
RISK ASSESSMENT IN CONSERVATION BIOLOGY

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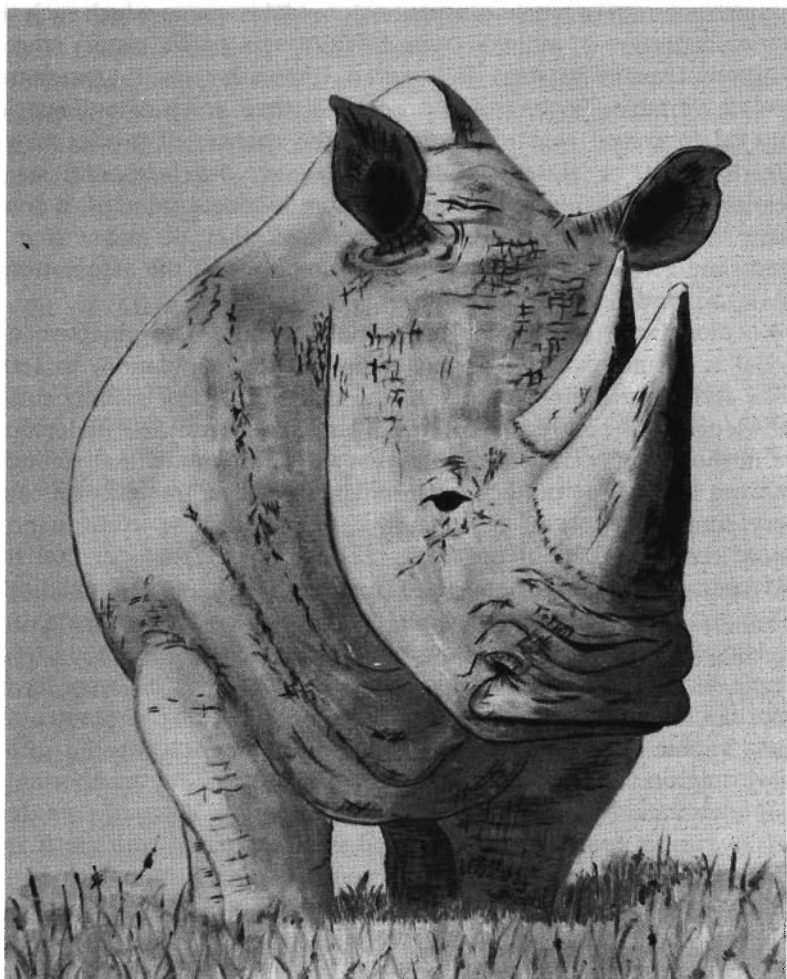
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2 White rhinoceros on Ndumu Reserve



To introduce the concepts we talked about in Chapter 1 in a more concrete fashion, we shall develop a stochastic model for a population of white rhinoceros (*Ceratotherium simum simum*). These particular animals live on the Ndumu Game Reserve in Africa and their demography is described by Conway and Goodman (1989). Ndumu is a small game reserve of about 116 km² on the Mozambique coastal plain. The population of white rhinoceros was established with the introduction of 20 individuals between 1961 and 1963. Currently, the population is increasing in size. Our aim is to build a model for the change in size of this population, but before we begin to write equations we shall introduce some general concepts that will be useful for this model and later on.

The complexity of a model must be a compromise between reality, available data and the use to which the model is put. When data concerning a population are scarce, any model of it must by necessity be simple. An unstructured, or single-dimensional, model is one in which such things as the proportion of individuals in different ages or life history stages, or in different spatial patches, are ignored. Population size is represented as a single variable, hence the terms unstructured and single-dimensional. Survival from one year to the next or the chances of producing viable offspring may be closely related to the age, developmental stage or location of an individual. When unstructured models are used, it does not mean that these factors are unimportant. Rather, it means that their effects are accounted for by a set of assumptions. If the assumptions are valid, the model will be adequate.

No model can replace the acquisition of data. The objective of the model is to improve our understanding of the population, to test our ideas and acquire more data with the ultimate aim of gaining sufficient knowledge to preserve the species. Thus, when data and understanding are in short supply, it is advisable to begin with a model that summarizes what we know. The predictions it makes should be treated with caution. Very simple models of population dynamics can be constructed that ignore considerations of the ages, life history or developmental stages, and spatial structure of species. The barest details of population distributions or individual behaviour may provide enough information to explain, in general terms, how population size is regulated. Usually, simple models for demographic risk assessment will be most useful to help us understand generalities such as the effect of environmental and demographic variability on population growth rates, or the effect of harvesting on expected population size. One of the most important uses of models is that they focus attention on important items of data that are missing, or on items of data that need to be estimated with much greater precision. This focus is related to sensitivity analysis, which we shall address in Chapter 3.

It is worth noting that simple models may in fact require as much information as models that account for details of population structure. If

there are fewer parameters in a model, there are more assumptions. For example, if we ignore the different ages of individuals, we assume age plays no important part in the average chances of an individual dying or reproducing. If we are to judge the validity of that assumption, we would need information on the relationship between age and vital rates.

As a result, conventional wisdom dictates that we should place little confidence in the accuracy of quantitative predictions made from simple, general models. These models often proceed from assumptions that are greatly oversimplified and are usually employed to generate qualitative answers to very general questions. However, if a model diverges from the details of the real world, it does not necessarily follow that it will be a poor predictor of ensemble properties such as the average population size at some time in the future, or the chances of crossing a given population size threshold. The values we assign to the parameters, and their relationships to one another in the model, embody all assumptions. We do not suggest that the kinds of models described below are sufficient for every case. Rather, when time is short and data are critically scarce, they may be the only methods. Conservation biology often deals with cases where time and resources are critically scarce. When urgent decisions are required and you have to decide one way or the other, it may be better to use a crude model than to use intuition alone.

2.1 FORMULATING A BIRTH-AND-DEATH MODEL

The total number of individuals (N) in a fixed region of space can only change because of births, deaths, immigration and emigration. Change in population size over a discrete interval of time from t to $t + 1$ can be described by the equation

$$N_{t+1} = N_t + B - D + I - E \quad (2.1)$$

where B and D are the total number of births and deaths respectively during the time interval from t to $t + 1$, while I and E are the total number of individuals entering and leaving the region during the same time interval. Of course, we may replace immigration and emigration by processes that are mediated by humans, such as introductions, harvesting or poaching. Change in population size from t to $t + 1$ is given by $N_{t+1} - N_t$.

For the moment, let us assume there is no immigration to, or emigration from, the rhinoceros population. We can rewrite Equation (2.1) in terms of the difference between the average per capita rate of reproduction, or birth rate, (b) and the average per capita death rate, (d). The two parameters, b and d , can also be considered as the probability of having offspring and the probability of dying between one time and the

next. We can calculate, in continuous time, the average rate of change in population size:

$$\frac{dN}{dt} = (b - d)N \quad (2.2)$$

where, by definition, the time interval, dt , had been reduced to become infinitely small. Thus, Equation (2.2) describes the instantaneous rate of population size change. This equation can be solved by integration to give the familiar equation for exponential population growth. At some time, t , in the future, given the initial population size, N_0 , the birth rate and the death rate, the size of the population will be

$$N_t = N_0 e^{(b-d)t} \quad (2.3)$$

where 'e' is a constant representing the base of natural logarithms. This equation may be written as

$$N_t = N_0 e^{rt}. \quad (2.4)$$

The difference between the birth and death rates, represented by the term r , is called the 'intrinsic rate of natural increase'. When the birth rate is greater than the death rate, the population will grow exponentially, irrespective of its initial size (unless, of course, the initial population size is zero).

We may replace the term e^r with the term λ (lambda). Alternatively, we let r be equal to the natural log of λ . λ is called the 'finite rate of increase' of a population and it is also called R . It represents the proportion by which the population changes at every time step. For example, if $\lambda = 1.1$, then the population increases by 10% every time step; if it is 0.5, the population decreases by half.

We can use this opportunity to introduce some more useful terminology. A **dependent variable** (or **state variable**) is the thing in the model you want to estimate (such as population size). It is the entity which 'depends' on the other factors. These other factors are called **independent variables**. A model is an equation describing the relationship between the independent variables and the dependent ones. The operations encapsulated in the equation describe the way you think the state variable is modified by the independent variables. **Parameters** are those components of a model that mediate the relationship between independent and dependent variables.

Equation (2.3) above constitutes a model, a mathematical expression that allows us to estimate the population size at any time in the future. It has one dependent variable, N , one independent variable, t , and two parameters, b and d . N_0 is an initial condition, the initial value of the dependent variable: it represents the size of the population at time zero, usually the present.

It is always a good idea to look at the qualitative characteristics of a model before you estimate parameters and make predictions. For example, Equation (2.4) predicts a very strong relationship between the expected population size and the difference between the per capita birth and death rates. We can tell this by inspection: the difference between the vital rates is an exponent (it is raised to the power 'e').

2.1.1 Model assumptions

Whenever a model is constructed, it employs a set of assumptions reducing the complexity of the real world to manageable proportions. Assumptions are all those things not dealt with explicitly in the model but which must nevertheless be true for the model to provide reasonably accurate predictions. The model above makes a number of them.

It is obviously a vast oversimplification. There is no attempt to model the dynamics of populations comprehensively. The probability of dying, d , and the probability of having an offspring, b , are not likely to be the same for different individuals in a population. They will surely depend to some extent on the age of the individuals. Furthermore, these rates are not likely to be constant over time. Nor are births and deaths likely to be independent events.

A list of all the assumptions, at least those of which we are aware, is:

1. Populations will grow or decline exponentially for an indefinite period. This implies that population density remains low enough for there to be no competition among members for limiting resources. There are no density-dependent effects.
2. Births and deaths are mutually independent.
3. Births and deaths are independent of the ages of individuals. In real populations, births, deaths and the propensity to immigrate or emigrate are age, sex and density dependent. However, it turns out that even if birth and death rates are age dependent, the mean rate per individual will remain constant if the proportions of the population in each age class remain constant over time (see Chapter 4). It is sufficient that, on average, the constant parameters apply equally and independently to all members.
4. Birth and death rates (and immigration and emigration rates) are constant in time. This assumption will be violated by any external influence such as an epidemic, or by genetic changes in the population, or by a change in the sex ratio (the relative numbers of males and females). Often, models of populations deal only with females, assuming there are sufficient males present for reproduction not to be limited by a lack of them.
5. There is no variability in model parameters due to the vagaries of the environment or the population's demography. The model for

exponential population growth above (Equations (2.2) and (2.4)) is clearly a deterministic model: there is no uncertainty in its prediction. It says that at some time, t , in the future, the population size will be N_t , and it can be calculated exactly by the right-hand side of the expression.

Obviously, we need to know quite a lot about a population to be able to make all of these assumptions.

2.2 PARAMETERS AND INITIAL CONDITIONS

White rhinoceros on Ndumu Game Reserve are difficult to observe because they inhabit dense woodland and thicket. As a result, demographic data are scarce. Conway and Goodman (1989) report that there are 57 white rhinoceros in the population. The mean density of the population is 0.49 km^{-2} , somewhat lower than densities of this species observed elsewhere in Africa. In areas of preferred habitat within the reserve, densities reach as high as 2.68 km^{-2} . The population consisted, in 1986, of 45 adults and subadults (18 males and 27 females), 4 yearlings and 8 juveniles.

It does not really matter if we build a model for both males and females, or for females alone. It is a realistic assumption that there will always be enough males to go around. Females are usually the limiting sex in reproduction. It is easier to base the model on females, ignoring the males in the population completely. Conway and Goodman estimated the per capita birth rate (the chance each female has of giving birth to a female calf that survives to the next census) at 0.14 per year. The per capita death rate, the chance each female has of dying, is 0.08 per year. Thus, the maximum rate of increase (r) we might expect, given by the difference between birth and death rates, is 0.06. In 1986, there were a total of 35 females present on the reserve.

Conway and Goodman (1989) observed a 50% death rate in the transition from juvenile to yearling. Clearly, death rates are not the same at different ages in this population. If any other age class suffered nearly as high a death rate, there would very soon be no rhinoceros left on the Reserve. However, it is not strictly important that death rates are different in different age classes if the proportion of the population within each age class remains more or less constant (see Chapter 4). We shall assume this is so.

For the purposes of developing management plans, let us assume the period of interest is the next 50 years. Our starting date will be 1986, the last year of reported observations. Our object will be to look at the predictions of the model as it is developed so far, and to develop it further to include features that make it more realistic.

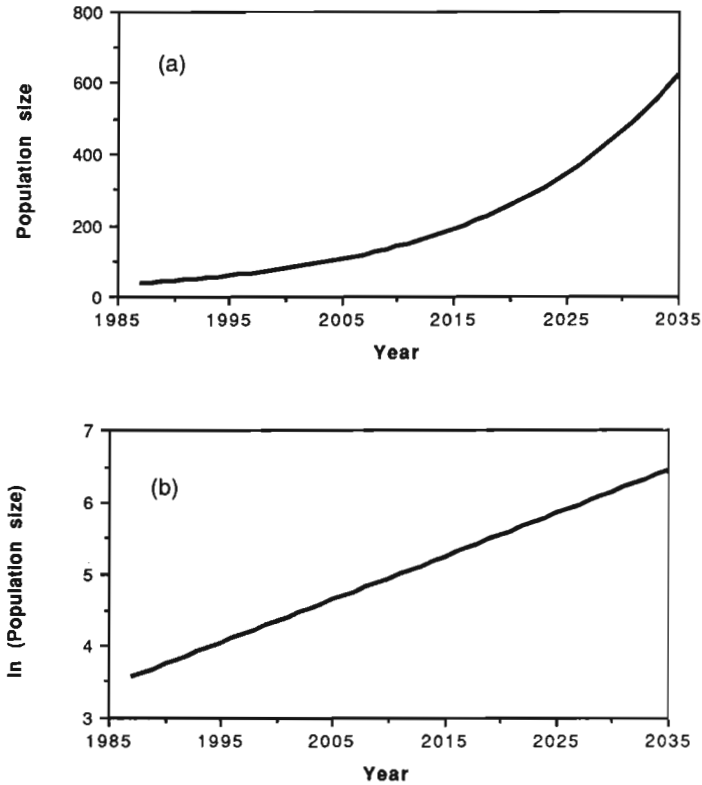


Figure 2.1 Deterministic prediction of an exponential model for growth of a white rhinoceros population: (a) population size is the number of females; (b) population size plotted on a log scale.

2.3 THE DETERMINISTIC PREDICTION

As a first step, we could evaluate the predictions of the deterministic version of our model. In this case, we have an analytical solution for N_t , given N_0 and r . We substitute the parameter values reported by Conway and Goodman in Equation (2.4), giving

$$N_t = 35 e^{0.06t}, \quad (2.5)$$

and solve the equation for each time step (Figure 2.1(a)).

The first thing to note is that the prediction is exact: there are no error bars or confidence limits. Second, if the population is allowed to grow for the next 50 years and there are no limits to the amount of habitat or other resources available, we could expect in excess of 650 females and a total population in excess of 1300 animals. When population size is plotted in a

log scale (Figure 2.1(b)), growth appears linear. This transformation is important if proportional changes in population size are more important than additive changes. Any of the predictions for population size in this chapter and the chapters that follow could be represented in a log scale.

These results are not particularly satisfying. A population of 1300 would result in densities of 13 animals per square kilometre, about twice the density observed in more optimal habitat elsewhere in Africa (Conway and Goodman, 1989). This density is clearly unsupportable in the Park environment. It is very unlikely that the population would continue to grow in an exponential fashion throughout the next 50 years. Resources on the reserve would become depleted as density increased and survivorship and fecundity rates would fall as a result. One of the important assumptions of our model, that birth and death rates are constant from year to year, would surely become invalid.

Another troubling feature of the model is that in calculating the exponential expectation above (Figure 2.1), we used real numbers. For example, the prediction for the population size in 1987 is 37.2 rhinoceros and in 1988 it is 39.5. Clearly, we cannot in reality have 0.2 of a rhinoceros. One element of realism we can add to our model is to use integer numbers. We shall address this problem first.

2.4 ADDING DEMOGRAPHIC STOCHASTICITY

death and
birth
rates are
constants
but
individuals
respond
randomly

Above, we noted that the mean population birth rate was 0.14, and the death rate was 0.08. These means apply to the population as a whole. Imagine the real population: we do not have 0.14 of each animal giving birth. Rather, a proportion of the population reproduces and it is impossible to say if a given animal will survive or will have offspring in any year. To model this aspect of a population, we could ask if each member of the population survives and, independently, if each member has offspring in any time step. A time step of a year seems appropriate because reproduction in the species is seasonal and the environment, especially rainfall, is highly seasonal (Conway and Goodman, 1989).

We account for two things by implementing the model in this way. We treat the population as composed of an integer number of individuals and we sample the survival and reproduction of members of the population, using the observed population size and the population average birth and death rates. The result is that our predictions will no longer be exact. A run of bad luck sampling the survival of individuals could lead to the extinction of any population, no matter how large the population size or how large the potential growth rate. These components of uncertainty are termed demographic stochasticity (see Chapter 1).

This approach is most effectively implemented on a computer. Most programming languages incorporate a random number generator. Usually, they generate a random number from a uniform distribution scaled

between 0 and 1 (that is, each value between 0 and 1 has the same probability of being sampled). The algorithm to calculate population growth is:

Algorithm 2.1 Exponential population growth with demographic variance.

1. For each time step from 1 to t , do steps 2 to 7.
2. Let $N(t + 1)$ take the value of the current population size, $N(t)$.
3. For each animal from 1 to $N(t + 1)$, do steps 4 to 7.
4. Choose a uniform random number, U_1 .
5. Choose a uniform random number, U_2 .
6. If U_1 is less than d , then decrease $N(t + 1)$ by 1.
7. If U_2 is less than b , then increase $N(t + 1)$ by 1.

Notice that the formulation in the Algorithm 2.1 is similar to, but not quite the same as, Equation (2.5), even if we ignore the element of demographic stochasticity it simulates. In the algorithm, we specify the average size of next year's population according to the equation

$$N_{t+1} = N_t + bN_t - dN_t \quad (2.6)$$

Thus, Equation (2.5) says that $N_{t+1}/N_t = \exp(b - d) = 1.062$ whereas Equation (2.6) says $N_{t+1}/N_t = 1 + b - d = 1.060$. Neither of these formulations is wrong. Rather, what is meant by b and d is slightly different. Because the population reproduces seasonally, in a more or less discrete period rather than continuously as, say, humans do, the definition of b and d encapsulated in Equation (2.6) is appropriate.

Notice also that Algorithm 2.1 simulates each individual separately. All the algorithms in this chapter use this approach to simulate demographic stochasticity because it makes the process easy to understand. By using Algorithm 2.1 we stipulate that a female can have no more than one offspring per year, and if $b = 1$ there won't be any uncertainty associated with births. These assumptions are probably alright for white rhinoceros, but not for many other species. In the chapters following Chapter 2, a more efficient and more general method is used that involves sampling the binomial and Poisson distributions.

In formulating the model above, we assumed that births and deaths are independent events. Two components of Algorithm 2.1 reflect this assumption. First, in steps 6 and 7, if an animal dies we allow it to have offspring in that same year. Second, we choose different random numbers to represent the survival and reproductive success of each individual in steps 4 and 5. We could, if we wanted, preclude reproduction if an animal dies by returning to step 2 if U_1 is less than d in step 6. The version of the model in Algorithm 2.1 was implemented and the results of the first two trials are shown in Figure 2.2.

It is clear that demographic stochasticity can have an important effect

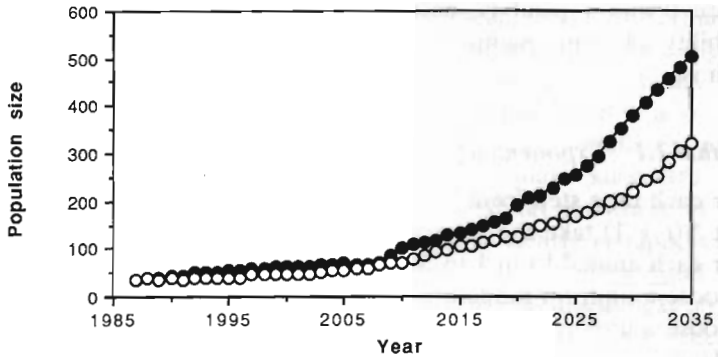


Figure 2.2 Two trials of a model for exponential growth of a white rhinoceros population incorporating demographic variance ($N_0 = 35$, $b = 0.14$, $d = 0.08$). The population size is the number of females.

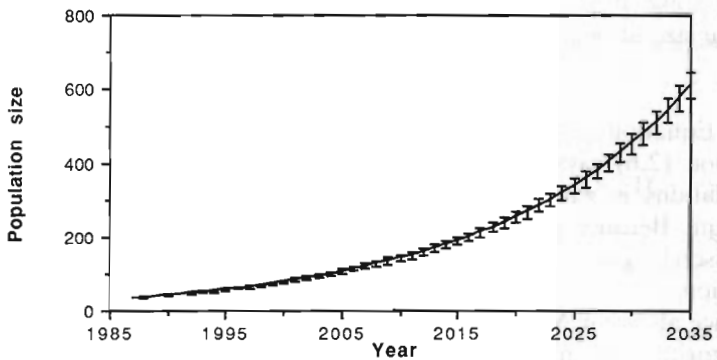


Figure 2.3 Mean and upper and lower 95% confidence limits for exponential growth of the white rhinoceros population, based on 100 replications of Algorithm 2.1. Population size is the number of females.

on estimated population size. This kind of variability is present in every population. The deterministic expectation (Figure 2.1) will be unlike most of the possible trajectories. It is fundamentally unrepresentative because it does not diverge from the pattern of smooth exponential increase. The second trial (Figure 2.2, open circles) falls well below the predictions of the deterministic version. We have done no more than take the trouble to treat our population as a finite set of integer numbers. If the trials are repeated many times, it is possible to calculate the mean and confidence limits of the population size at each time step. We simulated growth for the population 50 times using Algorithm 2.1 and performed these calculations for the above model (Figure 2.3).

The mean prediction of the stochastic model is similar to that for the

deterministic model (Figure 2.1). Notice that the confidence interval increases in width as time goes on (Figure 2.3). Our predictions become less and less certain, the further into the future we make predictions. This characteristic is a general result common to all stochastic models and it makes good intuitive sense.

The 95% confidence limits in Figure 2.3 are quite close to the mean, even after 50 years. On the whole, demographic stochasticity has often been considered unimportant in models of all but the very smallest populations because it has such a small effect. Demographic stochasticity is likely to be most important for rare species because the variance in population size it causes is related directly to the number of individuals in the population. As populations become larger, the effects get smaller, a phenomenon we shall return to below. We can see the qualitative effect of population size by considering the survivorship probability, 0.08, in isolation. If two females remain, the chance of extinction due to variability in sampling is $0.08^2 = 0.0064$. When there are 60 animals, the chance is 0.08^{60} , a very small number. Nevertheless, there remains some chance of important deviations from the deterministic model (Figure 2.2) and some chance, albeit small, of extinction through nothing more than sampling error. We shall return to the relationship between variance and population size in Chapter 3.

2.5 INTRODUCING A POPULATION CEILING

Conway and Goodman (1989) note that the population on Ndumu Reserve is below the carrying capacity of the environment. They expect the population to continue to increase, and they plan to remove individuals whenever the population exceeds about 60 adults. Given a constant proportion of about 20% subadults and juveniles in the population, this population ceiling translates to about 40 females.

The animals taken are to be used in establishing or supplementing herds in other areas. Another reason for the removals is that the area of suitable white rhino habitat on the Reserve, although small, supports a large number of other grazers and increased rhino numbers could be detrimental to the chances of persistence of other species.

We can model this aspect of the management of the population in a straightforward manner by using Equation (2.6). We include a population ceiling for females above which there is no reproduction, and we truncate the population to 40 whenever it exceeds that number. The model becomes:

$$\text{for } N_t \leq 40, \quad N_{t+1} = N_t + bN_t - dN_t \quad (2.7)$$

$$\text{for } N_t > 40, \quad N_{t+1} = N_t + bN_t - dN_t - H$$

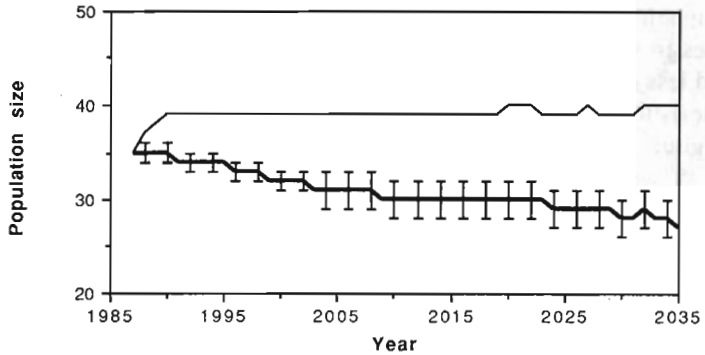


Figure 2.4 Size of the female rhinoceros population under two different scenarios. The thin line represents a management plan involving removal of animals only when the female population exceeds 40. The heavy line represents removing a number of animals that is proportional to 6% of the current population size, as well as animals whenever the female population size exceeds 40. The latter scenario may be interpreted as representing moderate to high levels of poaching. Both trajectories are based on 100 replications. The upper result is without confidence limits because they were too small to be drawn with accuracy. The error bars on the lower curve (removal of 6% of the population) are the 95% confidence limits. When just 2% of the population was removed, instead of 6%, the results were almost identical to the case of a simple population ceiling (the thin line).

where H is the harvest, equal to the number of females in excess of 40. This model may be implemented on computer using the same structure as Algorithm 2.1. The logic will be,

Algorithm 2.2 *Population growth to a ceiling with demographic variance.*

1. For each time from 1 to t , do steps 2 to 8.
2. Let $N(t + 1)$ take the value of the current population size $N(t)$.
3. For each animal from 1 to $N(t + 1)$ do steps 4 to 7.
4. Choose a uniform random number, U_1 .
5. Choose a uniform random number, U_2 .
6. If U_1 is less than d , then decrease $N(t + 1)$ by 1.
7. If U_2 is less than b , then increase $N(t + 1)$ by 1.
8. If $N(t + 1)$ is greater than 40, then let $N(t + 1)$ be 40.

This form of the model is equivalent to a management plan in which we only remove animals when the female population exceeds 40. The mean results of 100 replications of this model (Figure 2.4) show that the population is unlikely to deviate much from the imposed ceiling of 40 female rhinoceros. In fact, the 95% confidence limits are less than 1, even to the end of the simulation.

If managing this population involved nothing more than removing the excess animals each year, we would not anticipate too many problems from demographic stochasticity. However, even a modicum of intuition makes us feel uneasy about a population of 40 female rhinoceros surviving for the next 50 years. Too many things can happen.

Conway and Goodman (1989) mention the possibility of poaching, an activity responsible for the decline of rhinoceros populations elsewhere in Africa. Poaching may result in a constant number of animals lost from the population each year. Alternatively, if denser populations are easier to poach, it may be better expressed as a constant proportion of the population lost each year. Taking this latter alternative, we may rewrite the model in Equation (2.7). We let p be the per capita rate of loss due to poaching. That is, it is the average chance that an animal has of being taken by a poacher in any one year. Equation (2.7) becomes,

$$\begin{aligned} \text{for } N_t \leq 40, \quad N_{t+1} &= N_t + bN_t - dN_t - pN_t, \\ \text{for } N_t > 40, \quad N_{t+1} &= N_t - dN_t - pN_t. \end{aligned} \quad (2.8)$$

We make essentially the same assumptions about poaching as we do about births and deaths. The rate of poaching is independent of the other two events, it is independent of the age, size or sex of the individual, and it is constant in time. Again, using the same basic algorithm, we can write the logic for Equation (2.8) as:

Algorithm 2.3 Population growth to a ceiling, with demographic variance and removals proportional to current population size.

1. For each time from 1 to t , do steps 2 to 9.
2. Let $N(t+1)$ take the value of the current population size $N(t)$.
3. For each animal from 1 to $N(t+1)$, do steps 4 to 9.
4. Choose a uniform random number, U_1 .
5. Choose a uniform random number, U_2 .
6. Choose a uniform random number, U_3 .
7. If U_1 is less than d , then decrease $N(t+1)$ by 1.
8. If U_2 is less than b and $N(t)$ is less than 40, then increase $N(t+1)$ by 1.
9. If U_3 is less than p and U_1 is greater than d , then decrease $N(t+1)$ by 1.

We have assumed that the chances of dying, having offspring, and being taken by poachers are independent events for each animal. We have no data on the real levels of poaching on the Reserve. Assume that poaching occurs at a modest rate, say, one animal per year from a population of 50. In this case, the value of p will be around 0.02. Note from Equation (2.8) that the effect of poaching at this rate is identical to increasing the death rate from 0.08 to 0.10. The reason for the extra condition in step 9 in

Algorithm 2.3, 'if U_1 is greater than d ', should be clear enough. If U_1 is less than the death rate, d , then that particular animal has died. If an animal both dies and is taken by poachers in the same year, it amounts to the same thing as far as the population is concerned. The condition in step 9 avoids double counting the animal.

The average population size and confidence limits based on 50 simulations show that population size remains close to the ceiling of 40 females under the modest poaching rate of 2% per year. If the poaching rate is increased to 6% (equivalent to taking three animals out of 50 per year), the population size becomes very much more variable and the mean population size falls to less than 30 females after 50 years (Figure 2.4).

2.6 REMOVING CONSTANT NUMBERS

We know that rhinoceros are difficult to count, so it is unlikely that a management programme will be able to remove a constant proportion of the population. To do so, we would need to know the population size at the time the animals are removed. Instead, it is more likely that a specified number of animals would be removed each year. Conway and Goodman (1989) suggest the population at Ndumu could sustain the removal of two individuals (or one female) per year. Poaching may work essentially the same way if the number of animals taken is independent of the current population size.

Using the algorithms already developed as a template, it is easy to write a further algorithm for removing a set number of animals. For simplicity, we shall dispense with the population ceiling. Letting X be the number of animals taken, Equation (2.6) is modified to become

$$N_{t+1} = N_t + bN_t - dN_t - X. \quad (2.9)$$

The algorithm becomes:

Algorithm 2.4 *Exponential population growth with demographic variance and removal of a constant number of animals per year.*

1. For each time from 1 to t , do steps 2 to 7.
2. Let $N(t + 1)$ take the value of the current population size $N(t)$, less the number removed, X .
3. For each animal from 1 to $N(t + 1)$, do steps 4 to 7.
4. Choose a uniform random number, U_1 .
5. Choose a uniform random number, U_2 .
6. If U_1 is less than d , then decrease $N(t + 1)$ by 1.
7. If U_2 is less than b , then increase $N(t + 1)$ by 1.

We simulated this population model over 50 years, and repeated each trajectory 100 times. These simulations were performed twice each,

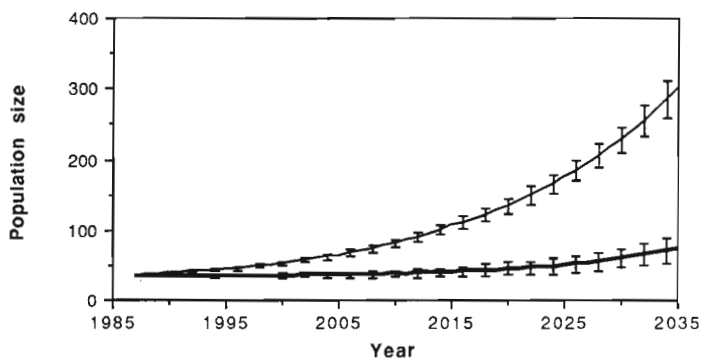


Figure 2.5 Mean population size and 95% confidence limits based on 100 replications for the rhinoceros population, assuming one female (thin line) and two females (heavy line) are removed each year.

letting X equal 1 and then 2 to represent the removal of either 1 or 2 females each year from the population.

The results suggest, at first glance, that the population could sustain the removal of two females per year and remain viable (Figure 2.5). The mean population size is higher, after 50 years, than the mean population size if we impose a strict ceiling (Figure 2.4). If it saves considerable time and money not to survey the population each year immediately prior to removing animals, we may be content to remove as many as two male and female pairs every year.

2.7 ENVIRONMENTAL VARIATION

So far, we have looked at nothing except the variation in population size that results from sampling a finite, integer number of animals from one year to the next. Populations are affected by other things, notably by the variation in the environment around them. Conway and Goodman (1989) observe, for example, that extended drought has probably depressed natality in the population of rhinoceros at Ndumu. Such variation, we assume, is fundamentally unpredictable.

Changes in environmental conditions will dictate fluctuations in the growth of a population. That is, environmental variation will affect the population through effects on survivorship and fecundity. When conditions are poor, food and water are scarcer, there is more competition with other grazers for the available resources, and fewer rhinos survive the year. Thus, environmental variation may be seen as something that varies the population mean birth and death rates.

Perhaps the easiest way to model this in a system without density dependence is to incorporate environmental variation through a degree of

*b and d
are
variables...*

random variation in the parameters for growth rate, b and d . As an equation, this may be written as

$$b_t = b + s \cdot y_t \quad (2.10)$$

and

$$d_t = d - s \cdot y_t \quad (2.11)$$

where b and d are the mean birth and death rates respectively of the population, y_t is a random variable with a mean of zero and a variance of 1, and s represents the standard deviation of the fluctuations. In the long run, the average of the y values is 0, so the average b_t is b and the average d_t is d .

We have assumed that variations in the birth rate and the death rate act in equal and opposite directions. If the random number is greater than zero such that the birth rate increases, then the death rate decreases. This means that if it is a good year for the survival of adults then it is also a good year for the survival of juveniles from birth to the time of the first census. We could have done it in other ways. It is unlikely that the two parameters for birth and death are as perfectly correlated as they are in Equations (2.10) and (2.11). We could choose different random numbers for each parameter, resulting in a correlation of zero between them. We could correlate the two random numbers so that if it is a good year for juveniles, it is likely (but not necessarily) a good year for adults. The correlation may even be negative if, for some reason, a good year for the survival of adults results in poorer survival of animals from birth up to first census. This will be true if the adults compete for the same resources as the juveniles, as adults are better competitors, and resources are limited.

The values corresponding to y_t are often assumed to be 'white noise': this term means that the random distribution from which y_t is drawn is the same at all times and there is no correlation between values selected for successive times. If species abundances are the result of several factors that act independently, the effect of these factors on population size will be additive. The Central Limit Theorem suggests that environmental variation acting in this way may best be represented by the normal distribution. If these independent factors act in a multiplicative fashion (i.e. their logarithms are additive), then the approximate distribution will be lognormal (for an introduction to the normal and lognormal distributions, and the Central Limit Theorem, see Sokal and Rohlf, 1981).

To represent these ideas, we must consider the structure of our model so far. The birth and death rates represent, for each animal in the population, the mean chance per year of having offspring or surviving. In our previous models, we have assumed them to be constant values. We are now saying these rates are not constant in time, and that they may

vary depending on how favourable or unfavourable the seasons turn out to be.

We shall assume that the environmental factors important for the growth of the rhinoceros population act independently and that their effects on the growth rate of the population are additive. For example, if rainfall is 10% above average, we might expect survival to increase by 10%. If some other important factor is 10% better than normal, we shall add another 10% to the average chance of survival.

All we need to do, at each time step, is to choose a random number from the standardized normal distribution with a specified standard deviation. This number will have a mean of zero. An algorithm for selecting a random number with a given standard deviation from the normal distribution is given in the Appendix, Section A.2.3. If the value we choose is negative, it represents a bad year for the population. The mean birth rate will fall and the mean death rate will rise (Equations (2.10) and (2.11)). Conversely, if the number is positive, it represents a good year, and mean birth rate rises and mean death rate falls. The magnitude we specify for the standard deviation represents the magnitude of the effects of environmental variation on the birth and death rates.

If we use the model for exponential growth in discrete time (Equation (2.2)) as an example and substitute Equations (2.10) and (2.11), it becomes

$$N_{t+1} = N_t + (b + s \cdot y_t)N_t - (d - s \cdot y_t)N_t \quad (2.12)$$

where the value y_t represents environmental conditions between times t and $t + 1$, and s represents the magnitude of their effect on the population.

The degree of correlation we employ must depend on empirical data. In the absence of any other information, we assume that the parameters have a correlation of 1 (that is, we use the same number to represent variation in both parameters). It would be better to assume there is no correlation between births and deaths if the factors that act on births are different from those that act on deaths. To solve Equation (2.12) and predict population size, accounting for both demographic and environmental variability, we need only introduce one more step to Algorithm 2.1, giving us

Algorithm 2.5 *Exponential population growth with demographic and environmental variance.*

1. For each time from 1 to t , do steps 2 to 8.
2. Choose a normal random number, Q_1 , with mean 0 and specified standard deviation.
3. Let $N(t + 1)$ take the value of the current population size $N(t)$.
4. For each animal from 1 to $N(t + 1)$, do steps 4 to 8.

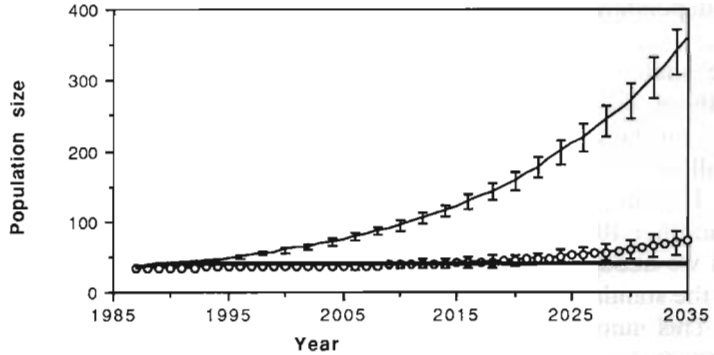


Figure 2.6 Predictions accounting for demographic and environmental variation for the size of the female rhinoceros population under three management scenarios: removal of animals when the population exceeds 40 (heavy line), removal of two females per year (circles) and removal of one female per year (thin line). The curves for the first two options are almost identical until about year 2015.

5. Choose a uniform random number, U_1 .
6. Choose a uniform random number, U_2 .
7. If U_1 is less than $(d - Q_1)$, then decrease $N(t + 1)$ by 1.
8. If U_2 is less than $(b + Q_1)$, then increase $N(t + 1)$ by 1.

To be realistic, b_t and d_t are truncated so they remain within the range $[0..1]$. The same applies to Equations (2.10), (2.11) and (2.12). Take two forms of the model developed above, Equations (2.7) and (2.9). These are, respectively, the equations for exponential growth to a ceiling and exponential growth with removals of a constant number of animals. The form of the equations, and the associated algorithms for the implementation of (2.7) and (2.9), may be modified in the same way as for the exponential model above (Algorithm 2.5). In Algorithms 2.2 and 2.4, just choose a normal random number (step 2 above), and modify the two steps for birth and death to include the variable Q_1 .

We don't know anything about the levels of environmental variability on Ndumu Reserve, or how they affect the reproduction and survival of individuals in the rhinoceros population. Assume that the effects of the environment are moderate. We shall use a coefficient of variation of 10% in birth and death rates. The mean birth rate is 0.14. Random variation of this magnitude will mean that in 95 years out of 100, the birth rate will be between 0.11 and 0.17, due to the effects of the environment. A coefficient of variation of 10% in death rate means that, 95 years out of 100, the death rate will be between 0.05 and 0.11. Using these parameters, it is unlikely that the mean population death rate will exceed the mean population birth rate in any one year, due to the effects of the environment alone.

For the exponential model with environmental and demographic variance, the expected (mean) population size remains the same as the deterministic model. The curves for all three scenarios (Figure 2.6) look very similar to the predictions for the same models accounting for demographic variance alone (Figures 2.4 and 2.5). The addition of environmental variance had done little more than increase the 95% confidence limits slightly. None of the management alternatives seems likely to drive the population to extinction.

As managers of the rhinoceros population, we may be tempted to look at Figure 2.6 and conclude that removing constant numbers from the population is a reasonable option. The growth rate, on average, is positive and the confidence limits when removing both one and two females are a long way from zero. While the variability expected as a result of imposing a ceiling is much smaller, the mean population size is well below the other two options at the end of the period. However, the confidence intervals shown in Figure 2.6 may be misleading. The distribution of the population sizes is strongly skewed, particularly towards the end of the simulations. For example, in the case involving the removal of 2 females per year (Figure 2.6), the mean population size at the end of 50 years is about 70 females, with confidence limits of about 20. However, 39 of the 100 trajectories (and the mode) are zero at 50 years, and most have population sizes of less than 15 females. A few trajectories reach population sizes in excess of several hundred, reflecting the small chance that environmental conditions are consistently good for most of the 50 year period. Thus, the confidence intervals underestimate the true magnitude of the variation. We shall test these conclusions by adding risk assessment to our stochastic models.

2.8 RISK ASSESSMENT

The only thing that may cause us concern about removing constant numbers of animals is that this management practice results in a much more variable prediction of the population size. The prediction of the model for the option involving removals when the population exceeds 40 females, that is, the option for a population ceiling, results in almost no important variation. It is too small to be shown on Figure 2.6. We should be comfortable in knowing that the population size will be close to 60 adults if our model is even approximately correct.

When we calculate the mean and confidence limits from a set of numbers, we are looking at the central tendency of our data. The behaviour of outliers is largely ignored. Estimating risk involves calculating the chances of extreme events. Extreme events in any population may result in population crashes or explosions. In the case of the rhinoceros on Ndumu Reserve, we want to know the chances that the population will become extinct at some time in the next 50 years.

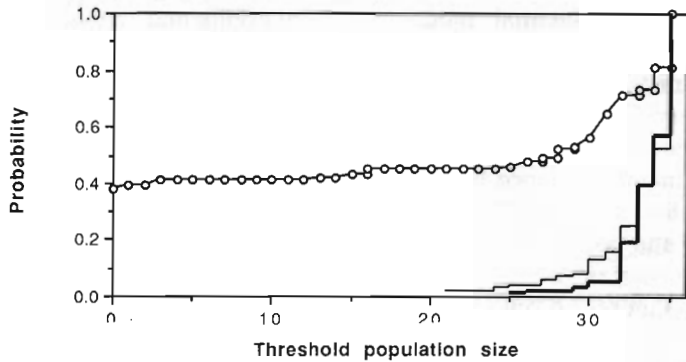


Figure 2.7 Quasiextinction curves for the predictions of the rhinoceros population size: ceiling of 40 females (heavy line), removing one female per year (thin line), and removing two females per year (circles). The simulations are represented in Figure 2.6 and are based on 100 replications. To construct the risk curves, the following procedure was used. From each replication of a simulation, the smallest size attained by the population between 1986 and 2035 was recorded. For example, the range of these values lay between zero and 35 for the simulation involving the removal of two females. Then, for each population size over the range of values (e.g. from 1 to 35), the proportion of the 100 values less than the given size was calculated. This gave a cumulative probability distribution representing the chances that the population will fall below the given (threshold) size at least once in the next 50 years. This process was repeated for each of the simulations in Figure 2.6, giving the three risk curves above.

The simulations performed to generate the three trajectories in Figure 2.6 involved estimating the population size at each time step over 50 years, after sampling survival and reproduction to account for environmental and demographic uncertainty. From the set of 100 replications of the simulation, it is possible to record not only the mean and confidence limits for each time step, but also the smallest value calculated during each replication. Each of the 100 trajectories that went into making the three mean curves in Figure 2.6 were probably different (see, for example, Figure 2.1). Some would have fallen below the mean trajectory and some above, depending on the vagaries of our random number generator.

To learn about the likelihood of extreme events, we need to look at the smallest population sizes found from each replication of the simulation. We may find that the predicted population size falls below, say, 20 animals, in a total of 40 out of 100 replications. We could then say there is a 40% chance that the population will fall below a population size of 20 at least once within the next 50 years.

If we record the smallest population size from each simulation, we can construct a graph of probabilities versus population size. A graph of this kind is known as a quasiextinction curve (Ginzburg *et al.*, 1982) because it

represents both the chances of extinction and the chances of falling below small population sizes. The smallest population sizes were recorded for each replication of the three simulations in Figure 2.6, giving the three curves in Figure 2.7.

Perhaps the most surprising thing about these analyses involves the removal of two females per year. Even though the mean population size for this management option is well above zero, and above the ceiling of 40 animals at the end of 50 years (Figure 2.6), there is about a 40% chance that the population will become extinct (Figure 2.7). These risks are a much more effective guide to the likely future of the population than are the mean trajectories in Figure 2.6. They reflect the very strongly skewed distribution of the underlying population. Thus, even though the average population size for the situation involving the removal of 2 females is 70 at the end of 50 years, the chance that the population is less than 70 females is about 80%. We occasionally use confidence limits when displaying expected population sizes in the following chapters even though they do not give an accurate representation of the true amount of variation, especially in cases where the risk of extinction is high. The safest option is to implement a ceiling and remove animals only when the population exceeds it. The chances that the population will fall below 30 females within the next 50 years is small. Even removing just 1 female per year results in an increased risk that the female population will fall below 30 animals. These risks are incurred by the population, not because of systematic pressure (in the sense of Shaffer, 1987), but because the variability in the average rate of population growth is greater when constant numbers are removed.

There is a good reason why the removal of constant numbers poses a greater threat to the population than does the imposition of a ceiling. When we remove animals it may be thought of as mortality, at least from the point of view of the rhino population. Removing animals in excess of 40 is the same as increasing the chances of mortality when the population becomes large. When the size falls below the ceiling, mortality rates effectively decrease because we no longer take animals. Thus, managing the population in this way has a stabilizing effect on the population size. We shall tend to push the population of females towards 40 individuals from above and below.

If we decide, on the other hand, to remove two females per year, our management activities will destabilize the population, making it more prone to population crashes and extinction. This is because the effective mortality rate (the sum of per capita death rates due to natural causes and removals) will increase when there are fewer rhinos. For example, if there are 100 females in the population, the effective mortality due to removals will be 2%. If there are 10 females, it will be 20%. This management scheme makes mortality inversely proportional to the density of the population and will tend to push it towards extinction.

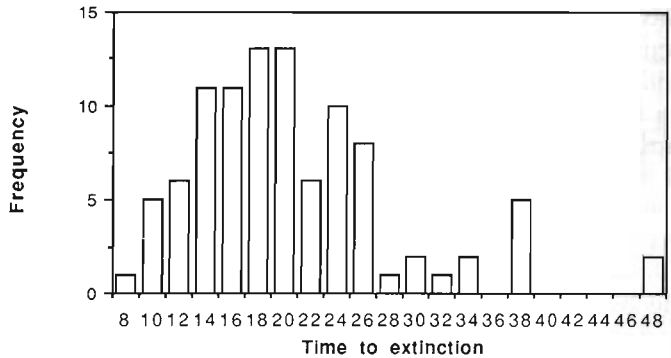


Figure 2.8 Histogram of time to extinction in 100 trials of the simulation of exponential growth of the rhinoceros population. The model includes demographic and environmental variance, and three females per year are removed from the population. A total of 97 replications out of 100 became extinct within 50 years and the remainder were extinct within 100 years. Only those that became extinct during the first 50 years are shown. The labels on the x-axis are lower class limits. Thus, the class labelled '8' represents all cases where the rhinoceros population became extinct during either the 8th or 9th year of the simulation. The label '20' contains the count of all replicates that went extinct during the 20th or 21st years.

2.8.1 Interpreting estimates of risk

If we find congruence between a model's predictions and observations of a population in the real world, it provides only weak inductive evidence that the assumptions of the model are correct. When models are tested against the real world, often we talk of model predictions. Predictions are of two kinds. Most often they refer to nothing more than the statistical fit of a model to a set of observations. The prediction of a regression model is the line that provides the least squares best fit to the data. In general, the more parameters one has in a model, the more variation of the data will be explained by the model. The second type of prediction is a forecast, wherein a model is used to predict events or values measured in the future. The parameters of a model are estimated from independent observations, and the forecast may be tested. Here, we have been forecasting the size of the rhinoceros population, but our interests are qualitative. The model is by necessity very simple because our data are limited.

A better model for these animals could include more factors to bring it nearer to reality. For example, it is unlikely that it would go unnoticed by the wildlife managers if the population size were to fall to 30, half its current size. If it did so, they would not continue to remove animals. In our models for constant removal, we continued to take rhinoceros, even when the population was close to extinction.

Conway and Goodman (1989) planned to remove two animals per

year. The effect of their management recommendations is likely to be a mixture of the model involving removals of a constant number per year, and the model for a population ceiling. We could build this into our computer model by, for example, allowing removals only when the population exceeds 40 animals. There are doubtless many other factors we could include if our knowledge was a little better.

Nevertheless, we have learned a few useful things. First, removing two females per year results in a more variable population size than removing females in excess of 40, even if the population's average net production is more than two females per year. This, in turn, increases the risks that the population will decline through chance events in survival and reproduction, and through a succession of poor years. Second, while wildlife managers are likely to be sensitive to the risks of declining population size, poachers are not. These results tell us that if poachers remove a constant number of two females or more per year, the population is endangered. If they remove as many as three animals per year, the population is almost certain to become extinct within the next 50 years (Figure 2.8). Poaching seems to pose a real threat because, even if moderate, its intensity may be independent of the existing population size. Poaching will destabilize the population. Careful management around the desired population ceiling may stabilize the population size and thereby reduce the chances of a severe reduction in numbers over the next 50 years.

The problems of the managers are complicated by measurement errors. Since they may not know the exact number of animals, sometimes animals may be removed when $N < 40$ and not removed when $N > 40$. This will increase the variation in population size and partially (even completely, if estimates of N have large errors) offset the stabilizing property of this management strategy. Its effectiveness depends on how precisely N is estimated.

When we simulate the scenario where three females per year are removed, the distribution of extinction times is skewed to the right and, as a result, most of the trials resulted in the population going extinct before the mean extinction time. About 60% of the replicates became extinct before the mean extinction time of 21.5 years. This example shows why it is important to know the complete distribution of extinction times, not just the average time (see Chapter 1).

The model described above is used as an exploratory tool. We have been interested principally in the qualitative results of different assumptions. We do not really expect the population to be 379 females, plus or minus 35, in 50 years' time if we remove exactly one per year. Too many things may happen in the intervening period to make the prediction realistic. The Reserve may expand or contract in area; we may develop a technique that makes counting rhinoceros easy; a catastrophe such as extreme drought or disease may eliminate the population in a single year.

These things are not accounted for in the model we developed. They may change our approach to modelling, or they may allow the implementation of different management practices. We do, however, expect that if we manage the population by implementing a ceiling, the population has a better chance of persistence than if we remove a constant number of animals. It appears to be important to remove animals only if we know the current population size.

2.9 SUMMARY

The processes of birth and death in a population determine changes in population size. The so called birth-and-death models can be used to predict population sizes at various times in the future. A model is constructed for white rhinoceros in Ndumu Reserve, providing an example of how to build a stochastic model.

The exponential model of population growth after 50 years predicts a population size greater than could be supported by the environment. Demographic variability adds an important component of uncertainty to the model's predictions. A modification to the model allows the evaluation of different management practices to limit the size of the population. Population variability will be minimized if animals are removed only when their abundance exceeds a specified threshold, but the effectiveness of this strategy depends on the errors associated with estimating population size. If constant numbers are removed from the population every year, regardless of its current size, the effect is destabilizing because the proportion removed increases as the population size decreases.

Environmental variation may be introduced to demographic models through the parameters for population mean birth and death rates. The effects of different impacts on the rhinoceros population can be estimated through the risks of population decline. Removing constant numbers from the population greatly increases the chances of extinction of the population.