig. 2. Frequency distribution of inter-calving intervals for black and white rhinos, Lapalala Wilderness Nature Reserve, 1990–2019. A total of 10 black rhino females and 21 white rhino females had more than one calving event.

season integrated EVI during the year of conception, whereas, for white rhinos, annually integrated EVI during the year of conception was in the top model. There was less support for rainfall or density variables, including the models with the competitor species (Tables S3–S6). There was also little evidence of an effect of variables based on El Niño or drought years for either species. For the black rhino population, there was no consistent evidence of an effect of EVI on age at first conception (Table 2). The two best-ranked models estimated hazard ratios with confidence intervals that overlapped 1. In the third-ranked model, the effect of NDVI did not overlap with 1, but the odds ratio unexpectedly suggested that calving decreased with each unit increase in wet-season maximum NDVI (Table 2). Contrary to the black rhinos, odds of having the first calf for white rhinos increased by a factor of 3.907 (1.755, 8.70) with each unit increase in annually integrated EVI (Table 2).

Calf sex

Calf sex ratios for both black and white rhinos were male-biased by the end of the study period, but they were only marginally different from equality (male:female ratios 1.5:1 and 1.13:1, respectively). Estimated odds of having a male calf was 0.752 (0.349, 1.617) times more likely for black rhinos than for white rhinos; however, the confidence interval contained 1, suggesting little meaningful difference between species. For each species by year, more female black rhinos were born during dry years (male:female ratio was 1:2) and more males born during normal/wet years (male:female ratio was 3.17:1). The estimated odds of having a male calf during wet years was 6.33 (1.543, 26.003) times the odds during dry years for black rhino. For white rhinos, however, sex ratios were equal in wet/normal years, but the odds of a male calf during dry years became 0.808 (0.339, 1.929) times that in wet years. Again, the confidence interval contained 1 suggesting little evidence of an effect in wet years. Thus, for black rhino, there was some evidence of a difference in response of sex ratios to dry *versus* normal/wet weather conditions.

Models with greenness variables had greater explanatory power for calf sex allocation for both species than other candidate models (Table 3). For black rhinos, the odds of having a male calf decreased by a factor of 0.121 (0.005, 0.785) with

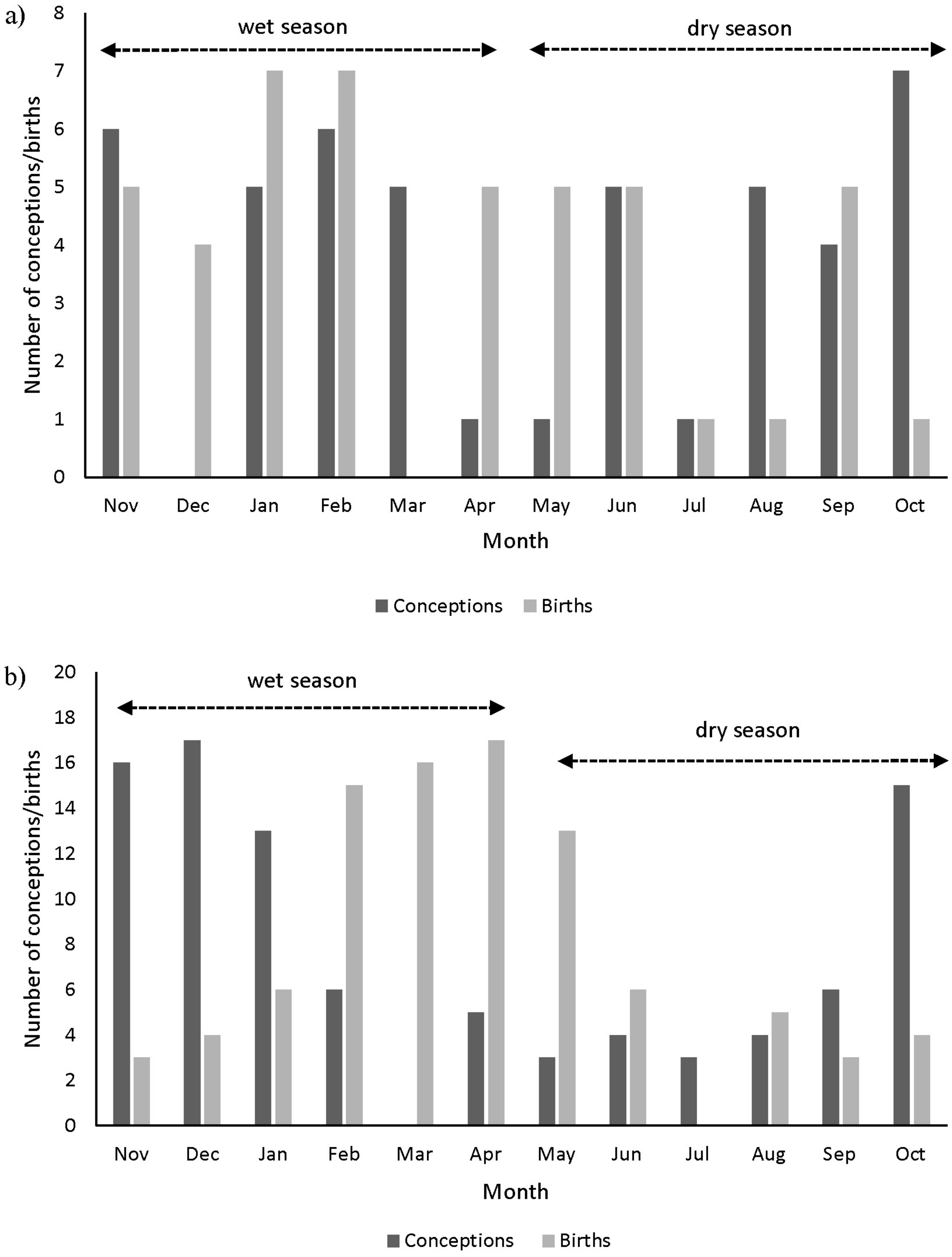

Fig. 3. Seasonal distribution of all conception and birthing events for (**a**) black and (**b**) white rhinos, Lapalala Wilderness Nature Reserve, 1990–2019.

each unit increase of vegetation greenness during the year of conception (Table 4). For the white rhinos, there was no consistent evidence of an effect of EVI on calf sex ratio (Table 4). Although the estimated hazard ratios had confidence intervals that overlapped 1, estimates suggested that the probability of having a male white rhino calf increased with EVI. Additionally, there was no

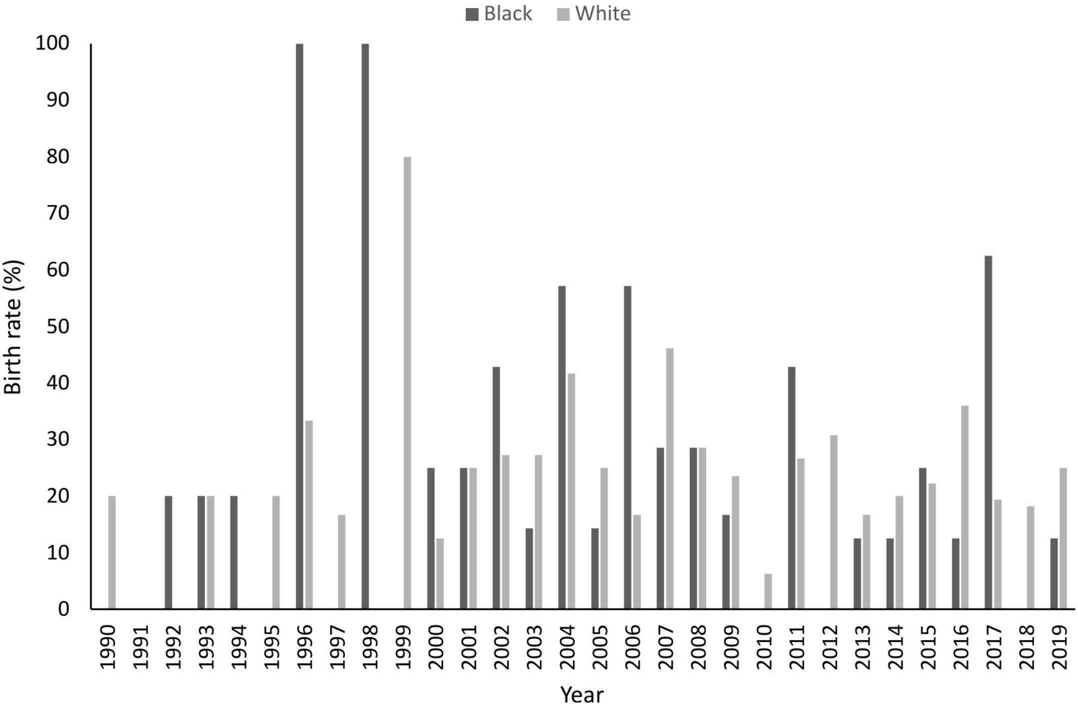

Fig. 4. The birth rate for black and white rhinos, Lapalala Wilderness Nature Reserve, 1990–2019. Years when the percentage of birth rate was 100% indicate a year where all adult females in the population successfully calved.

consistent evidence of an effect of rainfall and density on both species’ calf sex ratios. However, for both species, estimates for density suggested that male calves were favoured during years with low density compared to high-density years (Table 4).

DISCUSSION

The aim of this study was to assess the timing of reproduction events in black and white rhinos and to assess the influence of environmental fluctuations on the population’s reproductive parameters. Although white rhinos were more likely to conceive

Table 1. Metrics for model selection of Cox proportional hazard models to analyse age at primiparity of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019. Presented are models for which $w_i \geq 0.001$. Models with interacting variables also contain the individual additive variables.

Model	AICc^a	ΔAICc^b	w_i^c	K^d	Concordance^e
Black rhinos					
Wet-season integrated EVI during conception year	24.187	0.000	0.901	1	0.697 (0.118)
Origin × Wet-season Integrated EVI during conception year	26.452	2.264	0.094	2	0.758 (0.100)
Wet-season max NDVI during conception year	29.356	5.169	0.005	1	0.750 (0.067)
White rhinos					
Annually integrated EVI during conception year	196.498	0.000	0.906	1	0.673 (0.056)
Origin × annually Integrated EVI during conception year	198.768	2.270	0.094	2	0.677 (0.055)

[a] AICc = Akaike’s Information Criterion, corrected for small sample size.

[b] ΔAICc = AICc – min(AICc).

[c] w_i = Akaike weight.

[d] K = no. parameters.

[e] Standard error in brackets.

Table 2. Model coefficients from Cox proportional hazard models used to analyse age at primiparity of black and white rhinoceroses, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019. Presented are the greenness models used for interpretation.

Model	Stratum (Origin)	Estimate	S.E.	Hazard ratio	95% confidence intervals		*P*-value
					Lower	Upper	
Black rhinos							
Wet-season integrated EVI during conception year	All	–0.472	0.504	0.624	0.232	1.676	0.349
Origin × wet-season Integrated EVI during conception year	Lapalala	–0.508	0.545	0.602	0.207	1.750	0.152
	External	–1.059	0.739	0.347	0.081	1.478	0.351
Wet-season max NDVI during conception year	All	**–1.177**	0.560	**0.000007**	0.000	0.452	0.036
White rhinos							
Annually integrated EVI during conception year	All	**1.363**	0.408	**3.907**	1.755	8.700	0.001
Origin × annually Integrated EVI during conception year	Lapalala	1.349	0.428	**3.856**	1.738	8.695	0.002
	External	**1.358**	0.411	**3.888**	1.667	8.922	0.001

*Estimates and hazard ratios of predictors with standard errors excluding 1.000 are in bold.

Table 3. Metrics for model selection of generalized linear mixed models used to analyse calf sex ratios of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019. Presented are models for which $w_i \geq 0.001$.

Model	AICc[a]	ΔAICc[b]	w_i[c]
Black rhinos			
Wet-season integrated EVI during conception year	40.257	0.000	0.971
Wet-season integrated NDVI during conception year	43.783	3.525	0.029
White rhinos			
Annually integrated EVI during conception year	100.789	0.000	0.649
Wet-season integrated EVI during conception year	101.417	0.628	0.346
Annually integrated NDVI during conception year	105.679	4.889	0.005

[a] AICc = Akaike's Information Criterion, corrected for small sample size,

[b] ΔAICc = AICc – min(AICc),

[c] w_i = Akaike weight.

Table 4. Model coefficients from generalized linear mixed models used to analyse calf sex ratios of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019. Presented are models used for interpretation.

Model	Stratum	Estimate	S.E.	Hazard ratio	95% confidence intervals		*P*-value
					Lower	Upper	
Black rhinos							
Wet-season integrated EVI during conception year	All	**–2.114**	1.249	**0.121**	0.005	0.785	0.022
Wet-season integrated NDVI during conception year	All	**–1.632**	0.969	**0.196**	0.018	0.904	0.034
Conception during wet year	All	–0.821	0.769	0.440	0.091	1.989	0.286
Conspecific density during conception year	All	–0.049	0.099	0.951	0.765	1.147	0.615
White rhinos							
Annually integrated EVI during conception year	All	0.872	0.518	2.391	0.889	6.945	0.093
Wet-season integrated EVI during conception year	All	0.889	0.619	2.432	0.789	9.617	0.151
Annually integrated NDVI during conception year	All	0.466	0.506	1.593	0.596	4.474	0.358
Rainfall one month before conception	All	0.388	0.246	1.475	0.925	2.455	0.115
Conspecific density during conception year	All	–0.103	0.746	0.902	0.164	4.711	0.890

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

and calve at an earlier age than black rhinos, both species' reproductive events were not strictly seasonal as births occurred throughout the year. There were some differences between females born at Lapalala and external rhinos for both species regarding the conditions in which they reproduced, which we liken to a 'demographic heterogeneity' effect. In other words, they show variation at the individual level associated with differences in early life and access to resources (Kendall, Fox, Fujiwara & Nogeire, 2011; Stover, Kendall & Fox, 2012; Sky *et al.*, 2022) because conditions experienced throughout their life prior to Lapalala possibly influenced their nutritional gains and, consequently, their body condition. One difference between the two species, however, was how greenness affected birth sex ratios. Increased greenness was associated with a lower probability of conceiving a male black rhino, whereas increased greenness was associated with a higher probability of conceiving a male white rhino.

Seasonal distribution of births and conceptions

Both species reproduced and calved throughout the year. However, both had their conception peaks at times when conditions would be most favourable. For megaherbivores, because gestation exceeds 12 months, births tend to be spread throughout the year because there is low selective pressure favouring critical periods to coincide with nutritionally optimal periods during the year (Owen-Smith, 1988; Owen-Smith & Ogutu, 2013). Instead, oestrous cycling depends strongly on female condition, so that conception peaks will coincide with nutritionally optimal periods (Owen-Smith, 1988; Cook *et al.*, 2001; Owen-Smith & Ogutu, 2013). For black rhinos, conceptions peaked before the wet season and secondarily during the wet season (Fig. 3a), whereas conceptions peaked during the early wet season for white rhinos (Fig. 3b). Most woody plants will put on leaves and green before the first wet-season rains (Rutherford, 1980) and decline in nutritional quality at a slower rate than grasses (Pellew, 1983; Owen-Smith, 1994, 2008), suggesting that black rhinos would take advantage of this period to reproduce. The black rhino population in the Hluhluwe-iMfolozi Park also reproduced throughout the year, with two conception peaks in October and November and another between April and July (Hitchins & Anderson, 1983). The first peak occurs in spring and is associated with an improved nutritional state; however, the second peak is in autumn and possibly linked with photoperiod (Hitchins & Anderson, 1983). In contrast, herbaceous plants reach their nutritional peaks shortly after the first wet-season rains (Boutton, Tieszen & Imbamba, 1988; Owen-Smith, 2008) again suggesting that white rhino reproduction would be associated with the period during which grass quality increases (Ferreira, le Roex & Greaver, 2019; Truter, Mgqatsa & Parker, 2022). For white rhinos at Hluhluwe-iMfolozi Park, the peak is in November and again in February and is associated with the bimodal pattern in spring and summer rainfall (Owen-Smith, 1973). Except for elephants, most megaherbivores in rainfall-driven savannas show conception peaks in spring and summer when conditions are optimal, and birth peaks occur during the dry season (Owen-Smith & Ogutu, 2013).

Age at primiparity

The relationship between reproduction and greenness indices should be similar to that reported for reproduction and rainfall as greenness indices offer a direct measure of vegetation production (Goward & Prince, 1995; Huete *et al.*, 2002). Surprisingly, however, the age at which black rhinos conceived their first calf increased with increasing greenness (Table 2). Although the EVI model was not significant, we suggest that increases in wet-season integrated greenness and maximum NDVI during conception periods might indicate a shorter period of access to high-quality forage. Rapid vegetation green-up shortens the period of access to high-quality forage (Pettorelli *et al.*, 2007) or increased production of vegetation that the black rhinos may not have access to, *i.e.* vegetation that they do not consume or increased grass production. Early reproduction should be selected for as it increases lifetime reproduction (McGraw & Caswell, 1996; Martin & Festa-Bianchet, 2012). However, pregnancy requires sufficient energy and body condition, so much so that fertility will be delayed if those conditions are not met (du Plessis, 1972; Grimsdell, 1973). Furthermore, because rhinos are considered capital breeders, their reproduction can be suppressed as a response to unfavourable conditions (Hall-Martin *et al.*, 1975; Owen-Smith, 1988). By comparison, white rhinos had their first calf earlier when vegetation greenness was higher (Table 2). This suggests that they were more likely to reproduce when vegetation productivity was high (Rasmussen *et al.*, 2006), which would result in an increased body condition and trigger the onset of oestrous cycling. Additionally, most conceptions occurred at the beginning of the wet season, suggesting that females might take advantage of high-quality forage to build up body reserves and maintain the physical condition necessary to successfully conceive their first calf (Ryan, Knechtel & Getz, 2007; Pettorelli *et al.*, 2007; Therrien, Côté & Festa-Bianchet, 2007). Furthermore, the difference in responses to greenness variables might also reflect the differences in diet for the two species because the nutritional value of woody forage declines at a slower rate, compared to the nutritional value of grasses which declines almost immediately in response to environmental conditions (Pellew, 1983; Owen-Smith, 1994, 2008).

Calf sex ratio

Although the birth sex ratios remained male-biased by the end of the study period for both species, there was little evidence from the logistic regression models for a strong influence of environmental conditions on calf sex ratios. The probability of black rhinos conceiving a male calf decreased with increasing greenness, supporting the local resource competition hypothesis. In polygynous mammals, males are the dispersing sex. Therefore, rhinos in resource-limited environments and in poor condition should produce more sons (Clark, 1978). In support of our third hypothesis that the proportion of male calves would increase with rainfall and vegetation greenness, there were indications that females from both species were more likely to conceive males as rainfall increased. Furthermore, both species favoured male calves as population density decreased. However, the unsexed individuals could have affected these results. For instance, if these were male calves this would have made the support for our third hypothesis stronger if the calves were born during high productivity years, and weaker if they had been female calves. Additionally, because our variables were derived for each individual and each reproductive event, it is also possible that more males would have strengthened support for the influence of environmental conditions on sex allocation.

For black rhinos, higher rainfall during pregnancy increased the likelihood of having male calves at the Mkuze Game Reserve (Weladji & Leflamme-Mayer, 2011) and decreased the likelihood of having female calves at Pilanesburg (Hrabar & du Toit, 2005). There was no influence of rainfall detected on sex ratios for a population of supplementally-fed game-ranched white rhinos (Ververs *et al*., 2017). Therefore, periods of low vegetation availability did not have an opportunity to influence maternal condition or sex allocation (Law, Fike & Lent, 2014). Although only the greenness results were significant, both populations could potentially show stronger evidence in support of the extrinsic modification and Trivers & Willard hypotheses in future as the population grows, and with better data on maternal condition (Rachlow & Berger, 1998). White rhino mothers in the Hluhluwe-iMfolozi Game Reserve biased investment toward their sons compared to daughters and were more likely to respond to their son's calls (*i.e*. parental investment *via* nursing solicitations was greater for male calves (White *et al*., 2007)). On the other hand, birth sex ratios might be paternally mediated as the ratio of sex-determining chromosomes differ amongst males and is a function of male quality (Douhard, 2017). So rather than just maternal condition and investment influencing sex ratios, both parents might play a part in adaptive sex ratio manipulation (Douhard, 2017). We found evidence that the reproduction of both species was influenced by environmental factors and so it is possible that maternal conditions (and paternal quality) may affect sex allocation because male fitness is related to their growth and maternal investment (Clutton-Brock, 1988).

Effects of density on reproduction

There was little evidence for population density influencing reproductive parameters for both species. This was surprising, because density-dependence should reduce juvenile survival and fertility (Eberhardt, 2002), but increase age at sexual maturity (Sæther, 1997). Black rhinos reached sexual maturity at 6.5 years in a low-density black rhino population at Umfolozi Reserve and at 12 years in a high-density population at Hluhluwe Reserve (Hitchins & Anderson, 1983). White rhinos reached sexual maturity at 7.4 years in a low-density population and at 10.1 years in a high-density counterpart at Matobo National Park (Rachlow & Berger, 1998). In Lapalala the population densities of both black and white rhino were comparable to these low-density populations; however, the age at sexual maturity was more similar to the high-density ones. Since greenness and rainfall had the largest influence on age at sexual maturity in Lapalala, we suggest that both populations were more resource than density limited in the regulation of onset of sexual maturity. A threshold body mass must be attained before large herbivores attain sexual maturity and so reproduction can be suppressed as a result of resource scarcity caused by environmental variability (Hall-Martin *et al*., 1975; Owen-Smith, 1988; Andersen, Gaillard, Linnell & Duncan, 2000; Gaillard *et al*., 2000). Age at primiparity increased with resource limitation and lower-quality browse, with no effect of density, for subpopulations of black rhinos across Namibia (Muntifering, Guerier, Beytell & Stratford, 2023). In contrast, age at primiparity increased with density for the Umfolozi Game Reserve Complex (Hitchins & Anderson, 1983) and Pilanesburg (Hrabar & du Toit, 2005) black rhino populations. No effect of rainfall on age at primiparity was detected in the Pilanesburg population; however, density-dependence on primiparity was reduced during high rainfall years (Hrabar & du Toit, 2005) suggesting that increased resources relieved the rhinos of density-dependent effects.

The Pilanesburg black rhino population had shorter inter-calving intervals when rainfall increased, and this was linked to the relationship between rainfall and forage availability, negating density effects (Hrabar & du Toit, 2005). Mean inter-calving intervals at Lapalala were 2 years, 9 months and 3 years, 2 months for black and white rhinos, respectively, and falls within the moderate and poor fecundity categories (Du Toit, 2006). Inter-calving intervals vary amongst populations and individuals but are influenced by female age and forage availability and quality (Du Toit, 2006). After parturition, female body condition needs time to improve and build up reserves again because most of their energy was spent on late gestation, lactation and weaning (Therrien *et al*., 2007; Ogutu *et al*., 2014). And so, when wet-season rains are sufficient, female rhinos might be able to consume enough and highly nutritious food to recover body condition for the next conception (du Plessis, 1972); whereas, oestrous and fertility could be suppressed because of deteriorating food quality (Owen-Smith, 1988; Owen-Smith & Ogutu, 2013).

Lapalala might possibly be lower in productivity and nutrient status compared to other reserves, and so stochastic environmental events might further limit vegetation quantity and quality for the rhinos (McNaughton, Ruess & Seagle, 1988) and influence their reproduction before density-dependent effects can be observed. However, it is important to recognize that the determination of age at sexual maturity and inter-calving intervals in this study depended on the birth of the first known calf and subsequent calves. Therefore, increased age at sexual maturity and inter-calving intervals might have been influenced by the consequences of environmental conditions on female body condition, but also on pregnancies that were not carried to full-term, abortions and a combination of all three (Nhleko, Parker, Druce, 2017).

This study supports the notion that the reproductive phenology of megaherbivores is not based on anticipated conditions during births but rather conditions experienced during conception (see Owen-Smith, 1988; Cook *et al.*, 2001; Owen-Smith & Ogutu, 2013). Our findings suggest that the reproductive timing of black and white rhinos, especially the age at primiparity, is associated with resource availability as a result of environmental stochasticity and population density. Both rhino species at Lapalala exhibited slower life history traits and vital rates compared to other populations of similar sizes. This could be attributed to the low productivity of the region or lower habitat quality available for the rhinos. Both species are selective feeders and so if their preferred habitat is declining in either quantity or quality, we would expect that their reproduction would be slower (Chamaillé-Jammes, Fritz, Valeix, Murindagomo & Clobert, 2008). By recognizing the importance of food resources, local climate and population density on the vital rates of large herbivores, management at nature reserves can make informed decisions based on population performance and assist population recovery of vulnerable species as climate change will result in more variable conditions. Thus, while reproduction of black and white rhinoceroses appears related to resource availability, reproductive changes in response to climate variability are likely to be influenced by differences in the forage types that each species uses, which in turn will affect their abundance and longer-term conservation status.

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Supplementary material to:

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

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Table S1. Model descriptions: Cox proportional hazard models to analyse age at primiparity of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Table S2. Model descriptions: Generalized linear mixed models to analyse calf sex allocation of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Table S3. Model selection: Cox proportional hazard models to analyse age at primiparity of white rhinoceroses in relation to competitor density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Table S4. Model coefficients: Cox proportional hazard model used to analyse age at primiparity of white rhinoceroses in relation to competitor density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Table S5. Model selection: Generalized linear mixed models used to analyse calf sex ratios of black and white rhinoceroses in relation to competitor density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Table S6. Model coefficients: Generalized linear mixed models used to analyse calf sex ratios of black and white rhinoceroses in relation to competitor density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

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Table S1. Model descriptions: Cox proportional hazard models to analyse age at primiparity of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Model	**Age at primiparity was affected by…**
Rainfall 1 month before conception	total rainfall the 1 month up to conception date
Rainfall 6 months before conception	total rainfall the 6 months up to conception date
Rainfall 12 months before conception	total rainfall the 12 months up to conception date
Rainfall 24 months before conception	total rainfall the 24 months up to conception date
Conception in drought year	conceiving during a drought
Conception during wet year	conceiving during a wet year
El Niño year	El Niño-Southern Oscillation (El Niño) in year of conception
Wet-season rainfall prior to conception	wet-season rainfall experienced prior to conceiving
Rainfall during gestation	total rainfall experienced during gestation period
Rainfall 12 months before birth	total rainfall experienced 12 months before birth
Rainfall 24 months before birth	total rainfall experienced 24 months before birth
Annually integrated NDVI during conception year	annually integrated NDVI experienced during conception year
Maximum wet-season NDVI during conception year	maximum wet-season NDVI reached during conception year
Wet-season integrated NDVI during conception year	wet-season integrated NDVI experienced during conception year
NDVI during birth month	NDVI during birth month
Annually integrated NDVI during birth year	annually integrated NDVI experienced during calf birth year
Wet-season integrated NDVI during birth year	wet-season integrated NDVI experienced during birth year
Annually integrated EVI during conception year	annually integrated EVI experienced during conception year
Wet-season integrated EVI during conception year	wet-season integrated EVI experienced during conception year
Wet-season integrated EVI during birth year	wet-season integrated EVI experienced during birth year
Density during conception year	current density during the conception year
Prior density during conception year	prior density during the conception year, calculated over a two-year block
Prior density (F2) density during conception year	prior density during the conception year, calculated over a four-year block
Conspecific density during conception year	current conspecific density during the conception year
Prior conspecific density during conception year	prior conspecific density during the conception year, calculated over a two-year block

Table S2. Model descriptions: Generalized linear mixed models to analyse calf sex allocation of black and white rhinoceroses in relation to rainfall, greenness and density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Model	**Calf sex was affected by…**
Rainfall 1 month before conception	total rainfall the 1 month up to conception date
Rainfall 6 months before conception	total rainfall the 6 months up to conception date
Rainfall 12 months before conception	total rainfall the 12 months up to conception date
Rainfall 24 months before conception	total rainfall the 24 months up to conception date
Conception in drought year	conceiving during a drought
Conception during wet year	conceiving during a wet year
El Niño year	El Niño-Southern Oscillation (El Niño) in year of conception
Wet-season rainfall prior to conception	wet-season rainfall experienced prior to conceiving
Rainfall during gestation	total rainfall experienced during gestation period
Annually integrated NDVI during conception year	annually integrated NDVI experienced during conception year
Maximum wet-season NDVI during conception year	maximum wet-season NDVI reached during conception year
Wet-season integrated NDVI during conception year	wet-season integrated NDVI experienced during conception year
Annually integrated EVI during conception year	annually integrated EVI experienced during conception year
Wet-season integrated EVI during conception year	wet-season integrated EVI experienced during conception year
Density during conception year	current density during the conception year
Prior density during conception year	prior density during the conception year, calculated over a two-year block
Prior density (F2) density during conception year	prior density during the conception year, calculated over a four-year block
Conspecific density during conception year	current conspecific density during the conception year
Prior conspecific density during conception year	prior conspecific density during the conception year, calculated over a two-year block
Prior conspecific density (F2) during conception year	prior conspecific density during the conception year, calculated over a four-year block

Table S3. Model selection: Cox proportional hazard models to analyse age at primiparity of white rhinoceroses in relation to competitor density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Model	AICc[a]	ΔAICc[b]	w_i[c]	K[d]	Concordance[e]
White rhinos					
Grazer/mixed feeder density during birth year	81.158	0.000	1.000	1	0.552 (0.073)
Prior grazer/mixed feeder density in the conception year	109.792	28.634	0.000	1	0.473 (0.097)

[a] AICc = Akaike's Information Criterion, corrected for small sample size.

[b] ΔAICc = AICc – min(AICc).

[c] w_i = Akaike weight.

[d] K = no. parameters.

[e] Standard error in brackets.

*We attempted this analysis with the other large browsers, grazers and mixed feeders (blue wildebeest, buffalo, eland, elephant, hippo, impala, waterbuck and plains zebra) and we had difficulty getting the black rhino model for the primiparity analysis to converge, probably because of the smaller sample size and the incomplete count data (the census data for the other herbivores is not as comprehensive as the rhino data and only includes data from 2002–present, with large gaps).

Table S4. Model coefficients: Cox proportional hazard model used to analyse age at primiparity of white rhinoceroses in relation to competitor density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

					95% confidence intervals	
Model	Stratum (Origin)	Estimate	S.E.	Hazard ratio	Lower	Upper
White rhinos						
Grazer/mixed feeder density during birth year	All	0.163	0.165	1.177	0.852	1.625

Table S5. Model selection: Generalized linear mixed models used to analyse calf sex ratios of black and white rhinoceroses in relation to competitor density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

Model	AICc[a]	ΔAICc[b]	w_i[c]
Black rhinos			
Browser/mixed feeder density during conception year (animals/km^2)	37.361	0.000	0.778
Browser/mixed feeder density during conception year	38.622	1.261	0.222
White rhinos			
Browser/mixed feeder density during conception year (animals/km^2)	61.276	0.000	1.000

[a] AICc = Akaike's Information Criterion, corrected for small sample size.

[b] ΔAICc = AICc – min(AICc).

[c] w_i = Akaike weight.

Table S6. Model coefficients: Generalized linear mixed models used to analyse calf sex ratios of black and white rhinoceroses in relation to competitor density, Lapalala Wilderness Nature Reserve, South Africa, 1990–2019.

					95% confidence intervals	
Model	Stratum (Origin)	Estimate	S.E.	Hazard ratio	Lower	Upper
Black rhinos						
Browser/mixed feeder density during conception year	All	–0.433	0.383	0.649	0.253	1.280
White rhinos						
Browser/mixed feeder density during conception year	All	–0.111	0.221	0.895	0.579	1.403