

Population Growth, Sex Ratio and Reproduction of White Rhinoceros in South Africa

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Introduction

With the number of natural habitats rapidly dwindling, conservation of the white rhinoceros has become an unquestionable necessity. Intensive protection and the translocation of animals in reserves and private game farms has led to increasing population sizes (Emslie & Brooks 1999), but breeding animals in enclosures requires intensive management and knowledge of ecological factors affecting the population dynamics of the species (Ballenberghe & Ballard 1998). Density-dependent effects resulting from food competition, lead to changes in age of sexual maturity, litter size, first year survival, adult survival and sex ratios of young and adults which can have profound influence on the growth rates of a population (Ballenberghe & Ballard 1998). In natural situations, white rhino populations oscillate following the wet and dry phases of the rainfall cycle and individual animals (mainly subadult males) disperse where vegetation over utilisation occurs (Owen-Smith 1983). Captivity prevents dispersal and could cause population crashes in white rhinoceros, since they can not respond quickly enough to a deteriorating situation (Owen-Smith 1983). Thorough knowledge of the demography of a species and the ecological factors influencing it are therefore important for management of the species.

In the present study, the growth rate of a population of a white rhinoceros living on a game farm in South Africa was monitored, and the influence of management practices on the adult sex ratio, calf sex ratio and intercalving interval was analysed.

Methods

The study was carried out on a game farm in South Africa, which housed a population of white rhinoceros growing successfully since 1991. Location of the farm and total number of animals is not given for security reasons. However, it may be said, that the area covers several hundred km² and several dozen animals. All animals could be individually recognised and their ages were established by comparative horn and body analysis according to Hillman-Smith (1997), and by a photographic catalogue of known animals of different age. Hunting of adult males occurred shortly after introduction of the population, while subadult males were translocated in 1998 in order to prevent fighting between adolescents. The population size was established in 1998 when all animals of the population were

caught and ear notched. Demographic data of animals, including the number of introduced, hunted, translocated or deceased rhinos were obtained, by daily patrols and yearly animal counts. These data were supplemented by field observations between 1997 and 1999. Births occurring between 1992 and 1996 were calculated from the age of the animals, while all births occurring between 1997 and 1999 were recorded by direct observations of the female with her new-born. A population growth trend was calculated separately for each year, including all deceased and removed animals. From these data, an average annual population growth was calculated. The animals were grouped in three different age categories: calves (0 – 2 years of age), subadults (females of 2 – 4 years, males 2 – 6 years of age) and adults (females > 4 years, males > 6 years).

For data analysis nonparametric statistics based on two-tailed tests were used only. The calculation of the statistical tests were carried out using Microsoft Excel 1997, SPSS 8.0 and SsS 1.0. For descriptive statistics the median and interquartile ranges (IQR) were calculated giving 25 and 75% of the data range.

Results

Population growth

Since introduction of the animals in 1991/92 the population increased in average 15% per year. The relative number of animals per year increased over the whole time, but much stronger just after introduction of the population (fig. 1). Almost half of all females reproduced each year, mean natality rate (41%). The mortality rate was 2.25%.

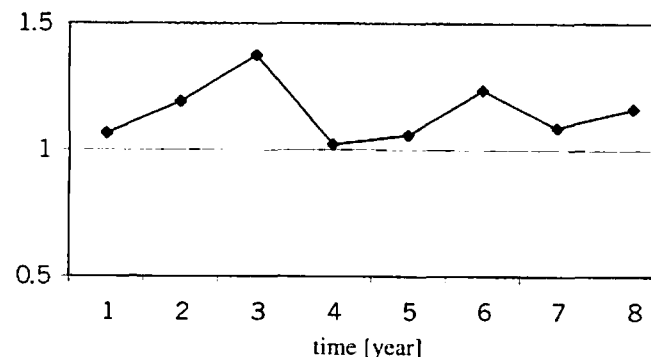


Fig. 1: Relative population growth in time. The graph shows the number of animals (including all deceased and removed animals) of one year relative to the following year (computed as N_{t-1}/N_t).

The population density during the year 1999 was 0.23 individuals/km² (including all deceased and removed animals).

Age and sex ratio

The population showed an over-representation of adult animals (55%) compared to subadult (25%) and calves (20%). Adult animals showed a significantly higher frequency of females

(89%) compared to males, G- test with Williams correction: $G = 13.3$, $p=0.0003$, fig. 2). Without hunting of adult males the frequency of adult males would be slightly higher (27%) compared to females (67%).

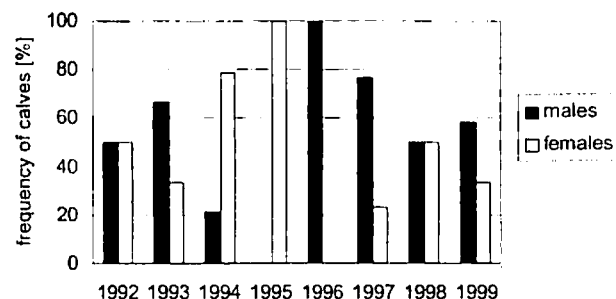


Fig. 2: Percentage of the age classes adult, subadult and calves of each sex after removal and death of some rhinos.

The sex ratio of the calves showed the opposite trend with a higher percentage of males (62%) compared to females (38%), but the sex ratio (1 male calf : 0.4 female calf) did not differ significantly (G-test with Williams correction: $G = 0.32$, $p = 0.32$).

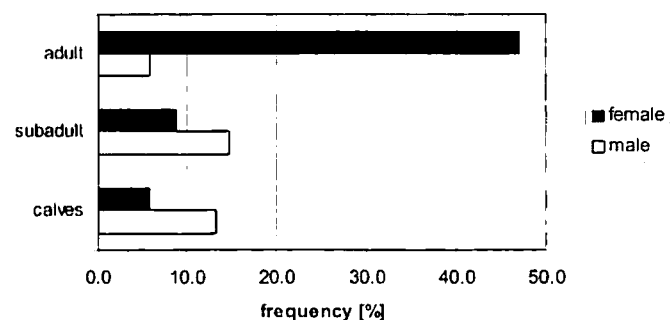


Fig. 3: Frequency of male and female calves occurring between 1992 and 1999.

The frequency of new-born male and female calves changed significantly over the time (G-test and Williams correction $G = 6.596$, $p = 0.01$). Male calves occurred in higher numbers between 1996 and 1999 compared to 1992 to 1995, while female calves were more frequent after introduction of the population (between 1992 and 1995).

Reproduction

Most calves (74%) were born between December and June with a peak in March. Intervals between successive births ranged from 1.2 years to 3.5 years (median = 2.3 years, IQR = 0.6). The time span between successive birth was significantly longer after a female calf was born (2.9 years, IQR = 0.75, Mann-Whitney- test: $Z = -2.65$, $p = 0.008$) and shorter after a male calf was born (1.9 years, IQR = 0.4).

After giving birth to a female calf it was less likely that the mother would give birth to another female (33% instead of expected 50%), but further data have to be collected to confirm this trend.

Discussion

Population growth

The annual growth rate observed in the study (15%) is among the highest rates reported for white rhinoceros: 10.4 in Whovi game Park, Zimbabwe (Rachlow & Berger 1998), 9.5% in Umfolozi-Corridor-Hluluwe Complex, South Africa (Owen-Smith 1973), 8.4% Krüger National Park, South Africa (Pienaar 1994). The high rate of increase is often discussed to be a consequence of the low population density. This applies for two studies sites, Umfolozi-Corridor-Hluluwe Complex, ± 2 animals/km² (Owen-Smith 1973) and Krüger N.P., 0.4 animals/km² (Pienaar 1994), showing higher densities and lower growth rates compared to my study site (0.23 animals/km²). However, lower growth rates still occurred in populations of similar population density: 0.23 rhinos/km² (Rachlow & Berger 1998) or lower density: 0.03 rhinos/km²: the northern subspecies *C. s. cottoni*, Garamba National Park, Zaire with a growth rate of 9.7% (Hillman-Smith 1997). High rates of population increase in our study might be a result of the extremely skewed sex ratio, with more females, all giving birth at their highest theoretically possible rate. A more balanced sex ratio, on the other hand, would either mean a much higher population density, or less females, with a consequence of a lower reproductive performance.

The over-representation of adult females compared to young animals indicates that the population is going to decline in numbers in the near future. The overall population mortality rate was low, similar to the one observed in Umfolozi (2.7%, Owen-Smith 1973).

Sex ratio

Hunting of adult males reduced the already low ratio of adult males (1 male : 2.5 females), to 1 male : 8 females, which is much higher compared to the proportion reported for the population in Umfolozi: 1 male: 1.02 females (Owen-Smith 1975). Eight females would have to share one male, if all were coming into oestrus at the same time. Previous studies indicated that a peak in fertile mating occurred between August and February, with a peak in October and November (Kretzschmar et al. 2001). Reproduction was therefore limited to a certain period of time. It is likely that the few adult males were not able to copulate with all females, though there was still a high natality rate of 41% compared to 34.2% at Umfolozi (Owen-Smith 1973). Thus the sex ratio should not become even more skewed in favour of females, because one potential limiting factor might be the minimum length of consort phase before a female accepts a male for successful copulation.

The sex ratio of the calves was reversed to that of the adults (1 male : 0.4 females). More than twice as many males than females were born during the last two years (1998 - 1999) but numbers were probably too low to show significant differences ($n = 13$). The frequency of new-born male and female calves changed significantly over the time. Male calves occurred in higher numbers between 1996 and 1999, while female calves were more frequently just after introduction of the population (between 1992 and 1995). Selection may have favoured the production of the sex that disperses after the local population has reached carrying capacity (McCullough 1979, de Gayner 1982 cited in Clutton-Brock & Iason 1986), or it might be more beneficial for a female to produce the less frequent sex, because of less competition between her offspring and others over reproductive possibilities.

Studies on different mammals showed that parents will increase their fitness by varying the sex ratio of their progeny in relation to differences in the costs and benefits of

producing a son or daughter (review Clutton-Brock & Iason 1986). Differences in intercalving intervals in the study population suggested, that female offspring were more costly to raise than males. Mothers that reared a female tended to experience an increase in interbirth interval between subsequent offspring and were less likely to produce a female the preceding year. Higher costs for the mothers to rear a young might have changed the sex ratio, favouring males in the second half of the study period. Density-dependent effects resulting from food competition could possibly explain the higher costs occurring for females, as no differences were observed in the amount of rain (measured on the study site) since introduction of the rhinos.

The study showed that high rates of increase do not guarantee continuous increase of the population. Growth rates, adult sex ratios and population density have to be monitored on a regular basis in order to intervene before numbers decrease. Hunting of males and highly skewed sex ratios will increase the frequency of male calves, which will subsequently reduce the growth rate.

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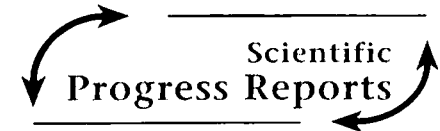
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