

THE WHITE RHINO OVERPOPULATION PROBLEM
AND A PROPOSED SOLUTION

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I. INTRODUCTION

The white rhino problem in the Umfolozi-Corridor-Hluhluwe Game Reserve Complex in South Africa encapsulates, in perhaps more acute form, the dilemmas of overabundance that have arisen with regard to elephants and hippos within the national park remnants of terrestrial ecosystems elsewhere in Africa. The impact on the vegetation of a grazing megaherbivore, such as the white rhino, is possibly more serious than that of elephants on the woody plant stratum, since it threatens the persistence of the ground cover of grasses and hence of underlying soils. While the southern white rhino was recently removed from the International Union for the Conservation of Nature and Natural Resources (IUCN) Red Data Book, populations of rhinoceros elsewhere in Africa plummet toward extinction. White rhinos are bumbling, inoffensive giants, for which culling by bullet would seem especially repugnant. Much of the Umfolozi Reserve is proclaimed as a wilderness area, and such operations intrude upon the aesthetic qualities for which it was set aside.

In this chapter I will analyze some of the facts of the white rhino problem based on my own research carried out between 1966 and 1971 (Owen-Smith, 1981). I will show the following:

- (1) The intrinsic eruption hypothesis is adequate to account for the overpopulation that has arisen.
- (2) Overpopulation must result from the time lags associated with age structure effects.

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(3) In the absence of barriers dispersal would have alleviated the biomass increase.

(4) Habitat changes involve complex interactions between plant species and topographic soil/nutrient conditions.

(5) In order to simulate former conditions with the least population disruption, removals should be concentrated within "vacuum zones" serving as population sinks.

(6) For current predator/prey theory to be practically relevant to plant/large herbivore systems, competitive relations between plant types and their interaction with external factors such as climatic cycles, fire regimes, and nutrient recycling must be taken into account.

II. WHITE RHINO POPULATION EXPANSION

Regular aerial censuses of the white rhino population within the Umfolozi-Corridor-Hluhluwe Complex have been carried out since 1959. Complete counts have been carried out by helicopter since 1970, while prior to that a fixed-wing aircraft was used. Comparison of results obtained by the two methods in 1970 suggested that the fixed-wing aircraft recorded only 60% of the white rhinos seen in the helicopter censuses. This correction factor must hence be introduced for the earlier counts. Since 1961, the rate of population increase has been slowed by the expanding removal program -- white rhinos being translocated to restock other areas and zoos (Fig. 1). To

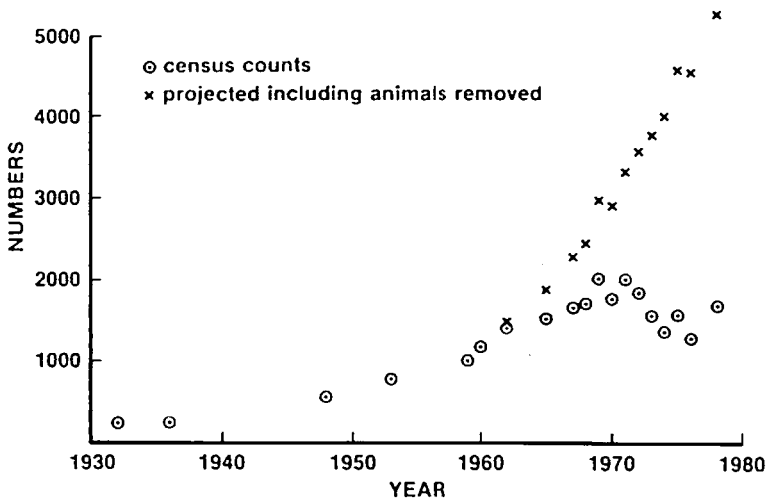


Fig. 1. White rhino population expansion, showing the effect of removals in checking the population increase in the Umfolozi-Corridor-Hluhluwe Game Reserve Complex.

estimate the true rate of population expansion, these animals have to be taken into account as well as their presumed recruitment (crudely estimated as 10%/annum). A log plot of the census data with these corrections reveals that the total white rhino population expanded at a constant rate of 9.5%/annum between 1959 and 1972 (Fig. 2). (Note that this is not the rate of density increase, since densities were controlled by the removal program.) Prior to 1959 the rate of increase was apparently somewhat slower, averaging about 6.3%/annum. It is clear that the entire population could well have arisen from fewer than 100 individuals prior to 1920, when effective conservation measures were first introduced. Rather than showing a density dependent decline, the rate of increase has apparently accelerated with increasing density. However, the high rate of increase exhibited over the period 1962 to 1971 could have been associated with the below-average rainfall that prevailed during this decade since the former distribution center of the subspecies lay in relatively arid savanna in Botswana.

This high rate of increase was the consequence of a high natality rate for so large a species and extremely low mortality rates. The mean intercalving interval averaged 2.4

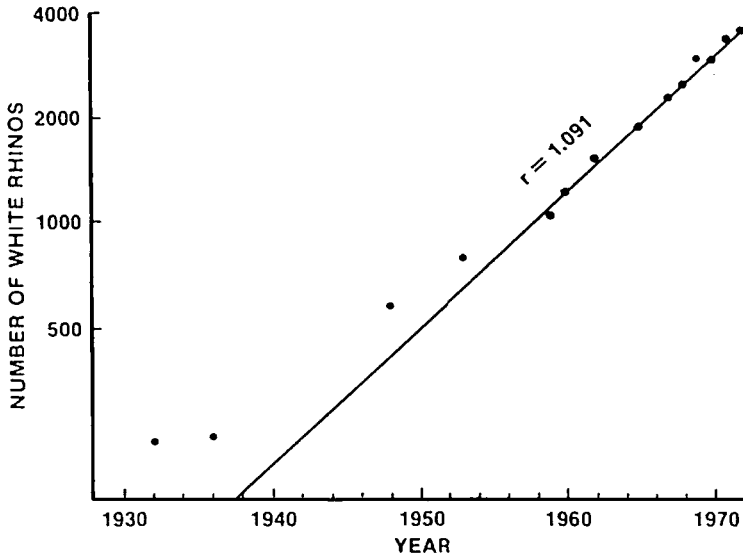


Fig. 2. Logarithmic plot of the projected expansion of the total white rhino population (including animals removed), revealing a constant rate of increase between 1960 and 1971.

years, with a shortest interval of 22 months. Animals introduced into other reserves have exhibited somewhat longer mean calving intervals. The mean annual adult mortality rates observed were 3% for males and 1.5% for females. Total infant losses, including prenatal losses and barren females as well as immediately postnatal mortality, amounted to 8%/annum. Thereafter juvenile mortality averaged 3.5%/annum. The age structure showed a marked preponderance of young animals, with 54% of the reconstructed 1969 population under breeding age (i.e., under 10 years for males and under 7 years for females). Predators, including lions and hyenas occurred in the reserve, but their increase had been recent and, with an abundance of alternative prey, their impact may have been insignificant although it could increase in the future. The population seemed to be increasing at very close to its intrinsic rate (r_{max}).

A major disturbance to the ecosystem was the virtual elimination of nearly all of the larger mammals, apart from the two rhinoceros species, during the anti-tsetse fly campaign carried out in the Umfolozi Reserve prior to 1950. However, during the 1960's large numbers of other ungulates followed by predators recolonized the area from the nearby Hluhluwe Reserve. In 1965 a rhino-proof fence was constructed around three sides of the Umfolozi Reserve, with the Black Umfolozi River providing the fourth boundary adjoining the Corridor between Umfolozi and Hluhluwe. White rhino capture and removal operations were initiated in 1961, but prior to 1967 most of the animals removed were taken from outside the boundaries of the reserve.

Regional breakdown of the rhinos counted in different censuses suggests that the population within the core area increased at a lower rate than that of the overall population. Between 1953 and 1962 the population in the section between the rivers of the Umfolozi Reserve increased by 5.2%/annum, while the population in the overall Complex increased by 7.6%/annum. Over the period 1967 to 1970 the population in the western, high density section of Umfolozi increased by 5.1%/annum, while the overall population increased by 8.6%/annum. This suggests a rate of emigration from high density areas of 3.5%/annum, despite the restrictions of the boundary fence (some of this difference, however, may have been the result of a more mature age structure in the core area). Animals colonizing new areas included subadults of both sexes plus some adult males, but no parous females.

The 1971 helicopter census counted 2,002 white rhinos within the 950-km² area of the Umfolozi-Corridor-Hluhluwe Complex. Of these, 1,529 occurred within the 477-km² area of Umfolozi Game Reserve, at a mean density of 3.2/km². Within the 21-km² area of my western study areas, the mean white rhino density was 5.6/km². There was no indication of any social

disruption to suggest that such densities were abnormally high for the species. Subordinate bulls share the territories of some territorial bulls even in low-density introduced populations, such as that in the Kyle Game Park, Zimbabwe (Condy, 1973). Only a few aged individuals showed any notable deterioration in body conditions during the dry season. However, although annual rainfalls were below average over the study period, the seasonal distribution was altered so that the winter dry periods were shorter than usual. In 1965 a 50% increase in mortality was reported, following the failure of the late summer rains. In 1933 following a severe drought, reportedly over 100 white rhinos died out of an initial population of perhaps 300 animals (Player and Feely, 1960). The most recent census carried out in 1978 indicates a total white rhino population of 1,677, only 16% lower than that present in 1970, despite the subsequent removal of 1,529 animals.

III. HABITAT IMPACT

The Umfolozi Basin is characterized by moderately fertile soils derived from alternating shale and sandstone beds of the Ecca Series of the Karoo sediments. The mean annual rainfall (1963 to 1978) measured at the Mpila camp is 690 mm. The typical vegetation is *Acacia* savanna ("Zululand thornveld"), with medium tall *Themeda triandra* predominating in the climax grasslands.

The changes in the vegetation that were occurring in the Umfolozi Reserve included the following:

- (1) The replacement of climax *Themeda* grasslands by extensive areas of short grass grassland, with creeping species such as *Panicum coloratum*, *Urochloa mossambicensis* and *Sporobolus smutsii* taking over.
- (2) Increasing prominence of areas of denuded and eroding soil.
- (3) The drying up of springs, and reduced flow of both Umfolozi rivers during the dry season.

The total large herbivore biomass within Umfolozi Game Reserve in 1970, based on the helicopter census data with corrections for undercounting of species other than white rhinos, amounted to 82 kg/ha. This is a minimum figure, since 14% more white rhinos were counted the following year (subsequently the numbers of other ungulates have been reduced considerably by culling). This is nearly twice the carrying capacity for biomass estimated on the basis of rainfall from the regression of Coe et al. (1976). However, it is only 40% of the biomass

existing in sections of the Rwenzori National Park, Uganda, with similar rainfall, that were reportedly showing good recovery from a previously overgrazed condition (Field and Laws, 1970). White rhinos comprised about 60% of the total biomass of grazing large herbivores in the Umfolozi Reserve but contributed only about 45% to total metabolic demands (based on body mass^{3/4}). However, as relatively inefficient digesters of forage, offtake of herbage by white rhinos is likely to be somewhat higher than is indicated by simple metabolic relationships. White rhinos are probably responsible for at least half of the total consumption of grass attributed to large herbivores.

White rhinos are capable of using both tall and short grasses, and with their lip plucking action can graze as close as within 2.5 cm of ground level. When subjected to repeated defoliation, erect tufted grasses such as *Themeda triandra* are unable to maintain enough leaf area to replenish root reserves, and eventually plants lose vigor and die. They are replaced by recumbent species which suffer proportionately less reduction in leaf area and which are also better adapted to exploit raised soil nutrient levels. Short grass grasslands are favored by white rhinos for grazing and become closely cropped quite early in the dry season. By promoting an increase in short grasses, which are relatively protein-rich, white rhinos increase the favorability of their habitat, considered in terms of the nutrient flow to their own population. As nonruminants, they can tolerate a high content of structural tissues in their diets, thereby increasing the rates of turnover and nutrient return from fibrous plant parts into the soil for subsequent plant growth. A fiber tolerant grazer such as a white rhino could exert a less detrimental effect on grassland vigor than a species such as impala which exhibits a selective removal of green leaves alone. McNaughton (1979) has shown for the Serengeti grasslands that aboveground production under a moderate grazing regime can be double that which occurs in an ungrazed state; some stimulation of production occurred even at levels of consumption amounting to 70% of the production measured under ungrazed conditions. At Umfolozi the invasion of grasslands by unpalatable species such as *Cymbopogon plurinodis* or *Bothriochloa insculpta* was not evident, possibly because of the intolerance of these species to high soil nutrient levels.

In terms of the production of animal biomass per unit of land area, the white rhino represents the most productive single species of large herbivore occurring in the Umfolozi ecosystem. It may well be that it is only in mixed species communities, including megaherbivores, that the full productive potential of habitats in terms of animal protein can be attained because of the ability of such species to make use of a much greater fraction of the vegetation than is the case for smaller herbivores. To some degree megaherbivores could possibly replace

fire in their effects on nutrient recycling, without the danger of nutrient losses that occur from the pulsed releases due to fire. Such acceleration of nutrient cycling rates could have a major effect on secondary productivity, not only of the mega-herbivore population itself, but also of the many other herbivores within the ecosystem (see Botkin et al., 1981).

However, white rhinos are dependent upon reserves of tall *Themeda* grassland to carry them through the late dry season. Furthermore, soils in short grass areas are exposed to the eroding influences of wind and early season thunderstorms. Pedestalling and reduced water infiltration result, which soon lead to reduced grass cover and rapid expansion of erosion gullies. At the same time, the short grass grasslands do not sustain fires and are thus readily invaded by woody plant seedlings, leading toward bush encroachment and reduced grass cover.

The rapidity with which the vegetation deteriorated over the short duration of my study was alarming. However, 1962 to 1971 was a decade of below-average rainfall, and thus some of the change was probably climatically induced. The situation was exacerbated by an influx of wildebeest and zebra into the region. Changes in the vegetation were spatially highly variable. Large areas of climax grassland on hillslopes remained relatively untouched by grazing animals. The western section, which sustained some of the highest white rhino grazing pressures, retained a mosaic of tall and short grassland areas with a good basal cover, probably aided by gentle relief and dolerite-influenced soils. Many of the areas showing the worst denudation were on deep alluvial soils which had been covered by thickets prior to the bush clearing which took place during the tsetse control operations in the late 1940's. These areas seemed to be reverting inexorably to their former vegetational state, though heavy grazing pressure was probably a factor promoting this trend. Much of the variability in consumption could be correlated with underlying soil fertility.

During the wet decade of the 1970's these trends were reversed, helped by extensive removals of grazing ungulates of all species. The white rhino removal quota was accordingly greatly reduced. However, rainfall was well below the average during the seasons of 1978-1979 and 1979-1980. Considerable alarm has once more been expressed over the rapidly spreading desertification of the area, and large-scale removals of all large herbivores, including white rhinos, are being carried out.

The margin between increased production and overutilization seems to be a delicate one. Simultaneous trends of increasing white rhino density and declining grass cover cannot persist for

long. A paradoxical situation exists in that the white rhino population has clearly not yet attained the carrying capacity of the environment in terms of the logistic model of population growth, while on the basis of vegetational changes the capacity of the vegetation to support even the existing white rhino population on a long-term basis has apparently been exceeded.

IV. DEMOGRAPHIC MODELS

Riney (1964) described the pattern of the eruptive fluctuations observed for introduced populations of large herbivores in New Zealand and suggested that they could arise in any situation where a large discrepancy was created between the potential carrying capacity of the vegetation and current population levels. Basically a time lag in population response results in a period of overshoot of the carrying capacity, initiating a downward trend in the capacity of the vegetation to support the herbivores. Eventually the herbivore population stabilizes at a rather lower density in a somewhat degraded habitat.

Caughley (1976a, 1977) developed analytical models of trophic level interactions between plants and herbivores. In these models both populations undergo a series of oscillations before settling down to equilibrium biomasses which are lower than those attained in the early phase. It is important to note that the effective plant biomass is that of potentially edible plant material available for consumption. Any increase in the productivity of vegetation in terms of edible material, such as a shift from climax to short grasses, would increase the equilibrium biomass of the herbivore population, while leaving that of the plant component unchanged. If the standing crop of edible plant material is reduced by consumption to less than half of that present under ungrazed conditions, persistent oscillations develop. Such a situation could be created by the delayed action of compensatory responses within the herbivore population. As stated by May (1976), sustained oscillations also result when time delays in the regulatory mechanism of the consumer population are long compared with the characteristic response time of the system. This seems to apply to the white rhino/grasslands relationship. A low intrinsic rate of increase of the animal population, while conferring the advantage that the population can maintain steady values over short-term environmental fluctuations, presents the disadvantage of slow recovery from large disturbances (May, 1976).

Such theoretical analyses bode ill for the likely trajectories of the white rhino/grassland interaction but do not necessarily chart out the actual pathway that will be followed in a real ecosystem where relationships are more complex. Thus it will be necessary to focus more specifically on the details of the white rhino population. Table I presents the detailed age structure of a hypothetical population increasing at a constant rate of 9.5%/annum with a stable age distribution. Age-specific parameters are the same as those observed in the real white rhino population. The proportion of immature individuals (subadults plus calves) in this population is a little higher than that observed in the real population (57% versus 54%). This discrepancy could be explained on the basis that the real population has not yet attained a stable age distribution, since its rate of increase was lower prior to 1960. The model population demonstrates, in only slightly exaggerated form, the extreme preponderance of young animals that characterizes an expanding population. Even if all reproduction was to cease instantly (say by 100% infant mortality), the size of the breeding segment of the population would continue to increase at 9.5%/annum for a further seven years. It is the adult segment that makes up most of the biomass, and thus exerts the greatest pressure on food resources. There is no way in which any realistic adjustment in breeding rates or infant mortality could act quickly enough to avoid a period of overshoot of carrying capacity; the severity of this overshoot will be greater the longer the period over which the population has been increasing at its intrinsic rate and the later the age of sexual maturity. It is for this reason that a laissez faire management policy towards the white rhino population cannot be advocated.

There is only one way whereby the expansion of the breeding segment could be halted immediately: by the sudden disappearance from the population, whether by emigration or culling, of the excess number of subadults just prior to their attainment of sexual maturity. In Table II, population A represents an example of a population with similar attributes to those of the real population where stability has been achieved solely by the emigration of surplus subadults at six years of age. The only other change in population parameters that has been allowed is a reduction in the specific natality per adult female to 0.33 (intercalving interval = three years), which is a likely result of the shift in the age structure of breeding females toward a higher proportion of older animals. This is based on the observation that the study population at Madlozi in the western high-density section of Umfolozi exhibited a mean natality rate over the four years observation period of 0.34 calves per adult female per year, while other study

TABLE I. Composition of Hypothetical Population Increasing at a Constant Rate of 9.5%/Annum, after Attainment of Stable Age Distribution^a

Age range	Number of individuals	Age range	Number of individuals	Age range	Number of individuals
0- 1	200	15-16	39	30-31	8
1- 2	177	16-17	35	31-32	7
2- 3	157	17-18	32	32-33	7
3- 4	140	18-19	29	33-34	6
4- 5	126	19-20	26	34-35	5
5- 6	113	20-21	23	35-36	5
6- 7	101	21-22	21	36-37	4
7- 8	91	22-23	19	37-38	4
8- 9	82	23-24	17	38-39	4
9-10	74	24-25	15	39-40	3
10-11	67	25-26	14	40-41	3
11-12	60	26-27	13	41-42	3
12-13	54	27-28	11	42-43	2
13-14	49	28-29	10	43-44	2
14-15	44	29-30	9	44-45	2

	Number	Percentage
Adult males (over 9 years)	363	19.0%
Adult females (over 7 years)	449	23.5%
Subadults (males 2.5 to 9 years; females 2.5 to 7 years)	644	33.7%
Calves (0 to 2.5 years)	455	23.8%
Total	1911	

Mortality of cohort (adults + subadults over 3 years)
= 26 or 1.8%

Specific natality: Fertile cohort = $\frac{202}{556} = .363$

Parous cohort = $\frac{202}{449} = .450$

Postparous cohort = $\frac{110}{357} = .308$

Proportion of individuals in age range 0 to 1 year = 10.4%

^aAssumptions: (1) size of total population = 1918 individuals; (2) age-specific sex ratios = 100:100; (3) mortality rates as follows -- juveniles (0 to 3 years) = 3.5%/annum, subadults (3 to 7 years) = 2%/annum, adults = 1.5%/annum, plus terminal mortality of all individuals reaching 45 years of age.

TABLE II. Composition of Two Hypothetical Stable Populations^a

Age range	Number of individuals		Age range	Number of individuals		Age range	Number of individuals	
	A	B		A	B		A	B
0- 1	155	75	15-16	28	30	30-31	23	20
1- 2	150	67	16-17	28	30	31-32	22	19
2- 3	145	60	17-18	27	29	32-33	22	18
3- 4	141	54	18-19	27	28	33-34	22	18
4- 5	137	49	19-20	27	27	34-35	21	17
5- 6	133	44	20-21	26	26	35-36	21	17
6- 7	32	40	21-22	26	26	36-37	21	16
7- 8	32	38	22-23	26	25	37-38	21	16
8- 9	31	37	23-24	25	24	38-39	20	15
9-10	31	36	24-25	25	23	39-40	20	15
10-11	30	35	25-26	24	23	40-41	20	15
11-12	30	34	26-27	24	22	41-42	19	14
12-13	29	33	27-28	24	21	42-43	19	14
13-14	29	32	28-29	23	21	43-44	19	13
14-15	29	31	29-30	23	20	44-45	19	13
			<u>Number</u>		<u>Percentage</u>			
			<u>A</u>	<u>B</u>	<u>A</u>	<u>B</u>		
Adult males (over 9 years)			435	431	23.6%	32.0%		
Adult females (over 7 years)			466	469	25.3%	34.9%		
Subadults (males 3 to 9 years, females 3 to 7 years)			495	243	26.8%	18.1%		
Calves (under 3 years)			<u>450</u>	<u>202</u>	24.4%	15.0%		
			Total					
			1846	1345				
Mortality of cohort (adults + immatures over 3 years)			43	63	3.3%	5.5%		
Proportion of individuals in age range (0 to 1 year)			155	75	8.4%	5.6%		

^aAssumptions: Population A -- as in Table I, with specific natality per postparous females of .33/annum, stability achieved by emigration or death of surplus subadults promptly at age 6; Population B -- specific natality = .25/postparous female/annum, first parturition at age 8, postnatal mortality (0 to 6 months) = 40%, immature mortality to age 6 = 10%/annum, subadult mortality to age 9 = 4%/annum, adult mortality = 3%/annum. Size of adult cohort in both populations adjusted to 900.

populations exhibited somewhat higher natality rates. To achieve equilibrium, the removal of 75% of the subadults reaching six years of age is required. However, if the process took the form of emigration spread evenly over the entire subadult period, then a specific emigration rate of only 20% per individual per annum would suffice. In terms of the overall population, the emigration rate amounts to 5.5% per individual per annum. This is only 1.5 times greater than the rate of dispersal that was estimated to be occurring from the population core between 1967 and 1970, despite the existence of the boundary fence at that time. (The proportion of subadults present in the model population A is, however, 17% lower than that estimated for the real 1969 population.) Thus it is quite feasible that the expanding population of Table I could be transformed smoothly into a stable population as in Table II entirely by a big enough increase in the dispersal rate.

Interestingly the mean adult mortality of population A in Table II is twice as great as that of the expanding population of Table I, though age-specific mortality rates remain the same in both. This difference is due to the much greater proportion of animals reaching the age of terminal senescence in population A (Table II). In the real population there should be very few individuals dying of old age, since such individuals would have been born during the 1920's, when the total population numbered only 200 to 300 individuals. Assuming that only 25% of the individuals born die of old age, it is projected that only 5 rhinos per annum would have died of old age in the entire population of 2,000 individuals in 1970 (assuming that none of these old individuals had been caught and removed elsewhere).

In the absence of opportunities for dispersal, equilibrium would have to come about through appropriate changes in fecundity and mortality rates. Population B in Table II exemplifies the possible characteristics of such a stable population:

- (1) The mean intercalving interval is increased to 4 years.
- (2) Age at first calving is retarded to 8 years.
- (3) Infant mortality is increased to 40%.
- (4) Juvenile and subadult mortality is increased to 10%/annum.
- (5) Adult mortality is increased to 3%/annum.

In this population only 33% of the animals are under breeding age. Such attributes would be expected only for a white rhino population living in poor condition in a degraded habitat. If all opportunities for dispersal are blocked, this is the type of population that must eventually result.

It is noteworthy that the black rhino in the neighboring Hluhluwe Reserve exhibited all the characteristics of such a population. A population estimated to number about 300 animals in 1961 had declined to 199 by 1972. Compared with the smaller but expanding population of black rhinos in the Umfolozi Reserve, the mean calving interval had lengthened from 2.3 to 2.7 years, infant mortality had increased from 9% to 63% (partly due to hyena predation), age at first calving had been retarded from 6.5 to 12 years, and mean adult mortality had risen to 5%/annum (P. M. Hitchins, unpublished data). The Hluhluwe black rhinos occurred at a mean density of 0.9/km² (compared with 3.2/km² for the Umfolozi white rhinos). Paradoxically, while both bush encroachment and grass disappearance were the major problems of habitat management in the Complex, the browsing species of rhinoceros was declining in numbers while the grazing species was still increasing at three times the density and six times the biomass.

V. MANAGEMENT SOLUTIONS

Management steps were urgently needed in 1970 to achieve the following objectives, given in order of priority:

(1) Reduction of the overall biomass of white rhinos and other grazing ungulates to a level which would halt further deterioration of the habitat.

(2) Transformation of the characteristics of the white rhino population to that of an equilibrium rather than an expanding population.

(3) Stabilization of the white rhino population at a level in balance with habitat resources, with the least disruption of natural population processes.

Table III outlines the removal program that I proposed in 1972 aimed at reducing white rhino biomass by one third and at the same time reducing the high proportion of immature animals in the population. The starting point was the population composition estimated for 1969, with account taken of the animals that were known to have been removed between 1969 and August 1971. The program required the capture and relocation of a total of 1,258 white rhinos over the four year period 1971 to 1975.

Independently, the need for a massive removal campaign had already been accepted by the Natal Parks Board. The removal quota was stepped up from 151 animals during the calendar year of 1971 to 448 in 1972, 293 in 1973, and 243 in 1974 (Brooks, 1974, and personal communication). In all, 1,093 white rhinos were captured over the four year period between mid-1971 and mid-1975, 13% fewer than I had proposed. However, the population remaining in September 1975 (extrapolated from a count covering Umfolozi only), numbered some 30% more animals than I had projected; that is, a population reduction of only 24% had been achieved. This suggests that the true population size is some 10% greater than is estimated even by helicopter census. The age structure recorded by Brooks in 1974 comprised 55% "adults" over about six years of age, which is the same as that which I had projected for the 1975 population. Subsequently with the return of high rainfall conditions the annual removal quota was reduced to 89 animals in 1975, 53 in 1976, 20 in 1977, and 38 in 1978 (P. H. Brooks, personal communication).

One of the problems which arose was a marked preponderance of males in the population; the sex ratio recorded in 1974 by Brooks, based on a sample of 563 animals, was 157 males: 100 females. This could not be explained by the small excess of females among the animals removed between 1967 and 1974 (93 males:100 females, $N = 1,475$). It must have been due to the male-biased sex ratio of calves born into the population that I had noted during my study period. Recent removals were aimed mainly at correcting this sex imbalance. Despite the disruptions caused by the removal operations and the male-biased sex ratio, the white rhino population has continued to expand at a rate of 6.5%/annum over the period 1970 to 1978 (including animals removed).

Notwithstanding these efforts the problem of ultimately stabilizing the white rhino numbers in the Complex still remains. Caughley (1977) discusses possible strategies for the control of populations based on a simple logistic model. If the basic assumption of a linear relationship between the rate of population increase and population density is valid, then culling of a proportion equal to half the intrinsic rate of increase would stabilize the population at half the density

that it would have attained in the absence of such removals (assuming no suppression of food production). Population oscillations would also be dampened, the effect being similar to that of adding a predator trophic level. In the case of the white rhino population this would require the removal of about 5% of the total population, or about 75 animals per annum from a total population of 1,500, if culling were unselective with regard to age and sex. This figure could be reduced by up to one third if removals were concentrated on subadults. With this culling strategy, the aim would be to reduce the rate of increase, and hence the degree of overshoot of their carrying capacity, thus suppressing or at least dampening oscillations in population size. The population would be allowed to move towards an equilibrium density similar to that which it would have attained in the presence of dispersal opportunities with whatever additional changes in natality and mortality rates that might be necessary.

The final problem to be considered is how best to carry out this culling. The ideal solution would perhaps be simply to remove the boundary fence, and to allow surplus animals to disperse into surrounding country where they could be harvested by the local people. Such a step seems to be politically impractical. The best alternative is to create dispersal sinks within the game reserve capable of absorbing the excess animals. This would entail creating vacuum zones, ideally situated near boundaries, from which all white rhinos that had settled there would be captured and removed at suitable intervals. The aim would be to create opportunities for dispersal processes to operate. Success would be dependent upon the adequacy of dispersal rates and also upon the size, situation, and habitat conditions offered by the vacuum zones. Culling methods would have to be carefully designed so as not to deter movements into vacuum zones. A possible strategy would be the complete removal of all resident rhinos from these zones at infrequent intervals, with several years elapsing between successive operations in the same area. It may still prove necessary to carry out some culling within the core zone to halt excessive habitat deterioration, but at least the extent of the interference with the population within this area would be minimized. A vacuum zone culling policy is appropriate, especially for those species for which dispersal appears to be the main process by which population size is regulated. This includes elephants as well as white rhinos and perhaps a range of other species as well. Its effectiveness remains to be tested in practice.

TABLE III. Suggested Removal Program to Reduce Biomass by One Third and Stabilize Population^a

Year	Removals				Age structure of population										
	Adult		Immature	Juvenile	Total	0-1	1-2	2-3	3-4	4-5	5-6	6-7	Adult+Subadult		Total
	♂	♀											♂	♀	
Early 1969															
Population						185	164	145	135	121	109	98	477	492	1926
Removed	13	36	109		158			32	29	26	22		13	36	
Remaining						185	164	113	106	95	87	98	464	456	
August 1970															
Population						207	179	159	110	103	92	84	498	500	1932
Removed	4	13	141		158			48	34	31	28		4	13	
Remaining						207	179	111	76	72	64	84	494	487	
August 1971															
Population						211	200	174	107	74	70	62	520	523	1941
Removed	26	49	183		258			74	46	32	30		26	49	
Remaining						211	200	100	61	42	40	62	494	474	
August 1972															
Population						196	204	193	97	59	41	39	509	499	1837
Removed	80	80	160	80	400	40	40	79	40	24	17		80	80	
Remaining						156	164	114	57	35	24	39	429	419	
August 1973															
Population						166	151	159	111	55	34	23	435	434	1568
Removed	80	80	160	80	400	41	39	71	49	24	16		80	80	
Remaining						125	112	88	62	31	18	23	355	354	

VI. DISCUSSION

The problem of the white rhino highlights many of the issues raised with regard to overabundant populations of large herbivores within national park ecosystems. Caughley (1976b) outlined various hypotheses that have been advanced to account for overpopulations of elephants and advanced a "stable limit cycle" hypothesis as a general explanation. However, this explanation is not applicable to the white rhino situation, where the periodicity of response in the vegetation is very much shorter than that of the animal population. The "intrinsic eruption" hypothesis as outlined originally by Riney (1964) is quite adequate to explain the development of an overexploitation phase. Time delays in population response are inevitable because of age structure effects, and the degree of overshoot will be accentuated by the extent to which the population was initially depressed below carrying capacity. Time lags will be especially severe for megaherbivores because of their several-year delay between birth and attainment of breeding age. Dispersal is the only population process sufficiently sensitive in its operation to dampen oscillations of herbivore numbers and vegetation biomass. Thus any hindrances to dispersal, in the form of barrier fences or merely fences surrounding settlements, can exaggerate and sustain the period of over-exploitation of the vegetation with potentially severe consequences for persistence of the ecosystem. I consider that this explanation is also quite adequate to account for elephant overpopulations; the common factor is initial population depression, due in the case of elephants to the ivory hunting which took place all over Africa around the turn of the century (see Spinage, 1973).

However, while dispersal may regulate local population densities, it cannot control overall population expansion, unless compensatory mortality occurs elsewhere. It seems that regions of favorable habitat generate a population surplus, which moves out to colonize surrounding areas of more marginal but thinly settled habitat. Presumably individuals may either remain in saturated habitats, where as subordinates they are unlikely to replace themselves genetically; or they may move out in the expectation that more favorable conditions for breeding might occur elsewhere. If it were not for the dynamic nature of environmental conditions, such movements would be genetically suicidal. Marginal habitats may thus serve as population sinks (Lidicker, 1975), absorbing the surplus animals produced in more productive habitats. Local environmental catastrophes such as drought could open up a

sufficient supply of favorable habitats for colonization so as to maintain the dispersal propensity, particularly for species which are capable of depressing the production of their own food resources in saturated habitats. If this account is correct, it implies that where free dispersal is inhibited, densities could rise to higher levels than those that would have prevailed under pristine conditions.

A policy of vacuum zone culling would seem to offer a number of advantages over alternative forms of management, whether by indiscriminate culling or by nonintervention:

(1) There would be no direct interference with the population in the core area where natural ecological processes could continue to operate.

(2) The animals dispersing into vacuum zones would presumably be the surplus individuals as determined by habitat conditions and social relationships with the core area, so that processes of natural selection could still operate.

(3) At the same time the ecosystem would be buffered against extreme fluctuations in herbivore density and vegetation resources. Such fluctuations would be likely to be exaggerated by the existence of a boundary, in contrast to the unrestricted conditions of the past, with the concurrent risk that critical thresholds for ecosystem persistence could be crossed.

(4) Within the core zone, wilderness qualities could remain untarnished by the roads or vehicle tracks that would otherwise be created by culling operations.

(5) If either live animals or their products -- such as meat, horns, or hides -- were of economic value, the vacuum zones could be conveniently situated near boundaries to facilitate the removal of these products for processing.

(6) A gradient in animal densities between the core area and the vacuum zones would be created, allowing greater opportunity to gain scientific understanding of the interactions between herbivores and vegetation -- a subject about which we are sorely lacking in knowledge.

(7) The creation of vacuum zones would enhance spatial heterogeneity in the vegetation, while at the same time population levels would still be allowed to fluctuate in response to changing climatic patterns. In this way reservoir areas would be created for those species of plants and animals that are vulnerable under overgrazed conditions on the one hand, and for those that depend on periodic overgrazing for their persistence on the other. In consequence both species diversity and ecosystem resilience would be increased (see Holling, 1973; Walker et al., in press).

The crucial unanswered questions concern the stability of the plant/soil system under the impact of intense grazing by white rhinos. It is easy to model the transformation of a white rhino population to a stable condition; but this is dependent on an assumption that a progressively worsening trend in the rate of replacement of its food resource is not initiated. While grazing may stimulate the production of leaf tissue, what is not observed is the compensatory reduction in root biomass that may be occurring. Smaller roots may leave plants vulnerable to mortality during periods of drought, and create openings in the soil that allow unpalatable plants to invade. Such trends could easily be self-reinforcing because of further consequences such as reduced fire intensity or increased soil erosion. Walker et al. (in press) describe cases where disturbing pressures can move a savanna community to an alternative stable state; for example the transformation by cattle overgrazing of an open savanna into a dense thicket with little grass cover. Exactly this type of change seems to have occurred in the Hluhluwe Game Reserve. Extensive areas, which in photographs taken during the 1930's appear as open grassland thronged by buffalo and zebra, now exist as thickets of woody shrubs such as *Acacia karoo* and *Euclea divinorum* occupied mainly by nyala and impala browsers which did not originally occur in the reserve. Apparently, this change was made possible by the absence of predators and led to the development of severe overgrazing before game culling was introduced as a policy during the late 1950's. Active management of both animal populations and fire has yet been unable to reverse this change.

So far the Umfolozi Reserve has undergone much less habitat change. Is this due to its lower rainfall, the less selective grazing impact of the white rhino, the occurrence there of browsers able to suppress woody plant invasion in its early stages, different soil conditions less favorable to woody plant encroachment, or is it just a matter of time?

Simple population models are hopelessly inadequate if theoretical predictions are to be relied upon by the managers who have to implement the policy. What is needed are total ecosystem models, comprising a set of detailed process models which are capable of being interlinked to form a functioning whole. These should incorporate not only plant/herbivore interactions but also competitive relationships between different plant types, their interactions with external conditions such as fire regimes, nutrient recycling, and soil movement, and the influences of climatic fluctuations and spatial variability. This is the challenge.

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