Translocation Strategies for the Conservation of the Black Rhinoceros (*Diceros bicornis*)

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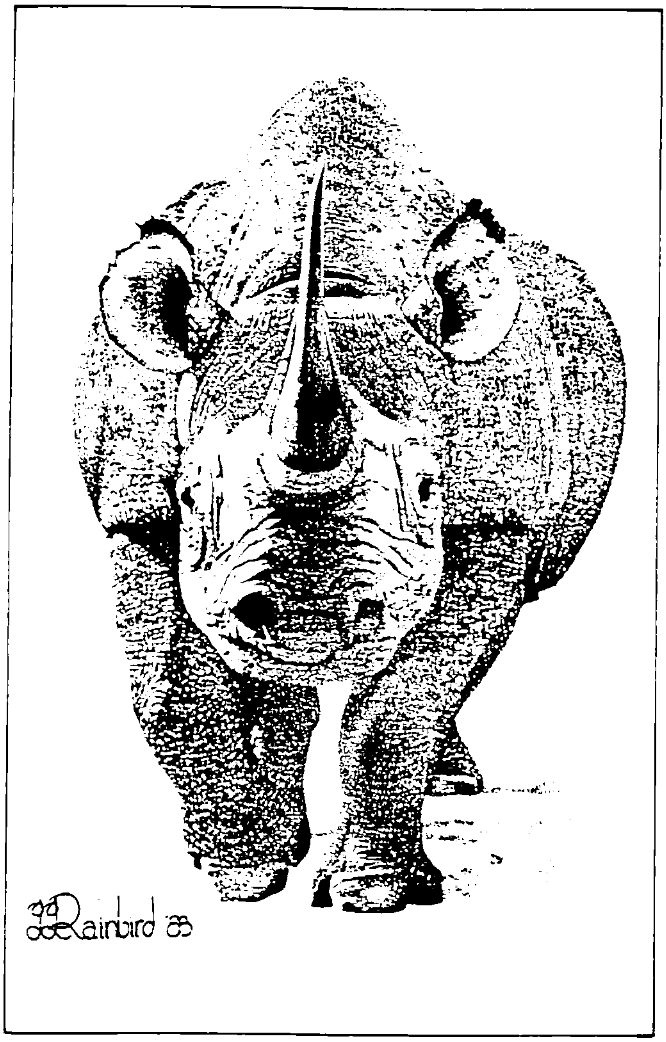

"Just because some of us can read and write and do a little math, that doesn't mean we deserve to conquer the Universe."

(K. Vonnegut, Hocus Pocus)

INTRODUCTION

The black rhinoceros *Diceros bicornis* is endemic to Africa and was once widely distributed south of the Sahara Desert. Its present distribution has been reduced and fragmented due to habitat destruction and poaching by humans. The black rhinoceros is now listed as an endangered species by the IUCN (1990) and as vulnerable species in the South African Red Data Book (Smithers, 1986). Some people even consider the black rhinoceros to be one of the most critically endangered species on earth (Brooks, 1989).

The dramatic decrease of black rhino numbers by 95 per cent over the last 20 years has been reviewed by Brooks (1989). Preservation of the species for the future appears bleak. The estimated population of 65 000 animals in 1970 has shrunk to fewer than 3 500. In many countries, *e.g.* Angola, Somalia and Botswana, black rhinos are now extinct or close to extinction. Only Zimbabwe, South Africa, Namibia, Tanzania, Kenya and Zambia have black rhino populations greater than 100 animals, but most of these populations are facing heavy poaching pressure and are decreasing.

South Africa and Namibia alone have populations which have increased over the last years due to effective anti-poaching measures (Brooks, 1989). For instance, all of

South Africa's black rhinos are kept in fenced and patrolled nature reserves. The total population of South Africa and Namibia comprises about 1 250 animals representing today over a third of the earth's remaining free-living black rhinos.

The species *Diceros bicornis* is divided into four subspecies of which three occur in South Africa (Brooks, 1989). There are about 735 of *D. b. minor*, 495 *D. b. bicornis* (including the Namibian population) and 21 of *D. b. michaeli*. Although there are some doubts about the justification of the subspecies classification (Prof. E. H. Harley, pers. comm.) these populations are managed separately to preserve their presumed genetic distinctiveness.

Since the species is highly threatened by extinction, a conservation management plan for southern Africa (South Africa and Namibia) was recently developed to increase its chances for survival (Brooks, 1989). The plan concerns the management of existing populations, the establishment of new populations and captive breeding programmes.

One of the plan's goals is to develop genetically viable populations of at least 2 000 animals of the subspecies *D. b. minor* and *D. b. bicornis* and to increase that of *D. b. michaeli* to 100 as rapidly as possible.

To achieve these goals, it is necessary to maximize the overall population growth of each subspecies by translocating animals from areas where density-dependent effects appear to be reducing the growth, to other areas where higher population growth rates can be obtained. This includes the establishment of new populations, as well as the supportive stocking of small, existing populations.

But what are the numbers, the ages and the sex ratio of the animals which should be translocated to maximize the growth of the entire population?

To answer this question, the aim of this project is to develop a mathematical model that represents the population dynamics of black rhinoceros. The model is applied to a single population to test different harvesting strategies. The maximum sustainable yield (MSY) of each of these strategies is assessed, as well as the population density level with the highest productivity. The reason for studying the MSY conditions of the model are as follows. Firstly, at MSY, the harvested population will generate the maximum number of animals for translocation. Secondly, the obtained MSY value for each harvesting strategy is used to compare the efficiency of each strategy.

In the next step, the model is extended to a metapopulation model consisting of a source population and a sink population. Animals are removed from the source population according to different harvesting strategies, and translocated to the sink population. With this model, simulations are performed to test if the strategy which yields the highest MSY, also maximizes the growth rate of the metapopulation.

METHODS

Available data

The objective of the model is to simulate black rhino numbers, so that different translocation policies can be tested. The literature is reviewed to find data on characteristics of black rhino and to determine the most important factors which influence the dynamics of a rhino population.

Age and population structure

Black rhinos may live for as long as 60 years, although 45 is the accepted average (Balfour and Balfour, 1991). In field studies, rhinos are classified into different age groups. These are:

- 0-1 year old : calves
- 1-2 year old : yearlings

- 2-8 year old : subadults

- ≥ 8 year old : adults.

Calves and yearlings stay together with their mothers. At 2-4 years of age, the young animals are rejected by the cow, either during the cow's next pregnancy or at the birth of the new calf (Moss, 1976).

Subadult animals are not fully grown. The growth continues until the animals are 7-8 years old. At this age they also start establishing their own home ranges.

Reproduction

Black rhinos breed throughout the year, and a single calf is born after a gestation period of about 15 months (Stuart and Stuart, 1988). Goddard (1967) found that black rhinos give birth in the Umfolozi Game Reserve as early as 6 years old. Hitchins and Anderson (1983) reported the first births at an average age of about 10.5 years in a high-density area.

Females have a calf about every three years, but it is assumed that rhinos should be able to produce every 22 months. Calving interval statistics from a variety of areas show a minimum interval between calving of 26 months, equivalent to 0.46 calves per cow/per year, and a maximum of 63 months, equivalent to 0.19 calves per cow/per year (Hitchins and Anderson 1983).

Mortality

Dead rhinos can be aged by examining of skull and tooth anatomy. Goddard (1970) gives a theoretical life table for black rhinos in the Tsavo National Park.

Due to nutritional stress, the mortality in the first three years of life is high, especially after weaning. Annual mortality in the first and second year was estimated to be 16% for a population that was assumed to be stable (Goddard, 1970), but higher mortality rates are possible (Hitchins and Anderson, 1983).

For animals 6-10 years old, there is high mortality due to fighting when they are trying to establish their home ranges for the first time.

Observations indicate a mean annual mortality value for 5-25 years old animals of about 10% (Goddard 1970).

In an extreme drought, the mortality rates rise from age 25 onwards and again after age 35, respectively (P. Goodman, pers. comm.).

There is no information in the literature on mortality rates relating to changing environmental conditions.

Predation

Predation has no impact on the survival of subadults and adults, but calves and yearlings are regular victims of lions *Panthera leo* and spotted hyaenas *Crocuta crocuta* (Hitchinson and Anderson, 1983). In particular, hyaenas play a major role in black rhino calf mortality (Kruuk, 1972).

Sex ratio

In several field studies, the adult sex ratio was even or did not differ significantly from parity (Frame, 1980; Hitchins and Anderson, 1983; Conway and Goodman, 1988).

The model

Since the the interactions of black rhinos with their environment and with other species are not well understood, a single-species model is used here which neglects most of the system interactions. It attempts to include as much available demographic data as possible. When there are insufficient data on black rhino population characteristics in the published literature (Goddard, 1967, 1970; Hitchins, 1978; Hitchins and Anderson, 1983) then empirically supported generalizations for large mammals are used (Eberhardt, 1977; Fowler, 1981; Laws, 1981). Furthermore, information and interpolations from other population models (Caughley 1976, 1981; Owen-Smith, 1983; Hearne and Swart, 1991; Starfield and Bleloch, 1991) are considered for the construction of the model.

Structure of the model

A population consists of individuals of both sexes. To keep the model flexible for further investigations at different sex ratios in translocated animals, populations are differentiated into the male and female components.

The model divides the female and the male components into distinct one-year age classes. Since the accepted average age at death is 45 (Balfour and Balfour, 1991), the number of age classes per sector is limited to 45.

The following notation is used:

$$P(t) = F(t) + M(t)$$

with $P(t)$ is the population vector at the year t, $F(t)$ is the female population vector and $M(t)$ is the male population vector.

The vector $F(t)$ and $M(t)$, respectively, consists of i age classes, *i.e.* $F_i(t), M_i(t)$; $i = 1,..,45$.

The model is deterministic, and it is assumed that the values attained in each age class (F_i, M_i) represent the numbers of individuals on average. The population that the model deals with is large enough so that, for example, demographic stochasticity, *e.g.* the chance variation in individual birth and death, can be ignored.

Density

The population dynamics of black rhinoceros are assumed to be density-dependent like that of other large mammals

(Fowler *et al.*, 1980). Density-dependent effects are related to the exploitation of the limiting resources.

To measure the impact of a population on resources, a population is converted into large stock units (Hearne and Swart, 1991). One large stock unit is equivalent to one adult in terms of its resource requirements. Calves (F_1, M_1) and yearlings (F_2, M_2) have lower requirements and, therefore, exert less pressure on resources. They are represented by only a fraction of a large stock unit. The total population P is calqulated in large stock units (LSU) as follows:

$$LSU_{(t)} = a_1 * (F_{1,t} + M_{1,t}) + a_2 * (F_{2,t} + M_{2,t}) + \sum_{i=3}^{45} (F_{i,t} + M_{i,t})$$

with $a_1 = 0.5$ and $a_2 = 0.67$.

The available resources in an area are represented by the ecological carrying capacity, CC, expressed in large stock units. The carrying capacity gives the number of animals that can be sustained in an area. If the population size is equal to CC, then the population exploits the available resources fully and the population is in equilibrium, *i.e.* the loss of animals is balanced by the increase of animals and the population growth is zero. The population density, D, is defined as:

$D_{(t)} = LSU_{(t)}/CC.$

In the model a density of 1 means that $LSU_{(t)}$ equals CC.

Fecundity functions

Eberhardt (1977) and Fowler (1981) suggest that fecundity, *i.e.* the interval between calving, is a declining function of density. The model follows the assumptions of Hearne and Swart (1991) that births only occur among adult females older than 8 years.

Although there is evidence that in black rhino populations females older than 45 years are still reproductively active (Goddard, 1970), births are limited to adult females not older than 43. The maximum age considered in the model is 45, and animals of this age would not be able to raise their calves successfully.

Density-dependent fecundity rates are obtained by linear interpolation between two data points (Starfield, 1991). Referring to the observations of Hitchins and Anderson (1983), a minimum of 0.46 calves per cow/per year at 25% of the carrying capacity and a maximum of 0.19 calves per cow/per year at 85% of the carrying capacity are the points for the interpolation (Fig. 1).

The sex ratio of neonates in the wild is even (Goddard, 1970; Hitchins and Anderson, 1983), so 50% of the offspring are female.

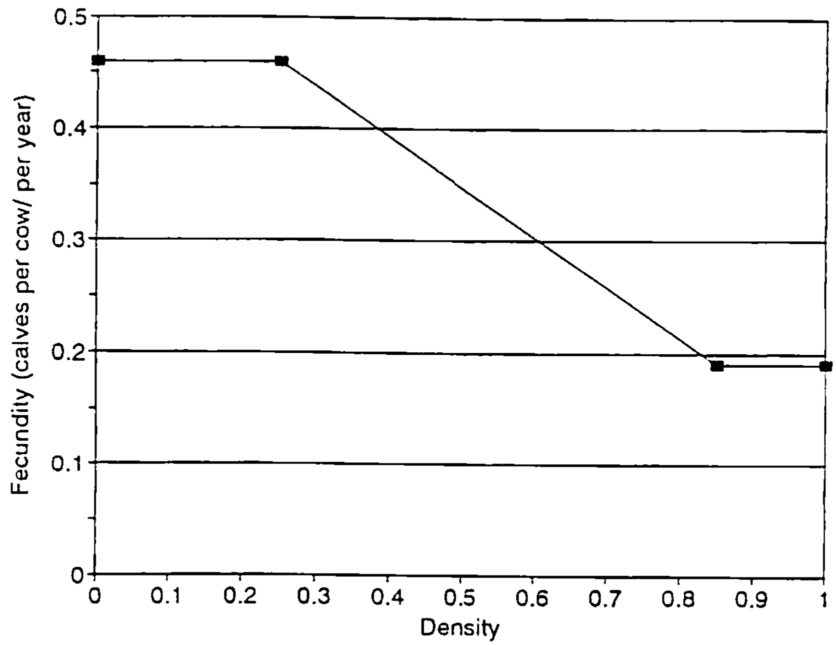

Figure 1 Fecundity as a function of population density resulting from the interpolation between a minimum value of 0.46 calves per cow/per year at 25% of CC, and a maximum of 0.19 calves per cow/per year at 85% of CC.

<u>Mortality functions</u>

According to Eberhardt (1977), an increase in juvenile mortality is one of the first signs of density-dependence. In contrast, the survival of adults in many large mammal populations is quite insensitive to density changes (Fowler 1981).

Observations indicate that for rhinos, adults older than 25 years have higher mortality rates than younger adults (Goddard, 1970) and that the mortality rate for adults older than 35 is even higher, when the population is close to carrying capacity (P. Goodman, pers. comm.).

Due to the lack of sufficient data to assess accurate mortality functions dependent upon density effects, these were estimated. Different combinations of mortality rates were tested to tune the model so that without predation the population is in equilibrium at its carrying capacity, *i.e.* the density equals 1.

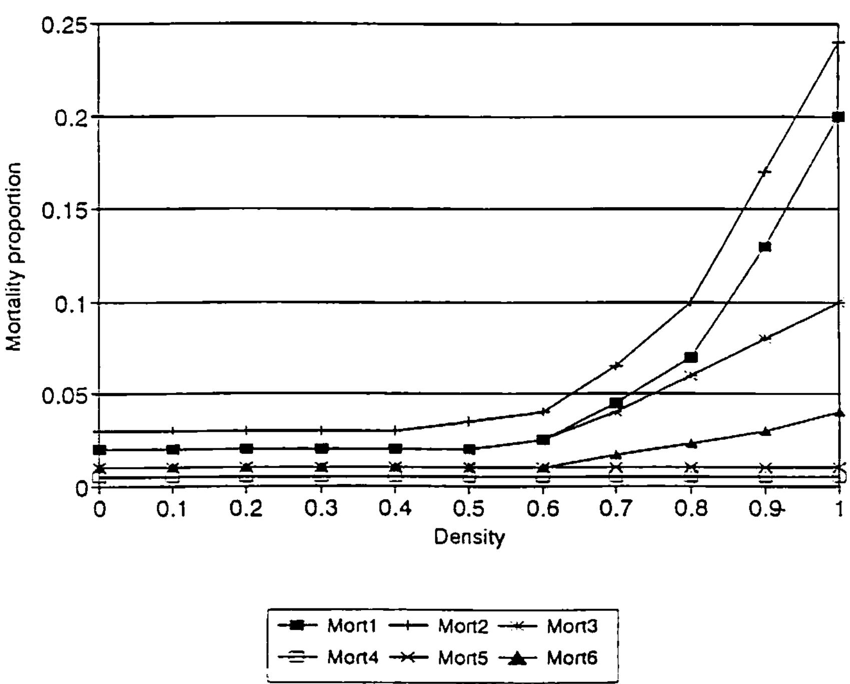

Figure 2 Estimated mortality for different age groups as a function of population density (see text).

Based on the above assumptions and on indications from field experiences (Goddard, 1970; Owen-Smith, 1973; Hitchinson and Anderson, 1983), the estimated mortality functions shown in Fig. 2 seem reasonable.

Predation rate

Predation, as mentioned above, plays a major role in calf mortality. Therefore, 16% of the calves (F_1,M_1) and 1% of the yearlings (F_2,M_2) are assumed to die due to predation (Hearne and Swart, 1991). As mentioned, the model is tuned by the mortality functions, so that the unexploited equilibrium is equal to the carrying capacity. Predation rates greater than 0 reduce the equilibrium point.

Poaching

Since poaching is infrequent in South Africa and Namibia, it is not explicitly considered in the model.

Translocation

The removal of animals for translocation purposes is confined to the subadult and adult groups (F_i, M_i; $i=3,..,45$) since calves and yearlings stay with the cows until at least two years of age.

The removal proportion for each age class depends upon the different harvesting strategies.

Time step

The model runs with a time step of a year since most censuses of black rhino take place at one-year intervals.

Formulation of the model

The model distinguishes between a harvested population and a stocked population. Both together make up the metapopulation with a flow of animals from the harvested population to the stocked population.

The harvested population (P)

Building upon the above made assumptions, the model for the harvested population, P, consists of following equations for the female component of the population, F:

$$F_{1,t+1} = 0.5 * \text{fecund}(\text{density}_{(t)}) * \sum_{i=9}^{43} F_{i,t+1}$$

$$F_{2,t+1} = F_{1,t} - \text{mort}_1(\text{density}_{(t)}) * F_{1,t} - \text{pred}_1 * F_{1,t}$$

$$F_{3,t+1} = F_{2,t} - \text{mort}_2(\text{density}_{(t)}) * F_{2,t} - \text{pred}_2 * F_{2,t}$$

$$F_{i,t+1} = F_{i-1,t} - \text{mort}_3(\text{density}_{(t)}) * F_{i-1,t} - \text{trans}_i * F_{i-1}$$

with i = 4..9

$$F_{j,t+1} = F_{j-1,t} - \text{mort}_4(\text{density}_{(t)}) * F_{j-1,t} - \text{trans}_j * F_{j-1}$$

with j = 10..25

$F_{k,t+1} = F_{k,t-1} - mort_5(density_{(t)})*F_{k-1,t} - trans_k*F_{k-1}$

with k = 26..35

$F_{l,t+1} = F_{l-1,t} - mort_6(density_{(t)})*F_{l-1,t} - trans_l*F_{l-1}$

with l = 36..45

where $fecund(density_{(t)})$ is the fecundity function, $mort_x(density_{(t)})$ is the specific mortality function of age classes x, $pred_x$ the specific predation proportion of age classes x. The age-specific translocation proportions, $trans_x$, are the input variables and depend upon the applied harvesting strategy. The fecundity function is given in Fig.1, the mortality functions in Fig. 2, and the predation proportions $pred_x$ (x=1,2) are 0.16 and 0.01, respectively.

The male component of the population is modeled in the same way.

Note that only mature females who have survived the year produce offspring.

The stocked population (P')

The model of the previous section represents a single population from which animals are removed. This is the model of the harvested population (P = F + M), also called the source population. In an area where no rhinos are present, a new population is established with the removed animals from the source population. The new population is the stocked population or sink population. The stocking of the population occurs continuously.

It is assumed that the new area has a very high carrying capacity, CC', in comparison to the source area, CC, so that density effects in the newly established population are small and, therefore, can be ignored. The values used in the model are CC = 500 and CC' = 2 000. This number is reasonable since the estimated carrying capacity for the Kruger National Park is about 3 500 (Balfour and Balfour, 1991).

The model for the stocked population, P', is analogous to the harvested population, P, except that the animals removed by translocation are added. For example, the transition for the female age class x looks like

$$F'_{x,t+1} = F'_{x-1,t} - mort_x(density'_{(t)}) * F'_{x-1,t} + trans_x * F_{x-1,t}$$

The metapopulation (META)

The metapopulation, META, consists of the harvested population, P, and the stocked population, P'.

$$META_{(t)} = P_{(t)} + P'_{(t)}$$

$$= M_{(t)} + F_{(t)} + M'_{(t)} + F'_{(t)}$$

Harvesting strategies

The manager is faced with a wide range of harvesting strategies for translocation purposes (Caughley, 1985).

Therefore, different strategies are tested to attain their maximum sustainable yield and their performance as translocation policies to maximize the growth of the metapopulation.

The first strategy, S_1, is straightforward. Subadults and adults (F_x, M_x; x:=3,..,45) are harvested with the same proportion, $trans_x$.

To test the differences of harvesting either immature or mature rhinos, two other approaches are introduced. The second harvesting strategy, S_2, considers only the subadults (F_x, M_x; x := 3,..,8) and the third, S_3, only adults (F_x, M_x; x := 9,..,45).

In practice, it is not feasible to harvest all age classes evenly, thus, a fourth approach, S_4, is to remove only animals from a single age class. The age classes 3-45 are harvested.

The exact determination of an animal's age is mostly impossible if the animal is unknown. To consider the possible variance in the age of a removed rhino, two other strategies are performed, referred to as window strategies. In one case (S_5), three age classes are combined within a window and are harvested in the same proportions. In the other case (S_6), five age classes are joined to a window. The window is then moved from one age class to the next. The first group, for example, consists of age class 3, 4 and 5, the next of 4, 5 and 6 and the last of 43, 44 and 45. This is analogous for the window with five age classes.

The different harvesting strategies are summarized in Table 1.

Testing for maximum sustainable yield (MSY)

The different harvesting strategies S_1-S_6 are applied to the source population P in order to assess its maximum

Table 1 Listing of the different harvesting strategies and the affected age classes. S_{4-6} are windows which are moved over the whole range of age classes.

Strategy	Range of harvested age classes	Note
S_1	3,..,45	subadults + adults
S_2	3,..,8	only subadults
S_3	9,..,45	only adults
S_4	x	single age class
S_5	x,..,x+2	window of 3 age classes
S_6	x,..,x+4	window of 5 age classes

sustainable yield (MSY) and the associated population density at MSY.

All strategies are tested using the following procedure.

In the beginning, the source population is stocked with a constant set of initial values. After reaching its equilibrium, *i.e.* its stable age distribution, the harvesting starts and animals are removed from the population according to the harvest proportion, $trans_x$. After reaching a new stable age distribution the sustainable yield is calculated.

This procedure is repeated for different values of $trans_x$ until the MSY is found. The proportion, $trans_x$, and the related density are recorded.

Testing for the optimal translocation strategy

The main purpose of the model is to find the optimal translocation strategy to optimize the growth rate of the metapopulation, called GRM.

Each strategy is used to manage the source population, P, of the metapopulation, META. The MSY for each strategy makes the most animals available for translocation. Therefore, the removal proportions obtained from the test for the MSY are used to remove animals from P and to translocate them to the stocked population, P', over a time period of 20 years. The size of the metapopulation, META, is assessed after each year.

Two scenarios are performed to measure GRM. In the first, called case 1, it is assumed that the source population, P, is unexploited and in equilibrium before the translocation operation begins.

In the second scenario, called case 2, the harvested population is considered to be in its MSY equilibrium state.

Sensitivity analysis

Since the model mainly consists of limited field data and of generalizations for large mammals, a sensitivity analysis was carried out to test its robustness. For example, the mortality functions used in the model resulted from its tuning, namely the testing of different combinations of mortality functions.

Therefore, a productivity curve for the first harvesting strategy, S_1, is again produced but the mortality rates are increased by 10%. This is repeated with a 10% decrease in the mortality proportions. The results are compared with the curve produced under the initial conditions. In the same way the fecundity function is analysed.

To test variations in the age of the first birth, sexual maturity is reached in one case a year earlier than assumed and in the other case a year later.

The same changes were tested for the growth of the metapopulation, GRM, over 20 years using S_1 to translocate black rhinos.

RESULTS

MSY of the harvested population

Figure 3 shows the sustainable yield dependent upon different density levels if the harvesting strategy, S_1, is used to remove animals from the population P. The maximum sustainable yield (MSY) is 17.00 animals per year, and this achieved by a harvest proportion of 0.06, at a density level of 58% of the carrying capacity, CC.

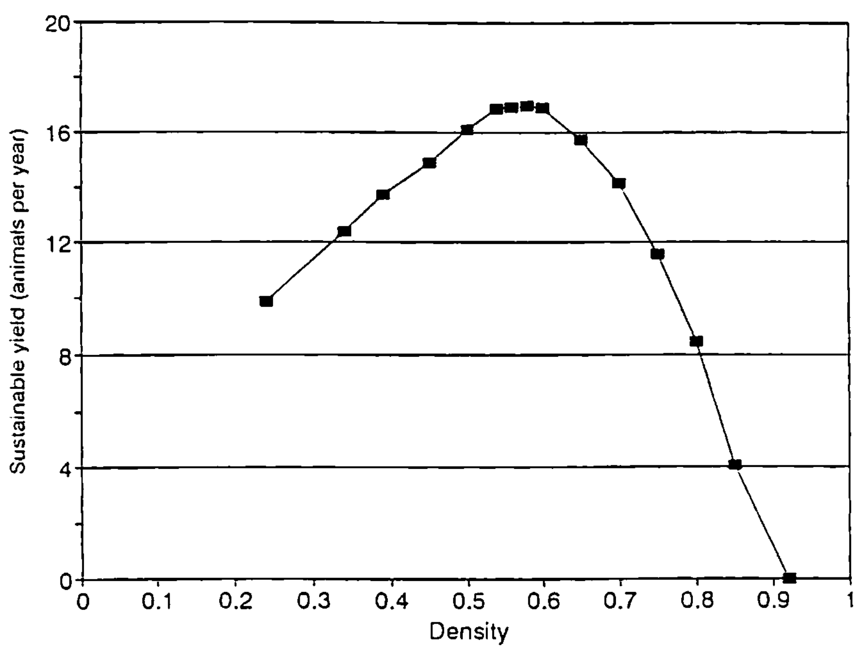

Figure 3 Sustainable removal rates for a black rhino population using the strategy, S_1, to harvest subadult and adult animals evenly.

Table 2 MSYs for the different harvest strategies and the associated densities and removal proportions, respectively. The listed removal proportions are used for the translocation in the metapopulation model.

Strategy	Harvested age classes	MSY (animals per year)	Density	Removal proportion ($trans_x$)
S_1	(3-45)	17.00	0.58	0.06
S_2	(3-8)	15.01	0.54	0.19
S_3	(9-45)	16.59	0.60	0.09
S_4	(3)	17.54	0.54	0.72
S_5	(18-20)	17.17	0.60	0.95
S_6	(18-22)	17.17	0.60	0.95

Table 2 contains the MSY values of all strategies (S_1-S_6), the related density levels and the harvest proportions, $trans_x$. The MSYs of S_4-S_6 displayed are associated with the age class and the window of joined age classes, respectively, which attained the highest MSY for the whole range of age classes.

It is interesting that the density resulting in highest productivity attained in this analysis, *i.e.* between 0.54 and 0.60, differs from that predicted by other models which obtain a value of 0.5 (*e.g.* Hearne and Swart, 1991).

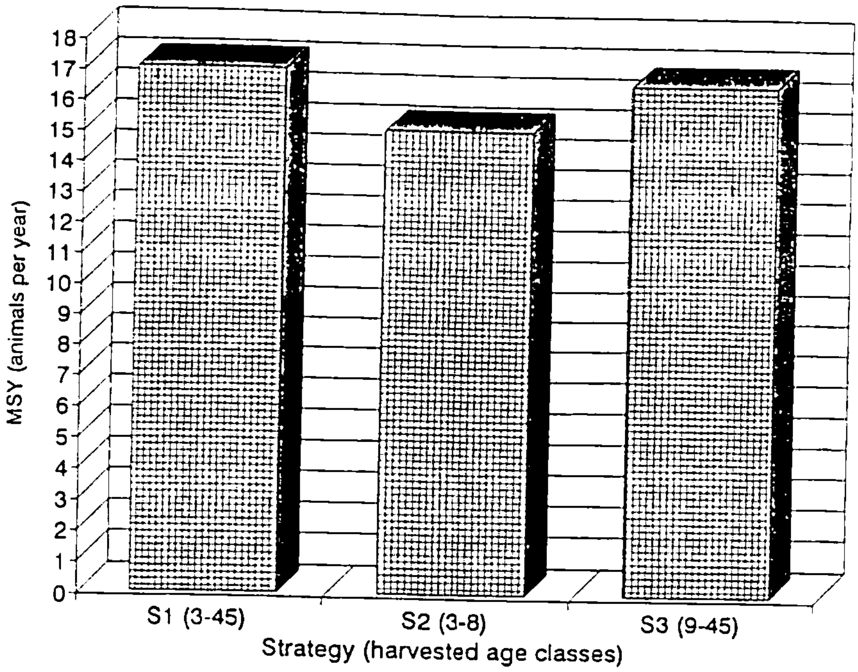

Figure 4 Comparison of the MSYs for the strategies, S_1-S_3. The highest MSY is attained if subadults and adults are harvested evenly (S_1), the lowest if only subadults are affected by the removal strategy (S_3).

Figure 4 compares the MSYs of the strategies S_1-S_3. The highest yield is attained if subadults and adults are harvested evenly, the lowest yield if only subadults are effected by the removal strategy.

In Figures 5-7, the MSY values of each age class and each window, respectively, produced by the strategies S_4, S_5 and S_6 are summarized. All three graphs are bimodal with the first peak representing the first age class of the subadult group. From there, the MSY values decline as long as immature animals are removed. From age class 9 onwards,

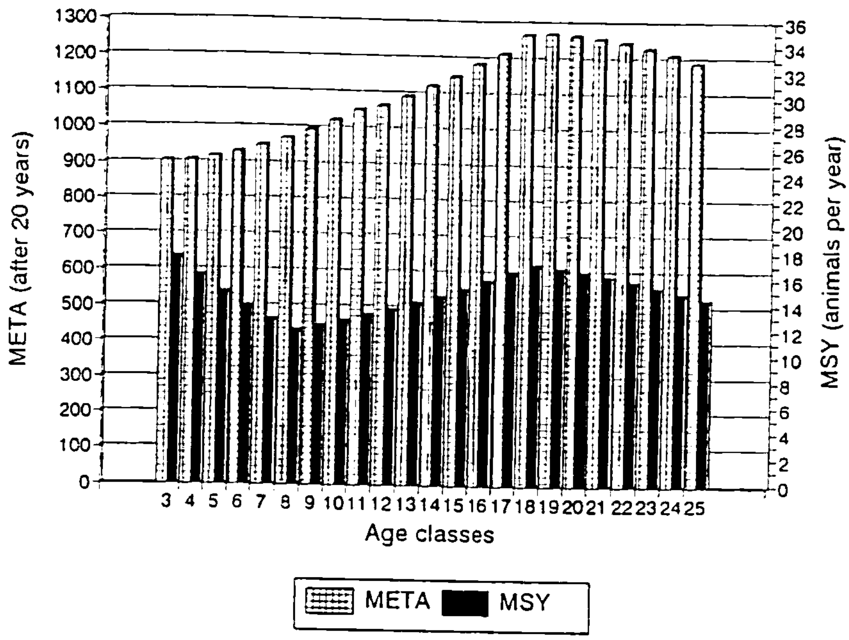

Figure 5 Comparison of the size of the metapopulation, META, after 20 years and the MSYs for the removal of rhinos from each age class according to translocation strategy, S_4.

when only adults are affected, the MSY values increase until the second peak at age class 18. Then the sustainable yield decreases again.

The strategy, S_4, has the highest sustainable yield at the first peak, *i.e.* harvesting of only 3 year-old subadults is attains the highest sustainable yield of all strategies (Table 2).

In contrast to S_3, the strategies, S_5 and S_6, which consist of windows of three and five consecutive age classes, allow the highest yield at the second peak, where adult animals are removed. Table 1 shows that both methods have the same values for their MSYs, the relating density levels and the removal proportions.

Figures 5-7 show that the first peak is reduced as the number of combined age classes is increased. This means that the wider the window, the more age classes are evenly harvested, and the higher the proportion of mature age classes, the smaller the first peak.

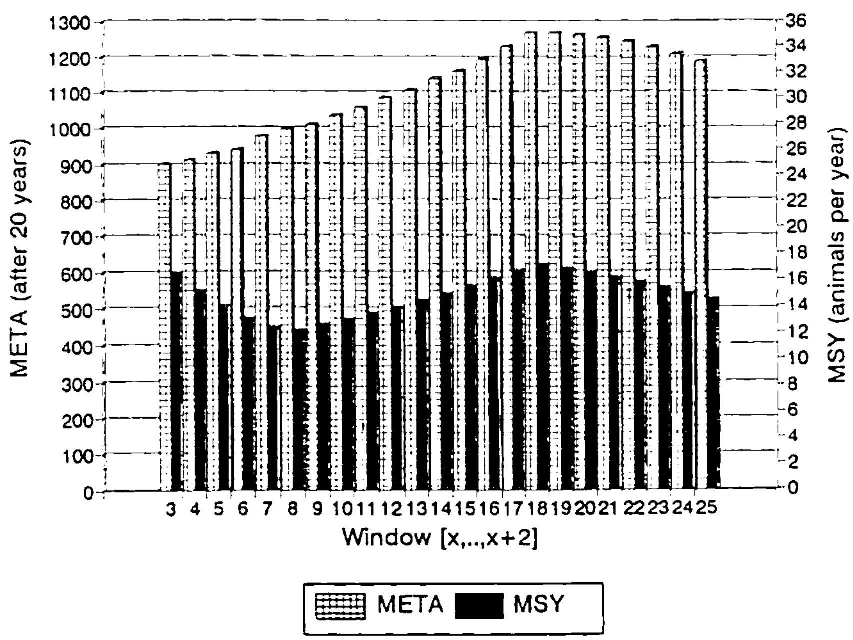

Figure 6 Comparison of the size of the metapopulation, META, after 20 years and the MSYs for the removal of rhinos from each window according to translocation strategy, S5. The window used here consists of three adjacent age classes, *i.e.* the first window joins the age classes 3, 4 and 5.

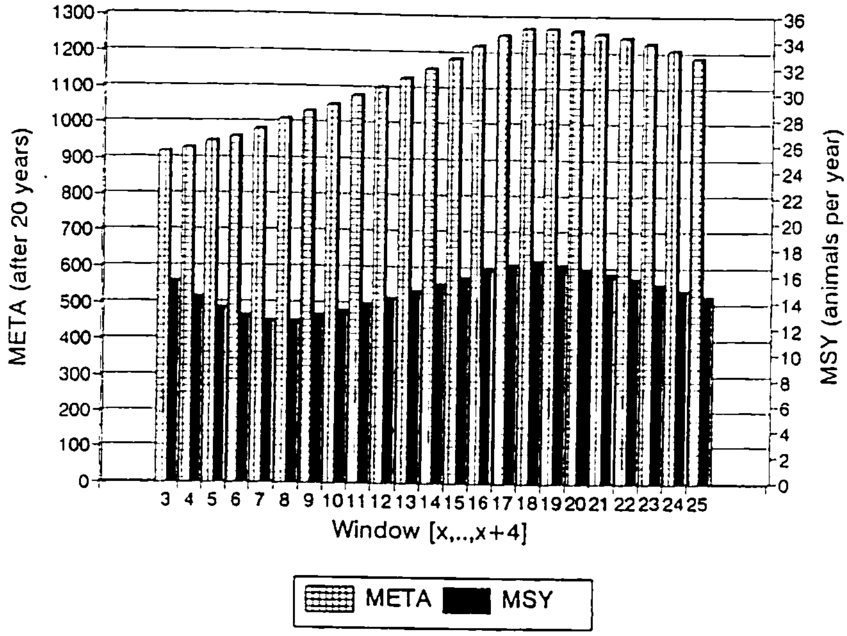

Figure 7 Comparison of the size of the metapopulation, META, after 20 years and the MSYs for the removal of rhinos from each window according to translocation strategy, S_6. The window used here consists of five adjacent age classes, *i.e.* the first window joins the age classes 3, 4, 5, 6 and 7.

Looking at the removal proportions in Table 1, the values for S_5 and S_6 are very high, namely 95% of the animals in the range of the window have to be removed to attain the MSY. In comparison with that, the removal proportions for S_1 and S_3 are markedly smaller. The stable age structure resulting from the application of S_5 and S_6, respectively, is very young. In the age classes younger than 18 years, there are enough mature rhinos to sustain the population, so that older animals can be removed without affecting the productivity of the population.

Optimal translocation strategy

The first scenario considers a source population, P, that is in equilibrium and not exploited. Animals are removed according to the MSYs attained in the previous test.

The results of the translocation policies (S_1-S_6) are summarized in Fig. 8. The graph shows the size of the metapopulation, META, after 10 and 20 years, respectively. Apparently, the strategy, S_4, with the highest MSY from the harvested population does not give the largest growth rate of the metapopulation, GRM, but S_3, where only mature animals are translocated, although the MSY of this strategy is one of the lowest.

All the strategies which include mature animals score higher GRMs than those which only consider immature animals.

S_1 and S_3 which translocate animals over a broad scope of age classes achieve larger metapopulation numbers than S_5 and S_6 whose exploited windows cover 3 and 5 consecutive age classes, respectively.

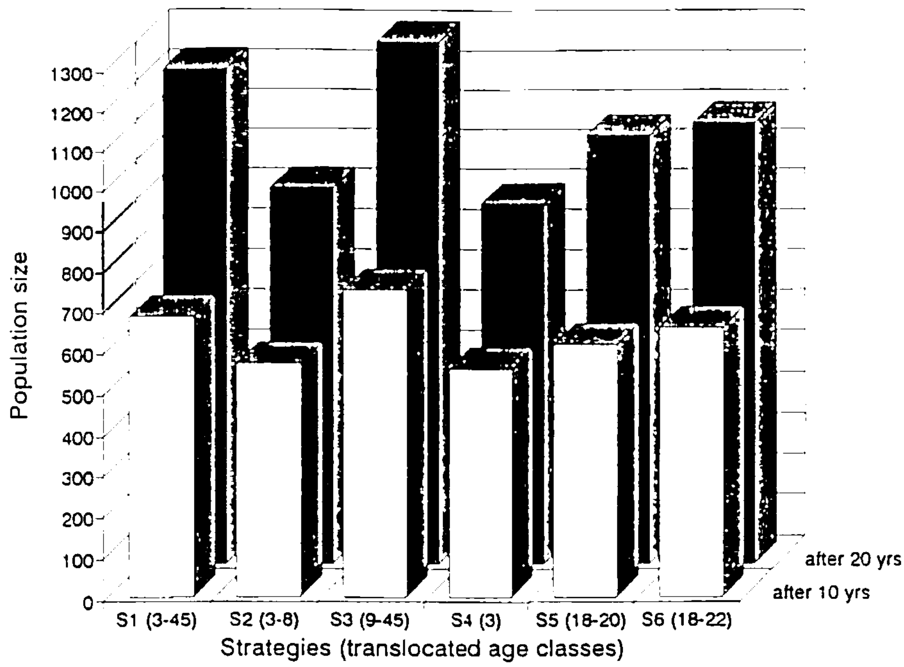

Figure 8 Comparison of the metapopulation sizes after 10 and 20 years respectively, according to the different translocation strategies for scenario 1. The source population is considered to be unexploited and in equilibrium before the translocation procedure starts.

The second scenario, case 2, assumes the harvested population, P, at its highest productivity level. Black rhinos are continuously translocated at MSY from P to the stocked population, P'.

Figure 9 shows the size of the metapopulation, META, after 10 and 20 years according to the applied translocation strategies (S_1-S_6).

Again the strategies which translocate only mature animals achieve over time the highest population sizes. In

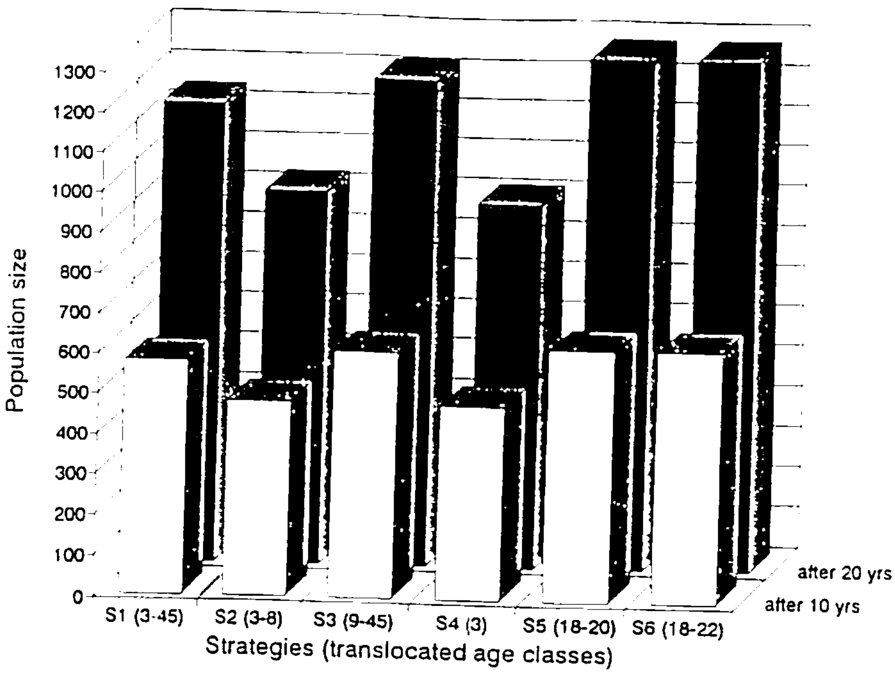

Figure 9 Comparison of the metapopulation sizes after 10 and 20 years, respectively, according to the different translocation strategies for scenario 2. The source population is considered to be at MSY level and in equilibrium before the translocation procedure starts.

contrast to Fig. 8, the strategies, S_5 and S_6, obtain the best results in terms of the GRM due to their high MSYs.

Table 3 compares the MSY and the size of the metapopulation in the two scenarios for all tested strategies. The translocation of immature animals results in about 30% lower metapopulation numbers in both cases.

The window methods, S_5 and S_6, produce smaller metapopulations after 20 years in the first scenario than in the second scenario. This is caused by the high harvest proportion (Table 2), where the yearly removal of 95% of

Table 3 Comparison of the MSY and the size of the metapopulation (META) after 20 years for each strategy. Scenario 1 starts at unexploited equilibrium and scenario 2 at exploited equilibrium. The strategy, S_3, has the highest MSY but as translocation policy scores the lowest population number.

Strategy	Harvested age classes	MSY (animals per year)	META (after 20 years)	
			Scenario 1	Scenario 2
S_1	(3-45)	17.00	1218.46	1137.43
S_2	(3-8)	15.01	920.71	922.92
S_3	(9-45)	16.59	1289.13	1208.04
S_4	(3)	17.54	882.23	904.37
S_5	(18-20)	17.17	1054.37	1269.22
S_6	(18-22)	17.17	1084.75	1269.25

the animals in the respective window disturbs the initially stable age distribution of the source population, P. This impact temporarily reduces the productivity of the population until a new stable age distribution is established at MSY, as it is in case 2.

Figures 5-7 elucidate again the importance of the translocation of sexually reproductive (as opposed to immature) rhinos in terms of optimizing the GRM. The figures compare the metapopulation after 20 years, corresponding to the MSY of the harvested population taken within each age class and window, respectively, for the strategies, S_4-S_6. The harvest of immature animals results in high MSY and consequently makes a maximum number of rhinos available for translocation. But, to maximize the growth rate of the metapopulation, GRM, it is more effective to translocate mature animals than immatures.

Likewise, the time until a rhino reaches its sexual maturity determines the outcome of the translocation strategy in terms of optimization of the metapopulation growth. For example, according to Fig. 5, about 30% more 3 year-old animals, which become first sexual reproductive in 6 years, can be translocated at MSY than 7 year-old animals, which reach maturity in 2 years. Nevertheless, the latter produce a *ca.* 5% larger metapopulation after 20 years.

The Figures 5-7 show again that the strategy, that can translocate the most mature rhinos at MSY, also attains the highest GRM.

Sensitivity analysis

The test for the maximum sustainable yield was repeated with changed parameters applying the removal strategy, S_1. Also, the different scenarios were again run through. The results of the sensitivity analysis are compared in Table 4, and Fig. 10 shows the sustainable yield curves for changed fecundity functions.

The model is less sensitive to variations of the mortality functions than to changes in the parameters affecting fecundity. A 10% variation of the mortality functions results in a 3% variation of the MSY and the size of the metapopulation, whereas a 10% change in fecundity functions leads to a 10% change in MSY and GRM.

The quantitative results are sensitive to variations of the input parameters, but the trends remain the same, so the model can be considered as robust in terms of qualitative results.

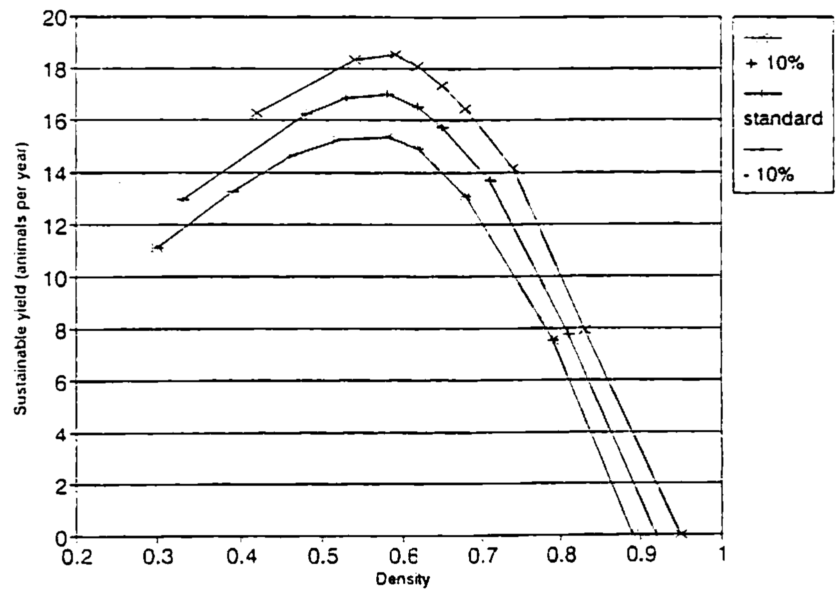

Figure 10 Sensitivity analysis of the sustainable removal rates for a black rhino population using the strategy, S_1. The fecundity function is unchanged or increased / decreased by 10%.

Table 4 Sensitivity studies on the result of the MSY and on the size of the metapopulation (META) after 20 years using the strategy S_1 to translocate black rhinos. Scenario 1 starts at unexploited equilibrium and scenario 2 at exploited equilibrium.

Parameters that differ from standard run	MSY (animals per year)	META (after 20 years)	
		Scenario 1	Scenario 2
None (i.e., standard run)	17.00	1218.46	1137.43
Mortality rates:			
- increased by 10%	16.52	1175.21	1096.91
- decreased by 10%	17.48	1266.92	1182.72
Fecundity rate:			
- increased by 10%	18.55	1330.95	1268.82
- decreased by 10%	15.35	1100.83	1014.57
Age at first reproduction:			
- a year earlier (7)	18.56	1328.45	1271.18
- a year later (9)	15.56	1122.91	1036.65

DISCUSSION

Hearne and Swart (1991) present a model of a rhino population in which the population is divided into eight groups according to age and sex. The first female group consists of calves (0-1 year old) and the second of yearlings (1-2 years old). The third group consists of subadult females between 3 and 8 years old and the fourth of fecund females older than 8 years. The male groups are divided in similar way. The transition from one group to the next is represented by differential equations, but age differences inside of the subadult and fecund groups are neglected.

According to Hearne and Swart (1991) a black rhino population attains its MSY at a density level of 50% of carrying capacity. This is in contrast to our model, that reaches MSY at a population density of 60% of carrying capacity. The latter result is consistent with the findings of Fowler (1980) that the MSY for large mammals occurs at a density level of about 60% of carrying capacity. The reason for the slightly skewed sustainable yield curve in the model used here is that most density-dependent changes occur at a population size close to the carrying capacity. For example, the slope of the mortality curves increases from a density of 0.6.

Thus, the density level for a managed black rhino population should be a compromise between high and low densities.

On the one hand, it is preferrable to keep populations of endangered species like black rhino at large numbers, since a large number of individuals reduces the risk of inbreeding and the loss of heterozygosity (Futuyma, 1986). Furthermore, game parks have an interest in relatively high densities, because it increases the chance of sighting a black rhino, thereby increasing the attraction of the park to tourists. On the other hand, conservation authorities which are interested in managing black rhinos at MSY should opt for a reduced density, to produce as many mature animals as possible to stock other areas.

A MSY level of 60% of carring capacity, instead of the value of 0.5 suggested by Hearne and Swart, allows a better trade-off between these opposing management goals.

Another result of Hearne and Swart (1991) which is in contradiction to the findings of the model introduced here concerns the MSY conditions. Hearne and Swart attain the highest sustainable yield for the removal of subadults. In our model, the strategy, S_2, that considers the subadult age classes from 3-8 and is comparable to Hearne and Swart's harvesting strategy scores the lowest MSY of all tested strategies.

The only strategy that attains the highest MSY for the removal of subadults is S_4. Although this strategy aims for the single age class 3, as soon as several subadult age classes are harvested simultaneously, as in S_5 and S_6, the largest MSY is attained by the removal of adults.

The objective of managing the harvested population at MSY is to make as many black rhinos as possible available for translocation to the stocked population. The results presented here show that the reproductive status of the translocated rhino is more important in terms of metapopulation growth than the amount of translocated animals.

The translocation of immature animals always has a negative effect due to the delayed reproduction as seen, for example, in the metapopulation growth for S_1. This strategy scores a higher MSY than S_3, but produces a smaller metapopulation after 10 and 20 years, respectively, due to the presence of subadults which are translocated.

Hearne and Swart are in agreement with the work presented here, that mature animals, which are able to reproduce in the new area immediately, should be preferred to immature animals to maximize the growth rate of a metapopulation, GRM. In our model, it is shown that the age of an immature animal, likewise, plays an important role in optimizing the GRM. Due to the time delay, the longer it takes an immature animal to become reproductive, the lower the metapopulation growth is.

Reproductive state and age are more important than the number of animals for deciding whether mature or immature rhinos should be translocated.

If only mature animals are considered, then the strategy that leads to the highest MSY is the most effective to improve the growth rate of the metapopulation by translocation. The more mature animals that can be translocated on a sustainable basis, the larger metapopulation size is after 20 years. This is shown in the second scenario in which the harvested population is assumed to be at MSY level and in equilibrium. The strategies, S_5 and S_6, which remove all 18 year-old and older rhinos, have the highest MSYs and, likewise, the best score for the metapopulation after 20 years.

These strategies, however, have the limitation that they are based on a stable age distribution that is very young. Over 95% of the rhinos are assumed to be younger than 19 years. Such an age distribution is highly productive but it is not very likely that this will be attained for black rhino populations. Removing 95% of rhinos from the age classes harvested by S_5 and S_6 is hardly practical and very expensive due to time and effort involved.

Furthermore, S_5 and S_6 are not appropriate starting points for harvesting an unexploited population, if the aim is to bring it to the MSY level, as seen in the first scenario. The high removal proportion of S_5 and S_6, respectively, leads to abrupt changes in the age distribution of the harvested population, so that its productivity is temporarily reduced. The strategies, S_1 and S_3, are rather practical due to their moderate translocation proportions.

In summary, the MSY values are less important in terms of maximizing GRM than the number of sexually mature animals that can be translocated on a sustainable basis. If the source population is not at its MSY level, managers should be careful to choose the appropriate strategy and removal rate to bring the population to this level. From the results of this model, the most appropriate strategy to bring a population to its MSY level is S_3, *i.e.* the even harvest of mature age, so that the changes in the age distribution are moderate. After reaching a stable age distribution, it is more effective in terms of overall growth to switch to strategies like S_5 and S_6, respectively, since they produce the most mature animals for translocations.

The sensitivity analysis shows that changes in reproduction parameters have stronger effects than changes in mortality parameters. This is in agreement with the results from models of other mammals (Caughley, 1977; Fowler and Smith, 1981; Starfield and Bleloch, 1991). Therefore, to enhance the population growth, the fecundity rate must be improved rather than the survival rate. If the mortality, however, exceeds the reproductive potential of a population, *e.g.* due to poaching, then the survival rate must be improved to stop the decline of the population.

A crucial assumption of the model is that rhinos can still reproduce when they are old (Goddard, 1970). This assumption needs further scientific foundation. If reproduction is decreases after the age of 30 years, then the growth rates of the metapopulation will be reduced but the qualitative results presented here are unaffected. However, if reproduction is diminished from the age of 20 years onwards, the qualitative results might change.

Another problem that was not further investigated in this project is the effect of the senescence of translocated mature rhinos on metapopulation growth. If, for example, translocated rhinos are too old, so that they die in the new area before they reproduce, then this will influence the overall growth adversely. In our model, the translocation of rhinos older than 30 years was not investigated closely. Therefore, the provisional recommendation at this stage is that the age of a translocated animal should not be over 30 years.

The current translocation policy favours subadult animals (Hearne and Swart, 1991) for several reasons. First, many subadults die due to fighting when trying to establish them, particularly in high density areas. Optimization of the growth of the metapopulation by translocation of adults, suggested by this model, depends upon the assumption that the subadults can fill the vacancies in the source population caused by the removal of adults, without an abnormal mortality due to fighting. Thus, the recruitment of subadults in areas from which black rhinos were removed should be monitored.

As mentioned above, the assumed age distribution for the translocation strategies, S_5 and S_6, are quite unrealistic. Additionally, it is unknown if a changed age distribution has negative effects on the social behaviour and structure of a rhino population. This might also modify the results of the model.

The second reason for the current translocation policy is that removing subadults decreases the probability of inbreeding because offspring are removed from their parents (P. Goodman pers. comm.). The model is not designed to test this assumption. However, if the removal of the offspring from their parents decreases the risk of inbreeding, then the translocation of the parents should have the same effect.

Nevertheless, despite the above mentioned objections, the main conclusion of the model remains the same. To maximize the growth rate of metapopulation consisting of a source population and a sink population, it is important to translocate as many sexually reproductive animals as possible on a sustainable basis.

SUMMARY

One of the goals of the conservation plan for the black rhinoceros in southern Africa (Brooks, 1989) is to maximize the overall growth of the existing populations. To achieve this goal, translocations of black rhinos from high-density areas to low-density areas must be carried out.

A metapopulation model that represents the dynamics of two rhino populations was developed to test the efficiency of different translocation strategies.

From the model presented here following conclusions can be drawn:

1) It is more effective to translocate mature rather than immature animals.

2) The growth rate of the entire population (metapopulation) increases if mature rhinos are translocated at MSY.

3) To attain MSY, rhino populations should be managed at about 60% of carrying capacity.

4) Populations serving as source populations for translocations should establish a young stable age distribution at MSY, *e.g.* most sexual reproductive animals should be younger than 18 years.

5) The reduction of source populations close to carrying capacity must be carried out carefully, since drastic changes in the age distribution of a population decrease its productivity.

6) Black rhinos which are translocated should not be older than 30 years. If reproduction is restricted from this age onwards, translocated rhinos should be younger than 25 years.

7) If the present translocation policy is to be continued, then older subadults are preferred to younger subadults, since they reach sexual maturity faster.

CODA

"Give me five parameters and I will draw you an elephant; six, and I will have him wave his trunk."

(J. Euler)

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