# Optimal translocation strategies for saving the Black Rhino 

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#### Abstract

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Over the past 30 years the black rhinoceros (Diceros bicornis) populations in Africa have dwindled dramatically. To enhance the survival prospects of the species, a national conservation strategy has been developed in South Africa. Its main goal is to formulate and implement policies to increase the southern African rhino population as rapidly as possible. This involves translocating animals from areas where the population is approaching the ecological carrying capacity and establishing new viable populations in other suitable reserves.

A non-linear differential equation model for a population of black rhino was developed. The model is used with a combination of analytical and numerical techniques to investigate a number of issues relating to the translocation of rhino from well-stocked, high-density areas to low-density areas with small herds or no herds. Firstly, the model is used to determine the maximum sustainable yield from the well-stocked reserves. The model is then applied to a newly established population to determine optimal import policies. Finally, the model is extended to include both an established exporting population and a new understocked importing population. Simulations are performed to give an indication of the number and age of animals which should be translocated to maximise the growth rate of the total rhino population in southern Africa.


## INTRODUCTION

The black rhinoceros (Diceros bicornis) populations in Africa have dwindled dramatically from 65000 head 20 years ago to about 3500 today. During this period twelve African countries lost their entire black rhino populations and presently at most six countries have herds exceeding 100 head.

In contrast, the black rhino population in South Africa and Namibia has increased four-fold to about 1000 head. With poaching a less serious problem in South Africa than the rest of Africa, the attainment of a sufficiently large population in this country, to ensure the survival of the species, has become the main goal of a national rhino conservation policy (Brooks, 1989). This involves the translocation of rhino from areas of high population density to other areas suitable for the establishment of new herds. At what rate and from which age and sex groups should animals be removed from high density areas so as to maximise the overall growth rate of the southern African population?

To answer the above question a mathematical model of a rhino population was developed. Three investigations were undertaken with the model. Firstly, we tried to determine the maximum sustainable yield of a wellstocked area. The assumption here being that the more animals that can be exported from this area on a sustainable basis the greater the likelihood of viable populations being established elsewhere and hence the faster the total population growth rate. This problem was solved by manipulating the mathematical problem into a form where it could be solved by linear programming techniques. Secondly, the translocation policy is considered from the perspective of maximising the growth rate of the new and newly established populations. The solution of this problem was achieved by analytically solving a linearised version of the differential equation model. Finally, the model is extended to include an exporting population (the founder population) and a newly established population (the translocated population). The translocated population imports from the founder population. Simulations are performed to test some translocation policies on the growth rate of the total (founder + translocated) population.

## FORMULATION OF THE MODEL

The population and behavioural biology of black rhinoceros is not well understood. Our current understanding stems from the several different sub-species of black rhino which occur in various localities throughout east and southern Africa. The model we develop incorporates information on black rhino population characteristics from the published literature (Goddard, 1967, 1970; Hitchins, 1978; Hitchins and Anderson, 1983) and other unpublished sources. Where no specific data for black rhino exist, we substitute with empirically supported generalisations for large mammals from the literature, notably Eberhardt (1977), Fowler (1981) and Laws (1981).

According to certain known characteristics of rhino and the ability of rangers to distinguish between different age groups in the field, the

TABLE 1
Division of the female population

| Group | Age (yrs) | Flows IN | Flows OUT |
| :--- | :--- | :--- | :--- |
| $F_{1}$ | $0-1$ | Births | Aging, death, predation |
| $F_{2}$ | $1-2$ | Aging | Aging, death, predation |
| $F_{3}$ | $2-8$ | Aging | Aging, death, translocation |
| $F_{4}$ | $8+$ | Aging | Death, translocation |

population is divided into eight groups according to age and sex. The various female groups, and the rates determining their levels are shown in Table 1. The male groups $\mathrm{M}_{1}-\mathrm{M}_{4}$ are divided in a similar way. Translocations remove animals from a founder population and add them to a translocated population.

From the table it should be noted that no migration occurs and that predation is confined to the younger groups. In South Africa poaching presently occurs infrequently and is ignored in the model. As the overall effect of poaching is to add to the total death rate of adult and sub-adult rhinos, its effect will be tested during a sensitivity analysis of death rates. Calves stay with the cows until at least two years of age, so removals (translocations) are restricted to the third and fourth age groups.

In order to measure the impact of a population on resources, a population is converted into large stock units. One large stock unit is defined as one adult in terms of its resource requirements. A younger animal exerts less pressure on resources and is therefore equivalent to only a fraction of a large stock unit. The total population measured in large stock units is denoted by LSU and calculated as follows:
$\mathrm{LSU}=a_{1}\left(F_{1}+M_{1}\right)+a_{2}\left(F_{2}+M_{2}\right)+a_{3}\left(F_{3}+M_{3}\right)+F_{4}+M_{4}$
where $a_{1}, a_{2}$ and $a_{3}$ take on the values $0.5,0.67$ and 1.0 , respectively.
Population density in a given region is defined as the ratio LSU/CC, where $C C$ is the ecological carrying capacity in large stock units of that region.

Observations indicate that births in the Umfolozi Game Reserve have occurred from as early as 6 years of age (Goddard, 1967) and in the high-density extreme in the Hluhluwe Game Reserve, first calves are dropped at around 10.5 years (Hitchins and Anderson, 1983). In this model it is assumed that all fecund females are in the fourth age group (which is true on average).

Fecundity, which is reflected by the interval between calving, is suggested to be a declining function of density (Eberhardt, 1977; Laws, 1981). Hitchins and Anderson (1983) summarised calving interval statistics from a
variety of areas and recorded a minimum interval between calving of 26 months ( 0.46 calves $\operatorname{cow}^{-1} \mathrm{yr}^{-1}$ ) and a maximum of 63 months ( 0.19 calves cow ${ }^{-1} \mathrm{yr}^{-1}$ ). The specific fecundity rate FF is assumed to have a maximum value of 0.46 for population densities below $25 \%$ of the carrying capacity; a minimum value of 0.19 for population densities exceeding $85 \%$ of the carrying capacity. Intermediate values of FF are obtained by linear interpolation between these two extremes.

The effect of density changes on the conception rate is represented by $\mathrm{FF}_{1}$, a first-order delayed version of the fecundity function FF , with delay time $T_{1}$. Thus:
$\frac{\mathrm{d}}{\mathrm{d} t} \mathrm{FF}_{1}=\frac{\left(\mathrm{FF}-\mathrm{FF}_{1}\right)}{T_{1}}$
It is only after some further delay (gestation period) that density-induced changes in the conception rate result in changes in the birth rate. Thus $\mathrm{FF}_{1}$ is subjected to a further delay to yield the specific birth rate $\mathrm{FF}_{4}$. This delay is modelled by the third-order delay equations:
$\frac{\mathrm{d}}{\mathrm{d} t} \mathrm{FF}_{\mathrm{i}}=\frac{\left(\mathrm{FF}_{i-1}-\mathrm{FF}_{i}\right)}{T_{2}} \quad i=2,3,4$
where $\mathrm{FF}_{2}$ and $\mathrm{FF}_{3}$ are intermediate variables and $3 T_{2}$ is the gestation period. The birth rate is therefore given by:
birth rate $=F_{4} \quad \mathrm{FF}_{4} \quad\left(\right.$ calves $\left.\mathrm{yr}^{-1}\right)$
Mortality is a function of age (Goddard, 1970) and density (Eberhardt, 1977; Fowler, 1981). Eberhardt (1977) proposed that one of the first signs of density-dependent stress was an increase in juvenile mortality. At the other extreme Fowler (1981) states that in many large mammal populations, adult survival is insensitive to changes in density. Observations indicate that for rhino, sub-adults have higher mortality rates than adults because they are subject to more social stress than adults, particularly when they are trying to establish their home ranges for the first time. Animals in the youngest two age groups are also subject to nutritional stress. Yearlings (age group 2) are weaned and so must depend on vegetation for food. They therefore have a higher mortality rate and are more susceptible to density stress than unweaned calves.

There is insufficient information available for a precise definition of the mortality functions but based on the above discussion and field experience the functions shown in Fig. 1 were considered plausible. In addition to natural mortality, deaths due to predation occur amongst the two younger groups.


Fig. 1. Mortality functions.

Observations indicate that half of all rhino births are female. The female sector of the population is therefore described by the following model equations:

$$
\begin{aligned}
& \frac{\mathrm{d}}{\mathrm{~d} t} F_{1}=0.5\left(F_{4} \mathrm{FF}_{4}\right)-F_{1} \mathrm{AGING}_{1}-F_{1} \mathrm{MORT}_{1}-F_{1} \mathrm{PRED}_{1} \\
& \frac{\mathrm{~d}}{\mathrm{~d} t} F_{2}=F_{1} \mathrm{AGING}_{1}-F_{2} \mathrm{AGING}_{2}-F_{2} \mathrm{MORT}_{2}-F_{2} \mathrm{PRED}_{2} \\
& \frac{\mathrm{~d}}{\mathrm{~d} t} F_{3}=F_{2} \mathrm{AGING}_{2}-F_{3} \mathrm{AGING}_{3}-F_{3} \mathrm{MORT}_{3}-f_{3} \\
& \frac{\mathrm{~d}}{\mathrm{~d} t} F_{4}=F_{3} \mathrm{AGING}_{3}-F_{4} \mathrm{MORT}_{4}-f_{4}
\end{aligned}
$$

where $\mathrm{AGING}_{i}$ is the specific aging rate of group $F_{i}\left(\mathrm{yr}^{-1}\right)$ MORT $_{i}$ the specific mortality rate function of group $F_{i}\left(\mathrm{yr}^{-1}\right)$, and $\mathrm{PRED}_{i}$ the specific predation rate of group $F_{i}\left(\mathrm{yr}^{-1}\right)$. The translocation rates $f_{3}$ and $f_{4}$ (head $\mathrm{yr}^{-1}$ ) are exogenously specified. The mortality functions are given in Fig. 1, and the predation rates $\left(\mathrm{yr}^{-1}\right)\left[\operatorname{PRED}_{i}(i=1,2)\right]$ are 0.16 and 0.01 , respectively. The specific aging rates $\left(\mathrm{yr}^{-1}\right)\left[\operatorname{AGING}_{i}(i=1,2,3)\right]$ are $1,1, \frac{1}{6}$ and were calculated from the time spent in each age group (see Table 1).

The male sector is modelled in a similar way.

## OPTIMAL HARVESTING OF A POPULATION

The model developed above can now be used to maximise the number of rhino that can be harvested from a reserve under sustainable conditions.

Thus, equilibrium solutions of the dynamic model are sought which maximise the rate at which animals can be removed for translocation.

The problem stated more concisely is to find a removal strategy ( $f_{3}, f_{4}$, $m_{3}, m_{4}$ ) and a density so as to maximise the rate of removals ( $f_{3}+f_{4}+m_{3}$ $+m_{4}$ ) subject to the constraints below, where $\boldsymbol{F}$ and $\boldsymbol{M}$ denote the column vectors $\left[\begin{array}{lllll}F_{1} & F_{2} & F_{3} & F_{4}\end{array}\right]^{\mathrm{T}}$ and $\left[\begin{array}{llll}M_{1} & M_{2} & M_{3} & M_{4}\end{array}\right]^{\mathrm{T}}$ respectively:
$\frac{\mathrm{d}}{\mathrm{d} t} \boldsymbol{F}=0$
$\frac{\mathrm{d}}{\mathrm{d} t} \boldsymbol{M}=0$
$M_{4}-F_{4}=0$
density $=\frac{\text { LSU }}{\text { CC }}$
$F_{1}, F_{2}, F_{3}, F_{4}, M_{1}, M_{2}, M_{3}, M_{4}, f_{3}, f_{4}, m_{3}, m_{4} \geqslant 0$
The social effects of a skewed sex distribution is not known. In the light of this uncertainty there is a reluctance to disturb the social order. Thus constraint (3) is included to maintain an equal sex distribution. Detailed expressions for constraints (1) and (2) are obtained from the dynamic model and require that the population be in equilibrium. These equations also show that the decision vector $\left(f_{3}, f_{4}, m_{3}, m_{4}\right)$ and density are implicit functions of the state variables $\boldsymbol{F}$ and $\boldsymbol{M}$. The problem is thus one of non-linear constrained optimisation.

Substituting the equations for the dynamic model into (1) and (2) and solving for $f_{3}, f_{4}, m_{3}, m_{4}$, we get:

$$
\begin{align*}
& 0=0.5\left(F_{4} \mathrm{FF}_{4}\right)-F_{1} \mathrm{AGING}_{1}-F_{1} \mathrm{MORT}_{1}-F_{1} \mathrm{PRED}_{1}  \tag{6}\\
& 0=F_{1} \mathrm{AGING}_{1}-F_{2} \mathrm{AGING}_{2}-F_{2} \mathrm{MORT}_{2}-F_{2} \mathrm{PRED}_{2}  \tag{7}\\
& f_{3}=F_{2} \mathrm{AGING}_{2}-F_{3} \mathrm{AGING}_{3}-F_{3} \mathrm{MORT}_{3}  \tag{8}\\
& f_{4}=F_{3} \mathrm{AGING}_{3}-F_{4} \mathrm{MORT}_{4}  \tag{9}\\
& 0=0.5\left(F_{4} \mathrm{FF}_{4}\right)-M_{1} \mathrm{AGING}_{1}-M_{1} \mathrm{MORT}_{1}-M_{1} \mathrm{PRED}_{1}  \tag{10}\\
& 0=M_{1} \mathrm{AGING}_{1}-M_{2} \mathrm{AGING}_{2}-M_{2} \mathrm{MORT}_{2}-M_{2} \mathrm{PRED}_{2}  \tag{11}\\
& m_{3}=M_{2} \mathrm{AGING}_{2}-M_{3} \mathrm{AGING}_{3}-M_{3} \mathrm{MORT}_{3}  \tag{12}\\
& m_{4}=M_{3} \mathrm{AGING}_{3}-M_{4} \mathrm{MORT}_{4} \tag{13}
\end{align*}
$$

The optimisation problem can now be restated as follows:

## Find

$F_{1}, F_{2}, F_{3}, F_{4}, M_{1}, M_{2}, M_{3}$ and $M_{4}$ to maximise the sum of the right hand sides of (8), (9), (12) and (13)
subject to
the equalities (3), (4), (6), (7), (10), (11)
and the inequalities
right-hand sides of (8), (9), (12), (13) $\geqslant 0$
and

$$
F_{1}, F_{2}, F_{3}, F_{4}, M_{1}, M_{2}, M_{3}, M_{4} \geqslant 0
$$

One the optimal structure of the population is determined the optimal removal strategy can be recovered from (8), (9), (12), (13). For a specified density, the optimal removal strategy can be determined by solving a linear programming problem. By specifying, in turn, a range of values for the density a series of linear programming problems can be solved. The results can then be compared to yield the optimal density and the corresponding optimal strategy at this density.

To illustrate this procedure we consider a population in a fixed area where the carrying capacity (cc) is 480 large stock units in total - this is the case in the province of Natal, South Africa (see later). The results are presented in Fig. 2 as the 'reference' graph where it is seen that the


- Reference $\quad-$ More sensitive $\quad$ Less sensitive

Fig. 2. Optimal removal rates (head $\mathrm{yr}^{-1}$ ) using the reference, more sensitive and less sensitive mortality functions, respectively.
population should be kept to a density of around $40-60 \%$. At this density the optimal strategy is to remove 9 males and 9 females from the third age group each year. Under current policy this is the preferred age group for capture and translocation. For current policy therefore we have determined the maximum sustainable harvest. There is some uncertainty as to the validity of some of the mortality functions. The mortality functions for age groups 1 and 2 are of particular concern as the function increases rather rapidly once density exceeds $60 \%$ of the carrying capacity. These functions were thus replaced by similar functions which assumed values about $10 \%$ greater than the original functions for densities of $50 \%$ and higher, i.e. the sensitivity of these functions to density has been increased. The problem of determining the optimal sustainable removal rate was then solved again. A similar procedure was followed for the mortality functions less sensitive to density. The results of both these exercises are also presented in Fig. 2. It is seen that the previously determined optimal strategy is not appreciably affected by these changes in the mortality functions.

In the next section we investigate whether this removal strategy is a good one from the perspective of achieving maximum growth in the newly established reserves.

## MAXIMISING THE GROWTH OF A NEWLY ESTABLISHED POPULATION

When density levels are low the dynamic model developed earlier is closely approximated by a non-homogeneous linear system of first-order differential equations. This is likely to be the case for the translocated population in the short term. This might even be true in the medium term if the current growth in the number of game reserves continues. An analysis of a linear model of the new populations is thus performed with a view to determining what input strategy would maximise its growth rate.

Removals from a well-stocked population would provide the source term for a new population. It was therefore assumed that the source term would comprise equal numbers of males and females in each age group. In this case it is only necessary to consider the female population as the rates affecting the corresponding male and female groups are the same.

From the original dynamic model it can be seen, for low population densities, that the female population can be represented by a linear system of differential equations of the form:
$\frac{\mathrm{d}}{\mathrm{d} t} \boldsymbol{F}=A \boldsymbol{F}+\boldsymbol{s} \quad \boldsymbol{F}(0)$ given
where the matrix $A$ is the following
$\left[\begin{array}{cccc}\left(-\mathrm{AGING}_{1}-\mathrm{MORT}_{1}-\mathrm{PRED}_{1}\right) & 0 & 0 & 0.5 \mathrm{FF}_{4} \\ \mathrm{AGING}_{1} & \left(-\mathrm{AGING}_{2}-\mathrm{MORT}_{2}-\mathrm{PRED}_{2}\right) & 0 & 0 \\ 0 & \mathrm{AGING}_{2} & \left(-\mathrm{AGING}_{3}-\mathrm{MORT}_{3}\right) & 0 \\ 0 & 0 & \mathrm{AGING}_{3} & -\mathrm{MORT}_{4}\end{array}\right]$

The coefficients of $A$ are constant for any specified density and are approximately constant for any variations in population such that the density remains less than $25 \%$ of the carrying capacity. The vector $s=$ $\left(\begin{array}{llll}0 & 0 & s_{1} & s 2\end{array}\right)^{\mathrm{T}}$ is the rate at which rhino are added to the population from an outside source. This rate is assumed constant and the total numbers fixed at $r$ animals per unit item. Thus we have:
$s_{1}+s_{2}=r$
The mathematical problem can now be stated as follows:

Find
$s_{1}, s_{2}$ to maximise $L(s)=F_{1}+F_{2}+F_{3}+F_{4}$, for arbitrary time $t>0$
subject to
(1), (2) and $s_{1}, s_{2}, F_{1}, F_{2}, F_{3}, F_{4} \geqslant 0$

To solve the problem we proceed as follows:
Let
$\boldsymbol{P}=\boldsymbol{F}+\boldsymbol{A}^{-1} \boldsymbol{S}$
then it follows from (1) that
$\frac{\mathrm{d}}{\mathrm{d} t} \boldsymbol{P}=\boldsymbol{A} \boldsymbol{P}$
Substituting data values into the matrix $A$ it is found that the eigenvalues $\lambda_{1}, \lambda_{2}, \lambda_{3}$ and $\lambda_{4}$ are real, non-zero and distinct. Corresponding eigenvectors $\boldsymbol{v}_{1}, \boldsymbol{v}_{2}, \boldsymbol{v}_{3}$ and $\boldsymbol{v}_{4}$ were then calculated to yield the general solution of (4):
$\boldsymbol{P}=c_{1} \mathrm{e}^{\lambda_{1} t} \boldsymbol{v}_{1}+c_{2} \mathrm{e}^{\lambda_{2} t} \boldsymbol{v}_{2}+c_{3} \mathrm{e}^{\lambda_{3} t} \boldsymbol{v}_{3}+\boldsymbol{c}_{4} \mathrm{e}^{\lambda_{4} t} \boldsymbol{v}_{4}$
for some constant vector
$\boldsymbol{c}=\left[\begin{array}{l}c_{1} \\ c_{2} \\ c_{3} \\ c_{4}\end{array}\right]$

Substituting back into (3) and solving for $\boldsymbol{F}$ gives:
$\boldsymbol{F}(t)=\left(\begin{array}{llll}\mathrm{e}^{\lambda_{1} t} \boldsymbol{v}_{1} & \mathrm{e}^{\lambda_{2} t} \boldsymbol{v}_{2} & \mathrm{e}^{\lambda_{3} t} \boldsymbol{v}_{3} & \mathrm{e}^{\lambda_{4} t} \boldsymbol{v}_{4}\end{array}\right) \boldsymbol{c}-\boldsymbol{A}^{-1} \boldsymbol{s}$
The vector $c$ can be determined from the initial conditions:
$\boldsymbol{F}(0)=\left(\begin{array}{llll}\boldsymbol{v}_{1} & \boldsymbol{v}_{2} & \boldsymbol{v}_{3} & \boldsymbol{v}_{4}\end{array}\right) \boldsymbol{c}-\boldsymbol{A}^{-1} \boldsymbol{s}$
Denoting the matrix $\left(\begin{array}{llll}\boldsymbol{v}_{1} & \boldsymbol{v}_{2} & \boldsymbol{v}_{3} & \boldsymbol{v}_{4}\end{array}\right)$ by $V$, we get:
$c=V^{-1} \boldsymbol{F}(0)+V^{-1} A^{-1} s$
and
$\boldsymbol{F}(t)=W V^{-1} \boldsymbol{F}(0)+\left(W V^{-1} A^{-1}-A^{-1}\right) s$
where
$W=\left(\begin{array}{llll}\mathrm{e}^{\lambda_{1} t} \boldsymbol{v}_{1} & \mathrm{e}^{\lambda_{2} t} \boldsymbol{v}_{2} & \mathrm{e}^{\lambda_{3} t} \boldsymbol{v}_{3} & \mathrm{e}^{\lambda_{4} t} \boldsymbol{v}_{4}\end{array}\right)$
To maximise $L(s), s$ needs to be chosen to maximise components relating to the second term in (5). Let $\left(b_{i j}\right)=\left(W V^{-1} A^{-1}-A^{-1}\right)$, then we need to maximise:
$\left(b_{13}+b_{23}+b_{33}+b_{43}\right) s_{1}-\left(b_{14}+b_{24}+b_{34}+b_{44}\right) s_{2}$
subject to the constraints given earlier. Denoting the multipliers of $s_{1}$ and $s_{2}$ in (6) by $\alpha$ and $\beta$ respectively, it is easily seen that for a maximum we require:
$\begin{array}{llll}s_{1}=r, & s_{2}=0 & \text { if } & \alpha>\beta \\ s_{1}=0, & s_{2}=r & \text { if } & \alpha<\beta\end{array}$
Numerical evaluation of the co-efficients of $\left(b_{i j}\right)$ revealed that $\beta>\alpha$ for all $t>1$ and that ( $\beta-\alpha$ ) increases with $t$. The results indicate that even allowing for inaccuracies in data the new population increases faster if a given number of animals in age group 4 are imported compared with the same number in age group 3. However, the sustainable yields from the source population are maximised when animals from the third age group only are translocated. In fact, for our source population with a carrying capacity of 480 large stock units, only 12 animals from the fourth age group can be translocated annually on a sustainable basis as opposed to about 18 from the third age group.

DETERMINING A TRANSLOCATION STRATEGY FOR THE WHOLE POPULATION

From the above results it is clear that a strategy aimed at maximising either the sustainable harvest of the founder population or the growth rate

TABLE 2
Initial values of the founder and translocated populations

| Group | Age (yrs) | Founder (head) | Translocated (head) |
| :--- | :--- | :--- | :---: |
| 1 | $0-1$ | 20 | 0 |
| 2 | $1-2$ | 16 | 0 |
| 3 | $2-8$ | 44 | 10 |
| 4 | $8+$ | 320 | 40 |

of the translocated population will not necessarily maximise the overall (founder + translocated) population growth rate. This matter is further explored by performing a number of simulations with a model that includes both an exporting (founder) population and a newly established importing (translocated) population. The dynamic model developed earlier is applied to the founder population with removals forming the input to a similar model for the translocated population. In this way the effects of a translocation policy on the total population can be evaluated.

Black rhinos of the southern-central subspecies available for translocation are found in the following game reserves in Natal: Hluhluwe, Umfolozi, Mkuzi, Ndumu and Itala (Brooks, 1989). There are a number of areas in southern Africa suitable for establishing or increasing populations of black rhino. Based on estimates for these areas the ecological carrying capacity of the total founder population is assumed to be 480 large stock units, that of the total translocated population 1920 large stock units and the initial values are given in Table 2. A period of 10 years was considered to be a suitable period over which to perform the simulations. After consideration of the results and discussion in the earlier sections of this paper it was decided to test translocation rates from 12 to 20 animals per year. To avoid social disruption as previously discussed the numbers translocated in any age class were equally divided among the sexes. For this reason only even numbers of total removals are considered. A translocation strategy can therefore be represented by two numbers $r_{3}$ and $r_{4}$, the numbers removed from the third and fourth age groups, respectively.

The results indicate that for any specified total translocation rate $r$ ( $=r_{3}+r_{4}$ ) the greater $r_{4}$ is, the greater will be the total population at the end of a 10 -year period. Thus, for a given total number of removals the best strategy is a pure strategy of translocating animals from age group 4 only and the worst strategy is the pure strategy of translocating animals from age groups 3 only. This is true for any given $r$ in the range of 12 to 20 . Some examples are shown in Table 3.

It would appear then that translocating adults (group 4) is more favourable to total population growth due to the immediate enhancement

TABLE 3
Performance of translocation strategies with nominal initial values

| Translocation strategy (head $\mathrm{yr}^{-1}$ ) |  | Population (head) |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Total | = | Founder | + | Translocated |
| $r_{3}$ | $r_{4}$ |  |  |  |  |  |
| 0 | 12 | 773 |  | 427 |  | 346 |
| 6 | 6 | 750 |  | 433 |  | 317 |
| 12 | 0 | 727 |  | 440 |  | 287 |
| 0 | 14 | 794 |  | 414 |  | 380 |
| 8 | 6 | 763 |  | 423 |  | 340 |
| 14 | 0 | 740 |  | 430 |  | 310 |
| 0 | 16 | 814 |  | 401 |  | 413 |
| 8 | 8 | 784 |  | 410 |  | 374 |
| 16 | 0 | 754 |  | 419 |  | 335 |
| 0 | 18 | 834 |  | 387 |  | 447 |
| 10 | 8 | 797 |  | 399 |  | 398 |
| 18 | 0 | 767 |  | 409 |  | 358 |
| 0 | 20 | 853 |  | 373 |  | 480 |
| 10 | 10 | 817 |  | 386 |  | 461 |
| 20 | 0 | 780 |  | 398 |  | 382 |

of fecundity in the new lower density environment. With sub-adults (group 3), there is some delay before they mature into fecund adults. After 10 years, for a translocation rate of 20 head per year, the total population attained by the two pure strategies differs by nearly $10 \%$.

Based on the nominal initial and parameters values it can be seen in Table 3 that translocating 20 adults (group 4) per year over a period of ten years will lead to a $90 \%$ increase in the total population (founder + translocated). Note that despite the removal of 20 animals per year the founder population declines by less than $10 \%$ over this period.

We now explore the dependence of these results on the initial and parameter values by performing further simulations. For various reasons including the preservation of an adequate gene pool, conservation authorities would find unacceptable any policy which leads to a severe decline in the founder population. For this reason any policy which leads to a decline in the founder adult population below 200 head is considered to be infeasible.

It was calculated earlier that if the founder population was to be kept in equilibrium at $60 \%$ of its carrying capacity then at least 18 animals can be translocated each year provided these animals were in the third age class. When the additional constraint was imposed on the problem that only animals from the fourth age group could be translocated then it was found

TABLE 4
Performance of translocation strategies for altered initial values

| Translocation strategy (head $\mathrm{yr}^{-1}$ ) |  | Population (head) |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
|  |  | Total | $=$ | Founder | + | Translocated |
| $r_{3}$ | $r_{4}$ |  |  |  |  |  |
| 10 | 6 | 729 |  | 365 |  | 364 |
| 16 | 0 | 712 |  | 335 |  | 377 |
| 12 | 6 | 737 |  | 349 |  | 388 |
| 14 | 4 | 732 |  | 354 |  | 378 |
| 16 | 2 | 727 |  | 359 |  | 368 |
| 18 | 0 | 722 |  | 363 |  | 359 |
| 14 | 6 | 744 |  | 333 |  | 411 |
| 20 | 0 | 730 |  | 348 |  | 382 |

that only 12 animals could be removed on a sustainable basis. These results suggest that if the initial structure of the founder population were such that the population could export 18 animals each year on a sustainable basis then there is a possibility that this would also be the best policy for the total population. Thus the simulations were repeated with this considerably changed initial structure. The initial values for the translocated population remains unchanged. This initial structure was expected to be more favourable to a policy of exporting animals from age group 3. Although a number of strategies were now infeasible, the results (table 4) for feasible strategies showed a similar pattern to those for the original initial values.

Further experimentation with the initial and parameter values was undertaken. In the case of the parameter values the mortality rates were increased by $20 \%$ and the fecundity rate simultaneously decreased by the same percentage. All the results strengthened the conclusion that, provided a strategy remained feasible, the greater the proportion of translocated animals that are in the fourth age group the more rapidly the total population will increase. However, the results also indicate the need for some caution regarding the actual number translocated per year. For example the translocation of 20 adults per year is no longer feasible for the changed set of parameter values. An inspection of the results from all our simulations indicated that a more cautious policy would be the translocation of 14 adults per year. With the nominal parameter values the total population would still experience an appreciable increase ( $75 \%$ ) over the 10 -year period.

## CONCLUSION

The stocking density and translocation strategy required to maximise the sustainable yield from a reserve well-stocked with rhino has been deter-
mined for the nominal parameter values. However, further analysis showed that following such a policy would not maximise the growth rate of the southern African population as a whole. Thus the survival prospects of black rhino would be enhanced by a change in the present policy of translocating animals from the third age group only to a policy of translocating as many from the fourth age group as the source population can tolerate.

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