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ALEX: A Model For The Viability Analysis Of Spatially Structured Populations

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Abstract

A new generic model for assessing the viability of spatially structured populations, ALEX (Analysis of the Likelihood of EXtinction), is described. Strengths and weaknesses of ALEX are discussed. ALEX only models one sex, ignores genetics, and is inadequate for modelling the dynamics of very small populations. However ALEX contains four features that make it useful for assessing the merits of different management options for populations that are distributed in a spatially complex landscape: (1) ALEX allows each patch to have different qualities including a habitat variable that may respond to catastrophes. In this way the dynamics of species which prefer a particular successional stage of a habitat can be modelled. (2) ALEX allows the user to specify a wide variety of catastrophic processes that affect and may depend on population size and/or the state of the habitat in a patch. (3) Sensitivity analysis is essential to the PVA process. ALEX allows automatic sensitivity analysis of most parameters. Although demographic stochasticity is modelled, ALEX can quickly simulate the dynamics of very large populations. (4) Modelling movement between patches by individuals is an important part of the dynamics of spatially structured populations. ALEX permits two types of movement by individuals. This allows the user to explore the importance of corridors, habitat selection, and mortality associated with dispersal.

Keywords: population viability analysis, computer simulation model, threatened species management, sensitivity analysis, risk assessment.

INTRODUCTION

Choosing between management options is fundamental to the conservation of rare and threatened fauna. Such options may include the dedication of protected areas (Armbruster & Lande, 1993; Lamberson *et al.*, 1994; Goldingay & Possingham, this issue), modification of disturbance regimes like fire and logging (Haig *et al.*, 1993; Virkkala *et al.*, 1993; Possingham *et al.*, 1994), capture of animals for captive breeding (Maguire *et al.*, 1987; Lacy *et al.*, 1989), harvesting (Hamilton & Moller, 1993), reintroduction (Burgman *et al.*, 1994; Southgate & Possingham, this issue), monitoring (Durant & Harwood, 1992), and the construction of corridors between existing habitat. For each type of management option there will be a range of suboptions. For example, where reserves are being set aside, the questions might be: how many, how big, and in what spatial arrangement?

To choose between management options we need to have a quantitative estimate of their merit for conserving the population in question (Maguire, 1991). As minimising the likelihood of extinction is usually the prime nature conservation objective for threatened populations, our task is to assign an extinction probability to each management option. Population viability analysis (PVA) (Shaffer, 1990; Burgman *et al.*, 1988; Boyce, 1992; Lindenmayer *et al.*, 1993a; Possingham *et al.*, 1993) -- the process of assigning an extinction probability, within a specified time frame and under particular circumstances -- has become a widely used tool for applied conservation biology.

The process of assessing viability usually involves the use of mathematical models that are explored using computer simulation. There are several general models available for assessing the viability of a single population; for example GAPPS (Harris *et al.*, 1986), RAMAS/age (Ferson & Akçakaya, 1990) and RAMAS/stage (Ferson, 1990). However, we know of only two other generic packages that can simulate the dynamics of spatially structured populations -- VORTEX (Lacy, 1993) and RAMAS/space (Akçakaya & Ferson, 1992).

In this paper we describe a new generic model for carrying out population viability analysis of spatially structured populations, the analysis of the likelihood of extinction (ALEX). ALEX has been used in

a variety of studies (Norton & Possingham, 1991; Lindenmayer *et al.*, 1993b; Possingham & Gepp, 1993; Possingham *et al.*, 1994; Goldingay & Possingham, this issue; Southgate & Possingham, this issue; Lindenmayer & Possingham, in press). The purpose of this paper is two-fold.

First, with the increase in popularity of complex simulation models there is concern over the underlying assumptions that are hidden within computer code. This paper explicitly describes the workings of ALEX and highlights its strengths, weaknesses and assumptions. Secondly, where time and money permit, the best approach for assessing population viability is to construct a specific model for a specific species (Lindenmayer *et al.*, in press). Detailed descriptions of existing models assist the development of new specific and generic models.

ALEX differs from other PVA models in a variety of ways leading to some important strengths and weaknesses.

Weaknesses

(a) Only one sex is modelled in ALEX and the age structure includes only three age classes. In this paper we assume that the limiting sex is female.

(b) ALEX is applicable to most vertebrates. Invertebrates and plants may require special models (Burgman & Lamont, 1992; Kindvall & Ahlen, 1992).

(c) ALEX ignores the possible effects of genetic structure on population viability.

Strengths

(a) ALEX allows for complex habitat spatial structure. Each patch has a unique location and the patches may differ in quality. Patches can be connected by corridors that facilitate movement.

(b) Two kinds of movement between different patches are allowed for in ALEX: 'diffusion' along corridors and 'migration'. The two kinds of movement can be used to model habitat selection, mortality induced by dispersal, density-dependent movement, and habitat corridors.

(c) For each patch ALEX follows a dynamic habitat variable. This habitat variable can be affected by, and affect, the likelihood of catastrophes. The habitat variable may affect the fecundity of animals in a patch. In this way we can accommodate species that respond to changes in the successional state of vegetation in a patch. The user can specify local and/or global catastrophes that interact with the populations and habitat in each patch.

MODEL DESCRIPTION

In this section we present an overview of the model structure and state variables, then a description of each process in the model.

ALEX is a Monte Carlo simulation model. Pseudorandom numbers are used to simulate the stochastic processes in the model. Each scenario needs to be run many times to gather statistics on the likelihood of extinction (Harris *et al.*, 1987). The user specifies the number of runs for each scenario and the length of the simulation in years.

The annual cycle of events modelled in ALEX is shown in Fig. 1. This structure is similar to most models intended to simulate the dynamics of animal populations which experience an annual cycle of events. The model may well suit some annual plants and insects that have only one breeding season per year (Hanski & Thomas, 1994). Changes in the order of events, for example when catastrophes occur compared to birth and death, could be important in some circumstances. Although ALEX does not allow changes in the order of events, careful parameterisation can accommodate most situations.

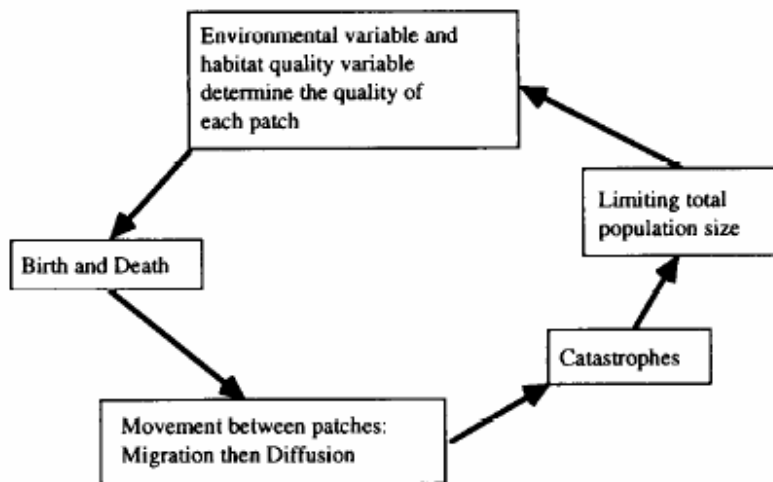


Fig. 1. Flow diagram showing the annual cycle of events simulated in ALEX.

Population structure, birth, death and environmental variability

The important state variables are the number, location and age class of each individual. Each individual in the model is assigned to one of three age classes - newborn (juveniles born that year), juveniles (individuals that are at least 1 year old but cannot reproduce) and adults. The user sets the number of years that individuals are newborn or juvenile; this number must be 1 or more. For example, the greater bilby *Macrotis lagotis* can breed the year after it is born (indeed even earlier, Southgate & Possingham, this issue) so we set the number of pre-adult age classes to 1.

For each age class there is an annual probability of death. This excludes death associated with catastrophic events. For each adult female that breeds there is a fixed probability distribution for the number of female offspring (male offspring are ignored as males are not modelled). Given data on the sex ratio at birth, number of litters, and size of litters, the user can calculate the probability of a certain number of offspring using a small program distributed with ALEX called BIRTHS.

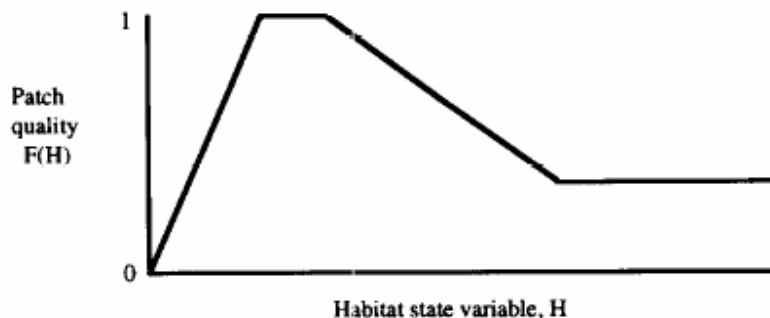


Fig. 2. Example of the impact of the habitat state variable on the quality of a patch and hence fecundity. This shows the postulated response of habitat quality for the southern brown bandicoot *Isoodon obesulus* to the time since the last fire, monitored using the habitat variable included in ALEX.

The population exists in a finite number of patches. These patches may be spatially discrete or they may be adjacent areas distinguished by different habitat attributes. Each patch has various attributes: position, area, A_i , maximum quality, B_i , and value of habitat state variable, $H_i(t)$, where t is an index of time in years and i is the patch index. These properties are fixed except for the habitat state variable which increases at a constant rate (and can be different for each patch) until it reaches a user-defined maximum value. The impact of the habitat state variable is moderated through a piecewise linear function, $F[H_i(t)]$. For example Possingham and Gepp (1993) used the function shown in Fig. 2 to model the relationship between the habitat state variable, in this case a

surrogate for time since fire, and its impact on breeding for the southern brown bandicoot *Isodon obesulus* in South Australia (see also Southgate and Possingham, this issue).

Environmental variability is modelled very simply. At the beginning of each year a normally distributed random variable, with patch-specific mean and variance, is selected for each patch. These may be fully correlated, uncorrelated, or partially correlated. The correlation of each patch is with respect to patch 1. For example, if a patch has a correlation coefficient of 0, its environmental variable is uncorrelated to patch 1, if the correlation coefficient is 1 then its environmental variable is perfectly correlated with patch 1, if -1 then its environmental variable is negatively correlated with patch 1. This does not allow for the full range of correlation structures (see Burgman *et al.*, 1993 for a description of a method for correlating more than two pseudo-random variables) and is being improved. The impact of the environment on the number of breeding females is modelled using an environmental modifier, M_e . The user sets an environmental value above which breeding is unaffected, $M_e = 1$, and a lower value below which there will be no breeding, $M_e = 0$. At intermediate values of the environmental variable the modifier is intermediate between zero and 1; see Fig. 3.

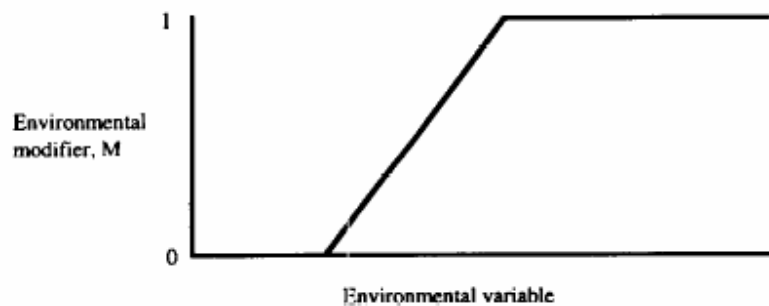


Fig. 3. Example of the relationship between the randomly generated environmental variable on the quality of a patch and hence fecundity.

The habitat state variable and parameters of a particular patch combine with an environmental variable to determine the 'quality' of the patch i , $Q_i(t)$, where

$$Q_i(t) = F[H_i(t)]M_iB_i$$

In turn the patch quality determines the maximum number of females that can breed in the patch, $X_i(t)$,

$$X_i(t) = Q_i(t)A/R,$$

where R is the minimum home range size of a breeding female. For example, if the patch quality is 1, the maximum number of breeding females is the patch area divided by the minimum breeding home range size, R . If patch quality, $Q_i(t)$, is 0.2 then the maximum number of breeding females in a patch that year is 20% of the patch area divided by R . The number of females that actually breed is the minimum of the number of females in the patch and $X_i(t)$.

This method of modelling variation in fecundity has a number of implications. The main advantage is that it enables the use of a fixed matrix (Possingham *et al.*, 1992) which contains the probability that a certain number of breeding females produce a certain number of offspring. The use of this matrix significantly increases the speed at which the model runs, particularly where the population size is large because pseudorandom numbers are not being generated for each individual. The biological implications of this method of incorporating environmental variability and habitat quality dynamics are not transparent. The key feature to note is that when patch quality is low, but positive, one or two of the females in a patch may still breed. This introduces a form of density-dependence which has two possible interpretations:

- (1) Most habitat is variable even within a patch and the best habitat in a patch is often occupied by the dominant females or groups. In years when the environment or habitat quality is poor, only these individuals may breed.
- (2) Habitat quality can be thought of as a modifier of the minimum home range required for a breeding female. The area required for a female to breed is the minimum area required, R , divided by the habitat

quality. For example, females in a patch with a quality of 0.5 need twice the area to breed as females in a patch with a quality of 1.

Movement between patches

ALEX allows the user to model two very different sorts of movement: movement to adjacent patches where there is no increased risk of mortality, called 'diffusion' in ALEX, and dispersal to a more distant patch associated with a substantial decrease in survivorship, called 'migration' in ALEX. Either, both, or neither movement submodel may be employed depending on the species concerned. The two movement submodels are described below.

Diffusion

Diffusion only occurs between patches that are connected by the user with a corridor. In general the user should connect a pair of patches with a corridor when they abut, nearly touch, or are linked by a corridor of suitable habitat. Diffusion is intended to reflect small-scale movement possibly associated with a change of territory position, but not associated with a significant increase in mortality. As with migration, each individual has an age-class specific probability of diffusing. The diffusion model has three optional features:

- (1) Each corridor connecting two patches is assigned a 'width'. The maximum number of individuals that can pass between two patches in each age class in each year is the corridor width divided by the square root of the minimum area required for breeding, R .
- (2) As with migration the user may set a density below which animals will not diffuse.
- (3) Diffusing individuals may preferentially move to a patch that currently has a higher quality. To reflect the fact that some animals can preferentially select better habitat that is nearby, the user chooses a parameter, E (non-negative), that reflects how good an adjacent patch needs to be to attract a diffusing individual. A diffusing animal will only move to one of the patches to which it is connected if the quality of the patch in which it currently resides $\times E$ is less than the quality of the patch to which it is moving. For example if $E = 0$ then there is no habitat selection and animals will move to any patch, while if $E = 1$ then individuals will only move to a better patch.

Migration

Each age class is assigned a constant probability of 'migrating'. Animals will only migrate if the density of animals in the patch is above some user-specified threshold (e.g. Verboom *et al.*, 1991). This is only sensible where individuals leave their natal home ranges yet live in a patch that is relatively empty. In these circumstances they are unlikely to risk long-distance dispersal. If an individual is deemed to be migrating in that year then the probability that it reaches another patch is a function of the distance between the two patches and the size of the target patch. If it does not successfully reach another patch then it dies. The probability of successful migration from a source patch to a target patch is $a \cdot \exp[-d/m]$, where d is the distance between the two patches, a is approximately the probability that a line drawn in a random direction from the centre of the source patch strikes the target patch, and m is the mean expected migration distance; see Fig. 4. We calculate the value of a using the

$$\begin{aligned} \text{formula} \quad a &= \arctan(r/d)/\pi && \text{for } d > r \\ &= 0.5 && \text{for } d < r \end{aligned}$$

where r is the radius of the target patch. Although this is only an approximation, the equation reflects the idea that large close patches are more likely to receive a migrant than small far patches. The user sets m , the average distance a migrating animal travels from its source patch.

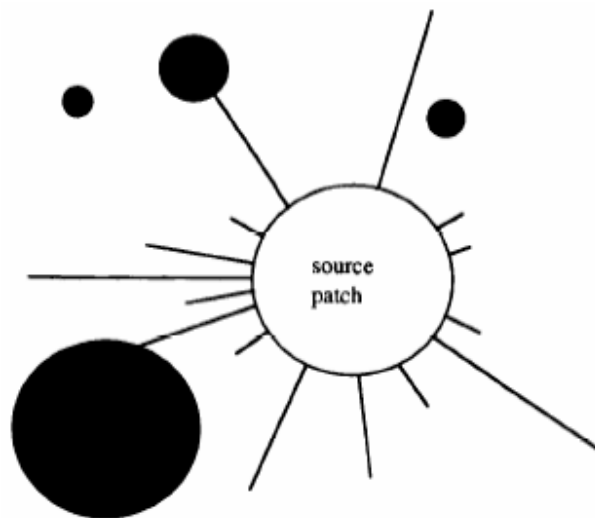


Fig. 4. Schematic diagram of the migration model in ALEX. Migrants emanate from the centre of a patch and die at a constant rate as they move outwards unless they strike another patch before dying. In this example two animals successfully moved to another patch and 13 died.

Catastrophes

Catastrophes are being perceived as increasingly important in determining the fate of threatened populations (Simberloff, 1988; Burgman *et al.*, 1993) and we attempt to give the user a range of options in ALEX for modelling real catastrophes.

Users can specify up to three different sorts of catastrophe. Each catastrophe has a variety of properties.

- (1) Some catastrophes affect the entire population, while others affect only parts of the population. A catastrophe may be either 'local' or 'global' in ALEX. When a global catastrophe occurs, all patches are affected; local catastrophes act independently on individual patches. These two options reflect only the extremes of all the possible correlations between catastrophic events in different patches.
- (2) The probability of a catastrophe may depend on the number of animals in the patch, $N_i(t)$, or the state of the patch habitat variable, or neither. If the catastrophe depends on either $N_i(t)$ or $H_i(t)$ then the user sets a piecewise-linear dependence function. For example, the chance of an epidemic may depend on the size of the population in the patch, while the chance of fire may depend on the time since the last fire. In the latter case the habitat variable can be used to monitor the time since the last fire.
- (3) Once a catastrophe occurs it reduces both the habitat variable and the population size by a random proportion, P . The user sets the range of this random proportion and P is chosen from a uniform distribution. 75% of the animals in a patch we might set the range for the proportion killed as between 0.5 and 1.0.

Limitation of total population size

The final stage of the population simulation is intended to stop the population becoming excessively large. The user sets a minimum living area for the species, L , so that the carrying capacity of a patch is A/L . If the total population in a patch has risen above the carrying capacity of the patch then individuals are removed until the population is equal to the carrying capacity. Individuals are removed preferentially from younger age classes.

Model results

To determine the probability that a population is extinct within a specific time it is necessary to simulate the population many times, recording the time to extinction for each run, and finally assembling the distribution of times to extinction. ALEX presents a histogram of the probability of extinction at any time

that is a multiple of one-tenth of the total run time. For example, given a run time of 500 years ALEX records the probability of extinction within the first 50, 100, 150 500 years.

Because ALEX does not model very small populations well the program records the time at which the population falls to a user-defined number, a quasiextinction event (Ginzburg *et al.*, 1982; Ferson & Burgman, 1990). In general this number should be at least 2, and in many circumstances higher. If more than half the runs in a scenario end in extinction then the model can calculate the median time to extinction, another useful measure of population viability (the first and third quartiles of the time to extinction are also calculated where possible). When dealing with real populations it is often useful to know how often a particular patch is expected to be occupied. ALEX generates the proportion of time each patch is occupied while the entire population is still extant. Similarly ALEX records the percentage of time each patch and the entire population is below a user-specified level. This is useful where the conservation objective is to maximise the proportion of time a population spends above a certain size.

Sensitivity analysis

Assessing the sensitivity of results to different parameters is an essential part of PVA. This is particularly true when choosing between management options for a particular species. Often the actual extinction probabilities will vary significantly as parameters are changed, but the important issue is whether or not the ranking of management options changes (Possingham *et al.*, 1993).

ALEX includes the ability to do some sensitivity analyses automatically. Most parameters in the model can be 'tagged' and varied automatically. The user specifies how the tagged parameter will vary from scenario to scenario, e.g. plus or minus 20%. Several parameters can be simultaneously tagged; however, each is varied separately and an automatic multivariate sensitivity analysis is not supported. Modifications are in progress to facilitate a more complete sensitivity analysis and allow some sensitivity analysis on the actual patch structure; for example, what happens if we remove certain parts of the patch structure.

DISCUSSION

The designer of a simulation package for applied population viability analysis treads a subjectively chosen path between many extremes. Some of these extremes are:

- (1) A complex model that is capable of accommodating any existing species and situation. Such a model would have an unmanageable number of contingencies and parameters most of which are not used in a specific case. Often by providing too many options the key issues are confused and users are intimidated by the volume of data that appears necessary for successfully using the package.
- (2) A model for a specific species under a particular circumstance addressing a few critical issues (McCarthy *et al.*, 1994). If time and money are not important, but the question is sufficiently important, this is the best option. Unfortunately this is rarely the case.
- (3) Individual-based models where many properties of each individual are included. In one extreme all individuals in a model are identical which facilitates analytic or numerical solutions. However, most applied population models follow, at a minimum, each individual's age. In addition we may also wish to specify many other properties of each individual including its: sex, genetic makeup, size, state of health, parasite load, precise spatial position, current home range size, and position in social structure, etc. These sorts of models are useful for very small, well-studied populations (Swart *et al.*, 1993).
- (4) Analytically or numerically tractable models that subsume most of the processes within a few parameters. For PVA these models need to be stochastic. The analytic study of stochastic extinction models is an exciting field that has great educational value (Goodman, 1987; Lande, 1993), but applied problems usually include complexities beyond the assumptions of these models. One of the greatest practical difficulties with analytic and numerical models can be estimating higher level parameters from data, although steps have been made to expedite this process (Talent, 1990; Mangel & Tier, 1994).

Ultimately the designer of a model must make subjective compromises between the different approaches. For the remainder of the discussion we explore the relative merits of the approaches used in modelling

different processes in ALEX. In some cases opinions about appropriate modifications and/or alternatives are suggested.

Variability

Because ALEX only models one sex, species in which both sexes can limit population growth rate are not modelled adequately. ALEX incorporates a simple age structure where individuals exist in one of three classes. Associated with each age class is a survivorship and only the adult class may breed. Where fecundity and survivorship change in a more complex fashion, approximations will have to be made in the parameterisation of the model. ALEX does not include genetics. These three limitations mean that ALEX may not model very small populations (e.g. less than 10) particularly well. In very small populations inbreeding depression may be important, the sex ratio is clearly important (10 males in a population with no females have a very different viability than five females and five males), and age-specific differences in fecundity and survivorship can be critical. For modelling very small populations explicitly individual-based models, like VORTEX (Lacy, 1993), may be superior. In general ALEX is targeted at larger populations and the problems of modelling small populations can be alleviated by setting a finite population threshold at which extinction is deemed to occur, i.e. quasi-extinction. For management purposes the model is often insensitive to changes in this population threshold.

We justify these shortcomings in two ways. First, when populations become extremely small and there is a complex interaction between genetic and demographic stochasticity (Lande, 1988), even detailed modelling is unlikely to permit accurate predictions. From the perspective of species recovery, when a once large population has fallen to this level one could consider that the recovery programme has failed. Certainly, even if recovery occurs from a few individuals, the genetic diversity of such a population would be negligible. Secondly, our approach allows the construction of fixed matrices that speed up the birth and death processes but accurately model demographic stochasticity (Possingham *et al.*, 1992). This increase in speed means that populations with thousands of individuals can be modelled quickly. Although the speed of a simulation model is not often considered important, where applied managers are interested in many options and testing the sensitivity of those options to parameter variation, speed is important. For example, in Lindenmayer and Possingham's (1994) work with Leadbeater's possum *Gymnobelideus leadbeateri*, about 1000 scenarios have been examined, each for 300 or more runs, about 50 habitat patches and hundreds of animals, over 750 years. The estimated number of animal years simulated in the project is over two billion. Using a fixed birth and death matrix means that actual birth and death rates cannot vary from year to year, or habitat to habitat. Variation in fecundity is modelled by varying the number of females that breed. Habitat quality and environmental variability do not affect survivorship in the model. Where survivorship is known to vary significantly from year to year the user may wish to specify a catastrophic process that generates the appropriate variation.

Habitat dynamics, catastrophes and movement

We believe that a strength of ALEX is the way in which it models habitat dynamics and associated catastrophes. The fecundity of many species depends on the successional state of the habitat it occupies. ALEX allows for habitat dynamics using one habitat dynamic variable (e.g. Southgate & Possingham, this issue). Despite this, three habitat variables were necessary to model the dynamics of the critical habitat components of Leadbeater's possum (Lindenmayer & Possingham, in press). We believe it is important to allow the probability of a catastrophe to depend on and affect the habitat or population size. The catastrophes in ALEX have been used to model fires, logging, drought and local predation events.

ALEX allows catastrophes to be either local or global. For some catastrophic processes that spread through the landscape, like fires and epidemic, a better model may be to include explicitly a mechanism for spreading. For example, we could assign a probability that a catastrophe starts in any patch, then a matrix of probabilities that determines how it spreads to other patches. However, if this in turn depended on the habitat quality and population size of a patch, such a model may become hard to parameterise. Because catastrophes are by definition relatively rare events, parameterising them is difficult.

When the quality of patches is modelled dynamically, and patch spatial structure is important, the modelling of movement between patches is likely to be important. ALEX provides a range of options for modelling movement; however, there are numerous methods that could be employed and until better data are available most movement models will be constructed subjectively. One key issue not dealt with by ALEX is differentiating movement events that cause an occupied patch to be supplemented, from movement events that result in colonisation of an empty patch.

Density dependence

For most species we have little or no information on the impact of population density on fecundity or survivorship, particularly rare species. Many population models use the logistic function, and other similar functions, to model the impact of density on birth and death. In our model, density dependence may occur through three mechanistic processes: in patches with low-quality breeding home range sizes effectively increase, there is a ceiling to the population size, and the user may set a population density threshold below which migration, and hence death through migration, do not occur. We are equivocal about the various methods that are employed and believe that this is one of the most difficult issues in population viability analysis modelling (Lande, 1993).

Model output and sensitivity analysis

Many authors focus on the mean time to population extinction as their model output. We believe that the median time to extinction is a more convenient to extinction for two reasons. To calculate the mean time to extinction we must follow every population to extinction -- often this is impractical. Secondly, the mean time to extinction may be increased significantly by a few extremely fortunate runs, while the median reflects the time to extinction of the average run. Sensitivity analysis is an integral part of population viability analysis. Assessing the significance of results will become an increasingly important issue (Ferson & Burgman, this issue; McCarthy *et al.*, this issue). This is particularly true for processes such as movement and catastrophes about which little may be known.

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