

Dynamics of a protected black rhino (*Diceros bicornis*) population: Pilanesberg National Park, South Africa

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Abstract

Achieving maximum productivity in remnant populations of black rhinoceros is crucial to the persistence of this species. It was, therefore, investigated whether the black rhino population of Pilanesberg National Park had become regulated by resource limitation 22 years after introduction in 1979. Inter-calving intervals (which are not restricted to yearly time increments, due to asynchronous reproduction) decreased with an increase in rainfall, while the percentage of male calves born increased with increasing rainfall. The percentage of reproductive cows achieving maternal success increased with increasing density until 0.085 rhinos/km², after which it decreased. This positive relationship at low densities is largely due to changes in the female age structure and the adult female/male ratio. The age at first calving tended to increase with increasing density, while mortality was not related to rainfall or density. It is concluded that the Pilanesberg black rhino population is showing the first signs of density dependence. It is proposed that black rhino conservators should monitor the percentage of cows achieving maternal success to detect early indications of density dependent resource limitation and use this as a criteria for decisions regarding metapopulation management.

INTRODUCTION

In just 18 years, from 1970 to 1987, black rhino (*Diceros bicornis*) numbers declined by 95% across the species' range (from 65 000 to 3800 animals: Muya & Ouge, 2000). Today, the species population not only remains at a critically low level, but is also fragmented into smaller, isolated populations. As a result, problems associated with small populations, such as environmental, demographic and genetic stochasticity, are quite probable (Woodroffe & Ginsberg, 1998). While subpopulations should ideally be large enough to prevent such problems from occurring in the long term (i.e. > 200 years), the small size of most protected areas makes this impossible for black rhinos (Foose *et al.*, 1993). Consequently, metapopulation management has been recommended for black rhino conservation, whereby the judicious translocation of animals between subpopulations should be maintained to prevent adverse genetic and demographic conditions (Foose *et al.*, 1993). In addition, achieving maximum productivity in all populations is crucial for decreasing their vulnerability to extinction. An understanding of black rhino demography and the factors affecting their productivity is therefore essential.

A central concern in population biology is the importance of density dependence in regulating population size (Hanski, 1990; Saether, 1997; Lundberg *et al.*, 2000). The results of several long-term individual-based population studies of ungulates have shown that in a predator-free environment, the population dynamics of ungulates are strongly influenced by a combination of stochastic variation in the environment and population density (Clutton-Brock *et al.*, 1987, 1992; Owen-Smith, 1990). Resource availability per individual is reduced at high population densities, affecting mortality, fecundity (calves born per adult female per year) and age at maturity (Saether, 1997). Both adult and calf mortality have been found to increase with the onset of resource limitation (Sinclair, Dublin & Borner, 1985; Clutton-Brock *et al.*, 1987, 1997; Mduma, Sinclair & Hilborn, 1999), while fecundity decreases due to increasing age at maturity (Gaillard *et al.*, 1992; Festa-Bianchet, Urquhart & Smith, 1994; Langvatn *et al.*, 1996) and increasing inter-calving interval (Fowler, 1981; Owen-Smith, 1990; Clutton-Brock *et al.*, 1991; Forchhammer *et al.*, 1998). Such effects of density dependence could have a significant effect on black rhino population performance, so the challenge is to maintain maximum reproductive performance while keeping subpopulations large enough to avoid stochastic demographic problems.

To minimise density-dependent effects in southern African subpopulations, the Rhino Management Group (RMG) recommends that populations be managed at 75%

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of ecological carrying capacity, K , with surplus animals being used for introductions elsewhere (Adcock, 2000). The difficulty, however, is in determining what K is, within the extent to which K is a useful concept in savanna ecosystems (see Illius & O'Connor, 1999). One method is to use the comparative approach, where population data from a number of areas of similar rainfall and habitat are used to derive a conservative estimate of K for the area in question (Bell, 1986). The RMG carrying capacity model is an example of such an approach, since 15 areas were compared across six variables (annual rainfall, rainfall concentration, minimum July temperature, soil fertility, browse availability and browse suitability: Adcock, 2001). A second approach, however, is to monitor a focal population over time to detect from population parameters when density dependent resource limitation comes into affect and then to apply adaptive management (Walters & Hilborn, 1984; Saether, Engen & Lande, 1996). This is a more effective approach (where and when possible) because K is not a set value, but rather a broad approximation that varies as conditions change (Macnab, 1985), for example as demonstrated in southern Africa where interannual rainfall variation is known to have a significant influence on ungulate population dynamics (Novellie, 1986; Owen-Smith, 1990).

A black rhino population that provides the opportunity to study the effect of increasing density and variable rainfall on population performance, is that of the Pilanesberg National Park (Pilanesberg). The population has not only been well monitored for nearly 20 years, but has also been steadily increasing in size during this period and has now reached its original estimated K of 0.1 rhinos/km² (Adcock, 2001). The aim of this study was, therefore, to determine whether, in the absence of hunting, the Pilanesberg black rhino population is showing signs of being at or near K and, if so, if density-dependent or density-independent factors are limiting population growth. The study set out to specifically investigate whether indicators of population performance (age at maturity, inter-calving interval, percentage of females achieving maternal success and mortality) changed predictably in response to increasing population density and rainfall.

Furthermore, we investigated whether variation in sex ratio at birth could be explained in this black rhino population by environmental factors that influence maternal condition. According to Trivers & Willard (1973), in species where one sex has a more variable reproductive success (such as males in polygynous species), natural selection will favour the ability of females to vary the sex ratio of their offspring in relation to their body condition. The degree of territoriality in black rhinos is debatable (Goddard, 1967; Frame, 1980; Kiwia, 1989) but territorial dominance is known to exist, suggesting that (Adcock, Hansen & Linderman, 1998) reproductive success between males is variable. We should thus expect black rhino females in poor condition at conception and during gestation to tend towards producing daughters, but when in good condition they should tend towards producing sons, assuming an offspring's future reproductive success is related to its size and/or condition at birth.

MATERIALS AND METHODS

Study area

Pilanesberg National Park is located in the North West Province of South Africa, between 25°22'S and 25°70'S and between 26°56'E and 27°14'E. It covers 476.41 km² of rocky hills and broad alluvial valleys in a weathered alkaline volcano (Adcock *et al.*, 1998). The habitat consists of *Acacia* and broad-leaf bushveld, ranging from open grassland to thicket. The mean annual rainfall is 630 mm, falling predominantly in summer. Winters are cold (average minimum 2.5 °C, average maximum 22 °C) and summers hot (average minimum 17.5 °C, average maximum 31 °C: Bailey, Brockett & Mentis, 1993). After the Park was proclaimed in 1979, 19 black rhinos were introduced between 1981–1983, and a further five individuals in 1989. The population increased steadily, allowing nine individuals to be translocated to Madikwe Game Reserve in 1996. By December 2001 the total population had reached 55 (Fig. 1).

Data collection

From 1981 to 1983 the population was monitored by Hillman (1982, 1983, 1984), but from 1984 to 1989 only annual helicopter counts were carried out. Older individuals were identifiable by recognisable characteristics such as ear tears and horn shape. Consequently, this enabled individual survival and female reproductive success (if they had a calf at foot or not) to be recorded during this period.

From 1989 monitoring efforts were increased and in 1991 an ear-notching program was started to enable the development of a rhino identification system, which has been updated almost annually. All black rhinos in the Park, except infant calves, are therefore individually recognisable. Reliable estimates of vital rates (survival, fecundity etc) of this wild population were therefore possible, as marked individuals could be accurately monitored in the long term (Gaillard, Festa-Bianchet & Yoccoz, 1998). Since 1989, ground monitoring was based on a game scout-training program, where game scouts were trained to collect information such as individual identification, sighting location and date. In addition, a full time black rhino monitoring officer has ensured the more intensive monitoring of each individual in the Park (i.e. seen at least once a year). Birth dates were determined by aging calves according to their body size and length of horn. Conception dates were calculated as being 15 months (Adcock, 2000) prior to the date of birth.

Population performance

All introduced rhinos were adults or sub-adults, resulting in the population age structure having an adult bias during the initial years following the introductions. In more recent years, however, the age structure has been skewed towards juveniles and sub-adults, as many calves have been born in the Park, but have not yet reached adulthood (Fig. 1). The population growth rate was therefore not used to assess population performance, since, even if all reproductive

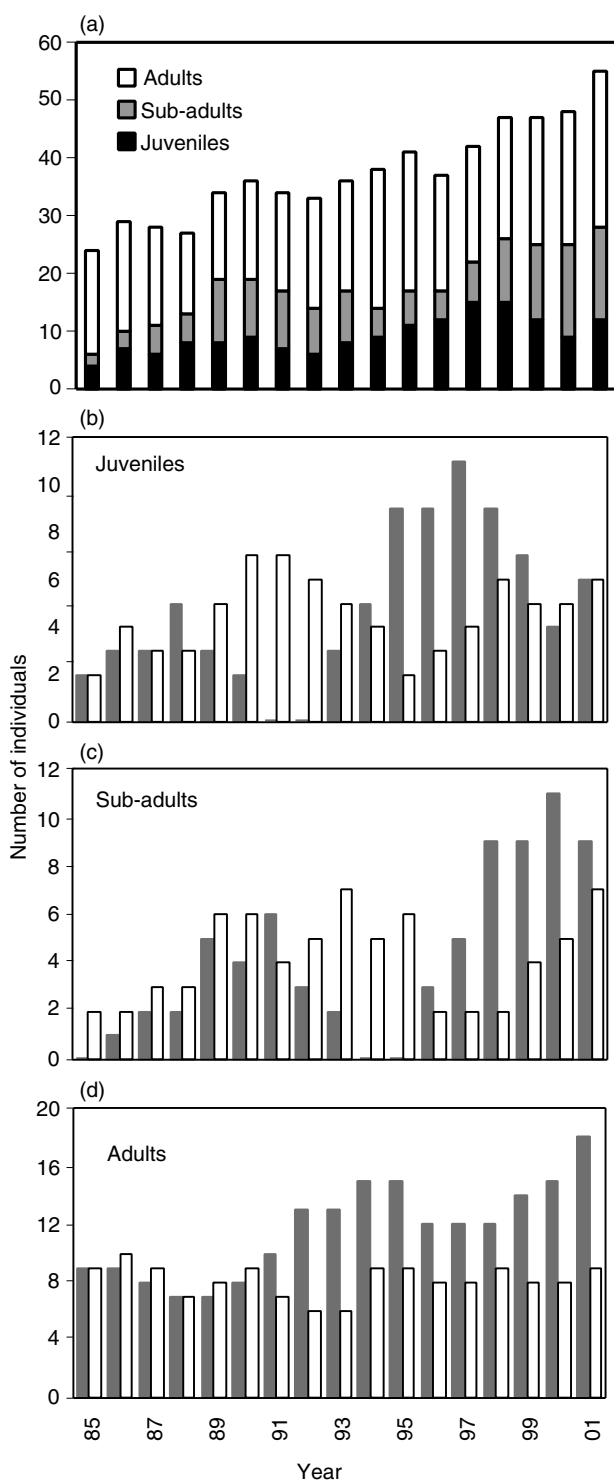


Fig. 1 (a) The number of black rhinos in Pilanesberg National Park from 1985–2001 (note that in 1996 nine individuals were removed from the Park). (b)–(d) The change in the number of juvenile, sub-adult and adult black rhinos in Pilanesberg National Park over time. Solid bars, females; open bars, males. Age classes as noted in the Methods.

females had a high reproductive success, their low numbers in the population would give a misleadingly low population growth rate (Saether, 1997). We therefore used inter-calving intervals (ICI), age at maturity (first calving),

mortality and the percentage of adult females achieving maternal success (raising a yearling) as performance indices.

For each calving event (except a female's first calf), we calculated the inter-calving interval as the number of years since the birth of the previous calf and assigned this value to the year in which conception took place. It is important to note that reproduction in black rhinos is asynchronous, with calves being born (and conceived) throughout the year. Inter-calving intervals are therefore not restricted to yearly time increments.

We calculated the percentage of adult females achieving maternal success for all females aged ≥ 6 years (the youngest age of first calving) and again for only those females that had started calving. This was to see whether the increasing number of young adult females (aged 6–8 years) in the population affected the percentage reproducing, as the probability of calving may be lower for this age group (Langvatn *et al.*, 1996; Adcock *et al.*, 1998). We determined mortality rates, calculated as the percentage of individuals dying per year, for juveniles (< 3 years old), sub-adults (males 3–7 years, females 3–5 years) and adults (males ≥ 7 years, females ≥ 5 years). We tested each index of population performance for associations with the population density and/or rainfall (see below). Density and rainfall were considered as independent variables, as they were not significantly correlated ($F_{1,13} = 3.705$, $P < 0.076$, $R^2_{adj} = 0.162$). Their weak relationship was most probably due to the occurrence of male deaths from fighting during low female/male ratio years, which happened to coincide with a period of low rainfall. Age at maturity was compared to the density and rainfall during the year of first conception and the 2 years prior to the conception year (with each year considered as a separate variable), as an individual's growth and development is influenced by resource availability over a number of years. Inter-calving intervals, the percentage of females achieving maternal success and mortality rates were compared to the corresponding density and rainfall (July–June) values for each year. Although shown graphically, the ICI value for 1986 (4.5 years) was not included in the analyses, as it is based on one individual and the validity of the long ICI is questionable due to the less intensive monitoring efforts at that time.

The monthly distribution of conceptions (averaged across all years) in relation to rainfall was also tested. We compared the number of conceptions per month to the mean rainfall for that month. For example, the number of conceptions that took place during January was compared to the mean rainfall for January.

We used multiple linear regression analysis to test for significance in relationships (Rosner, 1995; Zar, 1996) and statistical analyses were conducted using STATISTICA (Statsoft, 1991). All percentage data were arcsine transformed.

Calf sex

A direct comparison between female body condition at the time of conception and calf sex was not possible, since

Table 1. Results of four multiple regressions, each testing how a measure of population performance is affected by rainfall and density

Dependant variable	Independent variables	Regression coefficient (β)	Standardised coefficient (b)	<i>P</i> -value
Inter-calving interval	Rain	-0.0014 ± 0.005	-0.5787	0.0223
	Density	-9.5747 ± 7.005	-0.2976	0.1990
Maternal success (adult females)	Rain	0.0206 ± 0.0143	0.3049	0.1814
	Density	606.8092 ± 207.0157	0.6222	0.0150
Juvenile mortality	Rain	4.3757 ± 2.3208	0.5394	0.0838
	Density	-0.0001 ± 0.0002	-0.1584	0.5900
Adult mortality	Rain	0.0000 ± 0.0001	0.0747	0.7941
	Density	-2.8250 ± 1.4391	-0.5493	0.0732

R^2 adjusted and *P*-value for each multiple regression model:

Inter-calving interval – $R^2_{adj} = 0.477$, $P = 0.011$.

Maternal success – $R^2_{adj} = 0.498$, $P = 0.013$.

Juvenile mortality – $R^2_{adj} = 0.107$, $P = 0.201$.

Adult mortality – $R^2_{adj} = 0.147$, $P = 0.153$.

body condition data were not available. Relationships between body condition and extrinsic factors such as population density and climate have, however, been well documented (Kruuk *et al.*, 1999; Post *et al.*, 1999; Mysterud *et al.*, 2000). Therefore, assuming that female black rhino body condition is influenced by rainfall and the mortality of male and female newborns is equal, we calculated the number of male and female calves conceived during years with less than, and more than, 640 mm of rainfall (the mean annual rainfall over the study period). A chi-squared goodness-of-fit test, incorporating Yates correction factor (Everitt, 1977), was used to determine whether calf sex ratio differed significantly from the expected 50:50 ratio during years of high or low rainfall.

In addition, the sex of calves born to primiparous females, the tendency for individual females to produce one sex and trends in the sex of sequential calves born to individual females was investigated.

RESULTS

Population performance

The age at which females first calved ranged from 6–8.92 years ($\bar{x} = 7.25$, standard error (SE) = 0.22, $n = 12$) with 33% of females having calved before they were 7 years old, 83% before 8 years and 100% before 9 years. The age at first calving was not found to be related to the combined effect of density and rainfall ($F_{6,5} = 1.251$, $P < 0.412$, $R^2_{adj} = 0.120$), nor rainfall alone ($F_{3,8} = 2.077$, $P < 0.182$, $R^2_{adj} = 0.227$). Even though the relationship was not significant, there was a definite tendency for the age at first calving to increase with increasing density ($F_{3,8} = 3.461$, $P < 0.071$, $R^2_{adj} = 0.402$).

Inter-calving intervals ranged between 1.67 years and 5.17 years ($\bar{x} = 2.83$, SE = 0.11, $n = 47$). The negative relationship between ICIs and density was nearly

significant ($F_{1,12} = 4.508$, $P = 0.055$, $R^2_{adj} = 0.213$), yet a multiple regression including both rainfall and density showed rainfall to be the most important variable affecting ICIs (Table 1). When density was dropped from the model, the significance of the relationship with rainfall increased. ICIs were therefore best explained by rainfall alone, with intervals decreasing with increasing rainfall (Fig. 2). The timing of conceptions in the year was also related to rainfall, since the monthly number of conceptions increased significantly with an increase in monthly rainfall (Fig. 3).

No significant linear relationship was found between the percentage of females achieving maternal success and rainfall and/or density. When only data for densities of up to 0.085 rhinos/km² (the percentage of females achieving maternal success was highest below this density) were included in the analysis, however, the percentage of females achieving maternal success was significantly positively related to density (Fig. 4) and this relationship was strongest when rainfall was not included in the model (see multiple regression results, Table 1). An increase in density therefore resulted in an increase in the percentage of females achieving maternal success until a density of 0.085 animals/km², after which there began a decline with increasing density (Fig. 4). When only reproductive females were considered, i.e. excluding those females of 6 years and older that had not yet calved, the relationship with density was barely significant ($F_{1,11} = 4.937$, $P = 0.048$, $R^2_{adj} = 0.247$), indicating that the positive relationship with density was largely due to changes in the female age structure. There was, however, still a marked decline in reproductive success above a density of 0.085 animals/km². All juvenile deaths during this time were from mothers of 14 years and older and were, therefore, not due to an increase in young, less experienced, cows. Density, rather than female age structure, therefore best explains this decline in maternal success in recent years.

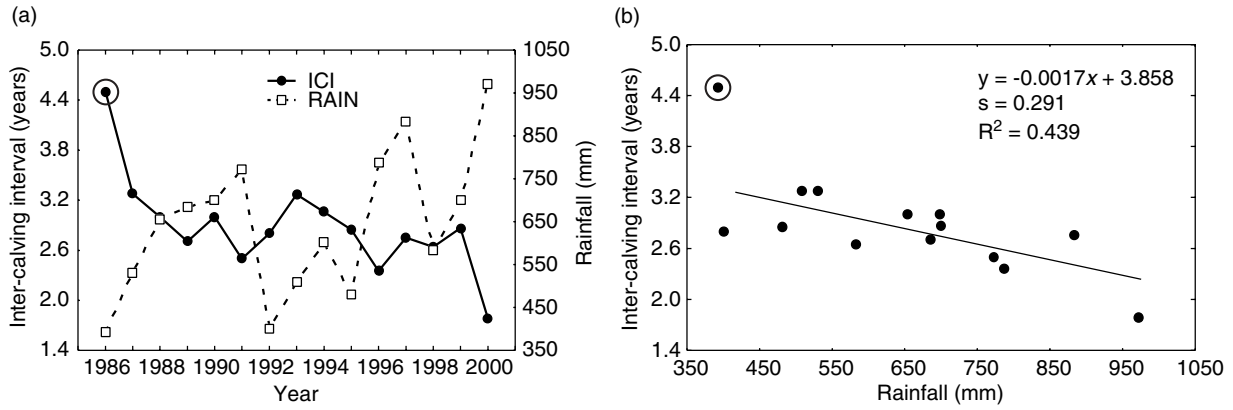


Fig. 2 (a) Graph of the annual mean inter-calving intervals (ICIs) and the mean annual rainfall (July–June). (b) Regression of the mean ICIs against mean annual rainfall ($F_{1,12} = 11.173$, $P = 0.005$, $R^2_{adj} = 0.439$), excluding data from 1986 (circled).

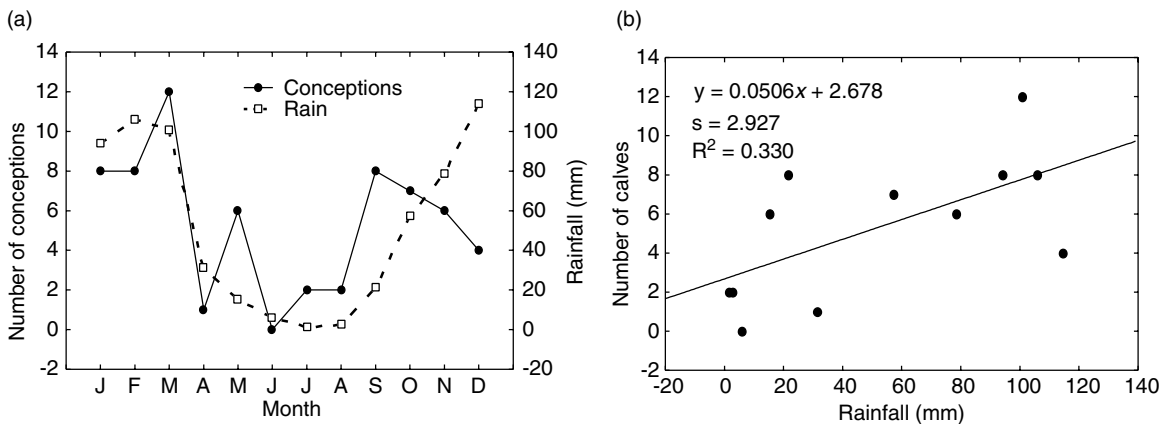


Fig. 3 (a) Graph of the monthly distribution of conceptions and the mean monthly rainfall over the duration of the study period. (b) Regression of the number of calves born per month against mean monthly rainfall ($F_{1,10} = 6.425$, $P = 0.030$, $R^2_{adj} = 0.330$).

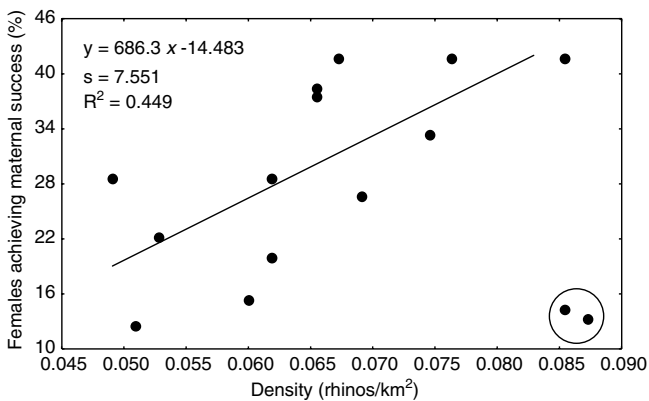


Fig. 4 The relationship between the percentage of females achieving maternal success and population density. Note that the regression excludes those points from the last 2 years (circled) when the density was ≥ 0.085 rhinos/km² ($F_{1,11} = 10.793$, $P = 0.007$, $R^2_{adj} = 0.449$).

To test whether the effect of density on maternal success (at low densities) was mainly due to a ‘year’ effect, ‘year’ was also treated as an independent variable. The percentage of adult females achieving maternal

success was positively related to year ($F_{1,11} = 9.748$, $P = 0.010$, $R^2_{adj} = 0.422$), while the relationship for the percentage of reproductive females was almost significant ($F_{1,11} = 4.739$, $P = 0.052$, $R^2_{adj} = 0.238$). This is to be expected when a small founder population is introduced into a closed system (as with the black rhinos in Pilanesberg), with population density increasing steadily over time. However, the decrease in significance of the relationship when only reproductive adult females were considered, together with the decline in maternal success in recent (high-density) years, indicates that maternal success is truly influenced by those variables changing over time (such as density and female age structure), rather than ‘year’ itself.

Twenty-two black rhino deaths were recorded from 1985 to 2001 (nine juveniles, zero sub-adults and 13 adults). For adults, the most common known cause of death was either fighting between males ($n = 3$) or old age ($n = 3$). The cause of all juvenile deaths and the remainder of the adult deaths are, however, unknown. Juvenile mortalities were highest during low rainfall years and recent high-density years (Fig. 5), yet neither juvenile nor adult mortality were significantly related to rainfall and/or density (Table 1).

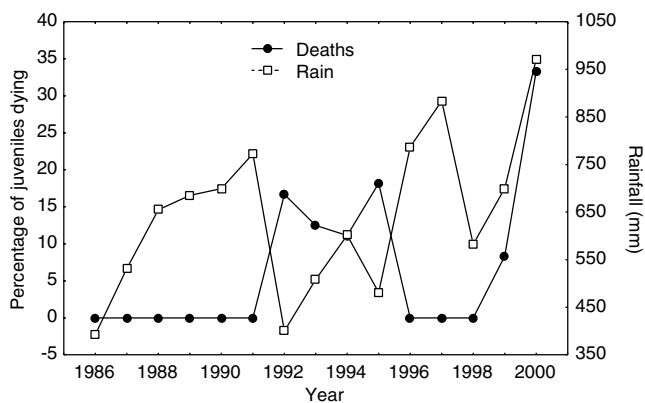


Fig. 5 Graph showing the percentage of juveniles dying each year compared to the annual rainfall (July–June).

Calf sex

Over the duration of the study period the calf sex ratio was exactly equal, with 27 males and 27 females being born. This ratio was not constant over time, however, as there were significantly more females conceived during years with below average rainfall ($\chi^2 = 3.885$, $df = 1$, $P < 0.05$) and significantly more males conceived during years with above average rainfall ($\chi^2 = 4.316$, $df = 1$, $P < 0.05$). It therefore appears that female body condition may influence calf sex in black rhinos.

Of the nine known-sex calves born to primiparous females, five were female and four were male. All, except for one out of 13 reproductive females, produced both male and female calves. The two females with the largest sample size of calves (six) both produced an equal number of males and females. There is, therefore, no tendency for primiparous females to produce a certain sex calf, or for individual females to produce one sex. However, for calves born to individual females, the occurrence of successive calves alternating in sex was almost double that of successive same-sex calves (17 versus 9 occurrences, respectively). There does, therefore, seem to be a trend for black rhinos to alternate the sex of their calves.

DISCUSSION

Population performance of the Pilanesberg black rhino population was found to be influenced by both density-dependent and independent factors. The percentage of females achieving maternal success was influenced by density, while inter-calving intervals were influenced by rainfall.

The increase in inter-calving intervals with decreasing rainfall is in accordance with the literature, as the links between rainfall and resource availability, and nutritional status and reproductive capacity, have been well documented. In African savanna ecosystems, for example, vegetation production has been found to be linearly related to rainfall where the total annual rainfall is below about 800 mm (Coe, Cumming & Phillipson, 1976; Rutherford, 1980). In addition, resource availability fluctuates over

time with the seasonality of rainfall (Rutherford, 1984; Ostfeld & Keesing, 2000). Individual growth and body condition depend on resource availability, which therefore influences reproduction. Age at first calving, for example, increases under conditions of resource limitation because the onset of puberty is dependent on body mass (Joubert, 1963; Hamilton & Blaxter, 1980). Inter-calving intervals are also affected, since evidence shows that under-weight females, or females on nutrient-poor diets, may fail to ovulate (Lindsay, 1976; Thomas, 1982). Periods of low rainfall must reduce the body condition of female black rhinos by reducing the quantity and quality of their food supply, that being forbs and woody browse (Goddard, 1970; Mukinya, 1977; Hall-Martin, Erasmus & Botha, 1982; Oloo, Brett & Young, 1994; Muya & Oguge, 2000), as confirmed by the positive association between the seasonal rainfall pattern and the occurrence of conceptions in the Pilanesberg population.

Population density would also influence resource availability, since the level of consumption and, hence, the period over which dietary components remain into the dry season, would depend on population density when the population size approaches K (Owen-Smith, 1990). Reproductive performance is therefore also density dependent (Albon, Mitchell & Stains, 1983). In the Hluhluwe–Umfolozzi Game Reserve, for example, the age at first calving in black rhinos was found to increase with an increase in population density, since the mean age at first calving was 6.5 years and 12 years in areas of low (0.1 animals/km²) and high (0.7 animals/km²) density, respectively (Hitchins & Anderson, 1983). In Pilanesberg, there was a tendency for age at first calving to increase with increasing density, yet even when the density was at its highest (0.12 animals/km²), females first calved between 6.83 and 7.13 years, which is comparable to the low-density Umfolozzi population. It should be noted, however, that the high rainfall received during high-density years could have reduced the effects of density in Pilanesberg.

Inter-calving intervals are also known to be influenced by density, with high densities resulting in an increase in the time between calves (elephant, Laws & Parker, 1968; white rhino, Rachlow & Berger, 1998). The trend in Pilanesberg was, however, opposite to this. Similarly, the percentage of adult females achieving maternal success (which is partly dependant upon ICIs) was positively related to density at low densities. This relationship did weaken when only reproductive females were considered, yet it was still significant and therefore could not be explained by female age structure alone. One other explanation for this unexpected pattern may be the Allee effect (Stephens & Sutherland, 1999). If densities are too low, for example, interactions between males and females in oestrus may be more infrequent, thereby decreasing mating opportunities. This has, however, not been reported for any other small rhino populations (Adcock *et al.*, 1998). Alternatively, the explanation could be that of social behaviour, since reproductive performance in black rhinos is known to increase with an increase in the female/male ratio (Adcock *et al.*, 1998). In Pilanesberg, the female/male ratio was particularly low

(≤ 1 female/male until 1991) in early, low-density years (Fig. 1), making this a probable explanation. The pattern of increasing reproductive performance with increasing density may, therefore, not be a typical response for black rhinos, but is rather due to the 'more favourable' adult sex ratio at higher densities in this case.

The decrease in calving success at densities ≥ 0.085 rhinos/km² suggests that density-dependent resource limitation may have begun to affect the population at this stage (Fig. 4), as rainfall was still above average and the female/male ratio had not decreased. Interestingly, no such trend was apparent in the ICIs. Inter-calving intervals are, however, only derived from the cows that calve, but the proportion of females reproducing successfully (which takes into account neonatal mortality) provides a more direct indication of how female reproductive success is influenced by environmental variation. In addition, juvenile deaths are reflected in 'maternal success' and, in this case, are largely responsible for the decline observed in recent high-density years.

The degree to which rainfall affects reproduction in black rhinos was also reflected in the effect on calf sex. As with numerous other ungulate studies (Saltz & Rubenstein, 1995; Wauters *et al.*, 1995; Cameron *et al.*, 1999; Kruuk *et al.*, 1999; Mysterud *et al.* 2000; Côté & Festa-Bianchet, 2001), the proportion of male calves born was positively associated with rainfall prior to and during the time of conception and, therefore, to food abundance and, presumably, body condition, as predicted by the Trivers–Willard Hypothesis. While such departures from expected calf sex ratio variations could potentially have applications for conservation monitoring, evidence supporting the Trivers–Willard hypothesis is mixed (Saltz, 2001; Carranza, 2002) and no mechanisms by which the hypothesis works have yet been proved in mammals.

In Pilanesberg, an index of black rhino population performance that was not influenced by rainfall or density, was mortality of sub-adults and adults. No sub-adult and only three adult mortalities (two due to old age) were recorded since 1994, in higher density years. This is not unexpected, first because the population density has been comparatively low until recently. Second, large-bodied mammals such as black rhinos generally exhibit a *K*-selected life-history strategy whereby lifetime reproductive success is dependent on a long life-span, during which starvation may be offset in times of resource limitation by temporarily forfeiting reproduction (Begon, Harper & Townsend, 1996; Coulson, Milner-Gulland & Clutton-Brock, 2000).

According to Eberhardt (2002), changes in vital rates take place as a specific sequence of events in response to increasing density. A reduction in early survival is expected to be the first response, followed by an increase in the age at first calving, then a reduction in reproductive rates and, lastly, an increase in adult mortality (note: opinions about this sequence may differ, see Gaillard *et al.*, 2000). The increase in juvenile deaths at high densities (reflected in the decline in maternal success), together with the trend of increasing age at maturity with increasing density, but the lack of response of ICIs and

adult mortality, suggests that the Pilanesberg black rhino population is responding in accordance with the sequence expected by Eberhardt (2002).

Considering the response of 'maternal success', the Pilanesberg black rhino population is starting to show signs of density dependence at its present density of 0.12 animals/km². With the first signs appearing at densities above 0.085 rhinos/km², *K* for Pilanesberg would be approximately 0.17 rhinos/km², assuming that density dependence begins at around *K*/2 (Caughley, 1977). This value of *K* is only valid under the present conditions, however, and is most probably an over-estimation of the long term *K*, since it was derived during a period of high rainfall. A more conservative estimate would therefore be closer to the previously estimated and model-predicted value of *K*, namely 0.1 rhinos/km². A carrying capacity of 0.1 rhinos/km² is relatively low compared to other reserves with similar rainfall. Ndumu Game Reserve, for example, supports a density of 0.38 rhinos/km² (Conway & Goodman, 1989) and Olduvai and Ngorongoro (Tanzania) support densities of 0.16 and 0.32 rhinos/km², respectively (Goddard, 1967). Pilanesberg's comparatively low carrying capacity may be due to a number of factors identified by Adcock *et al.* (1998), namely: the poor nutrient status of the Park, the extent of inaccessible steep and rocky terrain, the influence of frost on browse quality, competition with other browsers and the length of the dry season.

From this study, the assessment of population performance in response to increasing densities and variable rainfall has proved useful for assessing the ability of a reserve to support a black rhino population in the long term. More specifically, two points useful to the detection of density dependence and the future conservation of the species are highlighted. First, the index most sensitive to population density, namely the percentage of females achieving maternal success, has been identified. Second, the strong association between rainfall and population performance, even at low densities, highlights the need to assess performance during periods of high rainfall, since only then can a true reflection of density dependence be gained. The value of maintaining intensive monitoring programmes cannot be overstated. Detecting early indications of density dependence will allow subpopulations to be maintained at densities well below *K*, thus maximising population growth within a conservation strategy based on metapopulation management.

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