University of Nevada

Reno

Demography, Behavior, and Conservation of White Rhinos

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy
in Ecology, Evolution and Conservation Biology

by

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May 1997

UMI Number: 9728131

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May 1997

ACKNOWLEDGMENTS

I wish to thank Dr. William Nduku, director of the Zimbabwe Department of National Parks and Wild Life Management, and Mr. Rowan Martin, deputy director for research, for permitting me to conduct research in Zimbabwe and for their tireless support for conservation in their country.

My sincere thanks to Jon Cummings and Holly Haegerman for their generous contributions that made it possible for me to begin this project. I am especially indebted to Dr. Richard Faust and the Frankfurt Zoological Society who funded the majority of this project. Support also was provided by the Ecology, Evolution, and Conservation Biology program of the University of Nevada Reno, the World Wide Fund for Nature, the Rhino and Elephant Foundation, and the Rhino Survival Campaign of the Zimbabwe Conservation Trust.

Drs. Mike Kock and Mark Atkinson headed the dehorning projects, and provided invaluable support for this research. Mike was involved in many phases of the field work, and this project really was a team effort. Many other National Parks personnel provided help and advice, including Drs. Drew Conybeare and Peter Mundy, Mike Jones, Kathy Rogers, Norman Monks, Dr. Debbie Gibson, and Maggie Taylor. Thanks also to Dr. Piet Morkel for help in designing and fitting the radio-collars.

In both Hwange and Matobo National Parks, I was fortunate to meet and work with so many dedicated people. Wardens Frank Potts and Norman English were supportive of this project in the areas under their supervision. The help of many scouts and trackers made this project possible, and I thank them all. Fibion Ndwendi and

Jonas Gumede each spent over a year working with me. They taught me much about Africa and rhinos, and I will always remember their kindness and dedication.

There are so many folks in Zimbabwe who provided friendships, meals, push-starts, showers, and beds that the list is long and I am sure to leave a few out. Cathy Kerr, Claire Davies, Jill Spangenberg, Greg Rasmusen, Kim McCreery, Bob Robbins, Frank and Yazz Potts, and especially Dr. Joshua Ginsberg helped me to get my feet on the ground in Hwange, and I am very grateful for all their time and help. Piet and Yvonne Berkhout, David and Shelly Lasker, Cheryl and Martinus Nel, Colin and Sheryl Nott, Ian and Leanne Godfrey, Aubry Packenhum, Dave Hartung, Barney O'Hara, Dr. Kyle Good, Mark and Tracy Butcher, and Buck Rogers were a great help in many ways. Several tour operators provided logistical assistance and information on rhino citings -- thank you! Also, thanks to Tina Besthorn (the lion cub) for her field assistance and good cheer through everything from parasites to poaching. I thank my dear friends, Nathalie Jacquat, Ken Chuchro, and especially Jeff Keener for visiting me and helping with the field work.

Thanks to Beaux Berkeley for teaching me about rhino reproduction and fecal analyses. And on that subject, I wish to thank Dr. Ron Barry, Sherry and Josh Frick, and Dr. Mike Kock for one of the funniest evenings I have ever had. My sincere appreciation to Dr. John Kie for his assistance with home range analyses.

Many EECB and Biology students provided humor, ideas, music, and beers -- Dr. Rick Sweitzer, Alexine Keuroghlian, Don Eaton, Stewart Breck, Doug Smith, Ali Jones, Chris Mullen, and many others. Thanks you guys! Thanks also to Rina Shumer and the hydro-guys for help in printing and general good cheer. I appreciate the help of

Joan Rachlow, Mike Ashley, Dr. Matt Gompper, Wendy Kuntz, Eric Beever, and Veronica Johnson for reviews of proposals and manuscripts. My special thanks to Dr. Bill Povolny, who was supportive and understanding during the writing of this dissertation.

I am not sure how to express my appreciation to Dr. Joel Berger, my major advisor. He and Carol Cunningham first welcomed me to Reno, then to Africa, and back again. They taught me about rhinos, reserach, writing, etc. My sincere thanks to my committee members, Drs. Lew Oring, Steve Jenkins, Gary Haynes, Pete Stacey, and Hudson Glimp for their guidance and patience. Dr. Les Krysl served on my committee for two years before his untimely and early death, and I appreciated his input.

Lastly, want to acknowledge the support of my family. I am especially grateful to my sister and friend, JoAnn Krypel, who made two trips to Zimbabwe, carrying such necessities as chocolate and fine-spline free-wheeling hubs. As always, my parents, Joan and Bob Rachlow, have been a source of strength and encouragment for me. Further, they accepted more than their share of collect calls from Africa over the four years that I was in the field. Thank you!

ABSTRACT

Numbers of African rhinos have decreased markedly during the past 100 years, mainly due to poaching for their horns. Recent conservation efforts have included horn removal and establishment of heavily protected rhino reserves. In the absence of poaching, white rhino (Ceratotherium simum) populations can increase at rates of 5 to 10% per year, resulting in rapidly increasing densities within smaller reserves. The relationship between population density and demography of white rhinos in Matobo National Park, Zimbabwe, is examined in Chapter 1. Recruitment rates declined and ages at first reproduction increased with population density. Body condition was markedly affected by both population density and reproductive condition of females, suggesting that nutritional constraints may influence individual reproductive performance at higher densities.

Adult male white rhinos establish and mark territories from which other territorial males are excluded. However, at high population densities, only a small proportion of adult males successfully establish territories. Relationships among spatial patterns, age, body size, and testosterone levels of adult males are reported in Chapter 2. Spatial and behavioral associations with adult females did not differ between territorial and nonterritorial males. However, territorial males appear to discriminate among females based on their reproductive potential. Fecal testosterone levels were significantly higher in territorial males than in nonterritorial males, and this relationship was independent of age.

In Chapter 3, life history data from this and other studies were used to model growth and persistence of small populations of white rhinos. Variation in number of founders had large effects on the establishment of new populations. Population persistence reached a threshold at ≥10 founder individuals, which is in accord with empirical data for this species. Sensitivity analyses indicated that variation in mortality rates of adults and subadults can have substantial impacts on population persistence, but the results of the models did not change markedly in response to variation in mortality rates of calves. Both the magnitude of the carrying capacity and its standard deviation markedly influenced persistence.

Chapter 4 focuses on economic aspects of horn regrowth and the potential for harvesting rhino horns commercially. Regeneration of horns after dehorning was studied in separate populations of white rhinos in Hwange and Matobo National Parks, Zimbabwe. Both sex and age influenced the rate at which horns were regrown. Regenerated horn mass for adult males (>1.3 kg/yr) was almost twice the mass of adult females. Based on an economic model, dehorning at intervals of 1.2 to 1.5 years would maximize profits. However, these values likely represent minimum dehorning intervals for managers balancing profits with longer-term population management.

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INTRODUCTION

White rhinos (Ceratotherium simum) historically were widespread across southern African, and were common throughout much of Zimbabwe. By the late 1800's, hunting for horns, hides, and sport extirpated this species over most of its range. The last white rhino in Zimbabwe was reputed to have been shot in the 1880's. A program was initiated in the 1960's to reintroduce white rhinos into reserves throughout their historic range with surplus animals from Natal, South Africa. White rhinos were released into 3 reserves in Zimbabwe: Hwange National Park, Matobo National Park, and Kyle Recreation Park.

Intensity of rhino poaching rose sharply in Zimbabwe in the mid-1980's, and despite a substantial anti-poaching effort, numbers of rhinos killed by poachers continued to rise. A radical program was approved by the Zimbabwe government in 1991 to remove horns from the white rhinos in Hwange National Park. I began a research program there to evaluate the effects of horn removal on the survival, behavior, and reproduction of white rhinos.

During 1992 and 1993, the budget of the National Parks was severely restricted by a governmental restructuring program, and over 250 game scouts were laid-off. During this lapse in law enforcement, the population of white rhinos in Hwange Park was decimated by poachers, and fewer than 6 individuals were known to survive in late 1993. In response to marked declines in Hwange and other rhino populations in Zimbabwe, the Department of National Parks and Wild Life Management, established 4 intensive protection zones or rhino reserves, where both rhinos and resources for protection were concentrated. The only reserve designated for white rhinos was Matobo National Park, a small reserve of about 400 km^2, which contained a resident population of about 40 white rhinos. I continued field work at Matobo Park during 1994-95, and refocused the research to address questions about behavioral ecology and management of rhinos in small, insular reserves.

Conservation of rhinos within reserves and sanctuaries is becoming more common throughout Africa, and viability of populations outside of protected areas is likely to be marginal. Because effective protection from poaching is costly, rhino reserves tend to be small, and population densities relatively high. An understanding of the potential effects of increasing density and restricted dispersal on demography is important for development of conservation strategies for many rare species. My research examined effects of population density on demography (Chapter 1) and behavior (Chapter 2) of white rhinos in Matobo National Park, and empirical data on reproduction and survivorship were used to model consequences of different management strategies for reserve establishment (Chapter 3). Biological and economic aspects of horn removal were studied in two populations of dehorned rhinos, and an evaluation of horn harvesting is presented in Chapter 4.

In the absence of poaching, rhino populations can increase at rates of 5-10% per year, which may result in rapidly increasing densities within smaller reserves. In Chapter 1, two lines of evidence are used to examine the relationship between population density and demography of white rhinos in Matobo National Park: 1) a contrast between a fenced, high-density population and an unfenced, low-density group; and 2) an analysis of changes in demographic parameters within the fenced population over a 30-year period as density increased by >300%. Female reproductive parameters and population recruitment rates varied with density. Conservation plans for rhino reserves will need to consider the trade-offs between rates of reproduction and security in deciding when and how to regulate rhino numbers.

As population size increases and expansion is limited by reserve boundaries, changes in spatial relationships and mating patterns also may occur. Chapter 2 focuses on the territorial behavior of adult male white rhinos. Within the high-density group in Matobo Park, only 30% of adult males expressed territorial behaviors covering over 70% of the total area, including all of the large, open grasslands. Other adult males followed a nonterritorial tactic. Although adult males associated with females regardless of their territorial status, territorial males appeared to discriminate among female partners based on their reproductive value.

Demographic and behavioral data are used in Chapter 3 to explore issues relating to persistence of small and newly established populations. Probability of population survival is examined as a function of variation in numbers of founders and in the carrying capacity of the reserve. Persistence appeared to reach a threshold at founder populations of ≥10 individuals, a result supported by empirical findings. Carrying capacity and its variation interacted to affect the probability of persistence in the population models. Sensitivity analyses revealed that changes in age-specific mortality, especially of adults and subadults, can have a marked effect on population persistence. Although stocking small reserves well below their estimated carrying capacities may increase rates of population growth, those established with fewer than 10 founders may have higher probabilities of extinction. Management actions designed to increase survival of calves may be less effective in enhancing population persistence than actions that decrease adult and subadult mortality.

Horn removal from live rhinos has been conducted in Zimbabwe, Namibia and Swaziland in an effort to discourage rhino poaching. Although all trade in rhino products is banned at this time, establishment of a legal market for horn has been discussed as a means to raise revenue for rhino conservation. I measured horns before and after dehorning in Hwange and Matobo National Parks, and documented rates of horn regrowth. Both sex and age influence rates of horn regrowth; adult males regenerate almost twice the mass (>1.3 kg/yr) regenerated by adult females. Based on an economic model for harvest rotations, intervals for dehorning that maximize profits would range from 1.16 to 1.41 years, varying with both sex and age. However, these values may serve as minimum dehorning intervals to managers trying to balance profits with longer-term management goals.

Chapter 1: Reproduction and Population Density: Trade-Offs in Managed Ecosystems

Abstract: As human populations increase, wildlife is becoming increasingly restricted to protected remnants of ecosystems. One primary feature differentiating these protected areas from a "pristine" state is the presence of human boundaries that restrict or limit dispersal. The effect on large herbivore populations generally is an increase in population density within reserve borders. An understanding of the implications of restricted dispersal and increased population density on the demography and behavior of threatened, large species is critical to their conservation in managed systems. I investigated the relationship between population density and reproduction in white rhinos (Ceratotherium simum) in Matobo National Park, Zimbabwe. Two lines of evidence were examined: 1) a contrast in reproduction between a high-density and a low-density population; and 2) a longitudinal analysis of changes in reproductive parameters within a fenced population as density increased by >300%. Rate of growth of the fenced population was lower at higher population densities, and the recruitment rate decreased significantly with population density ($p = 0.018$). Individual reproductive parameters also varied with density. Age at first reproduction increased significantly, and females in the low-density group produced their first calves at significantly younger ages ($p = 0.036$). Body condition of the rhinos decreased between the wet and dry seasons, but the loss of condition was more pronounced in the high-density group ($p = 0.016$). Maternal females also lost significantly more body condition than non-lactating adult females ($p = 0.018$), a trend more evident in high-density populations. Because

most African rhinos exist in relatively small reserves, sound management of high-density populations will be important for long-term conservation planning. Managers of reserves will need to consider the trade-offs between enhanced safety from poaching and decreased reproduction in developing conservation strategies for rhinos and other rare, large species once confined to reserve systems.

Reproduction and Population Density: Trade-Offs in Managed Ecosystems

Introduction

Physical boundaries that limit or inhibit dispersal are becoming a prominent feature of many conservation areas. Even in protected areas without fences or other physical borders, a marked gradient in human activities at the edges often results in confinement of populations. Insularization of wildlife reserves can have numerous effects on the populations confined within the boundaries that increase vulnerability to local extinctions (Berger & Cunningham 1994a; Soulé et al. 1979; Wilcove et al. 1986; Wilcox 1980). An understanding of the potential impacts of restricted movement on population densities, behavior, and demography is required for sound management of confined populations.

The impacts of insularization may be most pronounced in species that, in unrestricted situations, range over large areas at relatively low densities. Among mammals, larger species have larger ranges (Belovsky 1987; Gompper & Gittleman 1991). In addition, conservation of viable populations of large-bodied carnivores requires even greater areas than those needed to sustain herbivore populations (Belovsky 1987; Mattson et al. 1996). As a result, small conservation reserves that effectively protect endangered, large herbivores are less likely to also support a full complement of their predators. The resulting trend is one of increased herbivore density initiated by restricted dispersal and exacerbated by a paucity of large carnivores (Clutton-Brock et al. 1982; Owen-Smith 1982). Thus, population densities of many large herbivores within smaller reserve systems might be expected to increase beyond densities observed in unrestricted populations in similar habitats.

Large, mammalian herbivores fall into the category of "K-selected" species, for which demographic patterns are influenced by variation in population densities (Owen-Smith 1988). Although to some extent, this is also true of small-bodied species (Krebs et al. 1973), density-dependent reproduction, mortality, and dispersal are especially conspicuous in large mammals (Fowler 1987). Declining resources have been related to lower levels of fecundity, delayed attainment of puberty, and increased mortality in ungulates (Albon et al. 1983; Jorgenson et al. 1993; Saether & Heim 1993; Skogland 1989). In the future, large-bodied mammals are likely to become more rather than less constrained to reserves, and the effects of changes in population density on their demography and conservation deserve attention.

Many of the most threatened or endangered mammals are unlikely to persist outside of protected conservation areas. For example, all five species of rhinos are uncommon outside of reserves today (Gakahu 1993; Kahn 1989). Although relatively large tracts of habitat still exist for African rhinos, poaching has decimated populations in areas outside of heavily guarded reserves. Recent conservation efforts for African rhinos have focused on establishment of rhino sanctuaries or intensive protection zones in which both rhinos and resources for anti-poaching are concentrated (Brett 1990; Nduku & Martin 1993). While this strategy has been successful in halting the rapid decline in numbers due to poaching, increasing population densities within the reserves will likely require changes in management practices.

Owen-Smith (1988) suggested that the demographic parameters most likely to respond to variation in population density in white rhinos (Ceratotherium simum) would be age at first reproduction, interval between births, and to a lesser extent, calf survivorship. I investigated the first two of these parameters using two lines of evidence: 1) a contrast between a fenced, high-density population and a lower-density population; and 2) an analysis of changes in demographic parameters within the fenced population over a 30-year period during which population density has increased by >300%. I examined population growth and recruitment in relation to population density, and determined the extent to which age at first parturition and interval between births increased with population density.

Methods

Study Area and Population

Matobo National Park (MNP) is located in southwestern Zimbabwe and encompasses over 425 km^2 of the Matobo Hills, characterized by rugged, granitic domes and kopjes (Wilson 1969). White rhinos were extirpated in Zimbabwe in the late 1800's, and reintroduced in 1962 in MNP (Roth 1967). Demographic data were available for the Matobo white rhino population since their reintroduction due to monitoring efforts by National Parks personnel. Written records and photographs were used to verify data on population size, translocations, births and maternal relationships of known individuals (Rachlow & Gumede 1994) as has been done in other retrospective analyses (Packer et al. 1991).

The white rhinos were released into a fenced area of approximately 105 km^2 within MNP known as the Whovi Game Park (WGP). Because the boundary of the WGP is fenced, population density increased with population size. Much of the terrain in MNP consists of granite domes and thickly vegetated rock kopjes that are not used by the larger grazing species. Grobler and Jones (1980) estimated that 51.9 km^2 of the total 105 km^2 of the WGP was available to grazers, and this area was used to calculate ecological densities (animals/available habitat; Eisenberg & Seidensticker 1976).

A second, smaller population of white rhinos was established within MNP, but outside of the fenced WGP in the Hazelside Area (HA). This area is about 3 times larger than the WGP, and rhinos did not use the entire area available. Therefore, movements of individuals in this second population were not constrained by a fence, and I estimated population density by calculating the size of the area used by the entire group based on 106 location points. Only one location per group or solitary individual per day was included in this analyses. The program CALHOME (Kie et al. 1996) was used to estimate a 95% group range (analygous to a 95% home range of an individual) using the adaptive-kernel method (Worton 1989). A smoothing parameter of 80% of the optimum calculated by the program was chosen because it lowered the least-squares-validation score (Worton 1989). Because the terrain in the HA is slightly less rugged than that in the WGP, a greater proportion of the total area was suitable for rhinos, and I used 60% of the total area used by this population to estimate the ecological density. This method realistically produces an estimate of maximum population density for the HA group. In the following analyses, the HA rhinos represent the "low-density" population and the WGP rhinos are considered the "high-density" group. Using a maximum density estimate for the "low-density" group is a conservative approach for these analyses.

Assessment of Body Condition

Body condition was assessed following a method outlined for white rhinos by Keep (1971), which scores condition visually based on reduction of fat deposits and muscle mass around the neck, scapula, spine, and sacrum. I photographed each rhino in the late wet season (7 April - 8 May) and again towards the end of the dry season (30 September - 2 November). Multiple photographs were taken of each rhino and scored on a scale from 1 to 4 at increments of 0.5 (Table 1). A score was assigned to each individual in each season.

Statistical Analyses

Mann-Whitney U tests were used in place of two-sample t-tests for comparing differences in body condition and reproductive parameters because sample sizes were too small to meet or to reliably test for the assumptions of parametric analyses (Zar 1984). Regression analyses (both simple and multiple linear) were used to examine relationships between reproductive parameters, population size or density, and rainfall. When necessary, data were log-transformed to correct for heteroscedasticity (Zar 1984). Means are reported ± standard errors of the means, and in all tests, a p-value of <0.05 is considered statistically significant.

Monthly rainfall totals were available from Park records and were used to examine the relationship between annual rainfall and reproductive parameters. Rainfall was highly variable; mean annual rainfall over the previous 45 years was 639 mm (range = 227 to 1097 mm; coefficient of variation = 0.368). Research in MNP demonstrated that yearly grass yield increased linearly with annual rainfall, especially in the thornveld habitat (Dye & Spear 1982). Because white rhinos are grazers, and an estimated 99% of their diet consists of graminoids (Owen-Smith 1973), marked variation in annual rainfall would result in large fluctuations in forage availability. Rainfall variables examined with respect to individual reproductive parameters include total annual rainfall in the year of birth, in the year of conception (birth - 2 years), and a mean annual total during the 4 years prior to a female's first conception (2 to 6 years before birth). The latter variable was used to explore the effect of rainfall during growth, which may influence age at puberty. I also tested the affect of variation in annual rainfall on recruitment rates of calves into the fenced population.

Because sample sizes for some of the statistical comparisons were small, estimated power of the tests using a power analysis program (Borenstein & Cohen 1988). However, I often used nonparametric tests for which formulas for power analysis were not available. In such cases, I reported the power analysis for the corresponding parametric tests, and assume that the power of the nonparametric test was lower.

Results

Reintroduction and Population Growth in the Whovi Game Park

The program to reintroduce white rhinos to MNP began in 1962 when 4 individuals were translocated from Umfolozi Game Reserve in South Africa and released into the fenced WGP. In 1966-67, an additional 8 white rhinos were added to this group bringing the founding number to 12 (7 females and 5 males) (Roth 1967). An additional 3 females and 1 male were added to the population from Swaziland in 1987. The population increased rapidly within the fenced area (Fig. 1), and 20 individuals were translocated out of the reserve between 1975 and 1986. The population in the fenced reserve has undergone two periods of growth between 1967 and 1974 (Early Period), and 1987 and 1994 (Late Period). Because management of this population included translocations out of the Park in the mid-70's and early-80's, these years were not used to calculate population growth rates. Rates of annual increase calculated for the Early and Late Periods were 10.4% and 6.6%, respectively (Fig. 1). Density in the WGP increased by over 300% from 0.23 rhino/km^2 in 1967 to 0.83 rhino/km^2 in 1994.

In addition to rates of population growth, other demographic characteristics of the WGP population differed slightly between the Early and Late Periods. Mortality rates for calves were lower during the Late Period, but adult mortality was higher (Table 2). The population age and sex structure in the WGP was strongly influenced by translocations both in and out of the reserve during the 1970's and 80's (Rachlow & Gumede 1994). The younger age structure during the Late Period (Table 2) resulted from selective removal of adults.

I examined data on recruitment rate of the WGP population in relation to population density. Because calving intervals ranged from 2 to 3 years, recruitment was summed over 3-year periods. This analysis revealed that number of calves recruited (survived >2 years) decreased significantly ($p = 0.018$) as the population density of adult and subadult rhinos increased (>2 years of age) (Fig. 2). Rainfall is highly variable in this semi-arid ecosystem (Fig. 3), and annual rainfall at the start of each 3-year period also significantly ($p = 0.032$) affected the recruitment rate (Table 3). The r-squared value indicated that over 80% of the variation in recruitment rate was explained by these two variables. The standardized regression coefficient for population density was larger than that for rainfall (Table 3) suggesting that the former had a greater influence on recruitment rate.

Individual Patterns of Reproduction

Female reproductive parameters varied with population density. Age at first reproduction for female white rhino in MNP varied from 6.5 to 11.5 years of age. Using data for all females, age at first reproduction increased significantly with population density in the year of conception (Fig. 4). About 40% of variation in age at first parturition was explained by this variable ($p = 0.011$). Annual rainfall and grass production are highly correlated in this environment (Dye & Spear 1982). Rainfall may influence reproduction either by affecting estrus or ovulation directly, or by affecting female growth and hence, age at sexual maturity. I examined the relationship between age at first calving and annual rainfall both in the year of conception and averaged over the 4 years prior to conception. Neither rainfall variable was significantly related to age at first calving (year of conception: $F=1.597$, $p=0.230$; 4 years prior to conception: $F=2.095$, $p=0.173$). Also, neither of these two rainfall variables significantly improved the regression of age at first parturition on population density.

A contrast of age at first calving between the low-density (HA) group and the high-density WGP rhinos revealed a similar relationship between population density and reproduction. I estimated the density in 1995 for the HA rhinos at 0.18 rhino/km^2. Age at first birth was significantly less for females in the HA population ($n = 4$) than for those in the WGP ($n = 9$) (Fig. 5). This contrast includes only females born during the period of 1982 to 1994, the time period for which data were available for both the high and low-density groups.

Intervals between births have ranged from 2 to 6 years for white rhinos in MNP. Because prenatal and neonatal mortality may not be detected, these values represent intervals between births of calves that survived for at least several weeks. A comparison of mean birth interval per female between the Early and Late Periods of population growth in the WGP revealed a slight, but non-significant difference (Mann-Whitney $U = 13.0$; $p = 0.144$). Mean intervals were 2.9 yr ± 0.103 yr ($n = 6$ females, 21 intervals) for the Early Period and 3.3 ± 0.183 yr ($n = 8$ females, 19 intervals) for the Late Period. Although formulas for power analysis are not readily available for nonparametric tests, the power for a two-sample t-test comparing these two means is 0.35 (Cohen 1988), and the power of a Mann-Whitney test is about 95% that of a t-test when both are applicable (Zar 1984).

Only one female in the low-density population has given birth to ≥ 3 calves, and the mean interval between calves was 2.25 yr (for 5 birth intervals). This value is lower than the mean intervals for all adult females ($n = 8$) during the same time period in the high-density population. The binomial probability of this result occurring by chance is 0.018, suggesting that the female in the low-density group experienced significantly shorter birth intervals than females in the high-density group. Obviously these data are limited because data from only one female in the low-density group were used in this comparison, and data from more individuals are required to provide a robust test.

Body Condition and Reproductive Status

Body condition varied only slightly among individuals during the wet season, but 90% lost condition during the dry season. Body condition of adults and subadults did not differ significantly between the sexes during the wet season (males: $n = 16$; $\overline{X} = 4.0 \pm 0.0$; females: $n = 20$; $\overline{X} = 3.9 \pm 0.06$) (Mann-Whitney $U = 136.0$; $p = 0.111$). However, power of a t-test on these data is only 34%, and sample sizes of 55 animals in each category would be required to detect the observed difference in the means at an alpha of 0.05 with 80% power. Despite my small sample sizes, body condition was clearly lower in females ($n = 20$; $\overline{X} = 3.0 \pm 0.12$) than males ($n = 15$; $\overline{X} = 3.5 \pm 0.1$) (Mann-Whitney $U = 74.0$; $p = 0.007$) at the end of the dry season.

Reproductive status affected female condition during the dry season. Although condition of maternal (lactating) females ($n = 9$) and non-lactating adult females ($n = 7$) differed only little during the wet season (Mann-Whitney $U = 48.0$; $p = 0.082$), lactating females were in significantly poorer condition during the late dry season (Mann-Whitney $U = 58.0$; $p = 0.018$) (Fig. 6). Again, the power to detect a difference as small as that observed during the wet season using a t-test is low (30%), and sample sizes of 27 would be required in each category to detect the observed difference in the means at an alpha level of 0.05 with 80% power. Therefore, female body condition may be affected by reproductive status throughout the year, but the differences become more obvious during the dry season.

Differences in body condition were significant between the high and low-density populations at the end of the dry season (sexes combined: $n = 32$ for WGP; $n = 7$ for HA; Mann-Whitney $U = 52.2$; $p = 0.024$) (Fig. 7), but not during the wet season (Mann-

Whitney U = 101.5; p = 0.406). This difference was apparent despite the fact that maternal females, which tend to exhibit the poorest condition during the dry season, comprised a greater proportion of the population in the HA population. As above, power for a t-test comparing body condition during the wet season was low (33%), and hence, body condition also may differ throughout the year, but differences become more pronounced during the dry season.

Discussion

Population Growth

Recruitment rate in a closed population is a population-level index of reproduction. The decrease in the recruitment of calves with population size in the WGP indicates that reproduction declined as the population size increased (Fig. 2). Population densities differed markedly between the Early and Late Periods, and differences in recruitment during these two periods probably provided a major contribution to the observed differences in population growth rates.

Rapid rates of increase have been reported in large herbivore populations following introduction into unoccupied habitats (Berger & Cunningham 1994a; Klein 1968; Leader-Williams 1980). The rate of growth of the white rhino population in the WGP following introduction (10.4% per annum) is among the highest rates documented for free-ranging populations of either species of African rhinos. A maximum rate of 9.6% per annum was calculated for white rhinos in Umfolozi Game Reserve, South Africa, and 10.5% was estimated to be a theoretical maximum (r_{max}) for the species (Owen-Smith 1973; 1988). A maximum rate of increase was estimated to be 6.0% in Ndumu

Game Reserve, a small South African reserve (Conway & Goodman 1989). However, a growth rate of 9.7% was reported for a small, low-density population of northern white rhinos (C. s. cottoni) in Garamba National Park, Zaire (Smith et al. 1993). The white rhino population in the WGP appears to have achieved a near-maximal rate of growth following introduction into this unoccupied habitat.

A comparison of mortality rates by age class reveals that rates of adult mortality were higher during the Late Period (Table 2). Population growth models for both black (Lacy 1987) and white rhinos (Owen-Smith 1988) suggest that even slight changes in rates of adult mortality can have large effects on population growth trajectories. Mortality from fight-related injuries is the most frequent cause of death identified in populations of translocated white rhinos in South Africa (Anderson 1993), and a major source of mortality among adult white rhino males in Kruger National Park, South Africa (D. Pienaar, pers. com.). Aggression may be exacerbated in rhinos confined to small reserves (Berger 1994). As population density rose within the fenced area, prevalence of fight-related mortality also increased and prompted managers to initiate the removal of rhinos from the WGP (Rachlow & Gumede 1994). Interestingly, 2 of the 5 adult deaths during the Late Period resulted from fighting among males. Although horn removal may reduce the probability of serious injuries from fighting in rhinos (Berger & Cunningham 1994b), one male was killed in a fight between two dehorned white rhinos during this study. The increase in adult mortality rates during the Late Period, due in part to rising levels of intraspecific aggression, likely contributed to depression of the population growth rate.

The population structure in the WGP has been strongly influenced by translocations both in and out of the reserve (Rachlow & Gumede 1994). Proportions of adult females (>5 years) in the populations varied slightly between these periods. Adult or potentially breeding females comprised 46.2% of the total population at the start of the Early Period in 1967 in contrast with 36.7% at the start of the Late Period in 1987 (Table 2). Therefore, differences in rates of population growth during these periods could be due, in part, to the larger proportion of adult females in the population during the Early Period, and to variation in age-specific mortality rates.

Individual Patterns of Reproduction

Theory predicts that females that reproduce early should gain a genetic advantage over those who delay reproduction (Cole 1954; Stearns 1976; 1992). However, trade-offs between growth and age at first reproduction may affect future fecundity or survivorship (Gadgil & Bossert 1970; Green & Rothstein 1991; Reiter & Le Boeuf 1991). Age at first reproduction can vary markedly in long-lived species, and delayed reproduction may be selectively favored under severe conditions (Goodman 1981; Williams 1966). The age at which mammalian females reach puberty and begin reproducing varies markedly with population density in numerous species (Albon et al. 1983; Fowler 1987; Jorgenson et al. 1993). Age at first calving also appears to be relatively sensitive to population density in African rhinos. In black rhinos, age at first birth was 6.5 years in a low-density population in Umfolozi Reserve, South Africa, and 12 years in a high-density population in the neighboring Hluhluwe Reserve (Owen-Smith 1981). In MNP, first births occurred at older ages in white rhinos as density increased

(Fig. 4), and females in the low-density population calved at significantly younger ages than did those in the high-density group (Fig. 5).

Birth intervals in rhinos and other nonseasonal breeders vary considerably, and may be relatively plastic with respect to population density. Although the sample sizes are small, data from MNP suggest that rate of calving is inversely related to population density. In black rhinos, a contrast between Hluhluwe (high-density) and Umfolozi (lower-density) Reserves revealed that the mean calving intervals were 2.7 years and 2.3 years, respectively (Owen-Smith 1981). A mean birth interval of 2.5 years was documented for white rhinos in Umfolozi Reserve, with a range of 1.8 to 3.5 years (Owen-Smith 1973). Although minimum calving intervals of 19 months (1.6 yr) have been documented in captive white rhinos (Rieches 1993), management practices are often employed to enhance reproduction in captive populations. Such reproductive rates are unlikely to be achieved by nursing females in the wild, and nutritional constraints may affect calving intervals at higher population densities.

Numerous factors likely interact to affect reproduction in female mammals. Several studies have identified a threshold body mass for reproduction among young female ungulates (Saether & Haagenrud 1983; Saether & Heim 1993), and the relationship between reproduction and body mass may be influenced by population density (Albon et al. 1983; Jorgenson et al. 1993). Other studies have distinguished between total body mass and body fat, demonstrating that fat reserves independent of body size, can positively influence reproduction in females (Albon et al. 1986; Thomas 1982). Although the index of body condition I used for the white rhinos is crude, it revealed seasonal declines in body condition related to both population density (Fig. 7) and reproductive status of females (Fig. 6). This suggests that competition among individuals is occurring in the high-density population and is affecting body condition during the dry season when forage availability is lower.

Annual rainfall and plant biomass exhibit a strong, positive correlation within soil types/vegetation communities in arid African systems (Bell 1984; Dye & Spear 1982). Rainfall significantly affected the recruitment rate in MNP along with population density, and together these variables explained >80% of the variation in recruitment. Given the relationship that I observed between body condition and reproduction, forage availability, through its interaction with both rainfall and intraspecific competition, is likely to affect the reproductive performance of individual females.

Management Implications

Due to relatively high rates of birth and low rates of mortality, white rhino populations have the capacity to increase rapidly. Because of the comparatively long period between birth and puberty in many large-bodied species, there is a delay between the times when reproductive rates decline and when number of breeding females added to the population also declines (Owen-Smith 1981). Further, mortality rates of adults are low and appear to be relatively insensitive to moderate shortages of forage unless densities become excessively high (Owen-Smith 1982). Hence, population-level responses to changes in forage per capita are relatively slow, and overuse and degradation of forage resources are likely to be subtle and require long periods to detect.

Owen-Smith (1982) modeled the effects of both restricted dispersal and variable rainfall on white rhino population growth. If dispersal is permitted in response to forage availability, the model suggests that white rhino numbers (biomass) would fluctuate with rainfall cycles. The absence of emigration, however, resulted in higher population peaks and long-term deterioration of the grassland resources, which in turn, lowered the carrying capacity and resulted in a large decline in the simulated white rhino population. Removal of subadults from the population may be the best option for regulating population densities within smaller reserves before an expanding population overshoots the carrying capacity and vegetation production is affected (Owen-Smith 1981). Similar feedback between population densities and subsequent vegetation changes have been observed in elk in the Yellowstone and Teton National Parks (Boyce 1989; Houston 1982).

Large fluctuations in forage availability because of rainfall variation make determining stocking levels or carrying capacities for large herbivores in small reserves difficult (Novellie et al. 1991). Managers will likely want to maintain populations well below the ecological carrying capacity to avoid ecosystem alteration (Berger & Cunningham 1994a). However, because large-bodied species require larger areas, total population sizes within smaller reserves are likely to be small, and few will reach numbers recommended for long-term population viability (Foose 1987; Gilpin & Soulé 1986). Indeed, this situation already exists for black rhinos, for which > 80% of the remaining individuals survive in populations of fewer than 100 individuals (Gakahu 1993). Management under these circumstances may need to consider exchange of individuals among populations in a metapopulation management approach (Foose 1987). However, translocation of rhinos is both costly and logistically challenging.

From a nonbiological perspective, other factors also will bear on management decisions for conservation of rare, large mammals within smaller reserves. Due to extreme levels of poaching, few African rhinos now persist outside of heavily guarded areas. Because of the difficulty of providing adequate levels of antipoaching protection in large, wild regions, most rhinos in Zimbabwe and Kenya are currently managed within rhino sanctuaries or intensive protection zones (Brett 1990), a trend that is increasing in South Africa and Namibia as well (Anderson 1993). Populations within these sanctuaries will continue to increase in the absence of poaching, and trade-offs are likely to occur between population densities and reproduction. From a numerical viewpoint, balancing numbers lost to poachers with the decrease in numbers of calves recruited, managers may choose to maintain higher density populations in safe areas. If management goals are to increase numbers of rhinos and to restock safe areas within their former ranges, then population densities within the rhino sanctuaries should be monitored and managed below the level where body condition affects reproduction.

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Table 1. System for scoring body condition of white rhinos used in Matobo National Park following the criteria outlined by Keep (1971).

INDEX SCORE	VISIBLE MUSCLE DETERIORATION
(4) Excellent	No visible muscle wasting, very rounded flanks and neck.
(3) Fair	Groove visible at the neck along the ligamentum nuchae, and the anterior of the scapula is visible.
(2) Poor	Muscles across the scapula are visible, and the skin fold on the flank is more pronounced.
(1) Very Poor	A marked groove is visible along the spine, and a hollow appears on the upper hind limb as a result of gluteus atrophy.

Table 2. Demographic characteristics of the white rhino population in the Whovi Game Park during the Early Period (1967-1974) and the Late Period (1987-1994).

PARAMETER	EARLY PERIOD	LATE PERIOD
Population Growth Rate*	10.4%	6.6%
Population Density**	0.23 rhino/km^2	0.52 rhino/km^2
Mortality Rates*	6.3% calves 0.0% subadults 0.0% adults	2.2% calves 0.0% subadults 2.7% adults
Sex and Age Structure**	8% calves 15% subadults 46% adult females 31% adult males	30% calves 17% subadults 36% adult females 17% adult males

* Rates expressed as percentage per annum.

** Values represent the status at the start of each Period (1967 and 1987).

Table 3. Results of single and multiple linear regression models for recruitment rate on population density for adults and subadults(>2 years of age) in the WGP and total rainfall.

Indep. variables	Std. coefficient	p-value	F-value	p-value	adj. mult. r^2
1. Density	-0.795	0.018	10.294	0.018	0.570
2. Density	-0.884	0.003	16.068	0.007	0.812
Rainfall	-0.491	0.032			

FIGURE LEGENDS

Figure 1. Numbers of white rhinos in the fenced Whovi Game Park within Matobo National Park, Zimbabwe. Rates of growth calculated for the Early Period (1967-1974) and the Late Period (1987-1994).

Figure 2. Recruitment rate (summed over 3-year periods) of calves that survived ≥ 2 years as a function of population density (animals ≥ 2 years of age). This relationship is significantly improved if mean annual rainfall for each 3-year period is entered into the regression (Table 3).

Figure 3. Total annual rainfall in Matobo National Park from 1960-1994. Mean annual rainfall was 632.8 mm (± 41.0).

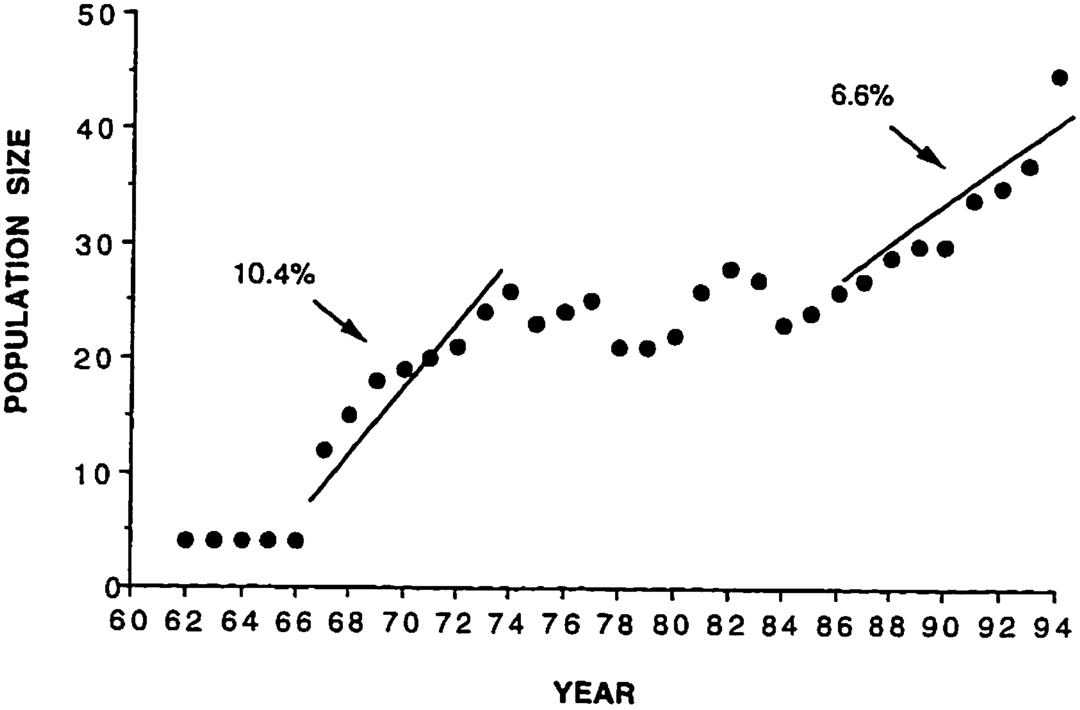
Figure 4. Age of first reproduction (log-transformed) in relation to population density for female white rhinos in Matobo National Park.

Figure 5. Comparison of age at first reproduction for females in the low-density (Hazelside Area) population ($\overline{X} = 7.4 \pm 0.375$ yr) and the high-density (Whovi Game Park) population ($\overline{X} = 10.1 \pm 0.684$ yr). This analysis includes females born between 1982-1994.

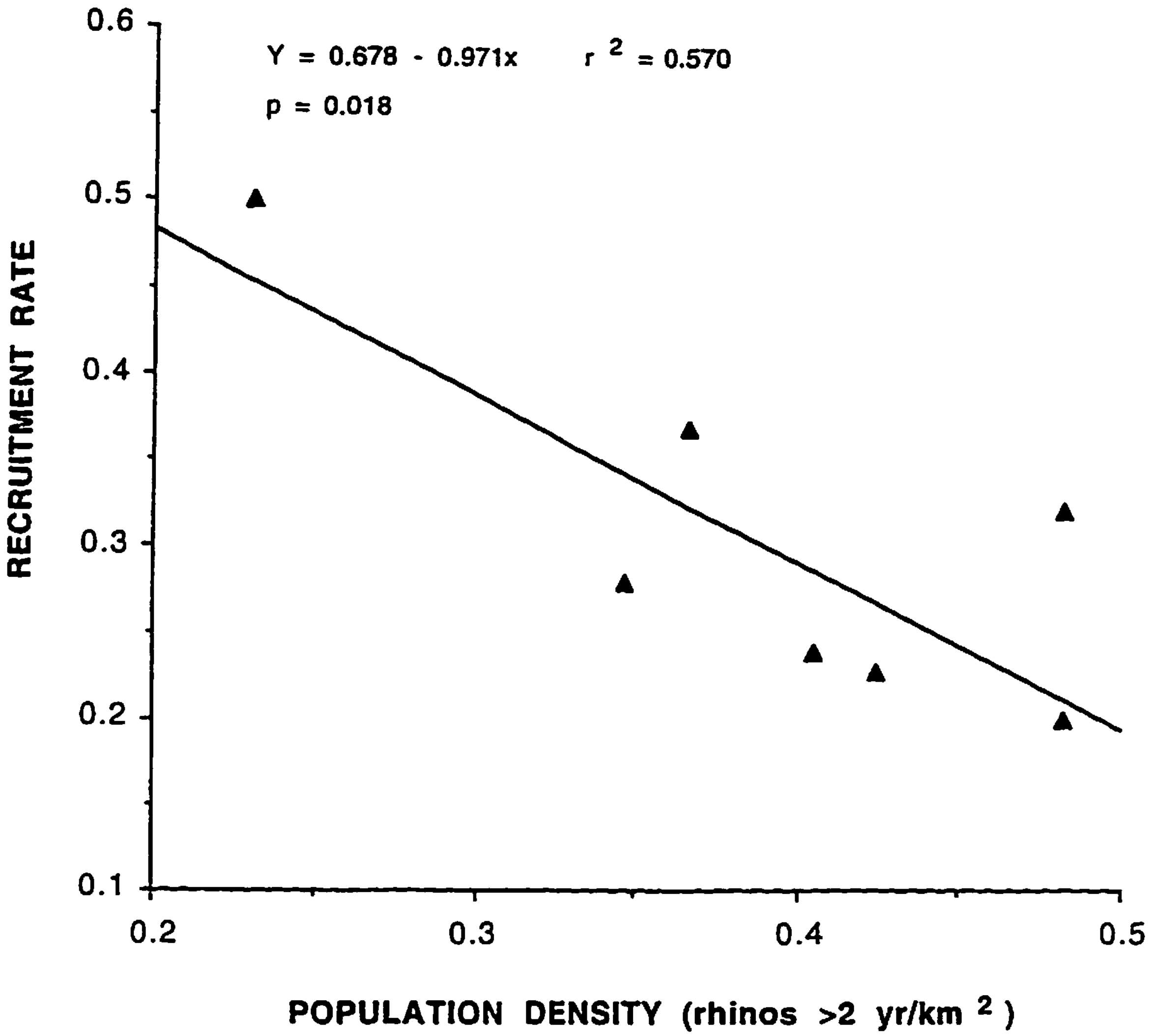
Figure 6. Comparison of body condition scores lactating and non-lactating adult females. Condition scores did not differ significantly during the wet season between non-lactating ($\bar{X}$ = 4.0 ± 0.00) and lactating ($\bar{X}$ = 3.8 ± 0.12) females. However, non-lactating females had significanlty higher scores ($\bar{X}$ = 3.4 ± 0.09) than lactating females ($\bar{X}$ = 2.7 ± 0.20) during the dry season.

Figure 7. Comparison of body condition scores for rhinos in the high and low-density groups. Condition scores did not differ significantly during the wet season between the low-density ($\bar{X}$ = 4.0 ± 0.00) and high-density ($\bar{X}$ = 3.9 ± 0.04) populations. However, animals in the low-density group ($\bar{X}$ = 3.6 ± 0.07) were in significantly better condition than those in the high-density group ($\bar{X}$ = 3.1 ± 0.10) during the dry season.

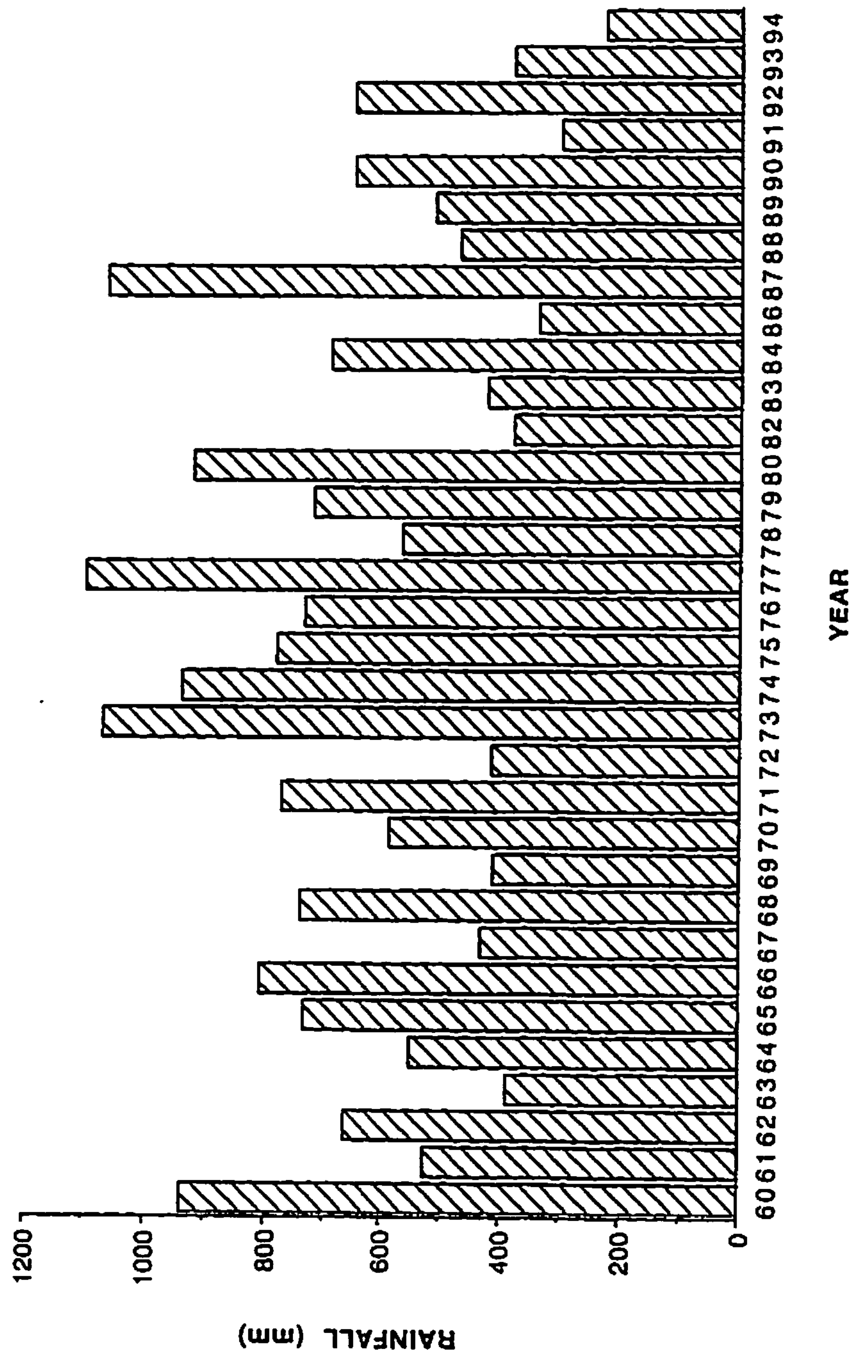
WHITE RHINOS IN THE WHOVI GAME PARK, ZIMBABWE



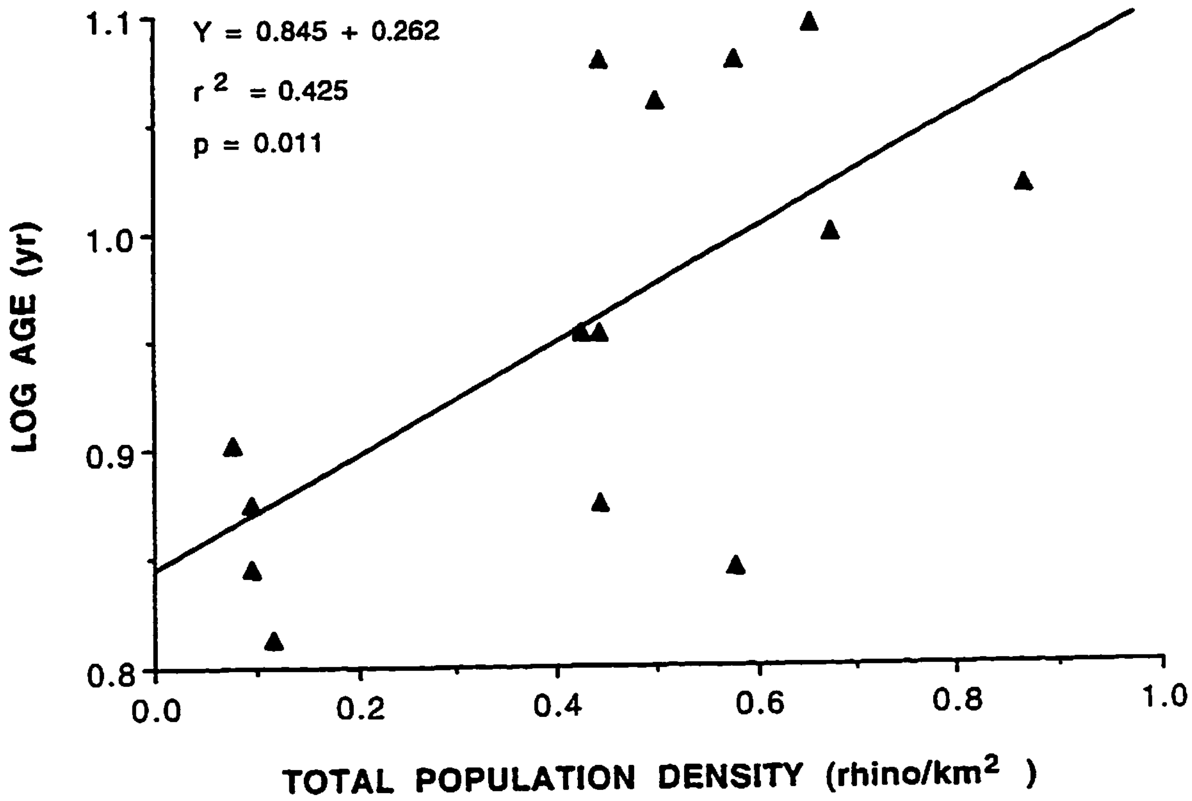
RECRUITMENT OF CALVES INTO THE WGP POPULATION



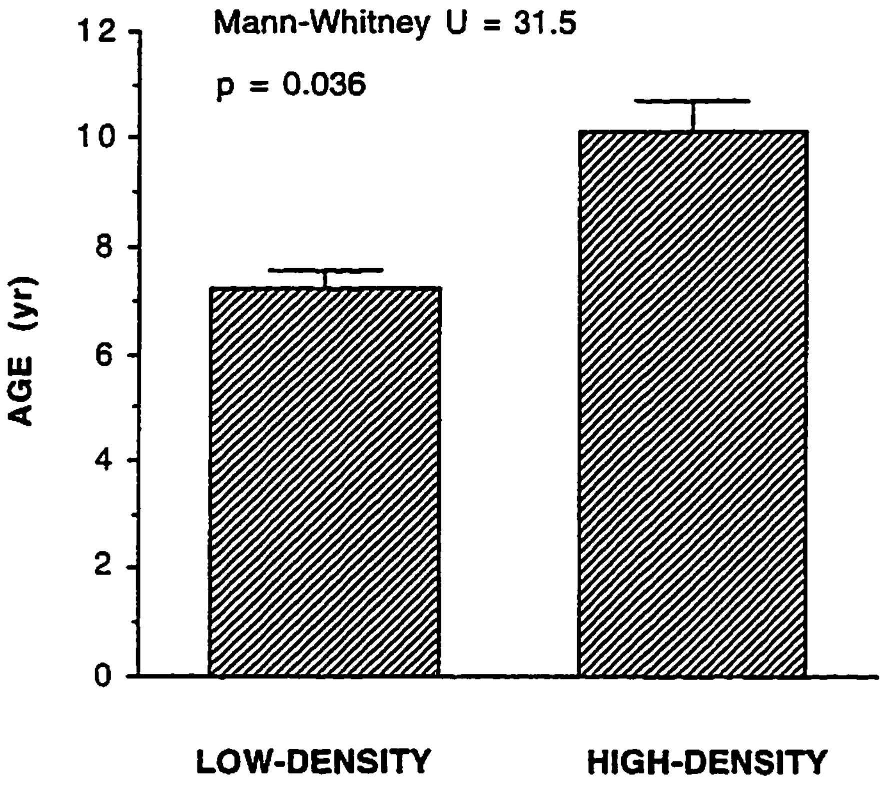
TOTAL ANNUAL RAINFALL IN MATOBO NATIONAL PARK, ZIMBABWE

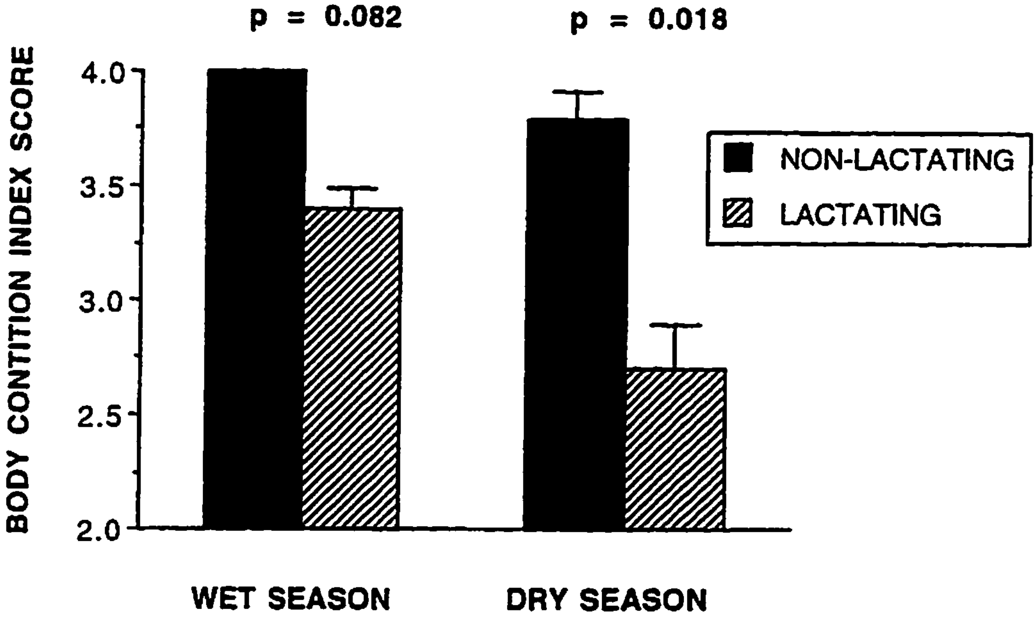


FEMALE AGE AT FIRST REPRODUCTION



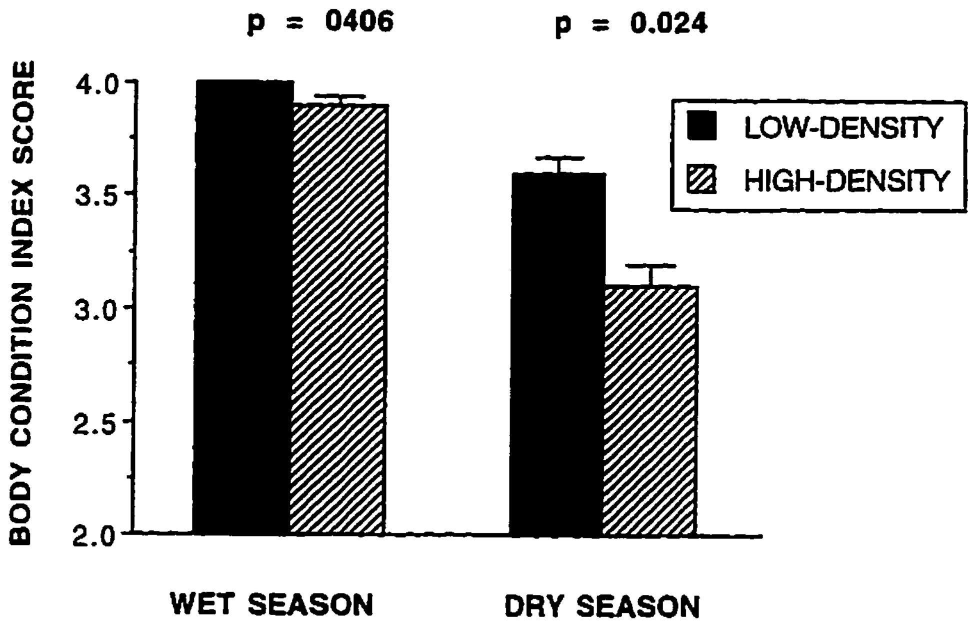
FEMALE AGE AT FIRST REPRODUCTION





SEASONAL CHANGES IN BODY CONDITION OF FEMALES

SEASONAL CHANGES IN BODY CONDITION OF WHITE RHINOS



Chapter 2: Age-Graded Correlates of Male Mating Tactics in White Rhinos

Abstract: When competition for mating opportunities among males is intense, younger, smaller males may opt for alternative tactics to gain reproductive opportunities. Demographic, social, and environmental conditions may affect the age at which males switch from one tactic to another. Territoriality is a common male reproductive strategy exhibited by many polygynous ungulates. Male white rhinos (Ceratotherium simum) establish exclusive ranges with scent-marking behaviors. Because only 33% to 67% of adult males in a population may establish territories that occupy all available space, other adult males are excluded from following the territorial tactic. I examined spatial relationships and scent-marking behaviors of adult male white rhinos in Matobo National Park, Zimbabwe. Correlates of male territoriality included age, body size, and testosterone levels. Patterns of range overlap and associations with adult females did not differ significantly between territorial and nonterritorial males. However, territorial males appeared to discriminate among females based on reproductive status, and they spent more time with females of higher reproductive potential. Although the territorial tactic may yield greater reproductive payoffs, genetic analyses are needed for possible confirmation. Knowledge about male reproductive competition and spatial patterns are needed for estimating the carrying capacity in small reserves.

Age-Graded Correlates of Male Mating Tactics in White Rhinos

Introduction

Reproductive strategies are shaped by natural selection favoring individuals with the greatest lifetime reproductive success. However, because not all individuals adopt the same reproductive tactics (Gross 1996), and competition for access to mates can be severe, young reproductive individuals sometimes opt for alternative mating tactics (Caro & Bateson 1986). This may be especially prevalent in species in which growth continues after sexual maturation, and competitive ability is related to age. For example, in a variety of large mammals including elephant seals (Mirounga angustirostris) (Le Boeuf 1974), red deer (Cervus elaphus) (Clutton-Brock et al. 1982), and horses (Equus caballus) (Berger 1986) young males do not defend harems. Instead, they attempt to copulate with females surreptitiously. Similar age or size-specific alternative tactics have been observed among taxa as diverse as dung beetles (Onthophagus sp.) (Cooke 1990), anurans (Arak 1983), guppies (Poecilia reticulata) (Reynolds et al. 1993), and pied-flycatchers (Ficedula hypoleuca) (Slagsvold & Saetre 1991).

The alternative tactics followed by smaller or younger males often seem to result in lower reproductive success than the tactic followed by more mature males (Dunbar 1982). However, even when male mating behavior appears to be influenced by age, not all mature individuals follow the same pattern. Environmental or demographic factors may constrain the number of males able to successfully employ optimal tactics, and force other mature males into "making the best of a bad job" (Dawkins 1980).

Demographic variation as well as individual characteristics that lead to competitive asymmetries may affect the age at which males switch from a less productive alternative to a more productive or optimal tactic (Gross 1996).

Among polygynous ungulates, territorial behavior is almost exclusively a male trait and it is believed to function primarily as a reproductive strategy to secure mates (Owen-Smith 1977), although it may also be important for resource defense in monogamous species (Komers 1996). Increases in population density may alter the intensity of male-male competition; under such conditions, the costs of territory maintenance may be so great, that alternative male mating tactics are favored, even among mature males (Dunbar 1982; Gosling 1986).

Studies of white rhinos in Umfolozi Game Reserve and Kruger National Park, South Africa, have described spatial patterns of adult males that consist of nonoverlapping ranges occupied throughout the year (Owen-Smith 1988; Pienaar et al. 1993). White rhino males exhibit characteristic scent-marking behaviors that function to delineate territories (Owen-Smith 1971, 1977). Mature males consistently perform these marking behaviors, and their expression is related to a system of exclusive space use and space-correlated dominance (Owen-Smith 1971). Although territoriality is a complex concept with various functional definitions (Maher & Lott 1995), the spatial patterns of adult male white rhinos appear to function as a territorial strategy for establishing access to estrous females within a male's territory (Owen-Smith 1971).

In this study I examined space use, scent-marking behavior, age, body size, and testosterone levels of territorial and nonterritorial adult male white rhinos. Range overlap and association behavior with adult females were examined for males exhibiting each tactic. Because females differed in their reproductive status, I asked whether territorial or nonterritorial males were possiby discriminating among females based on their potential reproductive value.

Methods

Study Area and Population

Data were collected from March 1994 to January 1995 in Matobo National Park (MNP), Zimbabwe. The park is located in southwestern Zimbabwe and encompasses over 425 km^2 of the Matobo Hills, a rocky region characterized by granitic domes and kopjes (Wilson 1969). Most of the white rhinos in MNP (n = 43) are contained within a 105 km^2 fenced area known as the Whovi Game Park (WGP). A smaller group of 9 rhinos exists outside of the fence in the Hazelside Area (HA) of the Park. These two areas are separated by a fence and a road, but consist of similar vegetation and habitat types. All adults and most subadults were identified by ear-notch patterns, and ages were known or estimates available from previous monitoring work in MNP (Rachlow & Gumede 1994). Sixteen adults were fitted with radio-collars during May-August 1994, and were followed at least weekly. I located other rhinos either visually or by following spoor with the help of a National Parks tracker. All locations were recorded in UTM coordinates using a 1:50,000 topographic map and/or a handheld global positioning system.

I collected measurements of body size from rhinos immobilized for radio-collaring. Total body length was measured along the spine from the base of the tail to the back of the skull. Chest girth was measured around the body behind the forelimbs and across the sternum. Nonlinear regression (Kaufmann 1981; Wilkinson 1990) was used to fit growth curves for these measurements as a function of age in males.

Few data are available regarding age at sexual maturity for African rhinos (Bertschinger 1994). Examination of the testes of two black rhinos indicated that spermatogenesis was not present in a 7-year old male, but was evident in an 8-year old (Hitchens & Anderson 1983). The youngest record of copulation in free-ranging male black rhinos was 4.4 years (Goddard 1970). The youngest age of a territorial male in MNP was 9 years, but considering that males are likely to become sexually mature at about 6 years of age, I classified males ≥6 years old as adults. Because Owen-Smith (1973) considered males ≥12 years old to be indistinguishable from older animals, I classified males from 6-11 years of age as young adults, and males ≥12 years old to be mature adults. The youngest age at first reproduction for females in MNP and in Umfolozi, South Africa, was 6.5 years (Owen-Smith 1988; Chapter 1) and hence, I classified females ≥6 years old as adults.

Behavioral Data

Observations were conducted during daylight between 0500 hr and 1900 hr, concentrating on the early morning and late afternoon periods when rhinos were most active. Rhinos were observed from distances of 50 to 200 m using 10x50 binoculars, usually on foot and often from rocky outcrops. Associations were recorded if individuals were ≤75 m (about 25 body lengths) of each other when first sighted, regardless of their activities during the observation period. Groups were identified when individuals were ≤45 m (15 body lengths) of each other, and exhibited synchronized activity patterns and cohesive behavior. Associations consisted of one or more groups, and patterns of association were analyzed based on proximity at first sighting to remove the potential bias of length of observation period. For each association observed, I recorded location, size, individual identity, habitat type, and initial activity. Scan-samples of focal groups were recorded at 5-minute intervals to quantify activity patterns (Altmann 1974). All occurrences of scent-marking behaviors (urination and defecation) were recorded. When possible,I followed groups on foot to continue observations of traveling individuals. Observations were suspended if the rhinos were disturbed by our presence and exhibited increased vigilance behavior for >5 minutes, or when a focal group was out of sight for >5 minutes. Following Owen-Smith (1973), I identified individuals that were consistently sighted together for periods of ≥1 month as a "stable group", and groups that persisted for shorter periods to be "temporary groups".

Spatial Use

Only one location per day was included for each individual, and the mean sampling interval between locations for all adults (n = 30) was 8.4 ± 0.8 days. Although questions regarding independence of data points exist in analyses of this type, sampling intervals that are sufficient periods for an animal to traverse its home range are often considered adequate to provide statistical independence (White & Garrot 1990). At Hwange National Park, Zimbabwe, I observed movements of 20 to 40 km per day by white rhinos, which suggests that individuals could easily cover their home ranges in MNP daily. Thus, I chose to include all daily locations in analyses of home range sizes.

Because territorial males move about their ranges very differently than females and nonterritorial males, two methods for estimation of home range sizes were used in this study. Territorial males delineate their ranges with marking behaviors, and rarely wander outside of these ranges (Owen-Smith 1971). Thus, the minimum convex polygon (MCP) approach (Mohr 1947) for calculating a home range adequately describes the area used by these males. However, females and nonterritorial adult males do not demarcate their ranges, and hence, are likely to move beyond the outermost locations that I observed. For this reason, an adaptive-kernel (ADK) method (Worton 1989, 1995) was used to estimate the size of the areas used by females and nonterritorial males. This method tends to produce a larger home range estimate than the MCP method because it calculates a probability density function for the home range of an individual based on the distribution of observed locations. For purposes of comparison with other studies, results from both methods are reported for females and nonterritorial males. Although the ADK method likely reflects the size of the area used by nonterritorial males more accurately than the MCP method, I used the MCP estimates for all males (territorial and nonterritorial) in the analyses to avoid a bias stemming from methodological differences.

The CALHOME home range analysis program (Kie et al. 1996) was used to estimate home ranges. When constructing an ADK estimate, CALHOME chooses a smoothing parameter assuming that the location data are normally distributed, and a measure of goodness-of-fit is provided based on least-squares cross-validation (LSCV) scoring (Worton 1989). However, location data rarely meet the assumption of normality, and if clumped, a better LSCV may be obtained using a smaller smoothing parameter. Following the recommendations of Worton (1989), I decreased the smoothing parameter to 80% of the predicted optimum, and then ran a second ADK analysis. I used and reported the analysis for each animal that resulted in the best fit to the data based on minimizing the LSCV score (providing that it did not cause the home range to become fragmented). Range estimates from rhinos in the WGP occasionally included regions outside of the fenced study area, although white rhinos were not observed to cross the fence. Thus, I calculated range areas and overlap values based on home range estimates that were corrected to exclude any area outside of the fence.

Home range polygon data from CALHOME were imported into a geographic information system (IDRISI) for analyses of range overlap (Eastman 1995). Range overlap was quantified among adult females, among adult males, and between females and males. Mean values are reported ± standard errors.

Fecal Assays

Fecal samples were collected from known individuals after observation of defecation, placed on ice for 1 to 4 hours, and stored in liquid nitrogen until thawed for steroid hormone analyses. A total of 0.5 g from each sample was extracted with 10 ml ethyl acetate-hexane (3:2 v/v). The organic phase from each extraction was decanted and air-dried at 37°C for 2-3 hours. The resulting residue was resuspended in 1.0 ml of phosphate buffer and frozen until assayed. The remaining fecal material from each extraction also was air-dried, and then weighed. A commercial testosterone radioimmunoassay kit (Diagnostic Products Corp.) was used to determine concentrations of testosterone. Sample extracts from females were analyzed for progesterone (P_4) using enzyme immunoassays following the methods of Munro and Stabenfeldt (1984). Concentrations were indexed to dried fecal weights, and results are reported in nanograms per gram of dried feces (ng/g df).

Because females potentially will vary in receptivity to males at different times during their reproductive cycles, I evaluated female reproductive status using a combination of fecal hormone analyses and the presence of calves. Mean interval between calves in MNP ranged from 2.25 yr to 3.3 yr (Chapter 1), and given a gestation period of 16 to 17 months (Owen-Smith 1988), females with young calves (<10 months) are unlikely to conceive. Analyses of fecal samples were used to identify the pregnancy status of females without calves, and those accompanied by older calves. Fecal progesterone (P_4) concentrations differed significantly (Mann-Whitney $U = 0.0$, $p = 0.004$) between samples collected from pregnant females during late gestation ($n = 4$, $\overline{X} = 2142 \pm 337.8$ ng/g df) and non-pregnant females ($n = 11$, $\overline{X} = 578 \pm 40.3$ ng/g df). Pregnant females and females with calves ≤ 10 months old, were classified as having "lower reproductive value" because they were unlikely to conceive in the near future, and non-pregnant females without calves or with calves >10 months old were classified as "reproductively valuable" females.

Results

Male Territorial Behavior

Data on rates of territorial marking behaviors were recorded during 205 hr of observations of adult males ($n = 14$; $\overline{X} = 14.7 \pm 2.1$ hr/male). Marking behaviors consisted of a scattering of dung with vigorous kicks of the rear legs both before and after defecation and spray-urination during which 2-5 pulses of urine were sprayed backwards, often after scraping the rear legs along the ground or over vegetation. Males expressing these behaviors consistently were classified as "territorial males".

Territorial males always were observed to defecate and urinate in these characteristic manners at a mean rate of 3.0 ± 1.19 acts/active hr. Nonterritorial males urinated in a stream like females, and did not scatter their dung. I observed 4 nonterritorial males (ages 6 to 10 years) begin to exhibit marking behaviors, but these behaviors were performed sporadically and less vigorously. Overall, nonterritorial males exhibited scent-marking behaviors at a much lower rate of 0.1 ± 0.08 acts/active hr.

The structure of the male territories in the WGP shifted after one territorial male (M-07) was killed in a fight with a neighboring territory holder in September 1994. Prior to the shift, only 3 males had established territories ranging in size from 1462 ha to 5041 ha (Table 1). One additional male (M-25) began to express marking behaviors on the edge of two established territories about 2 months prior to the shift, but restricted his movements to a relatively small area (Fig. 1a). Territory expansion occurred, in which two neighboring males incorporated portions of the vacant territory into their existing ranges, following the death of M-07 (Fig. 1b). I observed a sharp increase in rate of marking behavior in association with territory expansion; males increasing the sizes of their territories exhibited a 5-fold rise in rates of scent-marking (M-09: 0.36 to 1.98 acts/active hr; M-25: 1.32 to 6.42 acts/active hr). I did not observe a similar increase in marking behavior by the territorial male who did not expand his boundaries (M-05: 3.24 to 2.40 acts/active hr). No males were observed to enlarge territories without also increasing rates of scent-marking.

Territorial males used ranges that were essentially exclusive of those of other territorial males (Fig. 1). Mean overlap among territorial males (n = 3) was 9.4 ± 3.74% before the shift in territory structure, and 0.1 ± 0.07% after the restructuring. In contrast, nonterritorial males used ranges (100% MCP: $\bar{X}$ = 2151 ± 291 ha; see Appendix 1) that overlapped widely with those of other nonterritorial males ($\bar{X}$ = 26.8 ± 2.56%) (Fig. 2), as well as with those of territorial males ($\bar{X}$ = 29.2 ± 1.81% and 24.4 ± 1.85% before and after the shift, respectively). Overlap among nonterritorial adult males was significantly greater than that observed among territorial males either before (Mann-Whitney U = 23.0; p = 0.025) or after (Mann-Whitney U = 24.0; p = 0.014) the shift in territory arrangement. I did not observe cohabitation of one territory by territorial "alpha" males and subordinate "beta" males as described by Owen-Smith (1973).

Female Home Ranges

Numbers of locations ranged from 15 to 50 per adult female ($\bar{X}$ = 31 ± 3.24). Home range estimates for the WGP females calculated using the 95% ADK method ranged from 593 ha to 3651 ha ($\bar{X}$ = 1901 ± 188 ha) (Appendix 1). These ranges represent annual use areas for adult females. Although maternal females in both areas restricted movements when accompanied by neonates, I did not observe seasonal shifts in range use.

Overlap among adult female home ranges was extensive (Fig. 1). All females in the WGP shared portions of their ranges with ≥5 other adult females ($\bar{X}$ = 7.4 ± 0.6 females). Mean area of overlap between female pairs ranged from 20.5% to 58.0% of an individual's home range, and mean percent overlap among all females was 39.9 ± 4.05% in the WGP and 74.0 ± 5.38% in the HA.

Male - Female Range Overlap

Ranges of territorial males overlapped a mean of 10 female ranges (range = 6-15) before the shift in territorial structure, and a mean of 9 female ranges (range = 6-11) afterwards. Ranges of nonterritorial males overlapped a similar number of female home ranges ($\overline{X}$ = 10; range = 5-13) as those of territorial males.

Overlap among female home ranges created zones of high female density or "hot spots" (Fig. 1). I quantified female density within an individual male's territory as female-hectares (number of females x hectares of home range overlapped) included within each territory. This measure takes into account not only the number of female ranges that overlap with an individual male's territory, but also the extent of overlap. For example, a territory overlapping 10 different females for 1 km^2 each would have a lower value (10) than a second territory overlapping 5 females for 5 km^2 each (25). If male territories are established to monopolize mating opportunities in this species, then males should benefit from defending areas with high densities of potential mates, and I expected that female densities would be higher on territories than on the ranges of nonterritorial males. However, I found no significant differences in the density of females within a territory or range for males of different status either before the shift in territory structure (Mann-Whitney U = 15.0; p = 0.865) or afterwards (Mann-Whitney U = 17.0; p = 0.865). This pattern also was evident when overlap with reproductively valuable females (non-pregnant and without young calves) was contrasted between territorial and nonterritorial males. Although territorial males had over twice the density of high value females on their territories as nonterritorial males (T: 4210 female-hectares; NT: 2037 female-hectares), the differences were not significant (Mann-Whitney U = 6.0, p = 0.089 both before and after the shift). I calculated the power of a two-tailed t-test for this comparison using a power analysis program (Borenstein & Cohen 1988). Although nonparametric tests tend to be less powerful than parametric ones (Zar 1984), this estimate of power can serve as a rough indicator. In spite of small sample sizes, power was over 80% for this contrast, meaning that I had an 80% chance of detecting a difference at the 0.05 significance level. This suggests that pronounced differences in male-female spatial relationships did not occur between territorial and nonterritorial males.

Social Behavior

Males expressing territorial marking behaviors associated with other rhinos less frequently than nonterritorial males. I observed territorial males ($n = 5$) in association with other adults significantly less often than nonterritorial males ($n = 8$) (Mann-Whitney $U = 0.0$; $p = 0.003$) (Fig. 3). Mean percent of observations in which individual males were in association with adult females did not differ significantly between territorial and nonterritorial males (Mann-Whitney $U = 22.0$; $p = 0.770$) (Fig. 4), nor did the number of different females observed in association with each male differ significantly with male status (T: $\overline{X} = 3.4 \pm 0.25$; NT: $\overline{X} = 2.8 \pm 0.56$; Mann-Whitney $U = 10.5$; $p = 0.150$). However, territorial males spent a greater percentage of their total time with females in association with reproductively valuable females (T: $\overline{X} = 90.9\% \pm 6.20$; NT: $\overline{X} = 44.0\% \pm 13.01$; Mann-Whitney $U = 5.0$, $p = 0.027$) (Fig. 4). These data suggest that territorial males distinguished among females based on their reproductive status, and directed greater effort towards potentially valuable females.

All nonterritorial males formed stable groups (lasting $\geq$1 mo) with other adults, but only 60% of territorial males formed stable groups during this study. However, nonterritorial males rarely formed stable groups with reproductively valuable females. Territorial males formed stable groups with a significantly higher number of reproductively valuable females than nonterritorial males (T: $\bar{X}$ = 1.0 ± 0.32; NT: $\bar{X}$ = 0.25 ± 0.025; Mann-Whitney U = 8.0, p = 0.043). Six of the nonterritorial adult males formed stable groups with other nonterritorial adult males. In no cases did the territorial males form such alliances with other males, and one alliance between two nonterritorial males appeared to deteriorate after one of the males obtained territorial status.

Distances of separation between females and males were recorded during 138 observation periods involving 34 dyads of adults. I calculated mean values for each dyad, and then combined values for each adult male. Mean distances of separation to adult females did not differ significantly between territorial males (n = 5; $\bar{X}$ = 4.3 body lengths ± 0.389) and nonterritorial males (n = 8; $\bar{X}$ = 3.3 body lengths ± 0.399) (Mann-Whitney U = 12.0; p = 0.242). Statistical power to detect the observed difference using a t-test was low (34% power, meaning a 34% chance of detecting a significant difference at the 0.05 level), and hence, females may actively avoid or maintain proximity to males based on their territorial status, but I was not able to detect such a bias in these data.

Age, Body Size, and Testosterone

Although overlap existed in the ages of territorial and nonterritorial males, territorial males tended to be older (Fig. 5). Territorial males within the fenced area ranged in age from 9 to 25 years old ($\bar{X}$ = 16.0 yr ± 4.73), before the shift in territory structure. Mean age of the nonterritorial males was 8.75 yr ± 0.65 (Fig. 5). Ages of territorial and nonterritorial males did not differ significantly (Mann-Whitney U = 20.5, p = 0.076), and power to detect a difference of this size with a t-test was 74%. Thus, although territorial males were often older, there was considerable overlap between the male classes. Following the death of the oldest male which resulted from a fight, the mean age of territorial males in the fenced area was 11.7 yr (± 1.45). The only adult male in the HA was 30 years of age.

Because growth in mammals tends to be asymptotic, I used a sigmoid growth function, the von Bertalanffy growth curve, to model body measurements as a function of age (Kaufmann 1981; Leberg et al. 1989). Body length in males increased with age and approaches an asymptote at $\geq$14 years of age, whereas chest girth approached an asymptote at about 20 years of age (Fig. 6). No significant difference was observed in body length between territorial and nonterritorial males, but territorial males had significantly larger neck and chest girths (Table 2). This is not surprising because chest girth (Fig. 6), and probably neck girth, continue to increase in adult males throughout much of their lifespan, and territorial males tended to be older than nonterritorial males in this population.

Territoriality among adult male rhinos was positively related to fecal testosterone levels. Among adult males $\geq$6 years old, fecal testosterone was not significantly related to age ($n = 11$; $r^2 = 0.091$; $F = 0.904$; $p = 0.367$), and even when samples from 3 subadult males were included in the analyses, testosterone was not significantly related to age ($n = 14$; $r^2 = 0.180$; $F = 2.628$; $p = 0.131$) (Fig. 7). However, fecal testosterone levels were significantly higher in males expressing territorial behaviors ($n=5$) than in nonterritorial adult males ($n = 6$) (Mann-Whitney $U = 3.0$; $p = 0.028$).

Discussion

Territorial and Nonterritorial Tactics

Territorial males scent-marked and used areas that were exclusive of other territorial males (Fig. 1). Nonterritorial males did not exhibit scent-marking behaviors, and their spatial patterns differed markedly from those of territorial males. Ranges of nonterritorial males overlapped widely with ranges of other nonterritorial males (Fig. 2.). A notable difference in male spatial relationships in MNP compared to other populations of white rhinos was the lack of beta males sharing territories with alpha territorial males. It has been suggested that association between an alpha and one or more subordinate males is influenced by population density and lack of unoccupied area for dispersal of young adult males (Owen-Smith 1971, 1988). However, despite a high population density in the fenced area, nonterritorial males were not observed to form relationships with territorial holders. Instead, nonterritorial males tended to form stable groups with other nonterritorial males. Such male coalitions have been observed in felids, primates, and equids, and may function to improve the competitive ability of young males (Berger 1986; Caro 1994; Harcourt 1992; Packer & Pusey 1982). These male coalitions in rhinos may be an alternative tactic for dealing with intrasexual aggression in high density populations when there are few territorial males with whom a young adult males could form an "alpha-beta" relationship.

The relationship between fecal testosterone and territoriality establishes a link between physiology and territorial behavior in males. Because this relationship was independent of age, it suggests that territoriality and not just maturity are related to androgen levels. Urinary testosterone levels were significantly correlated with reproductive behavior and reproductive status in male African elephants (Loxodonta africana) (Poole et al. 1984). Among white-tailed deer (Odocolius virginius), serum testosterone levels were correlated with both male dominance and scent-marking (Millar et al. 1987). Territorial behavior and testosterone also were correlated in male Grevy's zebra (Equus grevyi) in a study documenting significantly higher levels of testosterone in the urine of territorial males than in samples collected from bachelor males (Chaudhury & Ginsberg 1990). Further, testosterone levels of territorial male Grevy's zebra were lower when they were absent from their territories. Numerous studies of birds also have established an association between territoriality, aggressive behavior, and testosterone levels in males (see Wingfield 1985, for a review). Although causal relationships between androgen levels and male reproductive behavior have not been fully explored, the link between territorial behavior and testosterone levels in male birds and mammals appears to be widespread.

Age and Reproductive Tactics

Theory predicts that males should defend territories only when the benefits outweigh the costs (Brown 1964; Owen-Smith 1977). Competition among male white rhinos may lead to fighting and fight-related injuries more frequently than behavioral observations suggest (Owen-Smith 1973). Fight-related mortality is believed to be the leading cause of death among adult white rhino males in Kruger National Park, South Africa (D. Pienaar, pers. com.), the most frequent cause of death identified in populations of translocated white rhinos in South Africa (Anderson 1993), and the source of highest mortality in black rhinos (Berger 1994). During this study, one territorial male was killed in a fight with a neighboring territory holder, and in a second incident, I observed a territorial male attack a subadult, knocking the younger male to the ground with repeated blows to the abdomen. If the territorial male had not been dehorned, this encounter would likely have been fatal for the younger male. Although serious fights are rarely observed, defense of a territory is a potentially risky venture, just as is the defense of estrous females in other male ungulates (Bergerud 1973; Clutton-Brock et al. 1982; Geist 1974).

For white rhinos, male reproductive success is likely to require that territorial status be maintained for a prolonged time period, especially because, unlike lekking ungulates (Clutton-Brock & Deutsch 1993), females are not clumped. Reproductive opportunities in African rhinos are both infrequent and unpredictable because free-ranging females reproduce at intervals of 2.5 to 4.0 years, and each estrous period may last for only a few days (Bertschinger 1994). Under these circumstances, males must secure a territory for a relatively long period of time to make it a reproductively cost effective tactic. White rhino males in Umfolozi Reserve, South Africa, had a mean territory tenure of 5.4 years (Owen-Smith 1973). Thus, males should accept the risk of territory establishment only when they will be able to hold a territory for a long enough period to receive the benefits in terms of a reproductive payoff.

Numerous proximate factors relating to the intensity of intrasexual competition may influence the strategy followed by individual males. Competition among males in the fenced WGP population is likely to be high for several reasons. Fenced reserves limit dispersal opportunities for young adult or subadult males. Owen-Smith (1982) documented that subadults of both sexes and adult males tended to move away from areas of high population density to occupy regions on the periphery of populations.

When dispersal is prohibited, the numbers of adult males would be expected to rise, thereby decreasing the operational sex ratios (Emlen & Oring 1977).

The influence of habitat on spatial relationships also may intensify male-male competition. Although the spatial pattern of territorial males in MNP is similar to that reported for other populations (Owen-Smith 1988), the sizes of male territories in MNP are much larger. Male territories and female home ranges have been observed to decrease as population density increases in several other reserves (Pienaar et al. 1993). However, the largest territory reported for a white rhino male was 1390 ha (Conway & Goodman 1989), which is smaller than the smallest territory in this study. Females in MNP also have large home ranges compared to those reported from other locations (Pienaar et al. 1993), and the high degree of habitat heterogeneity, lower plant productivity, or some combination of both in MNP may influence range size in this species. The sum result of limited dispersal, high population density, and very large male territories is that 67% of males over 6 years of age did not mark a territory. These males were faced with the "choice" between challenging one of the territorial males and risking injury and possibly death, or adopting a nonterritorial behavioral pattern.

Young males should be more likely to pursue an alternative mating tactic than older males for at least two reasons. First, they have a longer period of potential reproduction, and should be less likely to take the risks associated with territory establishment. Aside from fight-related mortality, survivorship of adult rhinos is high in areas where human predation is not prevalent (Owen-Smith 1988). Second, while body length reaches an asymptote at about 14 years of age, chest girth, which is related to mass, continues to increase for several more years (Fig. 6). In addition to having more social experience, older males are likely to be heavier than young adults. Thus, young adult males should be competitively disadvantaged in fights with prime age males, as shown among numerous long-lived mammals (Berger & Cunningham 1994; Clutton-Brock et al. 1982; Le Boeuf 1974; Poole 1989).

Reproductive Payoffs

From an ultimate perspective, individuals must balance the potential reproductive gain of a given strategy with that of reduced survivorship and diminished future reproduction (Gadgil 1972). Because reproductive success accrues over an individual's lifetime, increased survival combined with a lower annual reproductive output may result in a greater ultimate payoff (Stearns 1992). Although, a complete analysis of the payoffs of alternative reproductive tactics requires data about mortality and lifetime reproductive success of males following each tactic, as assessment of correlates of mating success is a useful gauge to approximate reproductive payoffs for males following different mating tactics.

Overlap with female home ranges should facilitate a male's ability to monitor the reproductive status of multiple females. Female rhinos do not exhibit overt visual signals of receptivity as do some female primates (Altmann 1980), and detection of estrus probably is accomplished via olfaction in rhinos (Owen-Smith 1973), particularly because males frequently perform flehman at urination and defecation sites. Male reproductive success was related to territorial overlap with females in several mammals including the common shrew, (Sorex araneus) (Stockley et al. 1996), Belding's ground squirrels (Spermophilus beldingi) (Sherman & Morton 1984), and red deer (Carranza et al. 1990). However, territorial and nonterritorial males did not differ in degree of overlap with adult females in this study.

Patterns of association with all adult females did not differ markedly according to male territorial status in this study. Although territorial males spent more time solitary than nonterritorial males, they spent roughly equivalent proportions of their time in association with adult females (Fig. 4). Males following both tactics formed stable groups with females in this study.

What are the payoffs for following a territorial tactic? Given that the territorial tactic is potentially costly in terms of energy and risky due to fighting among males, relatively large reproductive payoffs are to be expected. These payoffs may be subtle. For example, male bison discriminate among females, and older males spend less time with females, but concentrate their efforts on those with the highest reproductive potential (Berger 1989). White rhino males also appear to evaluate the reproductive potential of females, and to expend more effort towards females that are likely to come into estrus (Fig. 4). Therefore, although patterns of association and spatial overlap with females are similar in males following territorial and nonterritorial tactics, the reproductive consequences may differ markedly.

The degree to which female choice plays a roll in mate selection is unknown in this species. Proximity and tolerance of adult males by females may enhance their opportunity for gaining copulations. White rhinos have several behaviors for maintaining separation among individuals (Owen-Smith 1973), and when approached by males, females often respond with a space-retaining display and vocalization. However, this response appears to decrease following a period of association with an individual male.

Alternative male reproductive tactics have been recorded in many species of primates, in which males following nondominant tactics form affiliative relationships with females that increase their probability of mating (see Smuts 1987, for a review). Nonterritorial male white rhinos also may improve their chances of copulating by forming stable relationships with adult females.

Observations of copulations in wild rhinos are rare even during intensive studies, making it difficult to address the issue of male reproductive success behaviorally. Further, observed patterns of sexual behaviors may not be correlated with paternity (Amos et al. 1993; Ginsberg & Huck 1989; Pemberton et al. 1992). Ultimately, genetic analyses are needed to test assumptions about reproductive success and reproductive consequences of male mating tactics in white rhinos.

These issues are important for conservation of rhinos for at least three reasons. First, reproductive competition and spatial relationships among males may lower the carrying capacity of reserves below levels based on forage availability alone. Second, if territoriality results in high variance in reproductive success among males, then effective population sizes within reserves may be reduced, and loss of heterozygosity accelerated. Third, survivorship in adult rhinos is very high, and even slight increases in mortality rates can have significant effects on population growth rates (see Chapter 3). Because fight-related deaths are an important source of mortality in rhinos, increased male competition at higher population densities may undermine conservation efforts in smaller reserves.

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Table 1. Sizes of male territories in hectares using the 100% minimum convex polygon (MCP) method before and after the shift in territory structure in the Whovi Game Park (WGP).

Identification	100% MCP * (before shift)	100 % MCP * (after shift)
M-05	1733	1852
M-07	5041	dead
M-09	1462	1921
M-25	establishing	1733
M-31 **	3619	no change

* Area values for males in the WGP are adjusted to exclude areas outside of the fence.

** M-31 occupied the Hazelside Area.

Table 2. Characteristics of territorial and nonterritorial male white rhinos in Matobo National Park (mean ± SE).

Measure (cm)	n	Territorial	n	Nonterritorial	Mann-Whitney U	P-value
Body length	5	263.2 ± 8.81	4	250.0 ± 4.72	14.0	0.327
Chest girth	5	298.0 ± 11.78	4	254.0 ± 3.56	20.0	0.014 *
Neck girth	5	179.6 ± 4.00	3	159.3 ± 2.40	15.0	0.024 *
Testosterone (*)	5	54.2 ± 5.55	6	31.3 ± 3.96	3.0	0.028 *

(*) Testosterone is measured in ng/g dry feces.

FIGURE LEGENDS

Figure 1. Relationship between male territories and density of female home ranges in the WGP: A) prior to a shift in territory structure that occurred after the death of M-07; and B) territories after the shift. M-25 began expressing marking behaviors approximately 2 months prior to the territory shift, but did not consistently delineate a range with scent marking until after the death of M-07.

Figure 2. Home ranges of nonterritorial males estimated using the 100% MCP method.

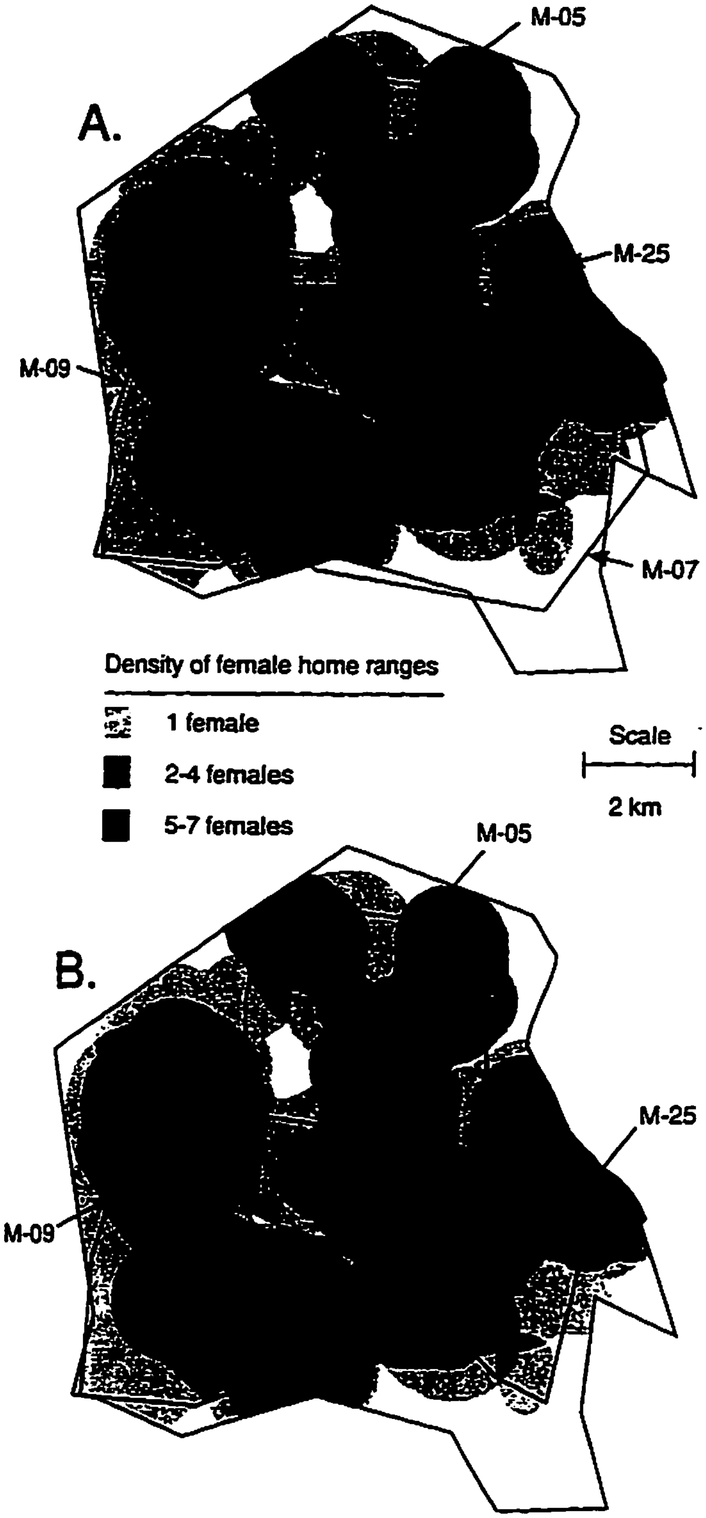
Figure 3. Percent of observations in which territorial males ($n = 5$) and nonterritorial males ($n = 8$) were solitary. Territorial males spent significantly more time alone (T: $\bar{X} = 50.0\% \pm 5.15$; NT: $\bar{X} = 8.1\% \pm 3.60$).

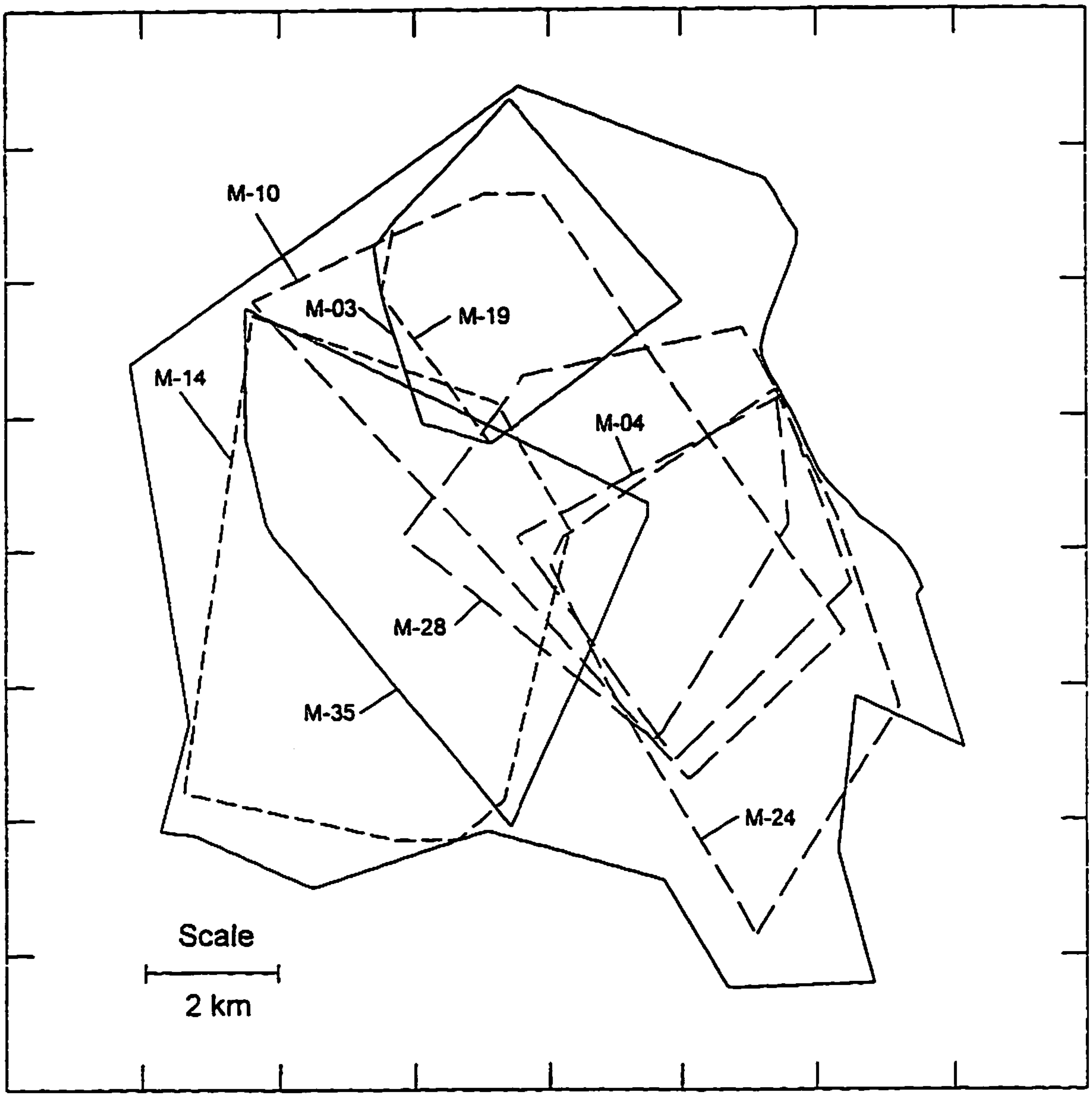
Figure 4. Territorial males spent a greater percentage of their associations with reproductively valuable females (Mann-Whitney $U = 5.0$, $p = 0.027$), although percent of all observations in which males were observed in association with ≥ 1 adult female did not differ significantly (Mann-Whitney $U = 22.0$, $p = 0.770$) between territorial males ($\bar{X} = 37.1\% \pm 7.15$) and nonterritorial males ($\bar{X} = 45.4\% \pm 12.15$).

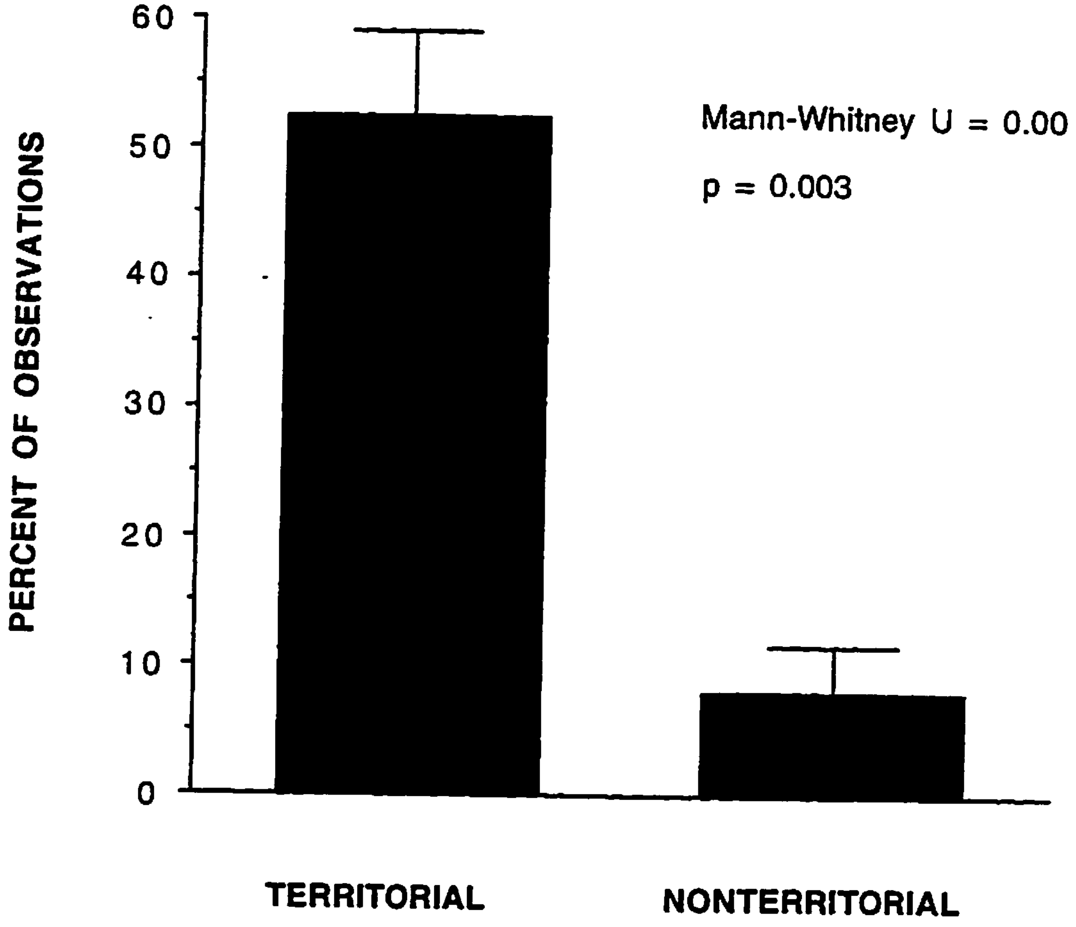
Figure 5. Age structure of adult males in Matobo National Park, Zimbabwe.

Figure 6. Measurements of male body size as a function of age fitted with von Bertalanffy growth curves. Fitted equations: chest girth = 306.7 - 150.6 * exp (-0.121 * age) and body length = 276.7 - 162.0 * exp (-0.197 * age). Chest girth continues to increase in males after body length approaches an asymptote at about 14 years.

Figure 7. Relationship between fecal testosterone (ng/g dry feces) and age. Even with the inclusion of samples from subadults, fecal testosterone levels did not increase significantly with age (F = 2.628; p = 0.131). The "new territorial male" (M-25) established a territory approximately 2 months prior to collection of this sample.

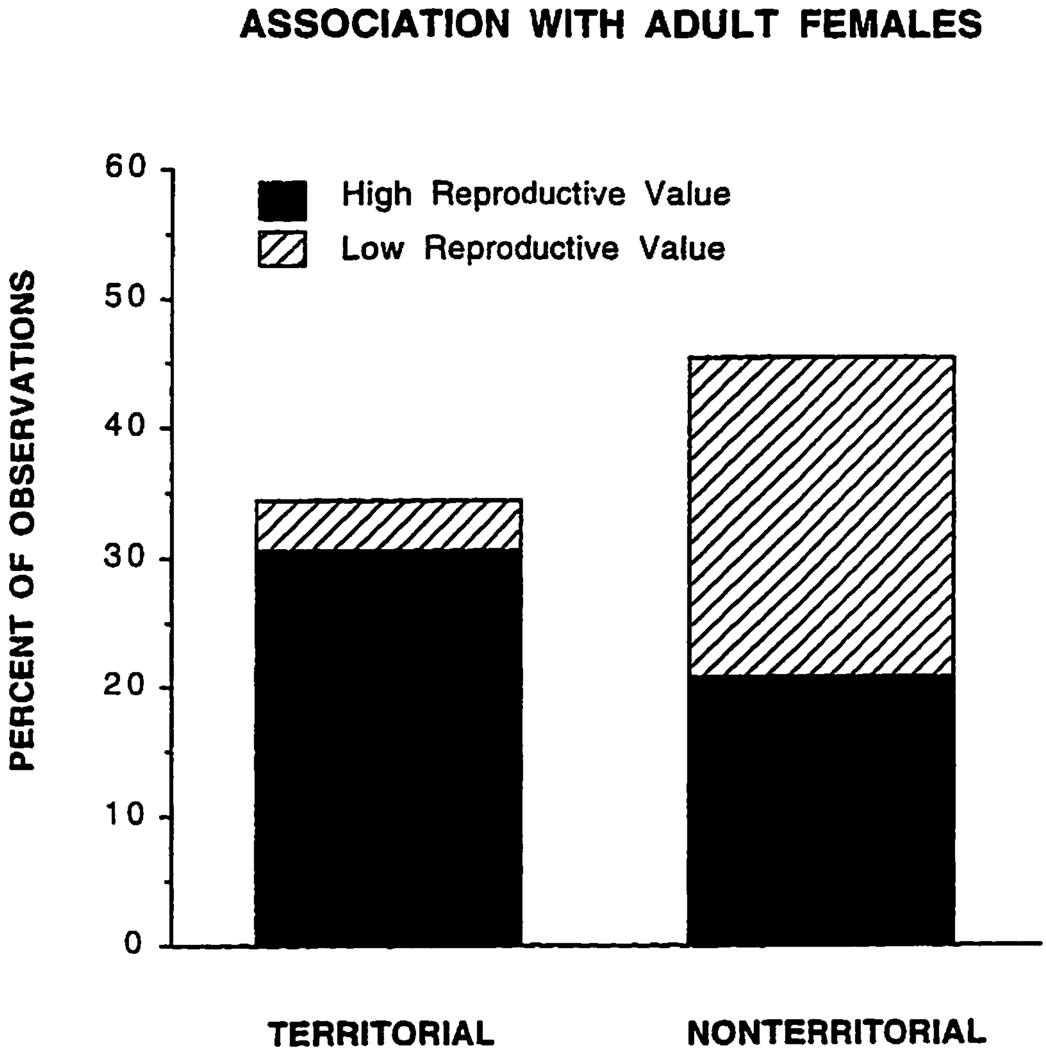

A.
M-05
M-25
M-09
M-07
Density of female home ranges
1 female
2-4 females
5-7 females
Scale
2 km
B.
M-05
M-25
M-09


M-10
M-03
M-19
M-14
M-04
M-28
M-35
M-24
Scale
2 km

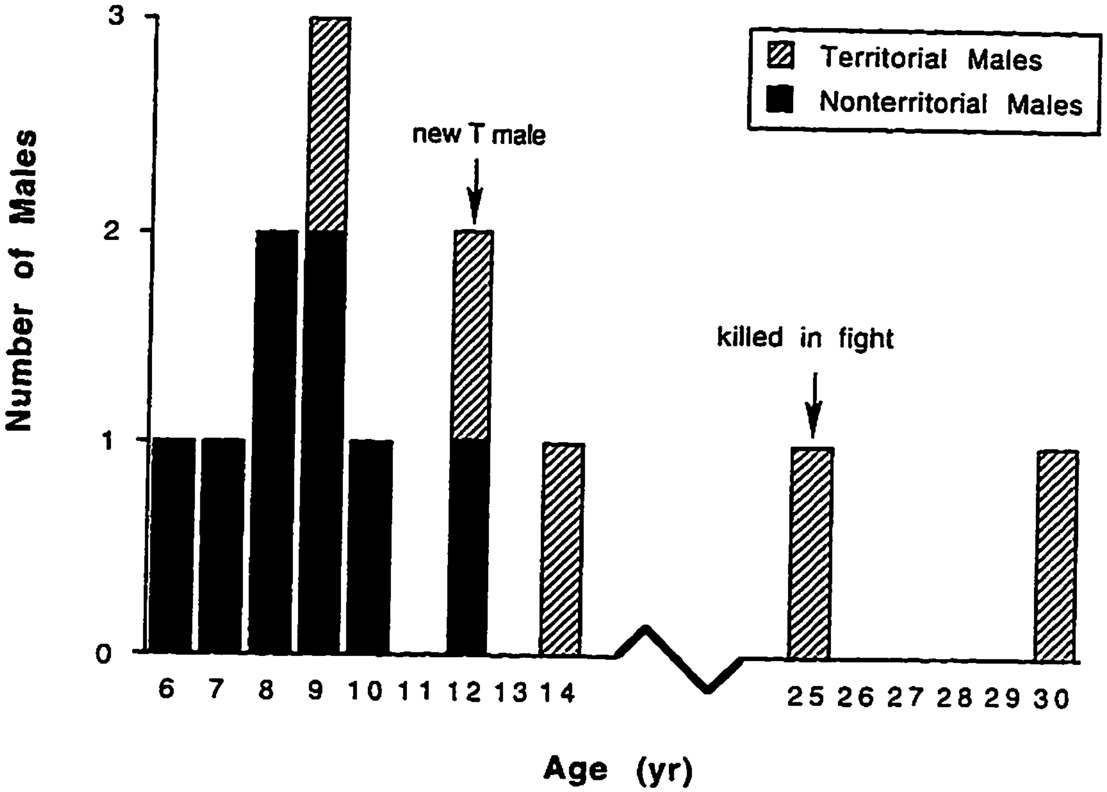


SOLITARY

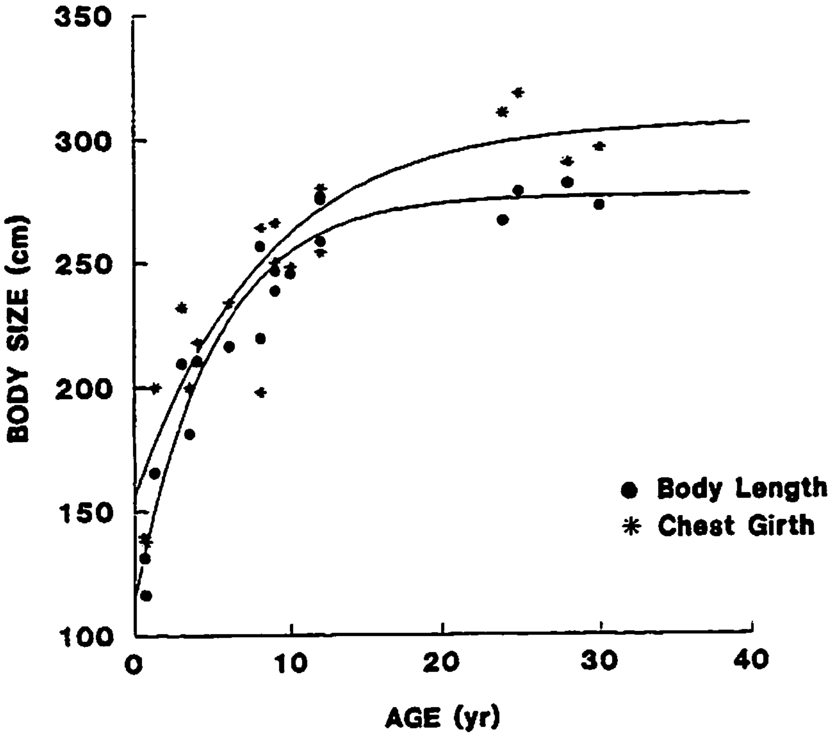
PERCENT OF OBSERVATIONS
60
50
40
30
20
10
0
Mann-Whitney U = 0.00
p = 0.003
TERRITORIAL
NONTERRITORIAL


ASSOCIATION WITH ADULT FEMALES
High Reproductive Value
Low Reproductive Value
PERCENT OF OBSERVATIONS
60
50
40
30
20
10
0
TERRITORIAL
NONTERRITORIAL

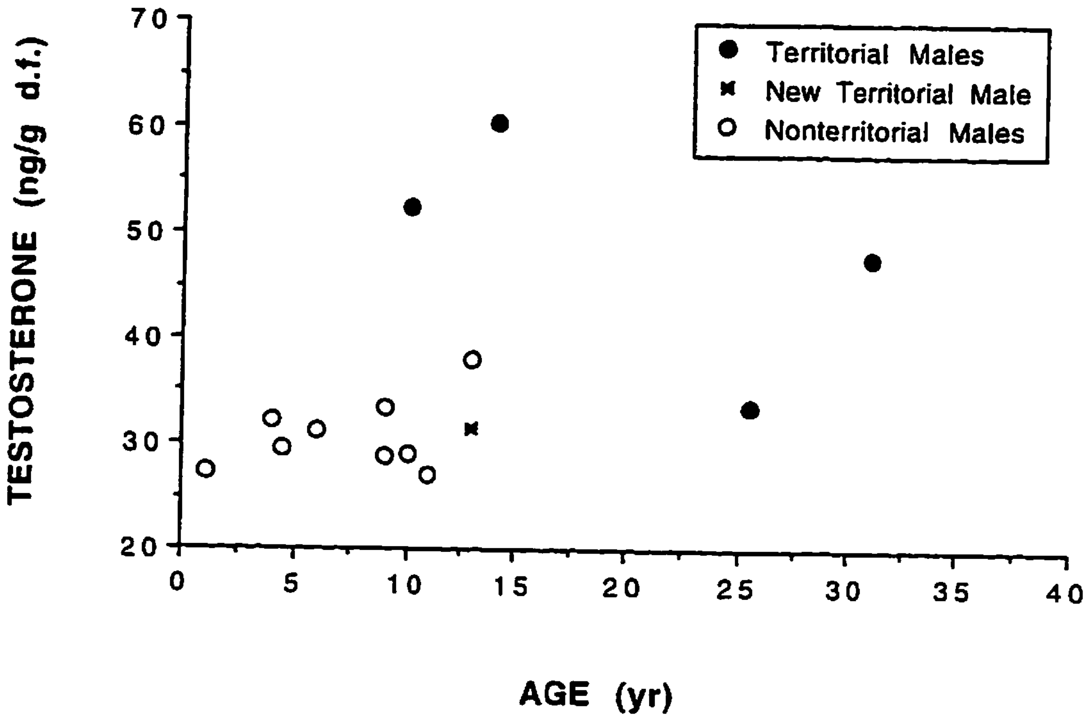
AGE STRUCTURE OF ADULT MALES



MALE BODY SIZE IN WHITE RHINOS



FECAL TESTOSTERONE LEVELS



Chapter 3: Management of White Rhinos: Establishment and Persistence of Small Populations

Abstract: African rhinos in many countries currently are managed in relatively small reserves where protection from poaching can be provided. I used empirical data on survivorship and reproduction to examine issues relating to establishment and persistence of small populations of white rhinos (Ceratotherium simum). Successful establishment of new populations was a function of founder size in these models. Populations established with <10 animals had a lower chance of persisting, even for 50 years. Both the mean and standard deviation of the carrying capacity had pronounced effects on both short and long-term population persistence. This suggests that larger reserves will be required to maintain populations in areas where the carrying capacity fluctuates widely. Population persistence was robust to increases in calf mortality. However, mortality rates >5% for adults and >10% for subadults markedly decreased probability of persistence. Management actions that increase adult and subadult survivorship may have the greatest impact on conservation efforts for white rhinos in small reserves. The models predicted that loss of genetic diversity would be affected by degree of polygyny. Management of breeding males may be warranted in small populations.

Management of White Rhinos: Establishment and Persistence of Small Populations

Introduction

In spite of the charismatic nature of large species, their conservation poses an enormous challenge. The needs of wildlife are often incompatible with human activities, and because many species of large mammals are potential threats to agriculture and human life, their survival outside of designated conservation areas is often low (Clark et al. 1996; Sukumar 1991). This is especially problematic for species whose body parts have commercial value (Heinen et al. 1995; Leader-Williams et al. 1990; Martin 1993). Populations of large species are becoming increasingly fragmented into small, insular populations within reserve boundaries (Berger & Cunningham 1994; Noss et al. 1996). Because population sizes in small reserves are generally low, these populations may be vulnerable to a suite of factors that threaten their persistence (Belovsky 1987).

Probability of extinction of small populations is increased by stochastic variation in environmental, demographic, and genetic factors, as well as by catastrophic events and deterministic factors such as habitat destruction or overexploitation (Gilpin & Soulé 1986; Shaffer 1987). Further, genetic diversity is lost more rapidly in small populations than in larger ones (Lande & Barrowclough 1987). Associations between population viability and individual components of fitness and heterozygosity have been documented in several species including oysters (Crassostrea sp.), brine shrimp (Artemia franciscana) (Mitton 1993), African lions (Panthera leo) (Packer et al. 1991), and wolves (Canis lupus) (Wayne et al. 1991). Loss of heterozygosity also can threaten the long-term persistence of small populations. For rapidly declining species, however, demographic threats are likely to be more critical for avoidance of extinction, at least in the short-run (Lacy 1987; Lande 1988).

For African rhinos, the overwhelming cause of population extinction has been overexploitation by humans (Berger 1994; Leader-Williams 1993). Black rhinos (Diceros bicornis) have dwindled from an estimated 60,000 to less than 2,500 in the past 30 years (Brooks 1993; Western & Vigne 1985). Although white rhinos (Ceratotherium simum) recovered from a bottleneck of 50 to 200 individuals earlier this century to >7,000 animals today (Brooks 1993; Owen-Smith 1973), poaching has extirpated reintroduced populations in Angola, Zambia, Botswana, and Mozambique (Brooks 1993; Gakahu 1993). In many countries, African rhinos have been translocated into protected reserves or sanctuaries, a strategy that appears to be successful in limiting losses to poachers (Brett 1990; Kock & Atkinson 1993). Intensive management in heavily-guarded reserves is likely to be one of the most viable methods for conserving rhinos in situ in the future.

Sound management strategies for small populations of rhinos that address the issues of short and long-term demographic viability are a prerequisite for developing comprehensive recovery plans. A strategy developed to guide introduction of black rhinos onto private properties in South Africa recommended that maximum founder densities should not exceed 37.5% of the estimated carrying capacities in order to maximize total population growth at a metapopulation level (Emslie 1994). However, many potential reserves are small with relatively low carrying capacities, and under these constraints, founder populations may consist of as few as 5-6 individuals.

Probability of successful establishment of rhino populations from such small numbers is questionable.

In addition to the number of founders, the carrying capacity of a reserve also will effect the probability of population persistence. Lande (1993) demonstrated mathematically that probability of persistence should increase exponentially with carrying capacity when growth is positive and density-dependent at population sizes below the carrying capacity. This appears to be the case in white rhinos (Chapter 1) and other large mammals (Fowler 1981). Therefore, a critical issue in planning for rhino reserves is the number of animals that can be supported within reserve boundaries, and the probability of persistence of different sized populations.

Stochastic models of population growth have been used in population viability analyses (PVAs) to evaluate probabilities of persistence under different scenarios (Boyce 1992; Gilpin & Soulé 1986). Because sufficient life history data often are lacking for long-lived species like rhinos, predictions of PVAs have been questioned (Harcourt 1995; Taylor 1995). However, sensitivity of model results to variation in individual parameters can be explored by systematically varying one parameter while holding all others constant. This process also can help to identify life history variables that have large effects on population dynamics.

In this paper, I used life history data for white rhinos gathered in Matobo National Park, Zimbabwe, and data from other African reserves to examine probabilities of persistence for populations in newly established reserves as a function of founder number and reserve carrying capacity. Sensitivity analyses were conducted to examine the effects of variation in several parameters on the model predictions. White rhinos exhibit a polygynous mating system, and behavioral data suggest that male reproductive success may be highly skewed (Chapter 2). Because polygyny in small populations can affect the rate at which genetic diversity is lost, I also examined how variance in male mating success might influence the rate at which heterozygosity is lost in small populations.

Methods

Modeling Approach

I modeled population growth based on estimates of reproduction and mortality observed for white rhinos using the VORTEX Version 7 population modeling program (Lacy et al. 1995). Estimates for the model parameters were based on my fieldwork in Matobo National Park, Zimbabwe, and on other studies of white rhinos in African reserves (Table 1). I examined probability of persistence as a function of the number of founders and the carrying capacity for populations projected for 50 and 200 years. These periods were chosen to represent short and long-term time frames over which management decisions could be made. The baseline model consisted of 15 founding individuals (7 males and 8 females) set to reflect a stable age distribution. I set the carrying capacity at 50 animals to represent a moderate-sized rhino reserve. The VORTEX program increases mortality rates when the simulated population exceeds the carrying capacity, thereby limiting the population size. I did not include inbreeding depression in these models. Values for all inputs into the baseline model are given in Appendix 1.

Parameter Estimates

Female Reproduction: White rhino females usually produce their first calf between 7 and 9 years of age, and births can occur throughout the year (Owen-Smith 1973). Both age at first reproduction in females and intervals between births appear to be sensitive to population density (Owen-Smith 1988; Chapter 1). Density-dependent reproduction is modeled in the VORTEX program using the following equation, which varies the proportion of adult females that breed as a function of the population size:

$$P(N) = P(0) - [(P(0) - P(K))\ (N/K)^{B}]$$

Values input into this equation include the percent of females breeding at population sizes near zero, $P(0)$, and at carrying capacity, $P(K)$. This model assumes annual reproduction, and I adjusted these input values to reflect the 2 to 4 year birth intervals observed for white rhinos (Table 1). At very low population densities, I estimated that 46% of females would breed in a given year, corresponding to a mean birth interval of 2.17 years. At densities close to carrying capacities, I estimated that 33% of females would breed in a given year, meaning that the average birth interval would be 3.03 years. These values are comparable to those observed in Matobo Park across a range of population densities (Chapter 1).

The exponent, B, in the above equation defines the shape of the function of percent of females breeding relative to the population size. In a review of density-dependence, Fowler (1981) suggested that the relationship between density and several life history traits is not linear in large mammals, and that a quadratic function could be used to describe the shape of this relationship. This corresponds to $B = 2$ in the above equation. I used this value in the base model, and varied the values from 1 to 16 in the sensitivity analyses. I omitted the term for an Allee effect (a decrease in reproduction at very low densities) from the VORTEX density-dependence equation because such an effect is unlikely to occur in rhino reserves, in which densities are generally higher than in free-ranging populations. Because it is not possible to vary age at first reproduction as a function of density in the VORTEX program, I used 8 years of age for first breeding in females, a value in the middle of the range recorded in wild populations (Table 1).

Male Reproduction: White rhino males exhibit a territorial spacing system that is believed to limit access to mating opportunities, and males begin to establish territories at 9 to 12 years of age (Chapter 2; Owen-Smith 1973). Proportions of adult males within a population that hold territories has ranged from 30% to 60% (Table 1). In the baseline model, I assumed that 45% of males ≥13 years of age bred each year.

Mortality: Mortality rates for white rhinos reported in the literature differ markedly. Estimates of mortality are generally higher for calves than for subadults or adults, and higher for adult males than for adult females (Table 1). I used values in the middle of the range reported for each sex and age class in the models (Appendix 1).

Sensitivity Analyses

I conducted sensitivity tests of several parameters for two reasons. First, because precise estimates are not available for many of the parameters, ranges of values were modeled to ask how error in the estimates affects the predictions. Second, sensitivity analyses can help to identify those parameters that influence the dynamics of a population, and can be used to guide management decisions (Lacy & Kreeger 1993).

I varied age-specific mortality rates, both the mean and standard deviation of the carrying capacity, and the shape of the relationship between population density and reproduction. Each parameter was varied independently, and probability of population persistence was recorded at 50 and 200 years. Additionally, I explored the rate at which heterozygosity was lost relative to the percent of adult males in the breeding pool.

Results

The baseline model predicted that a population with 15 founders in a reserve with a carrying capacity of 50 would increase to a mean population size of 36 animals (± 0.5) within 50 years, and then persist at a relatively constant size. Probability of persistence was high at 50 years (98.5%) and at 200 years (96.0%). The deterministic growth rate for this model, excluding density-dependence, was 6.4% per year. Following the release of 13 white rhinos into Matobo Park, the population increased rapidly at a rate of 10.4% per year for 10 years, but rate of increase declined with population density (Chapter 1). Although the Matobo population has been manipulated, the initial phase of population growth following introduction resembles that of the simulated populations.

Varying founder population sizes revealed a threshold for population persistence. Probability of persistence for populations with only 5 founders was much lower than that for populations with 10 to 20 founders (Fig. 1). Mean time to first extinction increased with size of the founder population from 23 years (± 2.1) for populations with 5 founders to 149 years (± 23.0) for populations with 20 founding individuals. However, after 50 years, probability of persistence for populations of 5 founders reached a plateau (Fig. 1).

This suggests that populations with few founders are vulnerable to extinction during the initial stages, but if they reach a size limited by the carrying capacity, their probabilities of persistence remain high.

Size of the population at carrying capacity also influenced the probability of persistence dramatically. For simulations with a carrying capacity of 20, probabilities of persisting for even 50 years were low (6.8%), and in none of the 500 iterations did the population persist beyond 100 years (Fig. 2). Increasing the carrying capacity to 40 resulted in a probability of persistence of 83.2% at 200 years, and carrying capacities of 60 or higher resulted in persistence probabilities of ≥98.0% (Fig. 2).

Variance in the carrying capacity had a pronounced effect on the predictions of the model. I used a standard deviation of 10% of the mean of the carrying capacity in the baseline model, and modified standard deviations from 0% to 20% of the mean of carrying capacities ranging from 20 to 80. Variance in the carrying capacity interacted with the population size at carrying capacity. Only the populations with carrying capacities of 60 or greater had high probabilities of persisting for 50 years when the standard deviation was increased to 20% (Fig. 3a). However, probability of persistence for 200 years was only 50.4% (Fig. 3b). The model predicts that populations with carrying capacities of 80 or greater would achieve high probabilities of persistence under the levels of variation in the carrying capacity used in these exercises.

Age-specific mortality rates also strongly influenced population trajectories. Probability of population persistence did not change markedly in response to variation in mortality rates of calves, but even modest increases in adult and subadult mortality rates resulted in marked changes in population persistence at 50 and 200 years. A threshold in persistence was apparent at rates over 5% for adults and over 10% for subadults. As adult mortality rates increased from 5% to 10%, persistence decreased from over 90.0% to 56.4% at 50 years and 6.2% at 200 years (Fig 4).

The shape of the relationship between population density and reproduction did not affect predictions of the model. I varied the exponent in the density-dependence equation, *B*, from 1 to 16, and in all cases the probability of persistence at 200 years remained high (> 95.0%) .

Patterns of male reproduction influenced the rate of loss of genetic diversity in these simulations. I modified the percent of adult males reproducing (degree of polygyny) from 100% to 25%. The mean expected heterozygosity (or gene diversity) remaining in the extant populations decreased at a slightly higher rate when only 25% of adult males bred, but marked differences were not apparent among the higher percentages (Fig. 5). Final population sizes at 200 years (range = 36 to 38) did not differ among these models. Therefore, population size did not confound the predictions about loss of genetic diversity in these models.

Discussion

Population Growth and Persistence

Population persistence was strongly affected by the number of founders, but appeared to reach a threshold above an initial size of 10 individuals (Fig. 1). Empirical data for white rhinos also support this result. White rhino populations have been established with as few as 4 individuals and as many as 24 in a South African program in which >1200 white rhinos were translocated to private lands over the past 35 years

(Anderson 1993; Buys & Anderson 1989). The fact that over 20% of the introduced populations of less that 10 individuals went extinct, and over half had declined in number (Buys & Anderson 1989) suggests that populations of less than 10 have a poor chance of persisting even for relatively short periods of time. Although numerous mortality factors, including hunting, may have contributed to these results, they lend empirical support to the predictions of these models that populations with fewer than 10 founders are unlikely to be successfully established. Stocking new rhino reserves well below the estimated carrying capacities may be desirable to encourage rapid population growth (Emslie 1994), but managers may sacrifice probability of persistence for short-term increases in rates of population growth

Both the carrying capacity and annual variation in the carrying capacity had profound effects on the probability of population persistence in these models (Fig. 3). These results suggest that, in environments where the carrying capacity fluctuates widely among years, larger populations are necessary to attain the same probabilities of persistence as those achieved by smaller populations in more stable environments.

Annual rainfall and plant biomass are strongly correlated in arid African systems (Bell 1984; Dye & Spear 1982). Variation in rainfall can result in fluctuations in forage availability, and hence, in carrying capacities for large herbivores in small reserves (Novellie et al. 1991; Owen-Smith 1982). Rainfall was highly variable in Matobo Park, with a standard deviation of >35% of the mean of 639 mm over the past 45 years (Chapter 1). Although the shape of the relationship between rainfall and carrying capacity for white rhinos is unknown, such high variability in rainfall may indicate that long-term persistence is significantly lower that based on expectations of mean carrying capacity alone.

Sensitivity Analyses

Identification and management of critical processes or life history stages that either erode or promote population persistence can help managers of rare species to avoid a triage situation. Population persistence is very sensitive to adult mortality rates based on this and other modeling exercises for black (Lacy 1987) and white rhinos (Owen-Smith 1982). Management actions that decrease adult mortality may increase the probability of persistence of small populations. Fighting was the leading cause of death identified in introduced white rhino populations in South Africa (Anderson 1993). As population densities increase within reserves, translocation of adult or subadult males may be warranted if incidence of fight-related injuries or mortalities rises. Additional mortality from poaching at even low to moderate levels could depress population growth and jeopardize persistence of small populations (Moehlman et al 1996).

The results of this modeling exercise were relatively insensitive to changes in mortality rates of calves (Fig. 4). These models suggest that management practices aimed at enhancing calf survivorship, such as predator control, may have less of an effect on population persistence than practices that enhance adult survivorship. Population densities of other grazing species may also affect the carrying capacity for white rhinos (Borthwick 1986; Owen-Smith 1988), and removal of predators might prove counterproductive if it resulted in increases in densities of other grazers like wildebeest, which have similar foraging patterns (Borthwick 1986).

Variance in male reproductive success influences the effective population size (N_e), and can markedly increase the rate at which genetic diversity is lost (Harris & Allendorf 1989). When degree of polygyny was increased such that only 25% of adult males bred, genetic diversity was lost at a faster rate (Fig. 5). Mean final population sizes did not vary with male mating patterns, indicating that the observed effect on heterozygosity was not confounded by variation population size. In these models, mating patterns affected genetic diversity directly.

The models used in these analyses likely underestimate the impact of variance in male reproductive success on heterozygosity in white rhinos. The VORTEX program selects the designated proportion of breeding males from all males randomly each year. However, white rhino males exhibit a territorial system, which is believed to control access to mating opportunities, and duration of male territory tenure can exceed 5 years (Owen-Smith 1971). If territorial males are solely responsible for breeding, and their tenure is lengthy, then loss of genetic diversity may occur at greater rates. However, paternity may not be directly correlated with observations of sexual behaviors, and genetic analyses are needed to assess actual differences in reproductive performance among males (Amos et al. 1993; Pemberton et al. 1992; Chapter 2).

From a genetic perspective, it may be possible to slow the loss of heterozygosity within small populations by limiting the breeding tenure of individual males, thereby decreasing the degree of polygyny. However, intensive management of rhino reserves as individual populations in a metapopulation of multiple reserves may be required to stem the loss of heterozygosity in isolated rhino reserves do to their small population size (Foose 1987).

The dynamics of white rhino populations may differ from the models constructed using VORTEX in another important way. Owen-Smith (1982) modeled population dynamics of white rhinos including density-dependent mortality, reproduction, and changes in the forage biomass. His models predicted that when dispersal is prevented, white rhinos would overshoot carrying capacity resulting in degradation of the habitat and subsequent reduction in the carrying capacity of the reserve. VORTEX does not permit populations to overshoot the set carrying capacity, and does not vary the carrying capacity with population density. Because white rhinos have high rates of adult survivorship and are relatively insensitive to short-term fluctuations in the carrying capacities, their populations may experience cyclic changes in size that lag behind those of the carrying capacity in enclosed areas (Owen-Smith 1982). Instability in population numbers may make smaller populations more prone to extinction over long periods of time than predicted using the VORTEX models. Therefore, predictions of these models should be viewed as optimistic.

For rapidly declining species, conservation strategies must be implemented that promote population persistence within a relevant time-frame (Berger 1994; Swart et al. 1994). Development of rhino reserves in many African nations appears to be successful at halting the precipitous decline of black rhino populations, and at increasing numbers of both black and white rhinos. Conservation efforts must now focus on establishment of new reserves, and long-term management of populations that are unlikely to persist outside of these sanctuaries. These models suggest: 1) that managers should focus on practices that increase adult survivorship; 2) that environmental variation that results in fluctuations in the carrying capacity may require larger reserves to achieve acceptable probabilities of persistence; and 3) that populations established with fewer than 10 founders have low probabilities success.

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Table 1. Observed values for reproduction and mortality of white rhinos in African reserves.

Parameter	Observed range	Source
Age females breed (yr)	6.5 - 7	Umfolozi, S.A. (Owen-Smith 1988)
	6.5 - >12	Matobo, Zimbabwe (chapter 1)
	8	Kyle, Zimbabwe (Condy 1973)
Age males breed (yr) *	12 (estimate)	Umfolozi, S.A. (Owen-Smith 1988)
	9	Matobo, Zimbabwe (chapter 2)
Birth interval (yr)	1.8 - 3.4	Umfolozi, S.A. (Owen-Smith 1988)
	2.3 - 3.3	Matobo, Zimbabwe (chapter 1)
	3.1 - 4.8	Kyle, Zimbabwe (Condy 1973)
% males breeding	60	Umfolozi, S.A. (Owen-Smith 1988)
	30	Matobo, Zimbabwe (chapter 2)
Calf mortality (%/yr)	3.5 - 8.3	Umfolozi, S.A. (Owen-Smith 1988)
	2.2 - 6.3	Matobo, Zimbabwe (chapter 1)
Subadult mortality (%/yr)	1.1 - 6.0	
	0.0	Matobo, Zimbabwe (chapter 1)
Adult mortality (%/yr)		
female	1.0 - 1.2	Umfolozi, S.A. (Owen-Smith 1988)
	0.0 - 2.7 **	Matobo, Zimbabwe (chapter 1)
male	3.0 - 3.6	Umfolozi, S.A. (Owen-Smith 1988)
	0.0 - 2.7 **	Matobo, Zimbabwe (chapter 1)

* Age at which males obtained territories is used as an estimate of the age at which males begin breeding.

** Adult mortality rates from Matobo National Park are for the sexes combined.

FIGURE LEGENDS

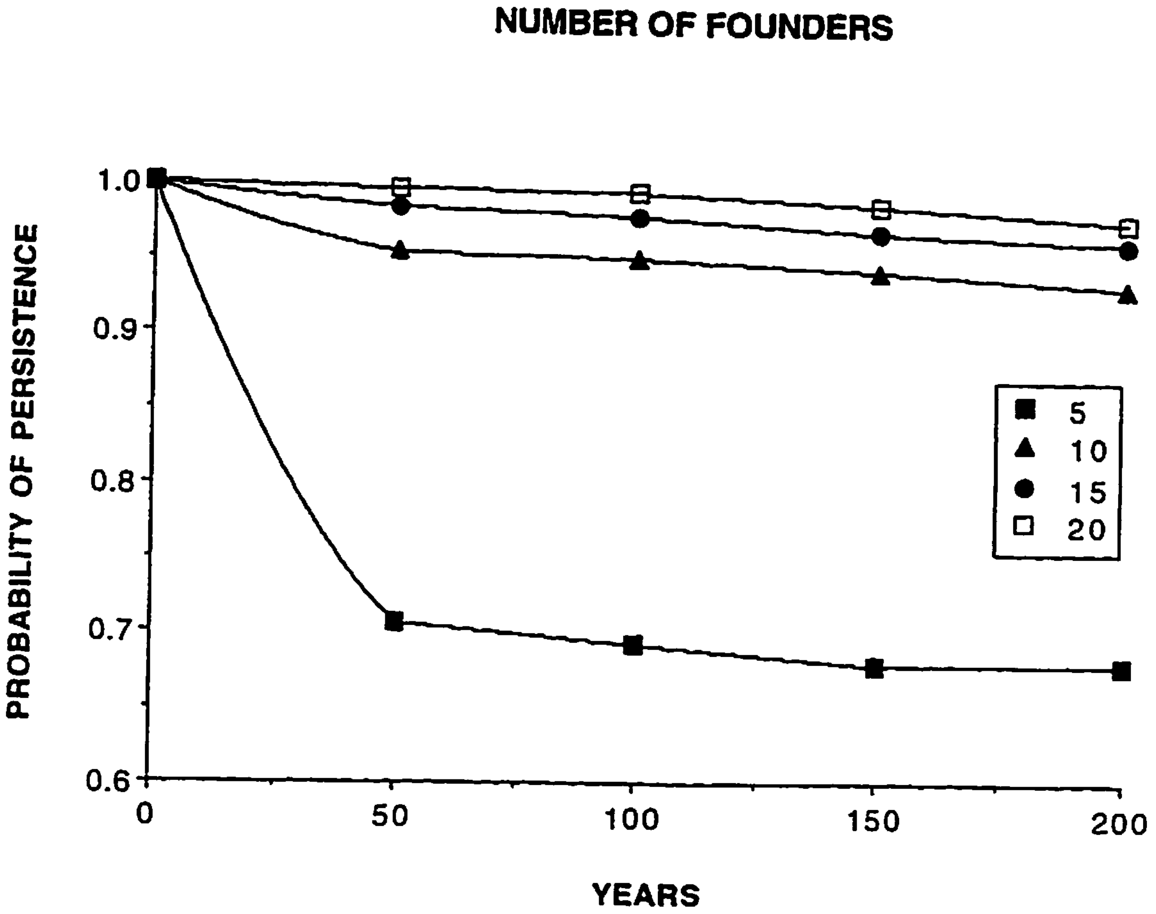
Figure 1. Probability of persistence as a function of the number of founders for initial populations of 5 to 20 individuals.

Figure 2. Probability of persistence as a function of the carrying capacity.

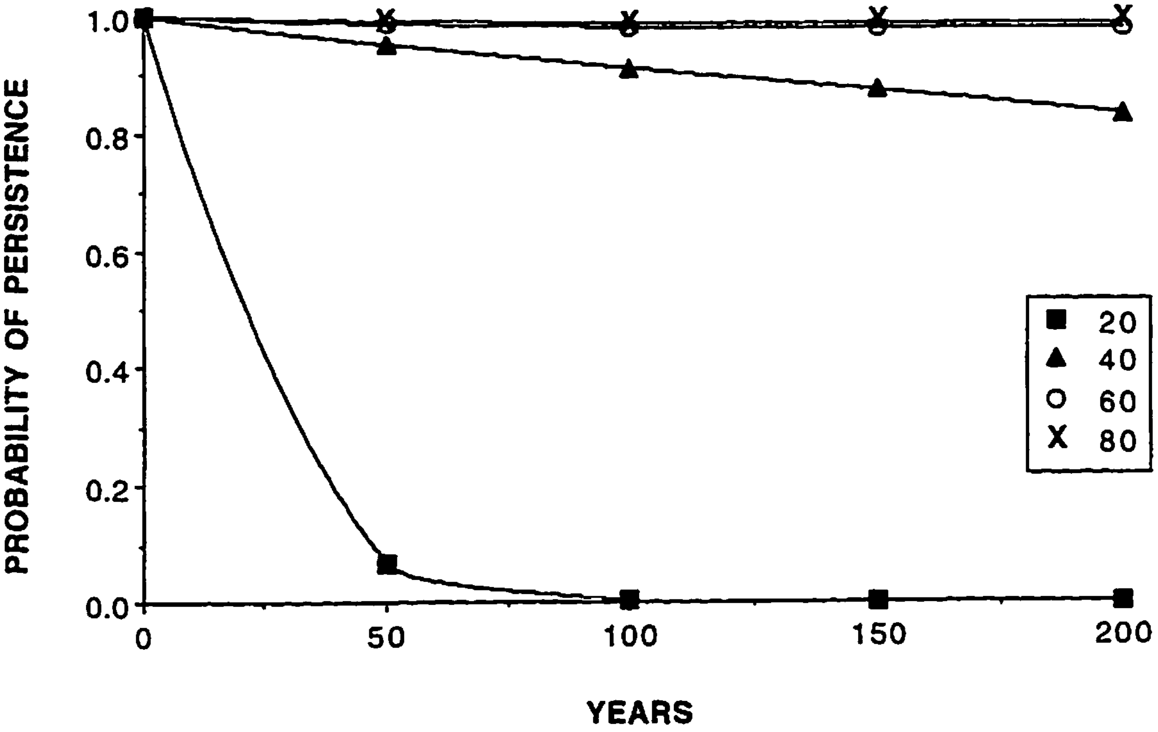
Figure 3. Persistence probability as function of the mean and standard deviation (0% □, 10% ▲, and 20% ●) of the carrying capacity at 50 years (a), and at 200 years (b). Increased variation in the carrying capacity resulted in decreased persistence for all carrying capacities <80.

Figure 4. Results of sensitivity analyses of mortality rates. Persistence probability as a function of age-specific mortality rates at 50 years (a), and at 200 years (b). Persistence was robust to variation in calf mortality, but adult and subadult mortality rates exhibited a threshold effect on persistence.

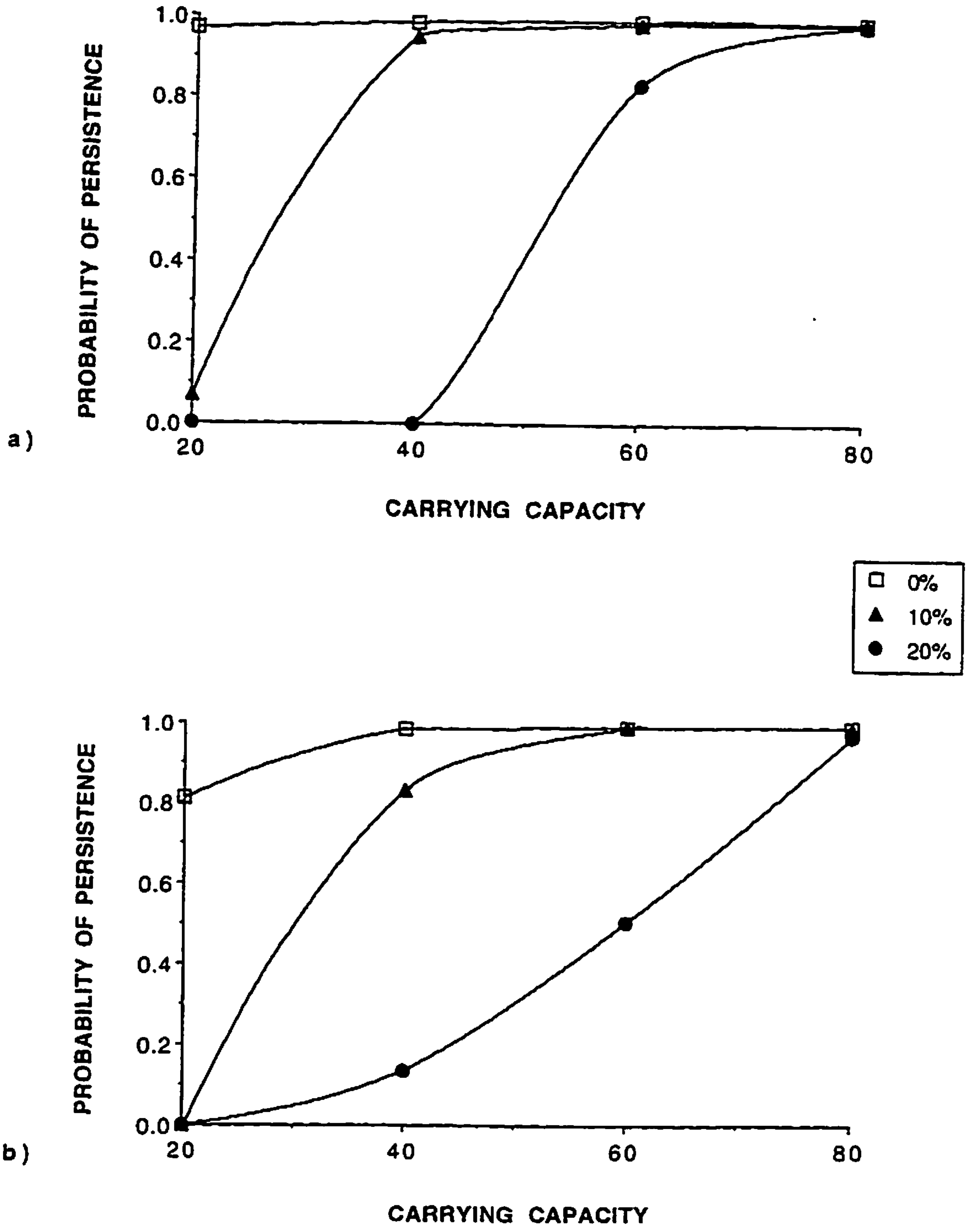
Figure 5. Results of sensitivity analyses of degree of polygyny. Mean expected heterozygosity in models with differing percentages of males (≥13 yr) in the breeding pool.


NUMBER OF FOUNDERS
PROBABILITY OF PERSISTENCE
1.0
0.9
0.8
0.7
0.6
0
50
100
150
200
YEARS
■ 5
▲ 10
● 15
□ 20

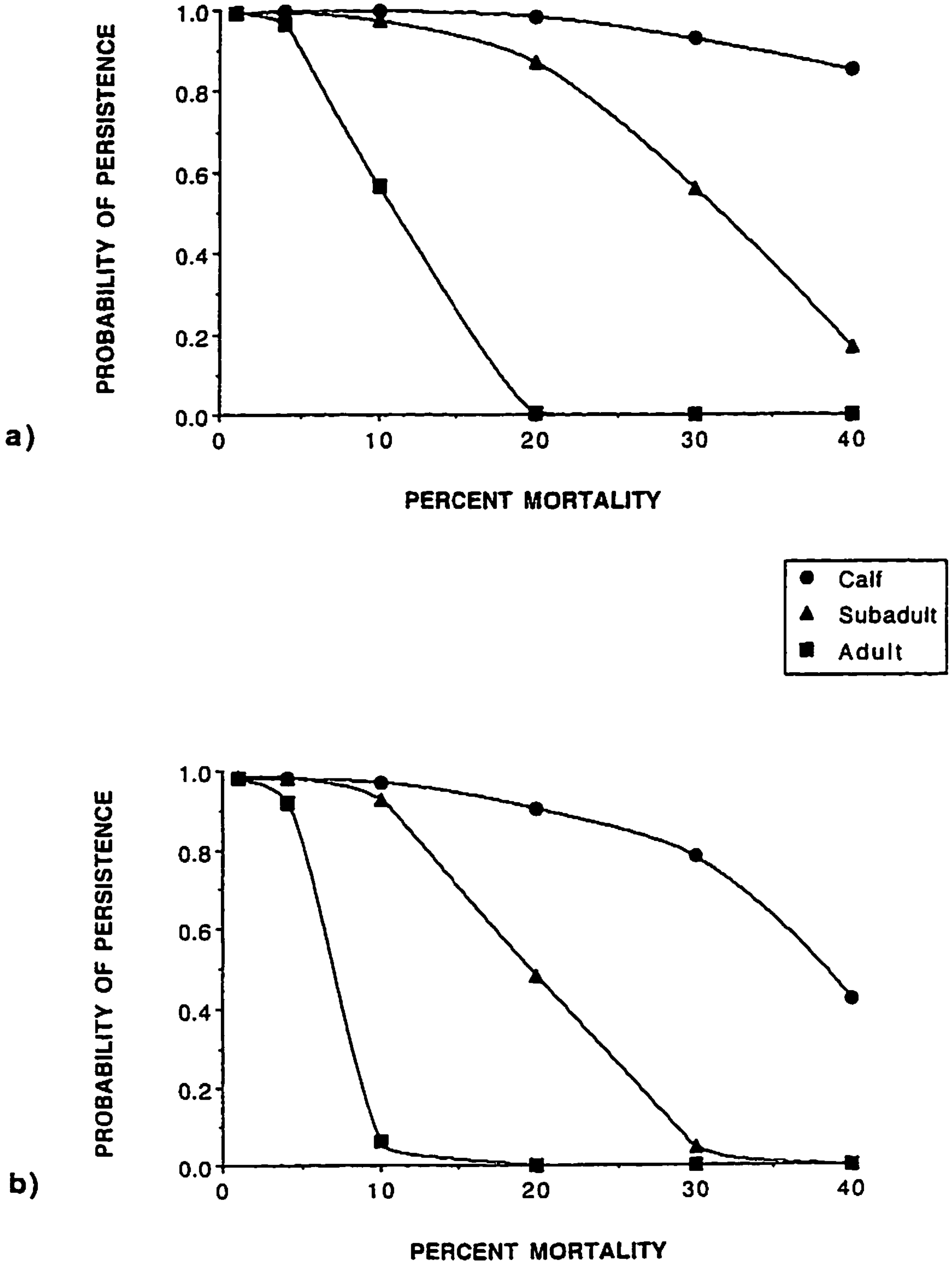
CARRYING CAPACITY

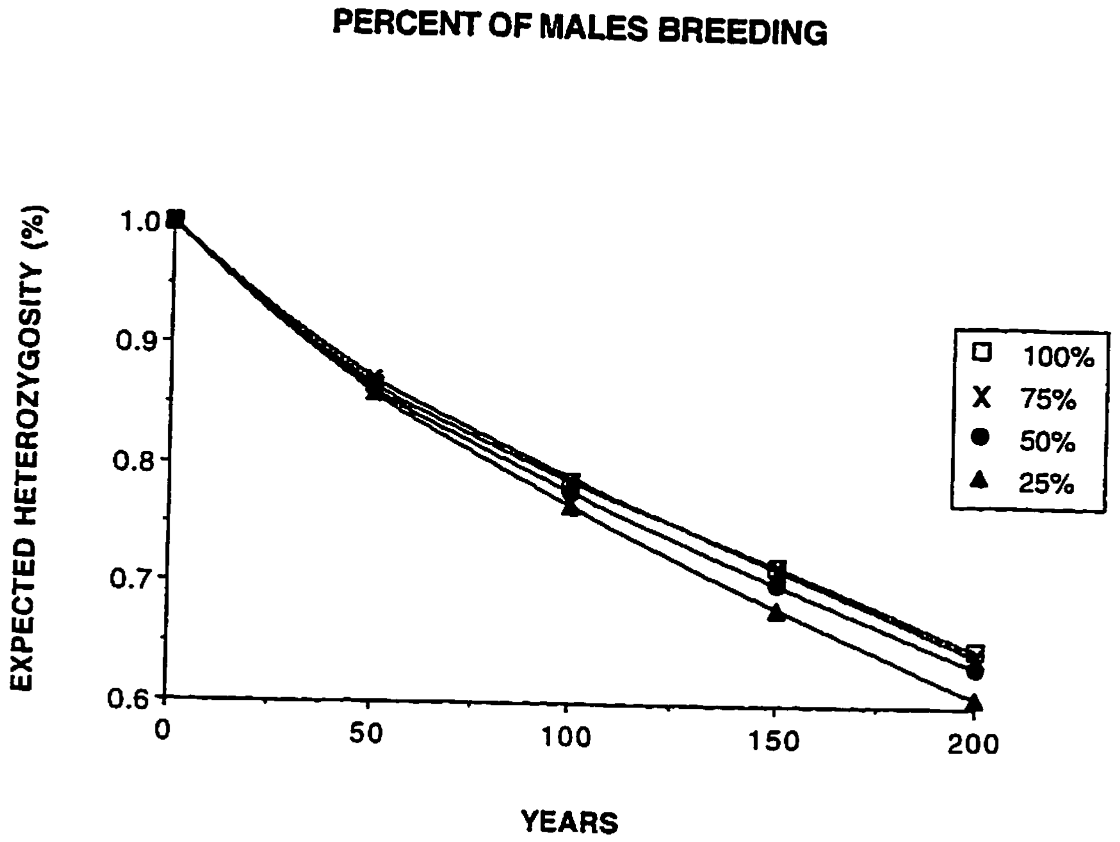


STANDARD DEVIATION AND CARRYING CAPACITY



AGE-SPECIFIC MORTALITY




PERCENT OF MALES BREEDING
EXPECTED HETEROZYGOSITY (%)
1.0
0.9
0.8
0.7
0.6
0
50
100
150
200
YEARS
□ 100%
X 75%
● 50%
▲ 25%

APPENDIX 1. Input values for parameters in the VORTEX Version 7 program (Lacy et al. 1995).

VORTEX parameter / option	Input value for baseline model
Inbreeding depression model	None
EV in reproduction correlated with EV in mortality	Yes
Number of catastrophes	1
Monogamous, polygynous, or hermaphroditic	Polygynous
Age females normally first breed	8
Age males normally first breed	13
Age of senescence, beyond which all animals die	36
Sex ratio at birth	0.50
Maximum number per litter	1
Density-dependent reproduction	Yes
Percent females breeding at *P*(0)	46%
Percent females breeding at *P*(*K*)	33%
SD in % females breeding	8.0%
Age-specific mortality in % (± SD in %):	
Females: calf 0 - 2 yr	5.5% (± 15.0)
subadult 2 - 6 yr	3.0% (± 10.0)
adult 6 - 36 yr	1.5% (± 5.0)
Males: calf 0 - 2 yr	5.5% (± 15.0)
subadult 2 - 6 yr	3.0% (± 10.0)
adult 6 - 36 yr	2.5% (± 5.0)
Probability of catastrophe	5.0%
Catastrophe severity for reproduction	0.75 (25% reduction)
Catastrophe severity for survival	0.75 (25% increase)
% adult males in breeding pool	45%
Carrying capacity	50
SD in carrying capacity	10%
Trend in carrying capacity	No
Initial size of population	15
Number males & females or stable age distribution	stable age distribution

Chapter 4: Conservation Implications of Patterns of Horn Regeneration in Dehorned White Rhinos

Abstract: The demand for rhino horn has led to drastic declines in numbers of rhinos in Asia and Africa. Although all trade in rhino products has been illegal since the mid-1970s, a lucrative illegal market flourishes and poaching continues. Horn removal from African rhinos has been conducted in Zimbabwe, Namibia, and Swaziland to deter poaching. Regeneration of horns following dehorning has created the potential for a sustainable harvest of rhino horn through dehorning programs. Establishment of a regulated legal market for rhino horn has been suggested to help fund rhino conservation programs in African countries. However, evaluation of an economic harvest of rhino horn from dehorning programs has been limited because few data on rates and form of horn regeneration exist. I offer measures of horn regrowth for two white rhino (Ceratotherium simum) populations studied in Zimbabwe between 1991-1995 because rate of horn regeneration will determine the interval at which rhino horns could be harvested profitably. Measurements of horn sizes were collected before and after dehorning, and mass to volume relationships were calculated. Von Bertalanffy growth curves were used to model horn size and rates of horn regrowth relative to age. Adult males had larger horn bases ($p < 0.001$) and faster rates of horn regrowth than adult females. Regenerated horn mass for adult males (>1.3 kg/yr) was almost twice the mass for adult females. Based on an economic model for profit maximization, optimal intervals for dehorning range from 1.16 to 1.51 years, varying with both sex and age. I suggest that managers use these values as minimum dehorning intervals in attempts to balance profits with longer-term management goals. Rates of horn regeneration are likely to be less important than law enforcement in determining the efficacy of dehorning as a deterrent to rhino poaching.

Conservation Implications of Patterns of Horn Regeneration in Dehorned White Rhinos

Introduction

The demand for rhino horn has pushed rhino populations in Asia and now in Africa into precipitous declines (Cumming et al. 1990; Leader-Williams 1992; Western & Vigne 1985). Although all trade in rhino products is banned under CITES, illegal trade in rhino horn continues today supporting aggressive poaching syndicates and a lucrative black market (Nowell et al. 1992).

Traditional conservation efforts for African rhinos have focused on military-style anti-poaching protection (Cumming et al. 1990). Such programs are costly, especially in areas with low densities of rhinos (Leader-Williams & Albon 1988; Martin 1993). Rarely have sufficient funds been available to support anti-poaching work in African nations; in the absence of adequate resources and field staff, poachers have rapidly decimated rhino populations (Borner 1981; Hillman-Smith 1990; Leader-Williams & Albon 1988; Milliken et al. 1993).

Since the ban on international sale of rhino products was mandated nearly 20 years ago, over 95% of Africa's black rhinos have been killed (Milliken et al. 1993; Western & Vigne 1985). Critics of the trade ban have argued for regulated, legal sale of rhino horns. Horn removal from live rhinos has recently added to the stockpiles of horn held by African governments. Further, profits from a sustainable harvest of rhino horn could be used to help support under-funded rhino conservation in developing nations (Kock & Atkinson 1993; Milliken et al. 1993; Sas-Rolfes 1990).

Empirical data about rates and form of horn regrowth following dehorning are needed to evaluate the efficacy of this strategy. Growth rates for intact anterior horns of black and white rhinos were documented when transmitters were imbedded into the horns (Pienaar et al. 1991). Regrowth for dehorned black rhinos has been measured at 6.0 cm/yr and 2.7 cm/yr for the anterior and posterior horns, respectively (Berger et al. 1993). Comparable data for white rhinos are lacking. Although Berger et al. (1993) observed that the horns of juvenile black rhinos regrew more rapidly, the relationships between horn growth, regrowth, sex and age are not well understood for either of the African species.

Data about horn regrowth are relevant to rhino conservation for two principal reasons. First, the efficacy of horn removal as a deterrent to poaching has been questioned, largely because horns regrow and thus, rhinos regain their value to poachers (Berger 1993; Milner-Gulland et al. 1993). Secondly, establishment of a legal market for rhino horn continues to be debated (Leader-Williams 1992; Nowell et al. 1992; Milliken et al. 1993). Dehorning of managed populations could provide a renewable supply of horn if the ban is lifted. However, data regarding horn regeneration must first be available and then evaluated to assess the feasibility of maintaining a sustainable yield through dehorning programs. My goal here is to present information regarding horn regeneration following dehorning of white rhinos as it relates to the latter of these conservation issues.

Background, Study Areas, and Methods

Two dehorned populations of white rhinos were studied in Zimbabwe during July 1991-January 1995. Field work was conducted in Hwange National Park (HNP) from July 1991 to September 1993. HNP is a 14,600 km^2 area in northwestern Zimbabwe on the eastern edge of the Kalahari sands (Jones 1989). Over 90 individuals were identified in HNP during this study. Matobo National Park (MNP) is located in southwestern Zimbabwe and encompasses over 425 km^2 of the Matobo Hills, characterized by rugged, granitic domes and kopjes (Wilson 1969). A total of 55 individual white rhinos were identified in MNP during 1994 (Rachlow & Gumede 1994).

Dehorning

Rhino horns appear solid, and consist of densely-packed microscopic protein fibers (Ryder 1962). Growth of horns occurs from a layer of vascular germinal tissue covering the nasal bones at the base of the horns (Bigalke 1945; Kock 1991). Seventy-one white rhinos were immobilized in HNP during May-November 1991, of which 59 were dehorned. Twelve calves were immobilized and ear-notched, but not dehorned. An additional 18 rhinos were immobilized in HNP in July-August 1992, of which 13 were dehorned. Thirty white rhinos were dehorned in MNP during October 1992, and an additional six subadults were dehorned during 1994. A chainsaw was used to cut off both horns just above the vascular tissue, and to trim the remaining horn stubs as closely as possible. All rhinos in both Parks were ear-notched during the first immobilization for individual identification.

I used several methods to age rhinos. Ages were known or estimated: (1) from previous monitoring work at MNP (Rachlow & Gumede 1994); (2) for calves in HNP based on body size in relation to adult females (Owen-Smith 1973); and (3) from tooth wear patterns following death and collection of skulls (Hillman-Smith et al. 1986). All other rhinos (n = 64) were placed into two broad age categories: subadults (2.5 - 4.5 years) and adults (> 4.5 years) based on body and horn sizes.

Horn measurements

Horns were measured on immobilized rhinos prior to dehorning. Basal circumference was measured for each horn along the horn-skin interface. Horn lengths were recorded along the front curve of the horns from the horn-skin interface to the horn tip. Measurements were recorded to the nearest 0.5 cm.

Rates of horn regrowth were calculated by comparing linear horn lengths (recorded from the mid-point of a lateral surface of the horn at the horn-skin interface to the tip of the horn) on the date of dehorning with actual measurements 0.8 - 2.2 years later. Linear lengths of regrown horn stubs were measured on 21 adults immobilized in HNP in July-August 1992 and on 14 adults immobilized for radio-collaring in MNP during 1994. Regrowth was estimated on an additional 18 rhinos in MNP using a photogrammetric device mounted on a 300 mm telephoto camera lens (Berger & Cunningham 1994). This device measures the distance between the camera and the animal accurately, resulting in a reliable method for scaling an object's size from photographs. Figure 1 shows the estimates of horn length from photographs of 25 horns compared with actual sizes determined using a tape measure ($y = -1.09 + 1.01x$; $r^2 = .99$). A correction factor was developed to refine the estimates of horn size (estimated size = 1.08 cm + 0.99 x photo-estimated size). The corrected horn length estimates were used to calculate linear rates of horn regrowth for rhinos that I did not immobilize again after dehorning.

Density of horns was determined from 49 white rhino horns by water displacement and calculation of mass/volume per horn. Horn density was used subsequently to calculate mass of horn regenerated following dehorning.

Data analyses

Basal circumferences of all adult males and females were compared using two-tailed, two-sample t-tests (Zar 1984). Mean values are reported ± 1 standard error. Because growth of mammals tends to be asymptotic, a sigmoid growth function, the von Bertalanffy growth curve, was used to model basal circumference as a function of age for each sex (Kaufmann 1981; Leberg et al. 1989). I modified an equation for exponential decay in an analogous fashion to the von Bertalanffy growth equation to fit the relationship between rate of horn regrowth and age. Nonlinear least squares estimation was used to fit the von Bertalanffy curves (Wilkinson 1990). The function for age-specific rate of horn regrowth was combined with that for age-specific basal circumference to estimate the volume of horn regenerated annually for each sex. The mean density of horn was incorporated into this equation to determine age-specific mass of horn regenerated annually.

Results

Horn sizes and density

Horn basal circumferences of adult males were significantly larger than those of adult females for anterior horns ($\overline{X}$ = 70.2 ± 1.58 cm for males; $\overline{X}$ = 60.9 ± 0.90 cm for females; $t = -5.365$; $df = 86$; $p < 0.001$) and posterior horns ($\overline{X}$ = 58.2 ± 1.87 cm for males; $\overline{X}$ = 49.3 ± 0.95 cm for females; $t = -4.452$; $df = 82$; $p < 0.001$). As with horn length, basal circumference increased rapidly with age for both sexes approaching an asymptote around 20+ and 15+ years for the anterior and posterior horns, respectively (Fig. 2; Appendix 1).

Mean density for all horns measured (n = 49) was 1.30 g/cm^2 (± 0.026). No significant difference was detected between the horns of males (n = 20) and females (n = 29) ($\overline{X}$ = 1.32 ± 0.03 g/cm^2 for males; $\overline{X}$ = 1.29 ± 0.04 g/cm^2 for females; $t = -0.571$; $df = 47$; $p = 0.571$). However, density of anterior horns ($\overline{X}$= 1.36 ± 0.12 g/cm^2) was significantly greater than the density of posterior horns ($\overline{X}$ = 1.20 ± 0.22 g/cm^2) ($t = 3.392$; $df = 47$; $p = 0.001$).

Horn regrowth

Linear rates of horn regrowth after dehorning decreased with age in both sexes for the first 10 years, after which rate of regrowth appeared to approach an asymptote (Fig. 3). Males had faster rates of regrowth than females for the anterior horns, and slightly faster regrowth for the posterior horns, but only 2 older males were sampled.

Because rhino horns are roughly conical in form (Fig. 4), I calculated mass of horn regenerated annually after dehorning using the equation for the volume of a cone (Pienaar & Hall-Martin 1993) (Appendix 1). I combined the von Bertalanffy growth curves for basal circumferences (Fig. 2) and the age-specific regrowth rates (Fig. 3) with mean horn density (anterior or posterior) for each sex independently. While females would reach a peak in horn regeneration at 8 years, mass of horn regenerated by males would approach an asymptote slowly at over 30 years of age (Fig. 5). The shapes of the functions of horn regeneration differ between the sexes because basal circumference approaches an asymptote at a later age for males than for females (Fig. 2). For much of their adult life span, males regenerate horn material at almost twice the rate of females (Fig. 5). This method for estimation of regenerated horn mass appears accurate because estimated horn mass was highly correlated with acutal measures of horn mass from 11 regrown horns collected from rhinos that died 0.8 to 2.0 years after dehorning (Pearson correlation coefficient $r = 0.976$; $p < 0.001$).

Discussion

Although data exist on horn size and regrowth after dehorning for black rhinos (Berger et al. 1993), there are none for white rhinos. Understanding patterns of horn growth and regrowth can be important in three principal ways. First, because legalization of the horn trade has been suggested as a possible way to generate revenue for conservation programs in southern Africa (Kock & Atkinson 1993; Milliken et al. 1993), it is necessary to predict how much horn might be harvestable. Second, because both sex and age affect horn size and mass, it is essential to know something about inherent variation and distribution of horn sizes within a population. Third, models that have examined the economics of dehorning and rhino protection have been forced to rely on assumptions about the constancy of growth, patterns that I am now able to refine. Here, I elaborate on these issues.

Rhino horns regorw throughout an individual's lifespan. However, wear at the tips of the horns may result in static or even decreasing horn lengths in older animals (Pienaar et al. 1991), although I observed little wear on the dorsal or lateral surfaces of regrown horn stubs, even two years after dehorning. Indeed, rates of regrowth after horn removal are similar to intrinsic rates of horn growth (the actual rate at which horns are produced) reported for white rhinos in South Africa (Pienaar et al. 1991). Regrowth rates for dehorned black rhinos also approximate those reported for intact horns in that species (Berger et al. 1993; Pienaar et al. 1991).

Both age and sex influenced horn regrowth in dehorned white rhinos. Linear rates of regrowth decreased with age in both sexes, but the horns of males regrew more rapidly (Fig. 3). Mean rates of horn regrowth for adult black rhinos in Namibia were 6.0 cm/yr and 2.7 cm/yr for the anterior and posterior horns, and regrowth was more rapid for the horns of juveniles (8.9 and 4.4 cm/year) (Berger et al. 1993). Thus, in both species of African rhinos, rates of horn regrowth appear to decrease with age, but the effect of sex has not been examined in black rhinos.

Mass of horn regenerated annually depends on the basal circumference and linear rate of horn regrowth. Because both of these attributes are strongly influenced by age in white rhinos, it is not surprising that marked differences occur in mass of horn regenerated relative to age. Likewise, white rhinos exhibit sexual dimorphism in horn size and regrowth, and consequently large sexual differences exist in the rate of horn regeneration (Fig. 4). Adult males produce almost twice the mass of horn annually as adult females of similar ages (Fig. 5c).

Mass of rhino horns is the key factor in determining their value because sale for medicinal consumption ultimately is priced per unit mass (Nowell et al. 1992). Rate of horn regeneration following dehorning is central to the issue of whether a sustainable harvest would be feasible if a legal market for rhino horn were established. Prices reported for retail sale of African rhino horns have ranged from $3250/kg to over $10,000/kg (Milliken et al. 1993). However, a price of $2000/kg has been noted for wholesale supply of horns by African governments if trade were legalized (Milner-Gulland et al. 1993). At this price, male white rhinos over 20 years old will regenerate, on average, over $2600 of horn annually.

Regeneration rates will influence the frequency of horn trimming necessary for a profitable yield. Milner-Gulland et al. (1992; 1993) adapted a forestry model for optimal harvest to suggest dehorning intervals for rhinos. This model considers two variables that influence the rotation time for harvest: 1) the cost-price ratio, which is the ratio between the cost of dehorning a rhino and the profit received from sale of the horns; and 2) the discount rate, which is the rate at which the potential for future profits decrease. Milner-Gulland et al. (1992) suggest that their model is insensitive to variation in the discount rate, and that a conservation agency with a strong interest in future yields may experience a very low discount rate. Thus, setting the discount rate equal to zero, the model can be simplified to:

$$V'(T)/(V(T)-c)$$

where T is the optimal rotation time with respect to profit maximization, $V(T)$ is the value of the horn at time t, and c is the cost of dehorning (Milner-Gulland et al. 1992).

The costs of dehorning rhinos vary with population density and methods used to locate individuals. In Zimbabwe, the costs have ranged from $350 to $1800 per rhino (Kock & Atkinson 1993). The higher values occurred in low-density populations that had experienced severe levels of poaching. Most rhinos surviving in Zimbabwe currently are managed within rhino sanctuaries or reserves. If horn harvesting in managed populations were to occur, values at the lower end of this range would be more realistic assuming that encounter rates do not change when individuals are dehorned at different intervals. Thus, using an average cost of $400 per rhino and the suggested wholesale price of $2000/kg for legal sale of rhino horn, a realistic cost-price ratio would be 0.2.

What predictions about horn harvesting follow from the economic model given my data on horn regeneration? Because rates of horn regeneration vary with sex and age, optimal frequency of dehorning for profit maximization also will vary among individuals according to these parameters. Optimal dehorning intervals for both sexes decrease throughout their lives, however the change is very slow, especially for older individuals. For example, optimal intervals for males are 1.38 yr at 3 years of age and 1.16 yr at 30 years of age. Because females regenerate less horn mass annually than males, optimal intervals for dehorning females always will be slightly longer than for males. Calculated optima are 1.51 yr and 1.40 yr for 3 and 30 year old females, respectively. In reality, this level of precision in predicting optima is largely academic because other factors such as availability of funding, equipment, personnel, and seasonal rainfall patterns are likely to influence the exact intervals at which dehorning could be accomplished.

Dehorning intervals calculated using this model are optimal only with respect to profit maximization. However, managers may consider other "costs" of dehorning, of which there may be many. Although mortality rates associated with dehorning both black and white rhinos in Zimbabwe have been very low (0% to 3%) (Kock & Atkinson 1993), the risk of mortality exists each time an animal is immobilized. Additionally, it is unclear whether frequent immobilization of animals with narcotic drugs might have long term effects. Finally, managers may wish to avoid disturbance of females with young calves and to adjust dehorning schedules for females accordingly. Thus, I suggest that dehorning intervals that maximize profits should be considered minimum intervals with respect to other population management objectives.

A second application of the economic model for horn harvesting has been to examine the effectiveness of dehorning in deterring rhino poachers (Milner-Gulland et al. 1992, 1993). Theoretically, rhino poaching should cease when the costs relative to the rewards become too great to provide incentives for poachers. However, this economic equation may not apply precisely to rhino poaching in Africa. Monetary rewards received by most poachers are an insignificant proportion of the potential value of the horns they have collected, and are only loosely related to horn size or mass (Milliken et al. 1993). A second challenge in applying a strict cost-price model to a poacher's decision to kill dehorned rhinos is that the cost of poaching is difficult to define in monetary terms. The Zimbabwean authorities maintain a shoot-to-kill policy for armed poachers in national parks (Martin 1993), and the real cost of poaching to the hunters is the risk of death or imprisonment (Milner-Gulland & Leader-Williams 1992). It is only at the level of African-based middlemen that the cost-price ratios become important (Milliken et al. 1993). Thus, there may be only an indirect relationship between the cost of poaching and the size or mass of horns obtained.

The cost or risk of being caught poaching is likely related to amount of monies allocated for anti-poaching activities. Where funds for law enforcement have been low, rhino populations have declined (Hillman-Smith 1990; Leader-Williams & Albon 1988). A dehorned population of white rhinos in Hwange National Park, Zimbabwe, experienced high levels of poaching after law enforcement in the national parks was sharply curtailed due to a lack of funding for anti-poaching work. Such factors as this funding crisis are likely to have an overriding impact on the success or failure of dehorning programs in deterring poaching. In reality, data on horn regeneration after dehorning is likely to be more useful in decision making about dehorning intervals for horn harvest rather than for predicting poacher behavior.

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FIGURE LEGENDS

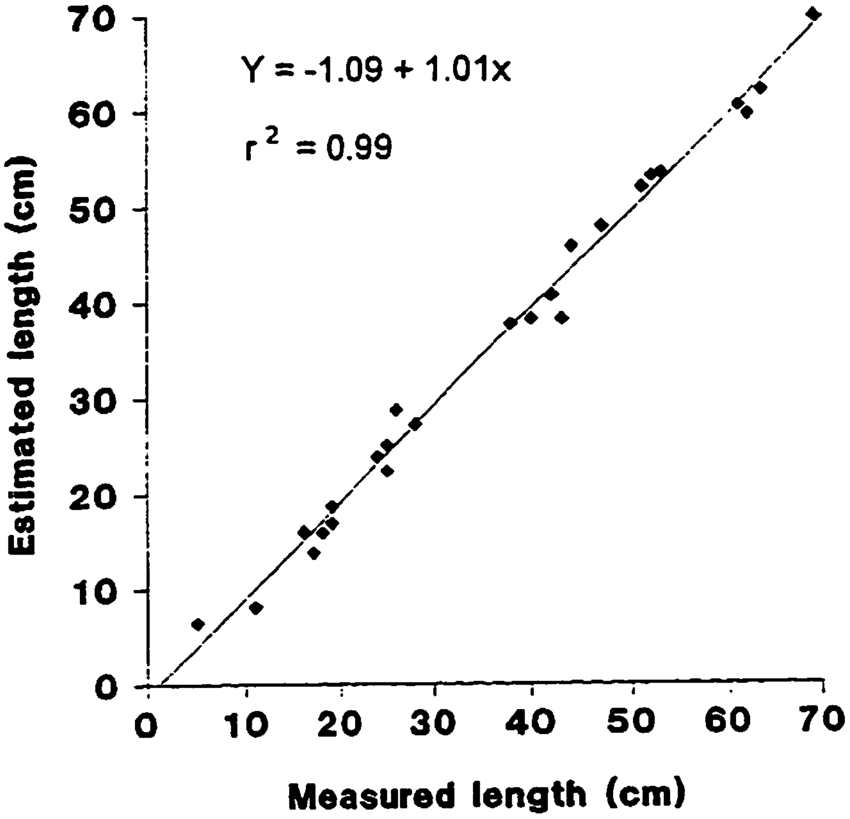
Figure 1. Regression of estimated horn lengths obtained using the photocalibration method on measured horn size. Estimates of horn lengths were corrected based on this regression (actual size = -1.09 + 1.01x estimated size; r^2 = 0.99).

Figure 2. Measurements of the curvilinear basal circumferences of horns of white rhinos fitted with the von Bertalanffy growth curves Y = a-b*exp(-c*age) for the anterior horns (a) and the posterior horns of males and females (b). Fitted values are given in Appendix 1.

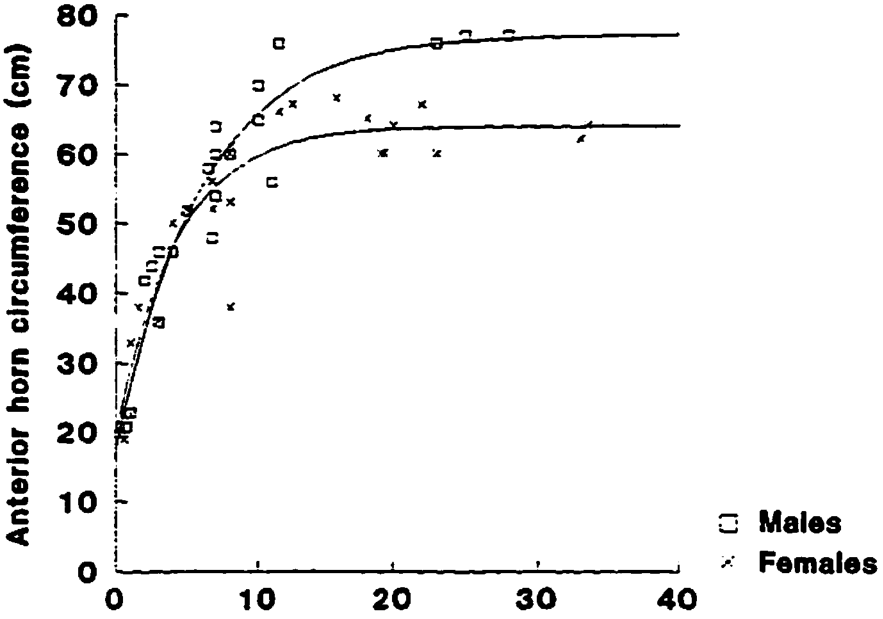
Figure 3. Rates of horn regrowth after dehorning for white rhinos fitted with von Bertalanffy-like modified equations for exponential decay Y = a+b*exp(-c*age) for the anterior horns (a) and the posterior horns of males and females (b). Fitted values are given in Appendix 1.

Figure 4. Horn regrowth in white rhinos two years after dehorning: 35-year old female (a) and 7-year old male (b).

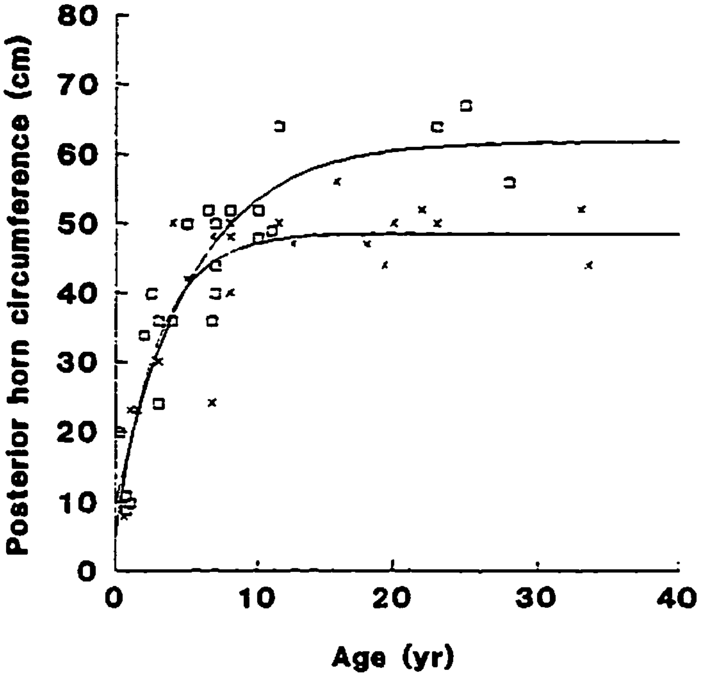
Figure 5. Annual rate of horn regeneration relative to sex and age of white rhinos: the anterior horns (a), the posterior horns (b), and the total of both horns (c).

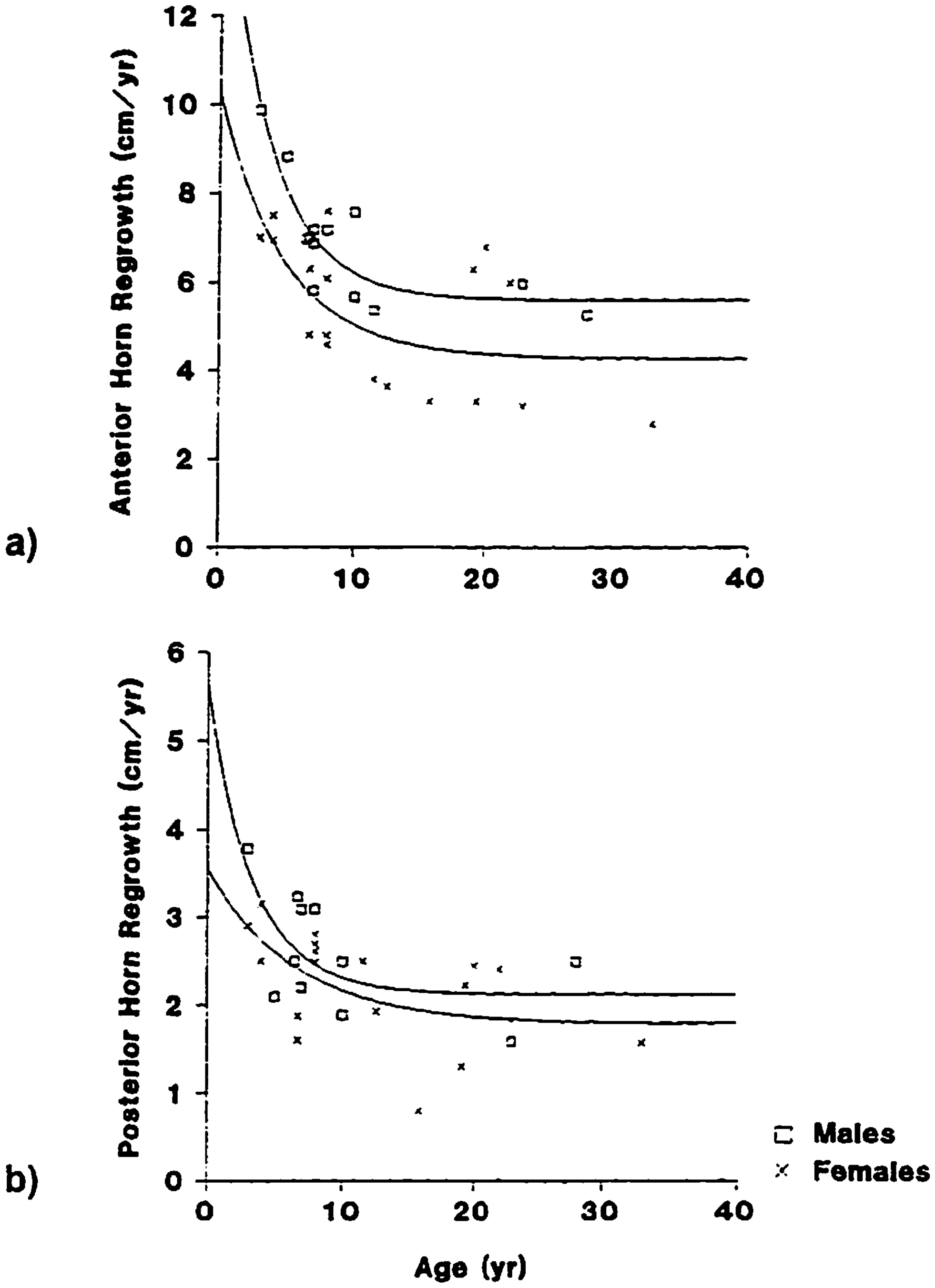

Y = -1.09 + 1.01x
$r^2 = 0.99$
Estimated length (cm)
0
10
20
30
40
50
60
70
Measured length (cm)
0
10
20
30
40
50
60
70

a)


Anterior horn circumference (cm)
0
10
20
30
40
50
60
70
80
0
10
20
30
40
☐ Males
× Females

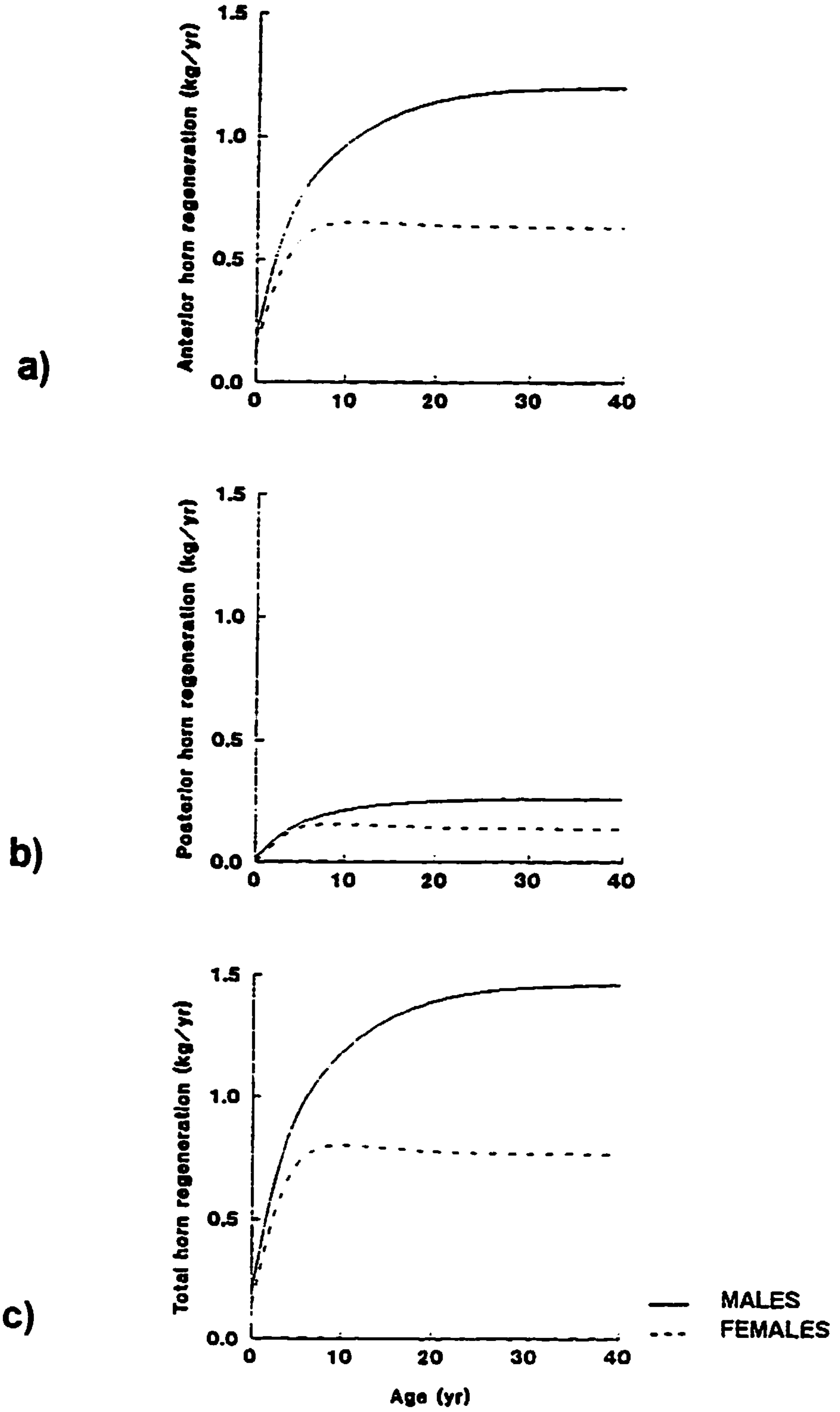
b)


Posterior horn circumference (cm)
0
10
20
30
40
50
60
70
80
0
10
20
30
40
Age (yr)


a)
Anterior Horn Regrowth (cm/yr)
0
2
4
6
8
10
12
0
10
20
30
40
b)
Posterior Horn Regrowth (cm/yr)
0
1
2
3
4
5
6
0
10
20
30
40
Age (yr)
□ Males
× Females

a)

b)


a)
Anterior horn regeneration (kg/yr)
1.5
1.0
0.5
0.0
0
10
20
30
40
b)
Posterior horn regeneration (kg/yr)
1.5
1.0
0.5
0.0
0
10
20
30
40
c)
Total horn regeneration (kg/yr)
1.5
1.0
0.5
0.0
0
10
20
30
40
Age (yr)
MALES
FEMALES

APPENDIX 1. Equations and fitted values for horn circumferences and rates of regrowth as a function of age for males and females.

Formula for the von Bertalanffy growth curves used to model basal circumference with age: $Y = a - b * \exp(-c * age)$.

Fitted values:

Horn Circumferences

Males: anterior: $a = 77.009$; $b = 59.356$; $c = 0.166$
posterior: $a = 61.749$; $b = 52.120$; $c = 0.184$
Females: anterior: $a = 63.844$; $b = 44.222$; $c = 0.238$
posterior: $a = 48.502$; $b = 43.172$; $c = 0.345$

Formula for the von Bertalanffy-like modification of exponential decay used to model decreasing rate of horn regrowth with age: $Y = a + b * \exp(-c * age)$.

Fitted values:

Rates of Regrowth

Males: anterior: $a = 5.616$; $b = 10.418$; $c = 0.286$
posterior: $a = 2.123$; $b = 3.489$; $c = 0.294$
Females: anterior: $a = 4.281$; $b = 5.979$; $c = 0.206$
posterior: $a = 1.792$; $b = 1.767$; $c = 0.156$

Equation for mass of regrown horns using the equation for volume of a cone:

mass = volume x density where volume = 1/3 (basal area x height), basal area = $\pi \times r^2$, r = horn basal circumference (cm) / 2 x π, and height = linear horn length (cm).

SUMMARY

White rhinos represent one of the success stories in conservation, having recovered from a single population of 50 to 200 individuals earlier this century to over 7,000 today. However, the demise of the white rhinos in Hwange National Park, Zimbabwe, the largest population outside of South Africa, should serve as a warning against complacency.

Horn removal from live rhinos has been employed as an emergency measure to deter poaching. However, in Hwange Park, it did not succeed due to a lack of law enforcement. Dehorning programs could provide revenue for rhino conservation efforts if a legal market were created. However, legal trade is unlikely to be established in the near future.

Survival of rhinos outside of protected reserves will remain low while trade in rhino horns fuels an illegal market. Even within guarded conservation areas, some losses to poaching should be expected. Establishment of rhino reserves, and sound management of small populations will be important for survival of rhinos in situ. This research focused on questions relating to conservation of rhinos within such reserves.

Although reproductive rates of white rhinos may be low compared to smaller-bodied species, their populations can increase at rates of up to 10% per year. Population densities can have a significant impact on body condition and reproduction. Managers of reserves need to consider trade-offs between population growth and population density. The territorial behavior of adult males within confined areas also may require management to meet long-term goals for maintenance of genetic diversity. Male mating patterns can affect the rate at which genetic diversity is lost in small

populations, but long-term data on variance reproductive success in both sexes are needed to confirm this result. Demographic models suggest that population persistence is strongly affected by rates of adult and subadult mortality, and by the mean and variation in the carrying capacity. Management actions that increase survivorship of adults are likely to have a greater impact on population persistence than those designed to improve calf survivorship.