



An assessment of the medium-term reproductive success of an extralimital white rhinoceros population

Anja Truter, Nokubonga Mggatsa & Daniel M Parker

To cite this article: Anja Truter, Nokubonga Mggatsa & Daniel M Parker (2022) An assessment of the medium-term reproductive success of an extralimital white rhinoceros population, African Zoology, 57:3, 145-153, DOI: [10.1080/15627020.2022.2132120](https://doi.org/10.1080/15627020.2022.2132120)

To link to this article: <https://doi.org/10.1080/15627020.2022.2132120>



Published online: 27 Oct 2022.



Submit your article to this journal [↗](#)



Article views: 10



View related articles [↗](#)



View Crossmark data [↗](#)

An assessment of the medium-term reproductive success of an extralimital white rhinoceros population

Anja Truter¹, Nokubonga Mgqatsa¹ and Daniel M Parker^{1,2*} 

¹ Wildlife and Reserve Management Research Group, Department of Zoology and Entomology, Rhodes University, Makhanda, South Africa

² School of Biology and Environmental Sciences, University of Mpumalanga, Mbombela, South Africa

* Correspondence: daniel.parker@ump.ac.za

The white rhinoceros (*Ceratotherium simum*) is threatened primarily due to continued poaching for its horns. In South Africa, partly to promote the conservation of the species, white rhinos have been introduced into areas where they did not occur historically (i.e. where they are considered extralimital). Few studies have investigated the conservation contribution of extralimital white rhinos to the overall national herd. We aimed to determine whether the white rhinos introduced to a private game reserve in the Eastern Cape province have been successful from a reproductive perspective. We calculated inter-calving intervals, age at first calving, sex ratios of calves, and recruitment rates for white rhinos at a single site between 1992 and 2019. The average net annual population growth rate for the population was 10%, which is higher than the recommended 5% by the Biodiversity Management Plan for white rhinos. Trends in density-dependent parameters such as age at first calving and inter-calving intervals also indicated that the study population is still well below the density at which ecological constraints may manifest. We demonstrate that an extralimital white rhino population in the Eastern Cape can be successful from a reproductive perspective.

Keywords: *Ceratotherium simum*, growth rate, life history, population dynamics, white rhino

Introduction

The reproductive parameters of large, herbivorous mammals are influenced by various demographic parameters including intrinsic population growth rate, inter-calving interval, age at first calving, conception rate, sex ratio of the population, the proportion of females giving birth per year, and the survival rate of calves (Balfour et al. 2019; Gaillard et al. 1998; Owen-Smith 2000; Rachlow and Berger 1998). These demographic parameters are also affected by various environmental drivers such as drought, disease, fire, floods, and human management which can all negatively affect reproductive success (Ferreira et al. 2019; Nhleko et al. 2017). The relative importance of these environmental and human factors differ depending on the species and the life history stage of the animal (Ferreira et al. 2019). For example, droughts can result in poorer food quality which can negatively impact adult female grazers, resulting in a decline in conception rates and, ultimately, fewer calves being born (Ferreira et al. 2019). Nevertheless, collectively these factors can influence herbivore reproductive parameters either through resource limitation (Coe et al. 1976), and are known as bottom-up factors, or through death or the fear of death (Hopcraft et al. 2010), and are known as top-down factors.

Density-dependent effects can also play a significant role in the reproductive parameters of large herbivores, whereby high-density populations may cause females to give birth to their first calves at an older age, and/or drive longer inter-calving intervals, resulting in slower overall intrinsic growth rates (Rachlow and Berger 1998). By contrast,

when large herbivores are found at lower densities, they tend to have their first calf at a younger age, have shorter inter-calving intervals and, consequently, have accelerated intrinsic growth rates (Rachlow and Berger 1998). Moreover, the sex ratios of calves born to large herbivores have also been linked to environmental conditions (Berkeley and Linklater 2010). Specifically, the physical condition of the female when she conceives influences the sex of the subsequent calf and has been demonstrated to be linked to the probability of the calf surviving once born (Berkeley and Linklater 2010). Significantly, sex-biased populations may present unique conservation challenges for threatened large herbivores such as the white rhinoceros (*Ceratotherium simum* Burchell, 1817).

Since the arrival of European explorers and hunters in South Africa in the early 1800s, white rhinoceroses (white rhinos hereafter) have been hunted (Carruthers 2005). In addition, white rhinos are also poached for their horns that are sold on Asian markets (Emslie et al. 2016). In combination, the hunting and poaching of white rhinos (top-down pressure) has resulted in their extirpation from several African countries, and severely depressed populations in others (Emslie and Brooks 1999; Player 1967). In 1930 in South Africa, only a small population of approximately 120 animals were left in the area known today as the Hluhluwe-iMfolozi Park (HiP) (Skinner and Chimimba 2005). The Natal Administrators Executive Committee was tasked to make recommendations to save the white rhino from extinction in South Africa (Player

1967). The decision was to relocate white rhinos from the HiP to other suitable reserves to increase numbers. The launch of what became known as “Operation Rhino” in 1960, and ran for approximately a decade, resulted in the relocation of about 4 000 white rhinos to eight other African countries and various reserves around South Africa (Player 1967; Skinner and Chimimba 2005). White rhino numbers gradually started to increase from 437 in 1953 to 18 064 at the end of 2017 (IUCN 2020). However, due to the increasing intensity of rhino poaching more recently, white rhino numbers have started to decrease (IUCN 2020).

Although the in-situ conservation of a threatened species within its native distribution range is preferred, ex situ conservation efforts, out of the native range can be used as an additional conservation measure (Kasso and Balakrishnan 2013). White rhinos in South Africa are a good example of the latter where they have been introduced as an extralimital species on various private game reserves across the country, including within the Eastern Cape province (Kraai 2010). Irrespective of whether a population is native or extralimital, some white rhino populations in South Africa are managed under the guidelines set out by the Biodiversity Management Plan (BMP) for White Rhinoceros in South Africa to achieve certain demographic and genetic goals (Emslie and Brooks 1999; Knight et al. 2015). To sustain the national white rhino herd, the BMP recommends a 5% growth rate for a population as a realistic target. However, individual rhino managers on private reserves are encouraged to achieve an intrinsic growth rate of between 7 and 9% to make removals and relocations possible (Balfour et al. 2019; Cousins et al. 2008; Knight et al. 2015). If such intrinsic growth rates can be achieved, private rhino owners can contribute to rhino conservation by countering the losses experienced through poaching (Cousins et al. 2008; Knight et al. 2015). However, where white rhinos are extralimital, it is conceivable that resource and condition constraints (bottom-up pressure) may negatively impact upon their vital rates, leading to reduced fecundity, survival, immigration and emigration. Nevertheless, with active management, the negative effects on population vital rates can be overcome through various interventions that alter conditions and resources and facilitate emigration and immigration. As such, extralimital populations may perform better than in-situ populations.

Here, we investigate the reproductive parameters of an extralimital population of white rhinos on a private game reserve in the Eastern Cape province between 1992 and 2019. We assess the reproductive parameters of age at sexual maturity, inter-calving interval, and recruitment rates and suggest potential drivers of the measured reproductive parameters. We predicted that since the population is actively managed to facilitate immigration and emigration via translocation, vital rates that are linked to such management interventions will respond positively. Specifically, we hypothesised that net annual growth rate would be increased by management interventions because the population would likely be maintained below its ecological carrying capacity. Similarly, we hypothesised that recruitment rates would be positive with active rhino management in place. However, since the population is an extralimital one and occurs at a site where bottom-up conditions may not necessarily be optimal,

rhino age structures (i.e., skewed towards older age classes) and sex ratios (i.e., skewed towards a male dominated population) will be indicative of a population under stress.

Methods

Study animals

The study site (details withheld for security purposes) introduced their first white rhinos in 1992 and this introduction included four adult cows, followed by an additional two adult bulls and one sub-adult heifer in 1993, making it a total of seven animals. Additional white rhinos were introduced during 2002 (two heifers and one sub-adult bull) and 2006 (two adult cows, both accompanied by calves). All white rhinos originated from HiP in KwaZulu-Natal, except for the two adult cows and calves in 2006 which came from the Kruger National Park. Since 2007, the study site has sold a total of 20 white rhinos, including nine adult bulls, four adult cows with calves at foot, three sub-adult bulls and three heifers. As in other species, these sales were to prevent inbreeding within the current population, prevent fighting and to supply newly established reserves with breeding stock (Benjamin-Fink & Reilly 2017), and to generate revenue to cover the costs of management and security.

Monitoring and individual identification

Since the introduction of rhinos to the study site, a wildlife monitoring system has been in place. The anti-poaching team was originally responsible for the monitoring of the rhinos and collected nearly daily data on births, deaths, overall health, and the physical locations of the rhinos. However, from September 2007, Anja Truter was appointed as the full-time rhino monitor. White rhinos at the study site were all microchipped in both horns and were ear notched to allow for individual identification (see Table 1 and Figure 4 for individual identification codes). Since rhinos can be reliably identified in the field by unique ear notches (Nhleko et al. 2017), Anja Truter made daily sightings of all rhinos (where possible) and their locations between 2007 and 2019. Records of any new births, deaths, and behaviours such as fighting, mating, dominant bull were also recorded.

Population growth

To determine the net population growth rate, annual growth percentages were calculated on 31 December of each year, whereby mortalities, sales and any additional rhino introductions were incorporated – also known as the instantaneous growth rate (Ferreira et al. 2012). Net population growth rate was calculated following Nhleko et al. (2017) and calculated as follows:

$$r = \left(\frac{\text{Prespop}_n}{\text{Prevpop}_n} \right)^{\frac{1}{\text{year}} - 1}$$

where, r equals population growth rate; Prespop_n equals total rhino present for specific year; Prevpop_n equals total rhino from previous year and year is the calendar year. To evaluate the influence of management removals of rhinos on the net population growth rate, we used the growth rate calculation above inclusive of all rhino removals between

Table 1: The age at first calving for seven female white rhinos on a private game reserve in the Eastern Cape, South Africa where the exact birth date of their first calf was known. Age at first calving is given in years and months, the year a female conceived and the age in years and months at conception. The gestation period of a white rhino is 16 months (Player and Feely 1960). Thus, age of first conception was back calculated from age at first calf using this information

Female rhino	Age at first calf in years	Age at first calf in months	Year conceived	Age conceived in years	Age conceived in months
W 51	7.0	84	August 2001	5.8	69
W 52	8.1	97	October 2006	6.9	83
W 54	9.1	109	August 2012	7.9	95
W 76	5.3	63	November 2013	3.1	37
W 515	5.2	62	October 2015	3.1	37
W 75	9.0	108	July 2015	7.8	94
W 103	5.1	61	September 2015	2.6	31

1992 and 2019 and exclusive of all rhino removals over the same period (Ferreira et al. 2012).

Inter-calving interval

To calculate the inter-calving intervals, only adult cows who gave birth to two or more calves during the study period were used (Hitchins and Anderson 1983). A total of 11 cows were used to analyse inter-calving intervals. Using these females, we were able to generate 54 separate inter-calving intervals. Inter-calving intervals were calculated by using the total months between any two successive births (Mostert et al. 2010).

Recruitment rate

Recruitment rate represents the number of calves born and still alive at the end of the year as a proportion of adult females (only females >7 years old) in a population at the start of each year. The calculation was adapted from Nhleko et al. (2017):

$$REC_t = \frac{\text{Surviving births}_t}{Ad F_{t-1}}$$

where, *Surviving births_t* equals to the number of calves that survived under the year of review and *Ad F_{t-1}* equals to the number of adult females (>7 years old).

Statistical analyses

A Kruskal-Wallis test was conducted to examine the net population growth rate over three periods (Period one 1992–1999; Period two 2000–2009; Period three 2010–2019). The periods were divided equally and done to determine whether active rhino management contributed to artificially increasing or decreasing annual growth rates. In addition, a Student's t-test was used to test whether there was a significant difference between the net annual growth rate inclusive of rhino removals and the net annual growth rate exclusive of rhino removals (i.e., the effect of active rhino management).

A Chi-square goodness-of-fit test was used to determine whether there was a significant relationship between age structure and sex with respect to rhino mortalities. Similarly, to determine whether there was any skew in the sex ratio of rhino calves born in such an extralimital environment, a Chi-square goodness-of-fit test was used.

Recruitment rates were calculated for the study period of 1992–2019. Data were tested for normality and a one-way ANOVA was used to determine any significant differences in the recruitment rates of the rhino population over the same three periods used for net annual growth rate. This test was used to determine whether active rhino management positively influenced recruitment rates.

The Kruskal-Wallis tests and one-way ANOVAs were both conducted using the statistical computer software R-Studio (Afero General Public Licence version 3, RStudio, PBC). The Chi-square goodness-of-fit tests and the Student's t-test were conducted using Microsoft Excel 2007 (Version 16.0.13029.20232; Microsoft Corporation, USA).

Results

Population growth rate

The white rhino population had a mean annual net growth rate of 10% per annum (Figure 1). This growth percentage included all mortalities, sales, and additional introductions over the 28-year study period. The mean annual net growth rate exclusive of rhino removals (i.e., representing the effect of active rhino management) was 11% per annum (Figure 1) and there was no significant difference between the two calculated growth rates over time ($t = 0.89$, $df = 25$, $p = 0.19$). In other words, the instantaneous annual growth rates were not significantly affected by active rhino management at the site. Similarly, despite visible fluctuations over time (Figure 1), there were no significant differences in the inter-annual growth rates among the three separate periods assessed ($H = 1.87$, $df = 2$, $p = 0.39$).

The number of mortalities between 1996 and 2000 exceeded the number of births, resulting in a low net growth rate (4%) during that 5-year period (Figure 2). Despite the number of deaths exceeding the number of births during this period, the relatively high number of rhinos introduced (Figure 2) would have maintained the overall positive growth rate. Regular live sales of white rhinos also took place from 2004 onwards. Although not significant, the year following sales generally resulted in a negative net growth rate, except for 2016 and 2017 (Figure 2). The high number of births during these years likely buffered the effect of the removals. Nevertheless, between 2009 and 2013, the net growth rate decreased in four consecutive years (Figure 1).

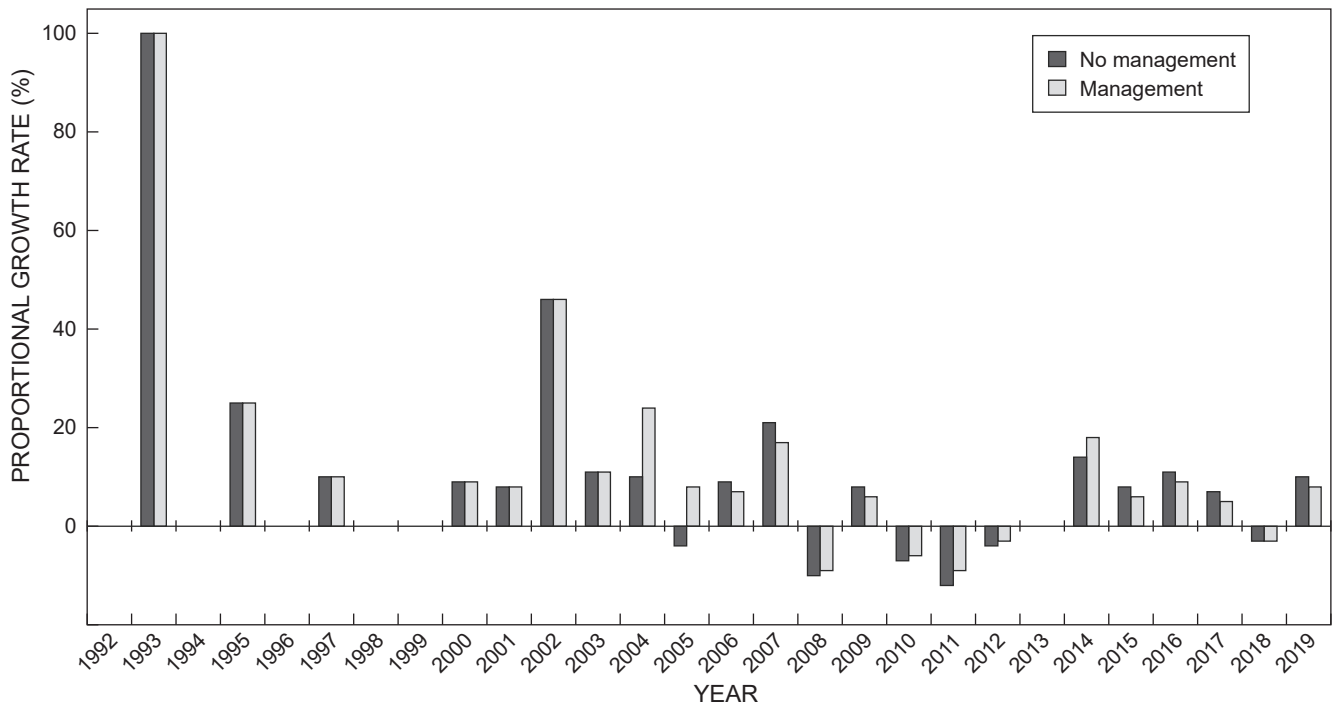


Figure 1: White rhino population growth rates between 1992 and 2019 on a private game reserve in the Eastern Cape, South Africa. Dark grey bars represent the instantaneous growth rate when management removals were not included and light grey bars represent when management removals were factored back into the growth rate

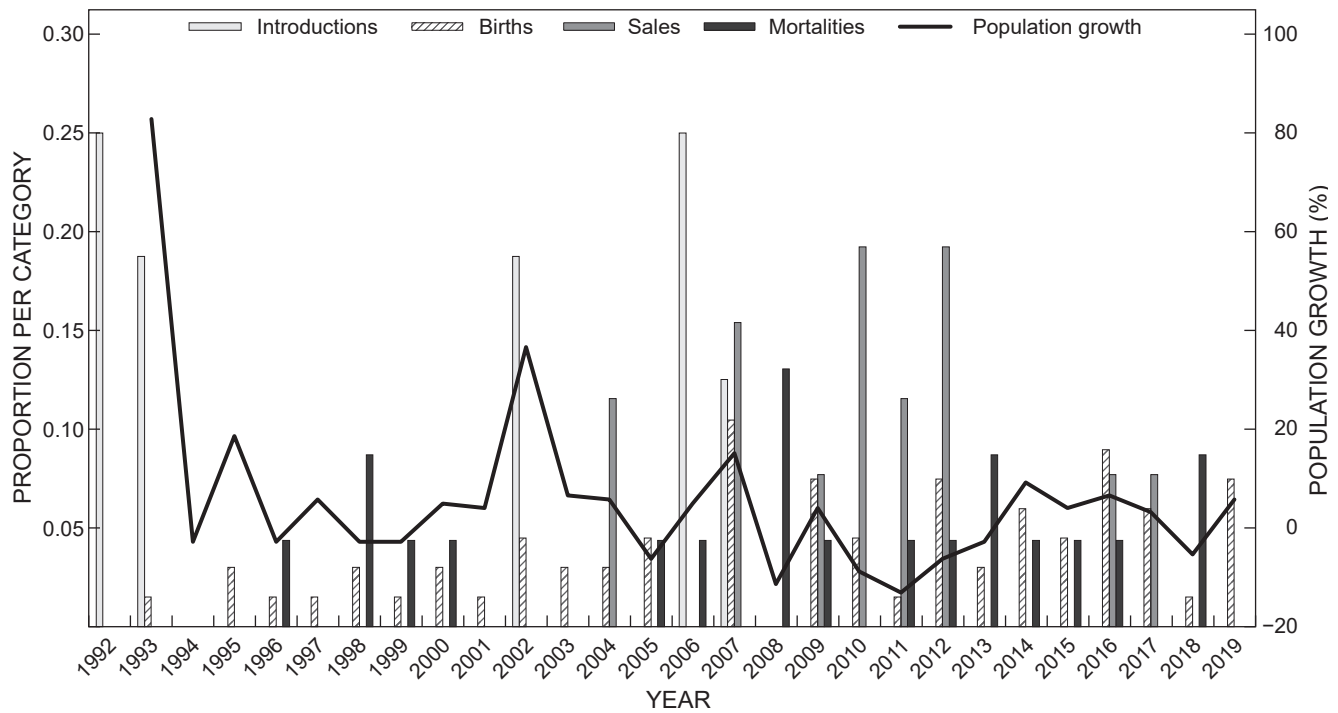


Figure 2: White rhino population growth rates for the years 1992–2019 on a private game reserve in the Eastern Cape, South Africa (line curve), including proportional; introductions; births of calves; sales and mortalities

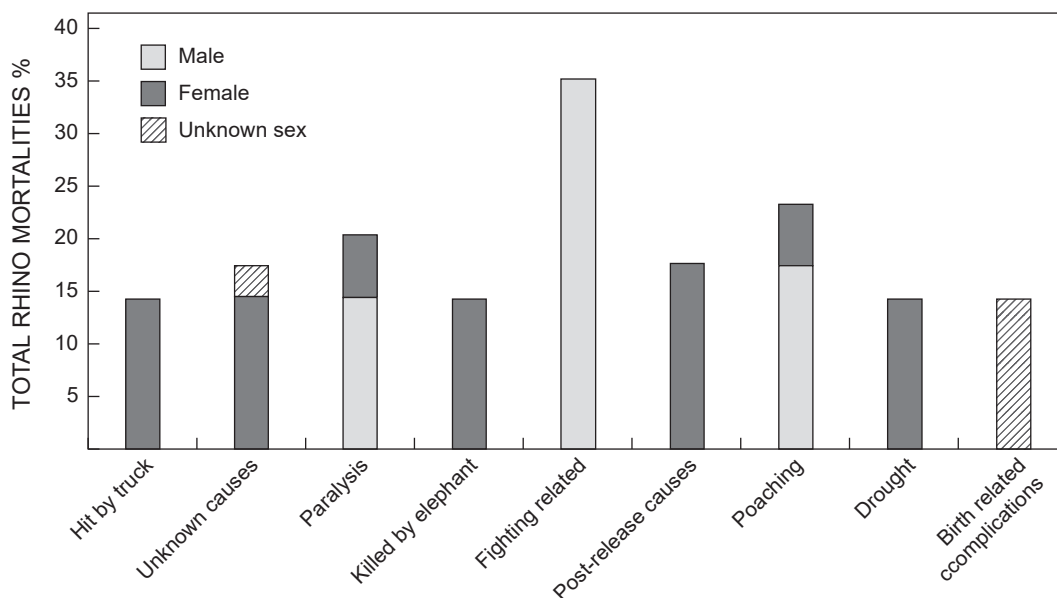


Figure 3: White rhino mortality record including cause of death and percentage of total mortalities recorded on a private game reserve in the Eastern Cape, South Africa. The sex ratio is indicated as a percentage for each cause of death

Mortalities and removals

Of the total mortalities recorded, 35% were due to fighting (Figure 3). The second highest cause of death was poaching, contributing to 17% of total deaths and comprised 50% female and 50% males. The third highest cause of death was paralysis (13% of total mortalities recorded) believed to be caused by *Clostridium* sp. Infections. Post-release causes and unknown causes, both contributing to 9% of total mortalities were the next most important drivers of mortality (Figure 3). There was no significant sex bias in the rhino mortalities observed during the study period ($\chi^2 = 4.35$; $df = 13$; $p = 0.83$).

During the study period, of the total white rhino sales 62% were males from different age classes (31% for ≥ 7 years, 19% for 3–7 years and 12% for 1–2 years) and 38% were females (15% for ≥ 7 years, 15% for 3.5–7 years, 4% for 2–3.5 years and 4% for 1–2 years).

Inter-calving intervals

Inter-calving intervals ranged between 1.6–3.8 years (19–46 months) with an average of 2.6 years (31 months). The shortest inter-calving interval recorded was 19 months. Two other cows both had the second shortest inter-calving intervals with an average of 24 months (2 years). Four cows had average inter-calving intervals longer than 30 months. Another cow had an inter-calving interval of 31 months, followed by a cow each at 32, 33 months and 34 months. Two other cows each had one inter-calving interval which exceeded 40 months. Another had an interval of 46 months in 1997 when she gave birth to her second calf and an older cow also had an interval of 46 months during 2003 and it was her third calf.

The most calves born to a specific cow was nine. The exact age of the cow is unknown and the only details available for her were that she arrived at the site as a sub-adult in 1993. She gave birth to her first calf during

May 1998 and could therefore be assumed to have been born between 1987 and 1990, making her between the ages of 30–33 years old. The second highest number of calves born was eight and from a cow presumed to be the oldest white rhino at the study site.

Sex ratio of calves

A total of 67 white rhino calves were recorded as being born on the study site during the study period. Of the 67 calves born, 39 (58.2%) were males, 26 (38.8%) were females and 2 (3.0%) the sex was unknown (Figure 4). However, there were no significant differences in the sex ratios of calves born over time ($\chi^2 = 12.34$; $df = 13$; $p = 0.11$). Of the 14 cows available for this assessment, four produced more male calves than females (Figure 4). Three cows produced calves in a 50:50 ratio, and three cows produced more female calves than males. Four cows only produced male calves and one cow only produced female calves (Figure 4).

Age at first calving

To determine the age at first calving, only seven females were used as they were the only rhinos whose birth dates were known and who (during the period of study) had their first calves (Table 1). The exact birth dates of cows introduced during 1992 and 1993 were unknown. In addition, no information regarding any of their previous calves was available. Thus, these animals had to be excluded from this assessment. The mean age at first calving was 84 months (7 years). The range was between 52 (4.3 years) and 109 months (9.1 years). The gestation period of a white rhino is 16 months (Player and Feely 1960). Thus, the youngest age at first successful mating was for one cow at 46 months (three years, ten months) and the oldest mating was for a cow at 93 months or seven years, nine months (Table 1).

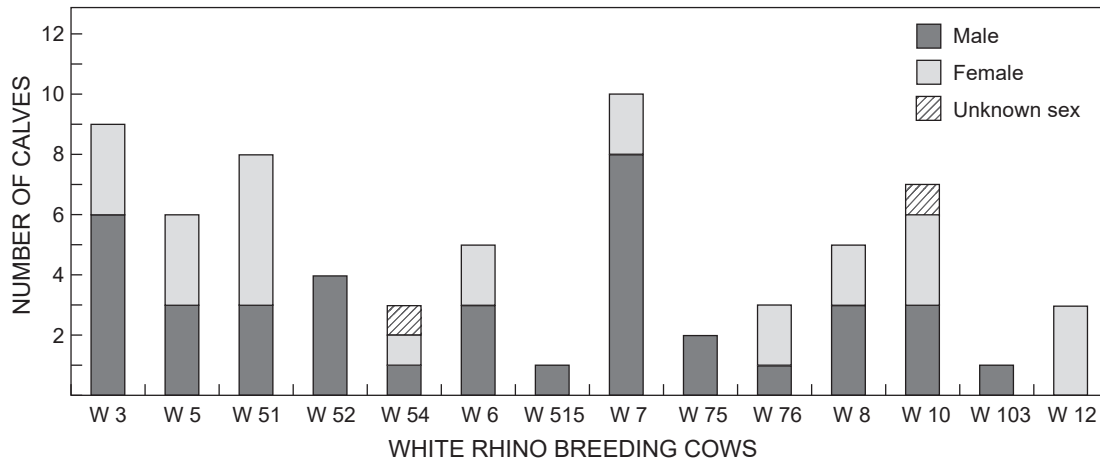


Figure 4: The sex ratio of calves born to white rhino cows on a private game reserve in the Eastern Cape, South Africa during the study period from 1992 to 2019. A total of 67 calves were born

Recruitment rate

The recruitment rate was lowest during 1994, 2006 and 2008 when no calves were born, followed by 2018 and 2011 (Table 2). The recruitment rate was at its highest during 2007 (Table 2). Nevertheless, there were no significant differences in the recruitment ($F_{(2, 24)} = 1.38; p = 0.27$) over time.

Discussion

Newly established large herbivore populations generally result in a rapid intrinsic growth rate following their introduction (Rachlow and Berger 1998). According to the white rhino BMP (Knight et al. 2015), the preferred intrinsic annual growth rate for rhino populations should be at least 5%. Balfour et al. (2019) further recommended that such growth rates should be kept between 7–9%, to include regular sales of animals. Importantly, the manipulation of the density of rhinos on a particular reserve is likely the best way to control the growth rate of the population (Balfour et al. 2019). Our data support this contention with evidence for our first hypothesis that population growth rates are positively influenced by active rhino management.

Game reserves and National Parks within South Africa show an intrinsic white rhino annual growth rate of between 2 and 9% (Knight et al. 2015). The intrinsic growth rate for the national herd averaged 6.6% between 1991 and 2012 has since been under enormous pressure due to the re-awakening of poaching for rhino horn (Knight et al. 2015). The national population intrinsic annual growth rate currently stands at 5%. However, if the losses from poaching are incorporated, South African white rhino populations are only currently increasing at a net rate of 2% (Knight et al. 2015).

Mortalities

The causes of mortality for white rhinos at the site were similar to what has been documented in other reserves. Fighting-related deaths contributed the highest percentage of deaths, and only involved male rhinos. This cause of death has been a regular occurrence on other reserves where fighting-related mortalities contributed to the highest

Table 2: The recruitment rates of the white rhinos on a private game reserve in the Eastern Cape, South Africa for the period 1992–2019

Year	Adult cows >7 years	Total calves born	Calves survived >1 yr	Deaths >1 year	Recruitment rate
1992	4				
1993	4	1	1		0.25
1994	4				0.00
1995	4	2	2		0.50
1996	4	1	1		0.25
1997	4	1	1		0.25
1998	4	2	1	1	0.25
1999	4	1	1		0.25
2000	4	2	2		0.50
2001	4	1	1		0.25
2002	5	3	3		0.60
2003	5	2	2		0.40
2004	5	2	2		0.40
2005	6	3	3		0.50
2006	7				0.00
2007	8	7	7		0.88
2008	8				0.00
2009	7	5	5		0.71
2010	7	3	3		0.43
2011	7	1	1		0.14
2012	7	5	5		0.71
2013	8	2	2		0.25
2014	8	4	4		0.50
2015	9	3	3		0.33
2016	10	6	5	1	0.50
2017	10	4	4		0.40
2018	9	1	1		0.11
2019	8	5	4	1	0.50
Average					0.37

number of deaths (Owen-Smith 2000). Fighting-related deaths is believed to be correlated with rhino densities (Rachlow and Berger 1998). Increased density within fenced reserves leads to aggression amongst rhinos, resulting in

increased fighting and deaths (Ferreira et al. 2019). Of the total fighting-related deaths (35%), 8.75% of the mortalities occurred during 2008. In both the Kruger National Park (hereafter KNP) and the HiP, mortality rates have been shown to increase during periods of drought (Ferreira et al. 2019; Owen-Smith 2000). Since the site received its lowest total yearly rainfall in 2008, it is possible that fighting-related mortalities in this fenced reserve were exacerbated due to limited grazing (Ferreira et al. 2019).

Inter-calving interval

Inter-calving intervals in white rhinos vary between two and four years (Owen-Smith, 2000). The longest single inter-calving interval was 4 years and 3 months (51 months). According to Hitchens and Anderson (1983), any inter-calving interval longer than 40 months or 3 years and 3 months could be due to the cow either losing the calf shortly after birth or because she aborted. In the population we studied, three cows had inter-calving intervals longer than 40 months. We therefore assume that three additional calves may have been born but were lost during the study period. According to Pienaar et al. (1992), in the KNP, the age of white rhino cows also influenced their inter-calving intervals. Younger cows tended to have shorter inter-calving intervals than older cows (Pienaar et al. 1992). However, in our study, although not tested statistically, female age did not appear to influence inter-calving intervals with younger cows having both shorter and longer inter-calving intervals compared to their older counterparts. Inter-calving intervals in Whovi National Park, Zimbabwe were strongly influenced by density (Rachlow & Berger 1998). In the low-density areas, the average inter-calving interval was 2 years 9 months, while in higher density areas the inter-calving interval averaged 3 years 3 months (Rachlow & Berger 1998). Similarly, the mean inter-calving interval recorded for HiP in KwaZulu-Natal was 2 years 6 months (Owen-Smith 2000). The shortest inter-calving for white rhinos (1 year 8 months) was also recorded in HiP (Owen-Smith 2000). Inter-calving intervals recorded by Kraai (2010) on various game reserves in the Eastern Cape ranged between 2 years 3 months to 2 years and 6 months.

Sex ratios

Sex ratios in rhino populations influence the reproductive parameters within the populations (Okita-Ouma et al. 2009). The Trivers-Willard hypothesis suggests that in a polygynous population, females will produce more male calves during favourable conditions than females (Cameron, 2004; Law et al. 2014). The hypothesis is that male offspring have a greater chance of contributing to the positive reproductive rate of the population than females during poor environmental conditions (Law et al. 2014). Therefore, rainfall may have a significant influence on the sex ratio of rhino calves (Law et al. 2014). Factors such as density and vegetation condition will also influence condition of breeding females which could lead to skewed sex ratios (Okita-Ouma et al. 2009). Facultative adjustment to calf sex allocation has been suggested by Owen-Smith (2000) due to the rhino's adaptable inter-calving intervals and a seasonal conception period. Importantly, skewed sex ratios within populations that are female biased will result in

an increased reproduction rate (Okita-Ouma et al. 2009). In a study conducted by White et al. (2007) in HiP, they found that mothers invested more time in raising male calves than female calves and would normally be followed by an extended inter-calving interval period. The results, although somewhat male-biased, showed no significant difference in calf sex ratios. As such, the reproductive success of our population does not currently appear to be compromised by a male-biased sex ratio or negatively affected by being extralimital, contrary to our third hypothesis.

Age at first calving

Age at first calving is dependent on various factors such as density, body condition and rainfall (Law et al. 2013; Rachlow and Berger 1998). In K-selected animals such as white rhinos, fertility is directly linked to the physical condition of the female and females will only reach sexual maturity once 80% of their bodyweight has been achieved (Law et al. 2013). Rainfall has been found to be one of the main contributing factors influencing demographic parameters in megaherbivores (Law et al. 2013). Low rainfall generally has a negative effect on breeding rhino cows whereby conception periods are delayed, resulting in prolonged inter-calving intervals and reduced population growth (Law et al. 2013). Density-dependence is also considered to negatively influence age at first calving when densities are high (Law et al. 2013; Rachlow and Berger 1998). In addition, female white rhinos that reproduce at an early age have a genetic advantage over other females and should produce more calves during their lifetimes, resulting in increased population growth rates (Rachlow and Berger 1998). There was no clear evidence that the age of first calving for rhinos at the study site was impacted by density-dependence in any way because of the variability observed in the ages at first calving likely due to the active rhino management practiced at the site. However, our relatively low sample of only seven females that were available for this analysis means that this contention should be interpreted with caution.

Recruitment rate

A population's recruitment rate can be used as an indicator of reproductive performance over time (Law et al. 2013). Recruitment rate is determined by the number of offspring a specific female produces in her lifetime. A decrease in calf survivorship can have a negative impact on growth rates in the long-term and is believed to be influenced by density (Rachlow and Berger 1998). At the study site, the recruitment rate did not change significantly over time, indicating that population growth has likely been consistent over time, and that calf survivorship has probably contributed to the continued growth of the population (Rachlow and Berger 1998). Thus, our second hypothesis is neither accepted nor rejected.

Conclusion

The white rhinos at the study site have thus far exceeded the objectives of the white rhino BMP with an average net annual growth rate of 10% over the last 28 years. Inter-calving intervals have decreased with increased density, indicating that the population is increasing at a

steady pace. However, inter-calving intervals have begun to increase latterly. Although the sex ratio of calves born was not significant, there were slightly more male calves born than females which could have a negative impact on the population growth rate in the future. Nevertheless, the reproductive performance of the white rhinos at the site is comparable with other endemic populations. We have demonstrated that an extralimital white rhino population can contribute to the ongoing conservation of this threatened species (IUCN 2020) in the face of poaching pressure (Emslie et al. 2016). However, the continued persistence of this extralimital population and its potential impact on the indigenous biodiversity of the Eastern Cape, which has not been adequately assessed, should be a key future research priority.

Acknowledgements — We thank all the members of the Anti-Poaching team and the site's wildlife department for their assistance and dedication.

ORCID

Daniel M Parker: <https://orcid.org/0000-0001-7555-5674>

References

- Balfour D, Barichiev C, Gordon C, Brett R. 2019. A Theory of Change to grow numbers of African rhino at a conservation site. *Conservation Science and Practice* 1: e40. <https://doi.org/10.1111/csp2.40>.
- Benjamin-Fink N, Reilly BK. 2017. Conservation implications of wildlife translocations; The state's ability to act as conservation units for wildebeest populations in South Africa. *Global Ecology and Conservation* 12: 46–58. <https://doi.org/10.1016/j.gecco.2017.08.008>.
- Benjamin-Fink N, Reilly BK. 2010. Annual and seasonal rainfall may influence progeny sex ratio in the black rhinoceros. *South African Journal of Wildlife Research* 40: 53–57. <https://doi.org/10.3957/056.040.0102>.
- Cameron EZ. 2004. Facultative adjustment of mammalian sex ratios in support of the Trivers–Willard hypothesis: Evidence for a mechanism. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 271: 1723–1728. <https://doi.org/10.1098/rspb.2004.2773>.
- Carruthers J. 2005. Changing perspectives on wildlife in southern Africa, C.1840 to C.1914. *Society and Animals* 13: 183–200. <https://doi.org/10.1163/1568530054927762>.
- Coe MJ, Cumming DH, Phillipson J. 1976. Biomass and production of large African herbivores in relation to rainfall and primary production. *Oecologia* 22: 341–354. doi:10.1007/BF00345312.
- Condy PR. 1973. *The population status, social behaviour and daily activity pattern of the white rhino (Ceratotherium simum) in Kyle National Park, Rhodesia*. PhD Thesis. University of Rhodesia.
- Cousins JA, Sadler JP, Evans J. 2008. Exploring the role of private wildlife ranching as a conservation tool in South Africa: Stakeholder perspectives. *Ecology and Society* 13: art43. <https://doi.org/10.5751/ES-02655-130243>.
- Emslie R, Brooks M. 1999. *African rhino: Status survey and conservation action plan*. IUCN, World Conservation Union.
- Emslie R, Milliken T, Talukdar B, Ellis S, Adcock K, Knight M. 2016. *African and Asian Rhinoceroses – Status, Conservation and Trade*. A report from the IUCN Species Survival Commission (IUCN SSC) African and Asian Rhino Specialist Groups and TRAFFIC to the CITES Secretariat pursuant to Resolution Conference 9.14 (Rev. CoP17) (CoP17 Doc. 68; p. 21). CITES. http://www.rhinosourcecenter.com/pdf_files/156/1560170144.pdf [accessed 22 September 2022].
- Ferreira SM, Botha JM, Emmett MC. 2012. Anthropogenic influences on conservation values of white rhinoceros. *PLoS ONE* 7: e45989. <https://doi.org/10.1371/journal.pone.0045989>.
- Ferreira SM, le Roex N, Greaver C. 2019. Species-specific drought impacts on black and white rhinoceroses. *PLoS ONE* 14: e0209678. <https://doi.org/10.1371/journal.pone.0209678>.
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG. 1998. Population dynamics of large herbivores: Variable recruitment with constant adult survival. *Trends in Ecology and Evolution* 13: 58–63. [https://doi.org/10.1016/S0169-5347\(97\)01237-8](https://doi.org/10.1016/S0169-5347(97)01237-8).
- Hitchins PM, Anderson JL. 1983. Reproduction, population, characteristics and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/ Corridor/Umfolozzi Game Reserve Complex. *South African Journal of Wildlife Research* 13: 78–85.
- Hopcraft JGC, Olf H, Sinclair ARE. 2010. Herbivores, resources and risks: alternating regulation along primary environmental gradients in savannas. *Trends in Ecology and Evolution* 25: 119–128. doi:10.1016/j.tree.2009.08.001.
- IUCN. 2020. *Ceratotherium simum*. In: Emslie R (ed.), *The IUCN Red List of Threatened Species 2020: e.T4185A45813880* [Data set]. International Union for Conservation of Nature. <https://doi.org/10.2305/IUCN.UK.2020-1.RLTS.T4185A45813880.en>.
- Kasso M, Balakrishnan M. 2013. *Ex Situ* conservation of biodiversity with particular emphasis to Ethiopia. *ISRN Biodiversity* 2013: 1–11. <https://doi.org/10.1155/2013/985037>.
- Knight MH, Emslie RH, Smart R, Balfour D. 2015. Biodiversity Management Plan for The White Rhinoceros (*Ceratotherium simum*) in South Africa 2015–2020. Department of Environmental Affairs, Pretoria.
- Kraai M. 2010. *White rhinoceros populations in the Eastern Cape: Distribution, performance and diet*. MSc thesis. Nelson Mandela Metropolitan University, South Africa.
- Law PR, Fike B, Lent PC. 2013. Mortality and female fecundity in an expanding black rhinoceros (*Diceros bicornis minor*) population. *European Journal of Wildlife Research* 59: 477–485. <https://doi.org/10.1007/s10344-013-0694-y>.
- Law PR, Fike B, Lent PC. 2014. Birth sex in an expanding black rhinoceros (*Diceros bicornis minor*) population. *Journal of Mammalogy* 95: 349–356. <https://doi.org/10.1644/13-MAMM-A-175>.
- Mostert B, Van der Westhuizen R, Theron H. 2010. Calving interval genetic parameters and trends for dairy breeds in South Africa. *South African Journal of Animal Science* 40: 156–162. <https://doi.org/10.4314/sajas.v40i2.57288>.
- Nhleko ZN, Parker DM, Druce DJ. 2017. The reproductive success of black rhinoceroses in the Hluhluwe–iMfolozi Park, KwaZulu-Natal, South Africa. *Koedoe* 59: a1386. <https://doi.org/10.4102/koedoe.v59i1.1386>.
- Okita-Ouma B, Amin R, van Langevelde F, Leader-Williams N. 2009. Density dependence and population dynamics of black rhinos (*Diceros bicornis michaeli*) in Kenya's rhino sanctuaries. *African Journal of Ecology* 48: 791–799. <https://doi.org/10.1111/j.1365-2028.2009.01179.x>.
- Owen-Smith RN. 2000. *Megaherbivores: The influence of very large body size on ecology* (reprint). Cambridge: Cambridge University Press.
- Pienaar DJ, Bothma JDP, Theron GK. 1992. Landscape preference of the white rhinoceros in the southern Kruger National Park. *Koedoe* 35: 1–7. <https://doi.org/10.4102/koedoe.v35i1.384>.
- Player I. 1967. Translocation of white rhinoceros in South Africa. *Oryx* 9: 137–150. <https://doi.org/10.1017/S0030605300006165>.
- Player IC, Feely JM. 1960. A preliminary report on the square-lipped rhinoceros (*Ceratotherium simum simum*). *Lammergeyer* 1: 3–21.

- Rachlow JL, Berger J. 1998. Reproduction and population density: trade-offs for the conservation of rhinos in situ. *Animal Conservation* 1: 101–106. <https://doi.org/10.1111/j.1469-1795.1998.tb00017.x>.
- Skinner JD, Chimimba CT. 2005. *The mammals of the southern African subregion* (3rd ed.). Cambridge: Cambridge University Press. <https://doi.org/10.1017/CBO9781107340992>.
- Van der Merwe P, Saayman M. 2003. Determining the economic value of game farm tourism. *Koedoe* 46: 103–112. <https://doi.org/10.4102/koedoe.v46i2.59>.
- White AM, Swaisgood RR, Czekala N. 2007. Ranging patterns in white rhinoceros, *Ceratotherium simum simum*: Implications for mating strategies. *Animal Behaviour* 74: 349–356. <https://doi.org/10.1016/j.anbehav.2006.12.011>.