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Using models in the management of Black rhino populations

Joris P.G.M. Cromsigt [a,*], John Hearne [b], Ignas M.A. Heitkönig [a], Herbert H.T. Prins [a]

[a] *Tropical Nature Conservation and Vertebrate Ecology Group, Wageningen University, Bornsesteeg 69, 6708 PD Wageningen, Netherlands*

[b] *School of Mathematics, Statistics and Information Technology, University of Natal, 3201 Scottsville, Pietermaritzburg, South Africa*

Abstract

A study was undertaken, modeling Black rhino, *Diceros bicornis*, populations from Hluhluwe-Umfolozi Game Reserve and Mkuzi Game Reserve, Republic of South Africa. This study had two specific goals. Firstly, we tried to find a simple model to predict the population number in the following year and give insight in the number of animals that can be removed from the population. Secondly, the use of different models gave us the opportunity to evaluate the effect of small differences in model structure on the outcome of the models. Five different models were tested, mainly focusing on the structure of density dependence. The density dependent model, that incorporated stronger density dependence at high densities, fitted best to the observed census values. The study, furthermore, indicated that the population in Hluhluwe-Umfolozi is stabilizing. The situation in Mkuzi was not that clear. Based on these results, managers should therefore be more careful with removing animals from this population. Finally the results clearly showed that different model structures can result in very different model outcomes. Besides in the values of the model parameters, this was also shown by different values for the population number where the yearly increase is maximal. Based on these results it does not seem wise to base management decisions solely on the outcome of one model. Therefore, we strongly encourage managers to compare the outcome from different model structures, based on different biological assumptions. © 2002 Elsevier Science B.V. All rights reserved.

Keywords: Black rhino; Density dependence; *Diceros bicornis*; Endangered species management; Population modeling; South Africa

1. Introduction

In the last few decades demographic models became an important tool in decision-making for the management of wildlife populations. A wide variety of examples are available where models are used as an evaluation tool for different management directions. These examples are found in

* Corresponding author. Tel.: +31-317-483174.
E-mail address: jcromsigt@hotmail.com (J.P.G.M. Cromsigt).

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the control of populations that cause socioeconomic concerns (McCarthy, 1996; Barlow et al., 1997) as well as in the conservation of endangered species (Crouse et al., 1987; Lande, 1988).

The development of the field of population viability analysis (PVA, Boyce, 1992) during the 1980s has stimulated the use of models by managers of endangered species enormously. Organizations like the US Fish and Wildlife Service and the World Conservation Union (IUCN) have used PVA for a wide variety of species (Boyce, 1992; Lacy, 1993). Especially the development of different commercial PVA software packages (Lindenmayer et al., 1995) has made the use of such models easily accessible to wildlife researchers, which has led to their widespread use (Lindenmayer and Possingham, 1995; Moehlman et al., 1996; Howells and Edwards-Jones, 1997).

However, Beissinger and Westphal (1998) discuss that the use of demographic models in PVA should be regarded with more caution. They warned that differences in model structure could have a major impact on model outcome. Through the emphasis on stochasticity in the use of PVA, the attention for deterministic factors has disappeared to the background. Especially the way effects of density are incorporated into the model seems to be of crucial importance (Mills et al., 1996; Brook et al., 1997). Furthermore, models are often used without first analyzing the data to explore what kind of model fits the observed data best. Therefore, Beissinger and Westphal (1998) suggest that researchers use different models starting with simple deterministic models before stochasticity is considered. The model that fits the observed data best should eventually be used to make predictions for management purposes.

The following study explores this approach of using different models for data on the Black rhino. Black rhino populations in Africa declined drastically over the last 20–25 years from around 70 000 individuals to approximately 2500 (Gakahu, 1993). The situation in South Africa, however, is promising with poaching currently a far less serious problem. The last estimate from the IUCN/SSC/African rhino Specialist Group in 1998 declared a total population size for the Black rhino in South Africa of 1043 individuals; this is approximately 40% of the worldwide population. Therefore South Africa is seen as an important stronghold for the survival of the species. Current management actions aim at sustaining a large Black rhino population in South Africa (Brooks, 1989 Conservation plan for the Black rhinoceros *Diceros bicornis* in South Africa, the TVBC States and SWA/Namibia. Unpublished report, Natal Parks Board, Pietermaritzburg, South Africa). An important tool in achieving this goal is translocation of individuals from areas with high densities to other areas with a suitable habitat (Hearne and Swart, 1991).

In deciding how many individuals can be removed from a population it is important to have a reliable estimate of the population number. To achieve these estimates yearly censuses are executed. These yearly censuses have two main problems. Firstly, they are expensive; a model that can predict the number of individuals in the following year, so that censuses do not have to be executed yearly, would be of great help (Goodman, Kwazulu Natal Nature Conservation Service, personal communication). A second important problem is the impression that the census methods give a biologically unrealistic variation in population numbers between years (Balfour, Kwazulu Natal Nature Conservation Service, personal communication). This variation could be intrinsic to the statistical methods that are used in determining the census population number. This variation is mainly caused by the small amount of data available, especially in the case of a low-density species like the Black rhino.

The present study has two goals. Firstly, we try to find a simple model that can predict the population number in the following year and give insight in the number of animals that can be removed from the population. Secondly, the use of different models gives us the opportunity to evaluate the effect of small differences in model structure on the outcome of the models, as suggested by Beissinger and Westphal (1998). In this respect, we specifically focused on the structure of density dependence.

2. Methods

2.1. Data

We used recent data originating from two sites in the northeastern part of South Africa, namely, Mkuzi Game Reserve and Hluhluwe-Umfolozi Game Reserve. The data set from Mkuzi GR existed of population size censuses from 1989 to 1998. Data on translocation of individuals, removals and/or introductions, were available from 1989 to 1998. The data set from Hluhluwe-Umfolozi GR was smaller. It consisted of population size censuses from 1990 to 1997 and data on translocation of individuals from 1990 to 1998. At the time of finishing this study a census number for 1998 for the population in Hluhluwe-Umfolozi was not yet available.

Table 1
Description of the different models on population size development that were explored

Model	Equation	Parameters
Exponential model	$N_{t+1}=N_t+r\times N_t$	$N(0)$, r
Logistic model	$N_{t+1}=N_t+N_t\times r \times(1-N_t/K)$	$N(0)$, r, K
Fowler model	$N_{t+1}=N_t+N_t\times r \times(1-(N_t/K)^n)$	$N(0)$, r, K, n
Logistic translocation model	$N_{t+1}=N_t+N_t\times r \times(1-N_t/K) -h$	$N(0)$, r, K
Fowler translocation model	$N_{t+1}=N_t+N_t\times r \times(1-(N_t/K)^n) -h$	$N(0)$, r, K, n

The parameters in the final column are the parameters, of which the value was optimized. Parameter h (number of removals minus number of introductions) had a known input value and is, therefore, not included in the last column. The parameters are explained as follows: r, the specific growth rate; N_t, the population number at time t; K, the carrying capacity; n, parameter which makes the relation between N_t and $(1-(N/K)^n)$ curvilinear.

2.2. General approach

We based our methods on an approach that was proposed by Fatti and Corrigall (Fatti and Corrigall, 1997. How many rhinos are there in the Hluhluwe-Umfolozi Game Reserve? Unpublished paper, ORSSA Conference, Illovo Beach, South Africa). Their approach assumes the following relationship between the modeled population number, $N(t)$, and the observed census population number, $P(t)$:

$$P(t)=N(t)+\varepsilon(t) \quad (1)$$

where $\varepsilon(t)$ is an error term that shows the difference between $P(t)$ and $N(t)$. If one assumes that this error term is only the result of random observational errors, it has expectance 0 and variance σ^2.

The best estimates for the initial population size $N(0)$ and the different model parameters of the model that predicts $N(t)$ are computed by minimizing:

$$\Sigma_{t=1}^{n}\varepsilon_t^2 \quad (2)$$

We minimized this sum of squares using the solver function in EXCEL (version Microsoft® EXCEL 97). With these estimates of $N(0)$ and the parameters of the model the best estimates for the population size at times 1 to n can be computed.

We applied this approach to different models (see below, Table 1) that predict $N(t)$ to find out what the influence of differences in model structure is on the outcome of the model. We specifically focused on the structure of density dependence.

2.3. Models

In all, we explored five models on population size development (Table 1). We followed a step-by-step approach, as suggested by Beissinger and Westphal (1998), to find a model that gives a reliable estimation of the population number in the following year. We started our exploration with a simple exponential growth model i.e. the Black rhino population grows with a constant specific growth rate r. This exponential model was used as a null against which to compare the

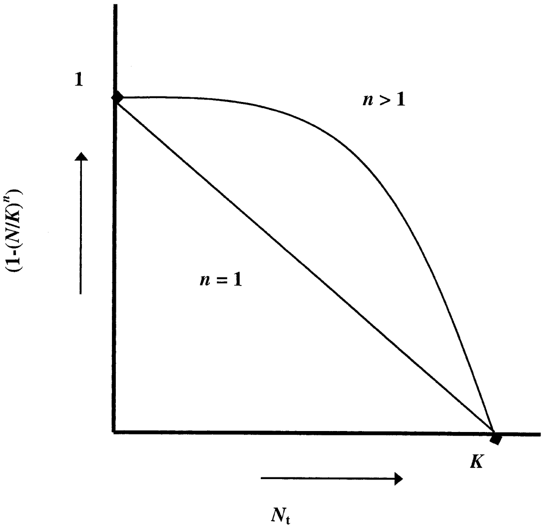

Fig. 1. Relationship between the factor that determines the intensity of density-dependence, $(1-(N/K)^n)$, and population size, N_t. If n equals 1 we get the logistic equation. If n is greater than 1 we get, what we have defined as the Fowler model. The size of n determines how steep the curve of the Fowler model declines.

density dependent models, which are introduced later in this chapter.

The 'exponential model' assumes that the population can grow endlessly. Black rhino populations in Hluhluwe-Umfolozi GR as well as Mkuzi GR originate from very small remnant populations and have both experienced strong increases in the last decades. An ongoing growth of the populations in these areas is, however, not very realistic. At high levels of density, the Black rhino population will become limited by a lack of natural resources and the population will possibly stabilize near an equilibrium density, often called the carrying capacity K. To explore whether the populations in Hluhluwe-Umfolozi GR and Mkuzi GR are approaching this density-dependent phase the simplest and most widely used equation, describing density dependence, the logistic equation, was used. We named this the 'logistic model'.

As early as 1981, however, Fowler suggested an important drawback of the logistic equation. He noted that the logistic equation assumes a linear relationship between N_t and the factor that determines the strength of the density-dependence, $(1-N/K)$, Fig. 1 ($n=1$). For large animals, however, he suggested that it is more realistic to assume that density-dependent factors play a more important role closer to the carrying capacity. To simulate this assumption an extra parameter, n, was introduced in the original logistic equation. This parameter n makes the relation between N_t and $(1-(N/K)^n)$ curvilinear and in this way makes the contribution of this factor relatively large close to the carrying capacity (Fig. 1, $n>1$). Because this last model is based on suggestions made by Fowler (1981), we called this model the 'Fowler model'. Next to this strong density dependence at high densities, the Fowler model also restricts the population growth rate at low densities. In this way it overcomes the problem of the logistic equation which results in unrealistically high estimates for the intrinsic growth rate for large animals, when extrapolating observed population numbers to zero.

As mentioned in the Section 1, however, high-density populations of the Black rhino are used as source populations of which animals are removed. This is especially the case for the population in Hluhluwe-Umfolozi. Both the 'logistic model' and the 'Fowler model' are therefore extended to models that include translocation of animals. This was achieved by adding a factor h to both models. The parameter h is defined by the number of removals minus the number of introductions per year. The fourth and fifth model in Table 1 show the 'logistic and fowler model', respectively, with translocation of animals being included. These models were named 'logistic translocation model' and 'Fowler translocation model', respectively.

2.4. Output

The results from the different models were evaluated by means of the following output. Firstly, the correlation coefficient of the modeled and census population numbers was calculated for the different models. It must be noted that the census numbers are auto-correlated and, for this reason alone, result in very high correlation coefficients. Therefore, in this study, the correlation coefficients are used to compare the fit of the different

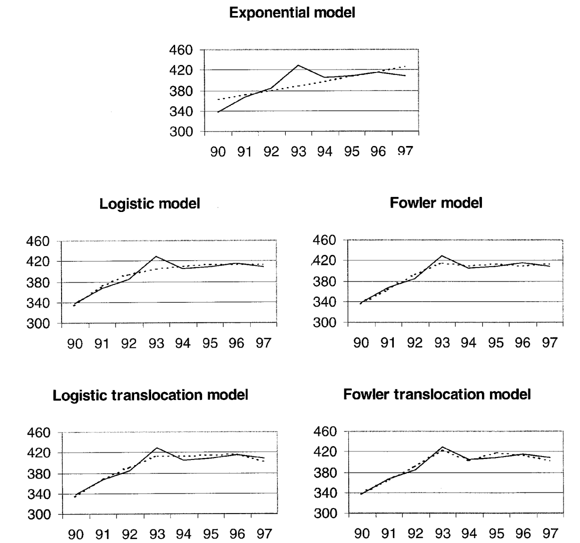

Fig. 2. Results of the analysis of the 5 models, as described in Table 1, with the data from Hluhluwe-Umfolozi Game reserve. The figures show the observed (solid line) and predicted (dashed line) population number on the y-axis against time in years.

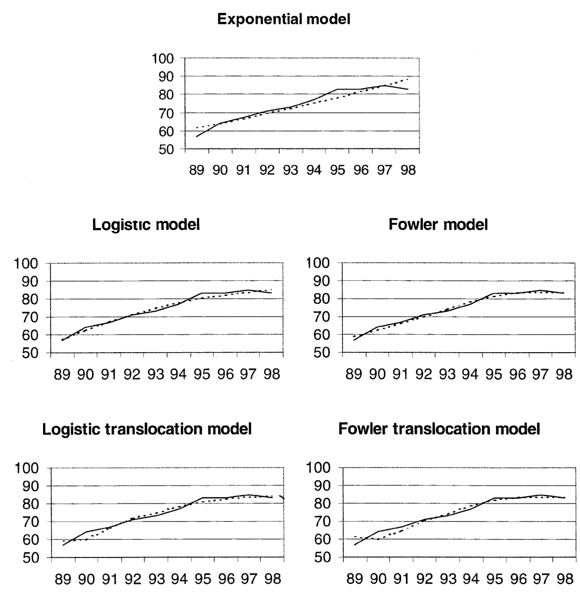

Fig. 3. Results of the analysis of the 5 models, as described in Table 1, with the data from Mkuzi Game reserve. The figures show the observed (solid line) and predicted (dashed line) population number on the y-axis against time in years.

models, rather than focusing on the absolute values of the correlation coefficients.

Secondly, the optimized values for the parameters in the different models (Table 1) give an idea on how realistic a specific model is. If, for example, the correlation coefficient for a specific model is very high, but the optimized value for the growth rate is biologically unrealistic, the model used is not very realistic. Finally, the standard deviations for the different ε's for the models were calculated. These standard deviations give an idea of the variation in the differences between modeled and census population numbers.

3. Results

The results of the optimization process of the different models to the observed data are presented for the data of Hluhluwe-Umfolozi GR and Mkuzi GR in Figs. 2 and 3 and Tables 2 and 3, respectively. The results are outlined below for each area separately.

3.1. *Hluhluwe-Umfolozi game reserve*

Fig. 2 and Table 2 show the results of the optimization process for the data of Hluhluwe-Umfolozi Game Reserve. The results clearly show that the 'Exponential model' (Table 2) did not fit as good as the other, density-dependent, models. It had a correlation coefficient of 0.76, compared with correlation coefficients higher than 0.90 for the other models, and a high standard deviation for the residual ε of 19.6.

When we compared the two density-dependent models (Table 2, 'logistic and fowler model'), results showed that the 'fowler model' fitted better than the 'logistic model'. This is shown by the slightly higher correlation coefficients for these models, differences of 0.03 and 0.02. However, the values of the specific growth rate r had unrealistically high values for the logistic model (0.59 and 0.47). For the 'fowler model', however, these parameters had realistic values of 0.08 and 0.1. This effect of the fowler model on the growth rate has already been discussed in Section 2.

The last step in building the simple model was including data on translocation. This improved

Table 2
Results of the optimization process for the models, outlined in Table 1, for Hluhluwe-Umfolozi GR

Model	r	K	N	N(98)	c.c.	s.d.
Exponential model	0.02	–	–	438	0.76	19.6
Logistic model	0.59	414	–	414	0.94	10.3
Fowler model	0.08	412	22	411	0.97	7.3
Logistic translocation model	0.47	451	–	406	0.96	8.0
Fowler translocation model	0.1	423	28	416	0.98	5.4

The symbols are explained as follows: N_t, the population number at time t; r, the specific growth rate; K, the carrying capacity; n, parameter which makes the relation between N_t and $(1-(N/K)^n)$ curvilinear; N(98), the predicted population number for 1998, based on the optimized values of the model parameters; c.c., the correlation coefficient between observed and predicted population numbers; s.d., the standard deviation of the remaining ε's.

Table 3
Results of the optimization process for the models, outlined in Table 1, for Mkuzi GR

Model	r	K	N	N(99)	c.c.	s.d.
Exponential model	0.04	–	–	92	0.95	3.0
Logistic model	0.25	89	–	86	0.99	1.5
Fowler model	0.06	84	19	84	0.99	1.3
Logistic translocation model	0.41	85	–	85	0.98	2.1
Fowler translocation model	0.1	84	10	84	0.97	2.3

The symbols are explained as follows: N_t, the population number at time t; r, the specific growth rate; K, the carrying capacity; n, parameter which makes the relation between N_t and $(1-(N/K)^n)$ curvilinear; N(99), the predicted population number for 1999, based on the optimized values of the model parameters; c.c., the correlation coefficient between observed and predicted population numbers; s.d., the standard deviation of the remaining ε's.

the fit of the model to the observed data (Table 2). The values of the correlation coefficients became larger and the standard deviations smaller.

We define the best fit as the model with the highest correlation coefficient and the lowest standard deviation. For the data from Hluhluwe-Umfolozi the 'Fowler translocation model' fitted best. The model predicts a population number of 416 animals in 1998 with a yearly growth rate of 10% and a carrying capacity of 423 (Table 2). The parameter n of the Fowler equation showed the high value of 28 (Table 2).

3.2. Mkuzi game reserve

Fig. 3 and Table 3 show that the results for the data of Mkuzi Game Reserve were partly the same as those for Hluhluwe-Umfolozi. The results from this data set also show that the Fowler model gave a better fit to the observed values than the logistic model. This, however, did not become very clear if the correlation coefficients were considered. The values of the correlation coefficients for Fowler and logistic models were equal (Table 3. 'Fowler model and logistic model') or differed slightly (Table 3. 'Fowler and Logistic translocation models'). The difference became clear again when the values of the intrinsic growth rate were considered. These values were unrealistic for the 'Logistic model' (Table 3) but realistic for the 'Fowler model' (Table 3).

In contrast with the results from Hluhluwe-Umfolozi, the 'exponential model' (Table 3) showed a high correlation coefficient of 0.95 for the data from Mkuzi. The value of the correlation coefficient for this model was still lower than for the density dependent models (Table 3) but the difference was small.

A second contrast with the results from Hluhluwe-Umfolozi was that including the extra data on the translocation of individuals did not improve the fit (Table 3).

The ‘Fowler model’ showed the best fit for the data from Mkuzi. Table 3 shows the values of the parameters for this model. A population number of 84 was predicted by the model for 1999. The population, as predicted by this model, grows with a specific growth rate of 6% and has a carrying capacity of 84 animals. For this data set n was 19.

4. Discussion

Below, the results are discussed according to the two goals of this study, as presented in Section 1; trying to find a model that can predict the population number in the following year and evaluating the effect of small differences in model structure on the outcome of the models.

4.1. Finding the proper model

As shown in the Section 3, the ‘Fowler model’ fitted best to the population censuses of both reserves. There were, however, two main differences between the results from Mkuzi GR and those from Hluhluwe-Umfolozi GR. For Mkuzi GR, in contrast to the results from Hluhluwe-Umfolozi GR, the fit did not improve with additional data on translocation of individuals. A more detailed analysis shows that translocation in Mkuzi GR took place only in 4 out of 10 census years. Five, 8, 1 and 2 individuals were translocated in 1989, 1990, 1991 and 1993, respectively. This corresponds to 8.8, 10.9, 1.5 and 2.7% of the observed population. In Hluhluwe-Umfolozi GR animals were removed annually, with an average of 2.6%. Hence, one would expect the population in Mkuzi GR to be affected by translocation in a similar way as the population of Hluhluwe-Umfolozi GR, especially in the years 1989 and 1990. The fact that this is not shown by a better fit of the models, incorporating translocation, suggests that there is an anomaly in the population censuses of especially 1989 and 1990. The censuses of these years are most probably overestimates.

The second difference concerns the quality of the fit of the exponential function to the census population numbers. The fit of this function is moderate for the data from Hluhluwe-Umfolozi GR. Only 76% of the variation in the census values can be explained by an exponential function, in contrast with 94% or more for the density dependent functions. This result indicates that the population in Hluhluwe-Umfolozi GR may have approached the equilibrium density. The results for Mkuzi GR are far less clear. The fact that the population number shows more or less the same value for the last four years gives the impression that the population is stabilizing. The optimization results, however, do not strongly support this notion. The census values show a very reasonable fit for the exponential function. The exponential function explained 95% of the variation in the census values. The density dependent functions show a slightly better fit of 99%. However, because there were only eight regression points, this small difference could be insignificant. On the other hand, this small amount of regression points can also mask the occurrence of density dependence, because the number of regression points with stable population numbers is to small for a clear difference in fit between the exponential and density dependent functions. Moreover, the transition from a growing to a stable population can occur over a narrow range in density. So, for the population in Mkuzi GR, it is difficult, based on the results of our study, to give a decisive answer to the question whether the population is already stabilizing.

4.2. The effect of small differences in model structure

We show the effect of relatively small differences in model structure by comparing the results from the ‘Fowler model’ and the ‘logistic model’. Results from both areas clearly show that the ‘fowler model’ gives a better fit than the ‘logistic model’. This is especially pronounced by the values of the growth rates. The ‘Logistic model’ only results in a good fit when values for the growth rate are unrealistically high (25% or more), as already discussed in the (Section 2) section. The ‘Fowler model’ shows a high correlation coefficient with realistic values of 6–10% for the growth rate, resembling those observed in the field

(Balfour, Kwazulu Natal Nature Conservation Service, personal communication). Other studies on rhinoceros already found comparable growth rates varying between 4.7 and 11% (Hitchins and Anderson, 1983; Moehlman et al., 1996; Loon and Polakow, 1997).

This study therefore supports Fowler (1981) contentions. The assumption of a nonlinear relationship between population size N and density-dependence results in a better, more realistic, fit than when a linear relationship is assumed (logistic equation). Furthermore the high values of n, predicted by the optimization process for both data sets, mean that the impact of density is only significant very close to the equilibrium density. This difference between the 'Fowler and the logistic model' has a direct implication for the management of the Black rhino. One of the current management goals is to maximize the total Black rhino population growth rate. To achieve this goal, populations should be held at a level where the increase in number of individuals is highest. Animals that have to be removed to keep the population at this level can be used to establish new or replenish small populations. This management regime was already proposed for Hluhluwe-Umfolozi GR by Hitchins and Anderson (1983) and is currently practiced. The two density dependent models, however, predict a totally different population number for which the yearly increase is maximal, N_{max}. For the 'logistic model' N_{max} equals $1/2K$. For the 'Fowler model' it equals:

$$N_{max} = \sqrt[n]{K^n/(n+1)}.$$

We calculated the N_{max} for Hluhluwe-Umfolozi GR and Mkuzi GR using the output presented in Tables 2 and 3 for the models that fitted best (423 for K and 28 for n for Hluhluwe-Umfolozi GR; 84 for K and 19 for n for Mkuzi GR). This resulted in an N_{max} for the 'logistic model' of 212 and 42 for Hluhluwe-Umfolozi GR and Mkuzi GR, respectively. However, for the 'Fowler model' these values are 375 and 72. Clearly there is a big difference between the two models regarding the number of animals that have to be removed from both populations to achieve maximal yearly increase. According to the 'Logistic model' around 50% of the animals should be removed (from total population sizes of 416 and 84 for Hluhluwe-Umfolozi GR and Mkuzi GR, respectively), instead of 10–15% according to the 'Fowler model'. So according to this study, in which the 'Fowler model' showed the best fit, the populations should be held 10–15% below equilibrium density. Comparing this result with the average removal rate during the past census years (2.6 and 3.3% for Mkuzi GR and Hluhluwe-Umfolozi GR, respectively), it argues for an increase in the yearly removal rate of around 10%, especially for Hluhluwe-Umfolozi GR, where the population seems to be around equilibrium density. So according to the 'Fowler model' the population does not have to be reduced much below equilibrium density to achieve maximum population growth rate. However, in this respect, it has to be noted that it can take some time before a population of large mammals responds. Density dependence in large mammals typically involves aspects that result in delayed effects after intervention in a population has taken place. These aspects e.g. include retarded age at first reproduction and a depression of high-quality vegetation after a period of high herbivore density, which takes some time to recover.

The example above shows the large difference in model predictions between two models with a relatively small difference in model structure. This result emphasizes that the choice of a model can have a big impact on management directions and that this choice should, whenever possible, be made on the basis of sound arguments. Moreover, the results from our study strongly support the point made by Beissinger and Westphal (1998) that models should be used with care in the management of wildlife populations. A strong interaction between managers and researchers and the comparison of the outcome of several model structures is crucial.

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References

Barlow, N.D., Kean, J.M., Briggs, C.J., 1997. Modelling the relative efficacy of culling and sterilization for controlling populations. Wildl. Res. 24, 129–141.

Beissinger, S.R., Westphal, M.I., 1998. On the use of demographic models of population viability in endangered species management. J. Wildl. Manage. 62, 821–841.

Boyce, M.S., 1992. Population viability analysis. Ann. Rev. Ecol. Syst. 23, 481–506.

Brook, B.W., Lim, L., Harden, R., Frankham, R., 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island Woodhen *Tricholimnas sylvestris* (Sclater). Biol. Conserv. 82, 119–128.

Crouse, D.T., Crowder, L.B., Caswell, H., 1987. A stage-based population model for loggerhead sea turtles and implications for conservation. Ecology 68, 1412–1423.

Fowler, C.W., 1981. Density dependence as related to life history strategy. Ecology 62, 602–610.

Gakahu, C.G., 1993. African rhinos: current numbers and distribution. In: Ryder, O.A. (Ed.), Proceedings of the International Conference on Rhinoceros Conservation and Biology. Zoological Society of San Diego, San Diego, pp. 160–163.

Hearne, J.W., Swart, J., 1991. Optimal translocation strategies for saving the Black rhino. Ecol. Model. 59, 279–292.

Hitchins, P.M., Anderson, J.L., 1983. Reproduction, population characteristics and management of the black rhinoceros *Diceros bicornis minor* in the Hluhluwe/Corridor/Umfolozi Game Reserve Complex. S. Afr. J. Wildl. Res. 13, 78–85.

Howells, O., Edwards-Jones, G., 1997. A feasibility study of reintroducing wild boar *Sus scrofa* to Scotland: are existing woodlands large enough to support minimum viable populations. Biol. Conserv. 81, 77–89.

Lacy, R.C., 1993. VORTEX: a computer simulation model for population viability analysis. Wildl. Res. 20, 45–65.

Lande, R., 1988. Demographic models of the northern spotted owl (*Strix occidentalis caurina*). Oecologia 75, 601–607.

Lindenmayer, D.B., Possingham, H.P., 1995. The conservation of arboreal marsupials in the montane ash forests of the central highlands of Victoria, south-eastern Australia. VII. Modelling the persistence of Leadbeater's Possum in response to modified timber harvesting practices. Biol. Conserv. 73, 239–257.

Lindenmayer, D.B., Burgman, M.A., Akçakaya, H.R., Lacy, R.C., Possingham, H.P., 1995. A review of the generic computer programs ALEX, RAMAS/space and VORTEX for modelling the viability of wildlife metapopulations. Ecol. Model. 82, 161–174.

Loon, R., Polakow, D., 1997. A conceptual model for assessing the economic feasibility of harvesting African rhinoceros horn. S. Afr. J. Sc. 93, 237–240.

McCarthy, M.A., 1996. Red kangaroo (*Macropus rufus*) dynamics: effects of rainfall, density dependence, harvesting and environmental stochasticity. J. Appl. Ecol. 33, 45–53.

Mills, L.S., Hayes, S.G., Baldwin, C., Wisdom, M.J., Citta, J., Mattson, D.J., Murphy, K., 1996. Factors leading to different viability predictions for a Grizzly Bear data set. Conserv. Biol. 10, 863–873.

Moehlman, P.D., Amato, G., Runyoro, V., 1996. Genetic and demographic threats to the Black rhinoceros population in the Ngorongoro crater. Conserv. Biol. 10, 1107–1114.