

Reproduction and population density: trade-offs for the conservation of rhinos *in situ*

Janet L. Rachlow and Joel Berger

Program in Ecology, Evolution, and Conservation Biology, University of Nevada, Reno, Nevada 89512, USA

(Received 25 April 1997; accepted 12 December 1997)

Abstract

As the human population increases, wildlife is becoming restricted to protected remnants of ecosystems with boundaries that limit dispersal. The effect on large herbivores generally is an increase in population density. We 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 of a fenced population as density increased by >200%. As density increased within the fenced area, the rates of population growth and recruitment of calves decreased, and the age at first reproduction for females increased significantly. Females in the low-density population produced their first calves at significantly younger ages than those in the high-density population. Loss of body condition was related to both population density and female reproductive status. Because most African rhinos exist in relatively small reserves, an understanding of the implications of restricted dispersal and increased population density on their demography is critical to their conservation *in situ*. Managers need to consider trade-offs between enhanced safety from poaching and density-dependent effects on reproduction in developing conservation strategies for rhinos and other rare, large species confined to reserve systems.

INTRODUCTION

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 (Berger & Cunningham, 1994; Arcese, Hando & Campbell, 1995; Campbell & Hofel, 1995). An understanding of the potential impacts of restricted movement on population densities, behaviour, 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 home ranges (Harestad & Bunnell, 1979; Harvey & Clutton-Brock, 1981; Gompper & Gittleman, 1991). In addition, the 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, smaller 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, Guinness & Albon, 1982; Owen-Smith, 1983).

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 (Kahn, 1989; Gakahu, 1993). Although relatively large tracts of habitat still exist for African rhinos, poaching has decimated populations in areas outside of heavily guarded reserves (Western & Vigne, 1985; Leader-Williams, 1988). 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; Martin & Vigne, 1997). While this strategy has been successful in halting the rapid decline in numbers due to poaching, rising population densities within reserves may require changes in management practices.

Large, mammalian herbivores fall into the category of 'K-selected' species, for which demographic patterns are influenced by variation in population densities (Fowler, 1987). Among ungulates, increases in population density

lead to lower levels of fecundity, delayed attainment of puberty, and increased mortality (Albon, Mitchell & Stains, 1983; Skoglund, 1989; Clutton-Brock, Price *et al.*, 1992; Jorgenson *et al.*, 1993; Saether & Heim, 1993). 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. We investigated the first two of these parameters using two lines of evidence: (1) a contrast between a high-density and a low-density population; and (2) an analysis of changes in demographic parameters within a fenced population over a 30-year period during which population density increased by >200%. We examined population growth and recruitment, age at first parturition, and interval between births as a function of population density.

METHODS

Study area and population

White rhinos were extirpated in Zimbabwe in the late 1800s, and reintroduced in the 1960s when animals were translocated from Umfolozi Game Reserve in South Africa. Matobo National Park (MNP) is located in south-western Zimbabwe, and encompasses over 425 km² of the Matobo Hills, characterised by rugged, granitic domes and kopjes (Wilson, 1969). In 1962, four white rhinos were released into a fenced area of approximately 105 km² within MNP known as the Whovi Game Park (WGP). During 1966–67, eight individuals were added to this group bringing the founding number to 12 (seven females and five males) (Roth, 1967). An additional three females and one male were added to the population from Swaziland in 1987. The population increased rapidly within the fenced area, and 20 individuals were translocated out of the reserve between 1975 and 1986 because of increased levels of aggression and fight-related injuries. A second population of white rhinos was established within MNP in 1978–79 when six of the rhinos removed from the fenced WGP were released in a region known as the Hazelside Area (HA).

Demographic data were available for the Matobo white rhinos 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).

We calculated densities for each population of white rhinos in MNP independently. 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 & Jones (1980) mapped the WGP and estimated that 52 km² of the total 105 km² (approximately 50%) was available to grazers. We used this area to calculate ecological densities (animals/available habitat; Eisenberg & Seidensticker, 1976).

The HA is about three times larger than the WGP, but because the rhinos used only a portion of the entire

region, we first estimated the size of the area used by this population, and then calculated an ecological density for that area. We estimated the size of the area used by the entire group ($n = 9$) based on 106 location points collected over a 13-month period during 1994–95; only one location per group or solitary individual per day was included in this analyses. The program CALHOME (Kie, Baldwin & Evens, 1996) was used to estimate a 95% group range (analogous to a 95% home range of an individual) using the adaptive-kernel method (Worton, 1989). Because the HA is slightly less rocky than the WGP, we estimated that 60% of the total area was suitable for grazers (in comparison with the 50% estimate for the WGP, see above), and this area was used to calculate the ecological densities for the HA population. In the following analyses, the HA rhinos represent the 'low-density' population and the WGP rhinos are considered the 'high-density' population.

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. We photographed each rhino in the late wet season (7 April to 8 May) and again towards the end of the dry season (30 September to 2 November). Multiple photographs were taken of each rhino and scored on a scale from one to four at increments of 0.5 (Table 1). An average score was assigned to each individual in each season.

We contrasted body condition of lactating and non-lactating females. All females with calves ≤2.5 years of age were observed nursing, and were classified as 'lactating'. Females without young, or accompanied by calves ≥2.5 years of age whom they were not observed to nurse, were classified as 'non-lactating'.

Statistical analyses

Mann–Whitney *U* tests were used for comparing body condition and individual reproductive parameters because sample sizes were too small to meet or to reliably test for the assumptions of parametric analyses (Zar, 1984). Regression analyses were used to examine relationships between reproductive parameters (recruitment rate and age at first reproduction) and population

Table 1. System for scoring body condition of white rhinos 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 around 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

density. When necessary, data were log-transformed to correct for heteroscedasticity (Zar, 1984). Means are reported \pm standard errors of the means.

RESULTS

Reintroduction and population growth in the Whovi game park

The population of white rhinos in the fenced WGP has undergone two periods of growth during which translocations did not occur: 1967–1974 (early period) and 1987–1994 (late period). Rates of annual increase calculated for the early and late periods were 10.4 and 6.6%, respectively (Fig. 1). The ecological density in the WGP increased by >200% during this time, from 0.23 rhino/km² in 1967 to 0.83 rhino/km² in 1994.

We examined data on recruitment rate of the WGP population as a function of population density. A simple linear regression revealed that recruitment rate of calves (calves that survived >2 years) decreased significantly ($P = 0.007$) with the density of adult and subadult rhinos (>2 years of age) (Fig. 2). Because rhinos are non-seasonal breeders and reproduce at intervals of 2–4 years, annual recruitment rates vary markedly, however, the decreasing trend in recruitment with population density is clear.

Individual patterns of reproduction

Female reproductive parameters varied with population density. Age at first reproduction for female white rhinos in MNP varied from 6.5 to 11.5 years of age (Rachlow, 1997). Using data for all females, age at first reproduction increased significantly with total population density in the year of conception ($y = 0.85 + 0.26x$; $F_{1,12} = 8.877$; $P = 0.011$; $r^2 = 0.425$).

A contrast of age at first calving between the low-density (HA) group and the high-density WGP rhinos revealed that age at first birth was significantly lower for HA females ($n = 4$) than for those in the WGP ($n = 9$) (Mann–Whitney $U = 315$, $P = 0.036$). Mean age at first

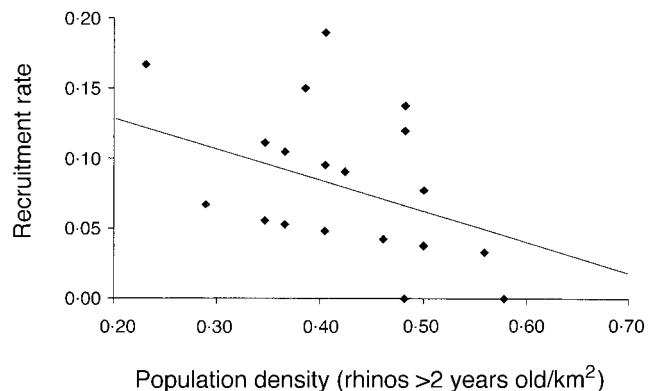


Fig. 2. Annual recruitment rate of white rhino calves as a function of population density of adults and subadults in the Whovi Game Park for the years of 1968–1993 ($y = 0.21 - 0.29x$; $F_{1,24} = 8.587$; $P = 0.007$; $r^2 = 0.264$).

birth was 7.4 ± 0.4 years in the low-density group and 10.1 ± 0.7 years in the high-density population. This contrast includes only females born during the period of 1982–1994, the time period for which data are available for both groups.

Intervals between births have ranged from two to six years for white rhinos in MNP. Mean intervals for females in the WGP were 2.9 ± 0.1 years ($n = 6$ females, 21 intervals) during the early period and 3.3 ± 0.2 years ($n = 8$ females, 19 intervals) during the late period. Only one female in the low-density population has given birth to more than three calves, with a mean of 2.25 years for five 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 females in the low-density group experienced significantly shorter birth intervals than females in the high-density group. Although intervals between calves appear to increase at higher population densities, data from more individuals are required to provide a robust test of this relationship.

Body condition and reproductive status

Body condition varied only slightly among individuals during the wet season, but 90% lost condition during the dry season. Loss of body condition by females was related to reproductive status. Although condition of lactating females ($n = 9$) and non-lactating adult females ($n = 7$) differed little during the wet season, lactating females were in significantly poorer condition during the late dry season (Fig. 3a). Differences in body condition also were related to population density. Rhinos >2 years of age in the high-density population ($n = 32$) were in significantly poorer body condition than those in the low-density population ($n = 7$) at the end of the dry season (Fig. 3b). This difference was apparent despite the fact that lactating females, which tend to exhibit the poorest body condition, comprised a greater proportion of the low-density population.

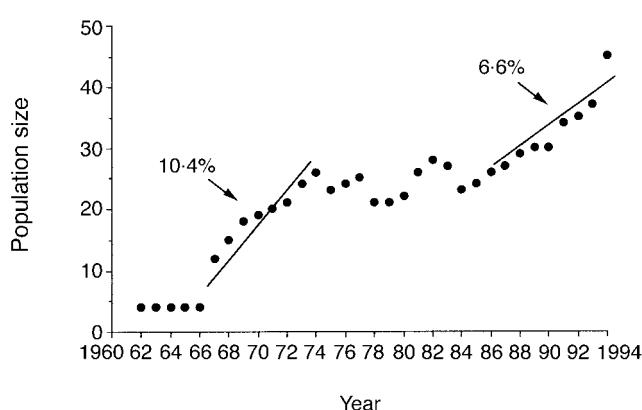


Fig. 1. Numbers of white rhinos in the fenced Whovi Game Park. Rates of growth per year were calculated for the early period (1967–1974) and the late period (1987–1994).

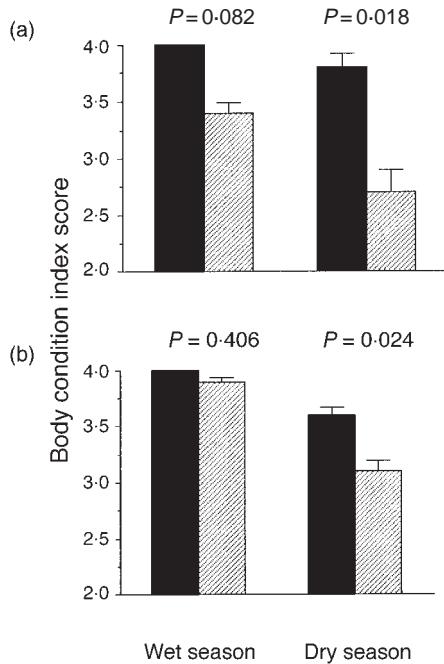


Fig. 3. Seasonal comparison of body condition index scores for white rhinos in Matobo National Park: (a) scores for non-lactating (■; $X = 4.0 \pm 0.0$) and lactating (▨; $X = 3.8 \pm 0.1$) females did not differ significantly during the wet season (Mann-Whitney $U_{[7,9]} = 48.0$). However, during the dry season non-lactating females had significantly higher scores ($X = 3.4 \pm 0.1$) than lactating females ($X = 2.7 \pm 0.2$) (Mann-Whitney $U_{[7,9]} = 58.0$); (b) condition scores did not differ significantly between the low-density (■; $X = 4.0 \pm 0.0$) and high-density (▨; $X = 3.9 \pm 0.0$) populations during the wet season (Mann-Whitney $U_{[7,32]} = 101.5$). However, animals in the low-density group were in significantly better condition ($X = 3.6 \pm 0.1$) than those in the high-density group ($X = 3.1 \pm 0.1$) during the dry season (Mann-Whitney $U_{[7,32]} = 52.5$).

DISCUSSION

Population growth

Rapid rates of increase have been reported in large herbivore populations following introduction into unoccupied habitats (Klein, 1968; Leader-Williams, 1980; Berger & Cunningham, 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 rhino. 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, 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, Mbayama & Watkin, 1993). The white rhino population in the WGP appears to have achieved a near-maximal

rate of growth following introduction into this unoccupied habitat.

Recruitment rate in a closed system is a population-level index of reproduction. The decrease in the recruitment of calves with population size in the WGP (Fig. 2) indicates that reproduction declined as the population density increased. Densities varied markedly between the early and late periods, and differences in recruitment during these two periods probably contributed to the observed differences in population growth rates (Fig. 1).

Individual patterns of reproduction

Females that reproduce early should gain a genetic advantage over those that delay reproduction (Cole, 1954; Stearns, 1992). However, early growth and maturation may affect future fecundity or survivorship (Gadgil & Bossert, 1970; Green & Rothstein, 1991; Reiter & Le Boeuf, 1991). The age at which mammalian females reach puberty and begin reproducing can vary markedly with population density (Laws, Parker & Johnstone, 1975; Albon, Mitchell, Huby *et al.*, 1983; Fowler, 1987; Jorgenson *et al.*, 1993). Age at first calving also appears to be 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 neighbouring Hluhluwe Reserve (Hitchens & Anderson, 1983). In MPN, first births occurred at older ages in white rhinos as density increased, and females in the low-density population calved at significantly younger ages than did those in the high-density group.

Birth intervals in rhinos and other nonseasonal breeders vary considerably, and may be relatively plastic with respect to population density. African elephant (*Loxodonta africana*) females in high-density populations exhibit longer intervals between births than those in lower-density areas (Laws & Parker, 1968; Laws, Parker & Johnstone, 1975). In black rhinos, a contrast between Hluhluwe (high density) and Umfolozi (lower density) reserves revealed that the mean calving intervals were 2.7 and 2.3 years, respectively (Hitchens & Anderson, 1983). A mean birth interval of 2.6 years was documented for white rhinos in Umfolozi Reserve, with a range of 1.8 to 3.5 years (Owen-Smith, 1988). Although the sample sizes are small, data from MNP suggest that rate of calving was inversely related to population density.

Numerous factors probably 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 (Laws, Parker & Johnstone, 1975; Albon, Mitchell & Staines, 1983; Clutton-Brock, Price *et al.*, 1987; 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 (Thomas, 1982; Albon, Mitchell, Huby *et al.*, 1986).

Although the index of body condition we used for the white rhinos is crude, it revealed seasonal declines in body condition related to both population density and reproductive status of females (Fig. 3). This suggests that competition among individuals occurred in the high-density population and affected body condition during the dry season when forage availability is lower.

Conservation implications

Due to extreme levels of poaching, few African rhinos now persist outside of heavily guarded reserves. Most rhino sanctuaries encompass relatively small areas because of the difficulty and expense of providing adequate anti-poaching protection in large, remote regions (Brett, 1990; Nduku & Martin, 1993; Martin & Vigne, 1997). Because rhino populations within these sanctuaries are likely to increase in the absence of poaching until density-dependent factors stabilise population growth (Owen-Smith, 1981), managers may eventually trade off reproduction for safety in following this conservation strategy.

One way around this dilemma is to maintain populations in reserves below ecological carrying capacities (Brooks & Macdonald, 1983; Owen-Smith, 1983). Indeed, management plans for rhinos in South Africa and Namibia have incorporated these ideas based on theoretical relationships between population growth and density (Emslie, 1994; Hall-Martin & Knight, 1994). The long-term data from Matobo Park provide empirical results to quantify such relationships, and demonstrate that density-dependent responses can have profound effects, even within a period of 30 years.

Maintenance of rhino populations in reserves at low densities, however, presents managers with another challenge. Because large-bodied species require large areas, total population sizes of rhinos within smaller reserves are likely to be low, and few will reach numbers recommended for long-term population viability (Gilpin & Soulé, 1986; Foose, 1987). This situation already exists for black rhinos, for which >80% of the remaining individuals survive in populations of fewer than 100 animals (Gakahu, 1993). Under these circumstances, managers may need to consider exchanging individuals among reserves in a metapopulation management approach (Emslie, 1994; Foose, 1987). However, translocation of rhinos is both costly and logistically challenging.

Non-biological factors also will bear on management decisions. Conservationists concerned about populations threatened by poaching may be constrained by limited resources for law enforcement, and may choose to maintain surviving individuals in higher-density populations within safe areas. From a numerical viewpoint, trading off numbers lost to poachers with the decrease in numbers of young recruited, this conservative strategy may be more prudent until resources can be secured to establish additional sanctuaries. However, if management goals are to increase numbers of rhinos and to restock safe areas within their former ranges, then population densities within rhino sanctuaries should be monitored

and managed below the level where body condition affects reproduction.

Acknowledgements

We thank the Zimbabwe Department of National Parks and Wildlife Management for permission to conduct this research. This work was supported by the Frankfurt Zoological Society, and World Wildlife Fund, and the Program in Ecology, Evolution, and Conservation Biology at the University of Nevada. Drs Mike Kock and Mark Atkinson provided invaluable assistance in the field. Many National Parks personnel contributed to this project, and we are especially indebted to Jonas Gumede. Thanks also to Josh Ginsberg for photographic coaching. Steve Jenkins, Lew Oring, Pete Stacey, Gary Haynes, Matt Gompper, and two anonymous reviewers who helped to improve the manuscript.

REFERENCES

- Albon, S. D., Mitchell, B., Huby, B. J. & Brown, D. (1986). Fertility in female red deer (*Cervus elaphus*): the effects of body condition, age, and reproductive status. *J. Zool., Lond.* **209**: 447–460.
- Albon, S. D., Mitchell, B. & Staines, B. W. (1983). Fertility and body weight in female red deer: a density-dependent relationship. *J. Anim. Ecol.* **52**: 969–980.
- Arcese, P., Hando, J. & Campbell, K. (1995). Historical and present-day anti-poaching efforts in Serengeti. In *Serengeti II: dynamics, management, and conservation of an ecosystem*: 506–533. Sinclair, A. R. E., Arcese, P. (Eds). Chicago: University of Chicago Press.
- Belovsky, G. E. (1987). Extinction models and mammalian persistence. In *Viable populations for conservation*: 35–57. Soulé, M. E. (Ed.). Cambridge: Cambridge University Press.
- Berger, J. & Cunningham, C. (1994). *Bison: mating and conservation in small populations*. New York: Columbia University Press.
- Brett, R. A. (1990). The black rhino sanctuaries of Kenya. *Pachyderm* **13**: 31–34.
- Brooks, P. M. & Macdonald, I. A. W. (1983). An ecological case history of the Hluhluwe-Corridor-Umfolozi Game Reserve Complex, Natal, South Africa. In *Management of large mammals in African conservation areas*: 51–78. Owen-Smith, N. (Ed.). Pretoria: HAUM Educational Publ.
- Campbell, K. & Hofel, H. (1995). People and wildlife spatial dynamics and zones of interaction: In *Serengeti II: dynamics, management, and conservation of an ecosystem*: 534–570. Sinclair, A. R. E. & Arcese, P. (Eds). Chicago: University of Chicago Press.
- Clutton-Brock, T. H., Albon, S. D. & Guinness, F. E. (1987). Interactions between population density and maternal characteristics affecting fecundity and juvenile survival in red deer. *J. Anim. Ecol.* **56**: 857–871.
- Clutton-Brock, T. H., Guinness, F. E. & Albon, S. D. (1982). *Red deer: behavior and ecology of two sexes*. Chicago: University of Chicago Press.
- Clutton-Brock, T. H., Price, O. F., Albon, S. D. & Jewell, P. A. (1992). Early development and population fluctuations in Soay sheep. *J. Anim. Ecol.* **61**: 381–396.
- Cole, L. C. (1954). Population consequences of life history phenomena. *Q. Rev. Biol.* **29**: 103–137.
- Conway, A. J. & Goodman, P. S. (1989). Population characteristics and management of black rhinoceros *Diceros bicornis* minor and white rhinoceros *Ceratotherium simum simum* in Ndumu

Game Reserve, South Africa. *Biol. Conserv.* **47**: 109–122.

Eisenberg, J. F. & Seidensticker, J. (1976). Ungulates in southern Asia: a consideration of biomass estimates for selected habitats. *Biol. Conserv.* **10**: 293–308.

Emslie, R. (1994). Regional conservation goals for black rhinos in Namibia/South Africa. In *Proceedings of a symposium on rhinos as game ranch animals*: 50–58. Penzhorn, B. L. & Kriek, N. P. J. (Eds). Onderstepoort: South African Wildlife Veterinary Association.

Fee, T. J. (1987). Long-term management of small rhino populations. *Pachyderm* **9**: 13–15.

Fowler, C. W. (1987). A review of density dependence in populations of large mammals. In *Current Mammalogy*, vol. 1: 401–441. Genoways, H. (Ed.). New York: Plenum Press.

Gadgil, M. & Bossert, W. H. (1970). Life historical consequences of natural selection. *Am. Nat.* **104**: 1–24.

Gakahu, C. G. (1993). African rhinos: current numbers and distributions. In *Proceedings of the international rhino conference*: 160–165. Ryder, O. A. (Ed.). San Diego: Zoological Society of San Diego.

Gilpin, M. E. & Soulé, M. E. (1986). Minimum viable populations: the processes of species extinctions. In *Conservation biology: the science of scarcity and diversity*: 13–34. Soulé, M. E. (Ed.). Sunderland: Sinauer Associates.

Gompper, M. E. & Gittleman, J. L. (1991). Home ranging scaling: intraspecific and comparative trends. *Oecologia* **87**: 343–348.

Green, W. C. H. & Rothstein, A. (1991). Trade-offs between growth and reproduction in female bison. *Oecologia* **86**: 521–527.

Grobler, J. H. & Jones, M. A. (1980). Population statistics and carrying capacities of large ungulates in the Whovi Wild Area, Rhodes Matapos National Park, Zimbabwe Rhodesia. *S. Afr. J. Wildl. Res.* **10**: 38–42.

Hall-Martin, A. J. & Knight, M. H. (1994). Conservation and management of black rhinoceros in Southern African National Parks. In *Proceedings of a symposium on rhinos as game ranch animals*: 11–19. Penzhorn, B. L. & Kriek, N. P. J. (Eds). Onderstepoort: South African Wildlife Veterinary Association.

Harestad, A. S. & Bunnell, R. L. (1979). Home range and body weight – a reevaluation. *Ecology* **60**: 389–402.

Harvey, P. H. & Clutton-Brock, T. H. (1981). Primate home range size and metabolic needs. *Behav. Ecol. Sociobiol.* **8**: 151–155.

Hitchens, P. M. & Anderson, J. L. (1983). Reproductive characteristics and management of the black rhinoceros in the Hluhluwe/Corridor/Umflozi Game Reserve Complex. *S. Afr. J. Wildl. Res.* **13**: 78–85.

Jorgenson, J. T., Festa-Bianchet, M., Lucherini, M. & Wishart, W. D. (1993). Effects of body size, population density, and maternal characteristics on age at first reproduction in bighorn ewes. *Can. J. Zool.* **71**: 2509–2517.

Kahn, M. (1989). *Asian rhinos: an action plan for their conservation*. Gland, Switzerland: IUCN.

Keep, M. E. (1971). Observable criteria for assessing the physical condition of the white rhinoceros *Ceratotherium simum* in the field. *Lammergeyer* **13**: 25–28.

Kie, J. G., Baldwin, J. A. & Evans, C. J. (1996). CALHOME: a home range analysis program. *Wildl. Soc. Bull.* **24**: 342–344.

Klein, D. R. (1968). The introduction, increase and crash of reindeer on St Matthew Island. *J. Wildl. Mgmt* **32**: 350–367.

Laws, R. M. & Parker, I. S. C. (1968). Recent studies on elephant populations in East Africa. *Symp. zool. Soc. Lond.* **21**: 319–217.

Laws, R. M., Parker, I. S. C. & Johnstone, R. C. B. (1975). *Elephants and their habits: the ecology of elephants in North Bunuoro, Uganda*. Oxford: Clarendon Press.

Leader-Williams, N. (1980). Population dynamics and regulation of reindeer introduced into South Georgia. *J. Wildl. Mgmt* **44**: 640–657.

Leader-Williams, N. (1988). Patterns of depletion in a black rhinoceros population in Luangwa Valley, Zambia. *Afr. J. Ecol.* **26**: 181–187.

Martin, E. B. & Vigne, L. (1997). Good news for rhinos. *Swara* **20**: 13–14.

Mattson, D. J., Herrero, S., Wright, R. G. & Pease, C. M. (1996). Science and management of rocky mountain grizzly bears. *Cons. Biol.* **10**: 1013–1025.

Nduku, W. K. & Martin, R. B. (1993). Development of the Zimbabwe national conservation strategy for black rhinoceros. In *Proceedings of the International rhino conference*: 186–195. Ryder, O. A. (Ed.). San Diego: Zoological Society of San Diego.

Owen-Smith, R. N. (1981). The white rhino overpopulation problem and a proposed solution. In *Problems in management of locally abundant wild mammals*: 129–150. Jewell, P. A., Holt, S. & Hart, D. (Eds). New York: Academic Press.

Owen-Smith, R. N. (1983). Dispersal and the dynamics of large herbivores in enclosed areas: Implications for management. In *Management of large mammals in African conservation areas*: 127–140. Owen-Smith, N. (Ed.). Pretoria: HAUM Educational Publ.

Owen-Smith, R. N. (1988). *Megaherbivores: the influence of very large body size on ecology*. Cambridge: Cambridge University Press.

Rachlow, J. L. (1997). *Demography, behavior, and conservation of white rhinos*. PhD dissertation, University of Nevada, Reno, Nevada, USA.

Rachlow, J. L. & Gumede, J. (1994). *The white rhino of Matobo National Park: 1962–1994 population management and individual histories*. Zimbabwe National Parks Research Report.

Reiter, J. & Le Boeuf, B. J. (1991). Life history consequences of variation in age at primiparity in northern elephant seals. *Behav. Ecol. Sociobiol.* **28**: 153–160.

Roth, H. H. (1967). White and black rhinoceros in Rhodesia. *Oryx* **9**: 217–231.

Saether, B.-E. & Haagenrud, H. (1983). Life history of the moose (*Alces alces*): fecundity rates in relation to age and carcass weight. *J. Mamm.* **64**: 226–232.

Saether, B.-E. & Heim, M. (1993). Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. *J. anim. Ecol.* **62**: 482–489.

Skoglund, T. (1989). Natural selection of wild reindeer life history traits by food limitation and predation. *Oikos* **55**: 101–110.

Smith, K., Mbayma, A. & Watkin, J. (1993). Pachyderms and threats increasing in Garamba National Park, Zaire. *Species* **20**: 30–32.

Stearns, S. C. (1992). *The evolution of life histories*. Oxford: Oxford University Press.

Thomas, D. C. (1982). The relationship between fertility and fat reserves of Peary caribou. *Can. J. Zool.* **60**: 597–602.

Western, D. & Vigne, L. (1985). The deteriorating status of African rhinos. *Oryx* **19**: 215–220.

Wilson, V. J. (1969). The large mammals of the Matopos National Park. *Arnoldia* **13**: 1–32.

Worton, B. J. (1989). Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* **70**: 164–168.

Zar, J. H. (1984). *Biostatistical analysis*. 2nd edn. Englewood Cliffs: Prentice-Hall, Inc.