Ecological Modelling (1995) 82 (2) : 161-174. http://dx.doi.org/10.1016/0304-3800(94)00085-V
http://www.sciencedirect.com/science/journal/03043800

A Review of the Generic Computer Programs ALEX, RAMAS/space and VORTEX for Modelling the Viability of Wildlife Metapopulations

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Abstract

An assessment is presented of three computer packages, ALEX, RAMAS/space and VORTEX, that have been developed for analyses of metapopulation viability. Their usefulness was assessed in the context of the need to understand the assumptions and limitations of the programs. The study examined many attributes of these programs, ranging from availability and "user-friendliness" to the mathematical structure and procedures underpinning the sub-models. Key features and strengths of, and differences between, the various programs were highlighted. They are structured differently and vary in the way processes such as environmental and demographic variation are modelled. Many of these differences reflect what the architects of the programs consider to be the most important factors influencing the viability of metapopulations. These differences mean that the programs may produce different results even for investigations of the same populations. The selection of the most appropriate program should be based on a range of key criteria including: (1) the key question(s) and objectives of the study, and, (2) the strengths, limitations and assumptions that underpin the program and how these match the attributes, life history parameters and available data for the target species. The processes of data assembly, running the programs and reading the accompanying documentation give the user an improved understanding of population behaviour and dynamics. The wide variety of threatened taxa and diversity of conservation problems highlight the value of a broad range of sound, well-developed and relatively error-free packages for simulating metapopulation viability. However, in some cases it may be more appropriate to develop a new program that is tailored specifically to the requirements of a particular management problem.

Keywords: management strategies; model comparison; population viability

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1. Introduction

Population viability analysis is the quantitative evaluation of all factors and their interactions that act on populations and contribute to their risks of short- and long-term decline or extinction (Boyce, 1992). Such analyses enable wildlife managers to forecast the fate of populations, allowing the development of preemptive management actions and strategic research programs (Clark et al., 1991; Lindenmayer et al., 1993a,b). Viability analyses are a key component of many endangered species management and recovery plans (Mace and Laude, 1991; Possingham et al., 1993) and in Australia they have been recommended for use as a tool for quantifying the impacts of land use practices by estimating their effects on extinction probabilities (Resource Assessment Commission, 1992). The use of viability analysis offers a range of benefits for the development of strategies to conserve threatened species. Some of the most important of these are allied with the quantitative and objective nature of the technique (Lindenmayer et al., 1993a). Its application can help place a quantitative value on the opportunity costs of proposed resource development. The use of the approach may also overcome some of the problems associated with potentially subjective judgements made by wildlife biologists and managers who may have pre-determined opinions about the conservation status and management of populations they know well.

Computer simulation programs are being used increasingly in the assessment of the viability of populations of threatened or vulnerable organ-isms and in the development of applied conservation strategies (Table 1; Thomas et al., 1990; Haig et al., 1993; Lindenmayer et al., 1993a,c). There are many programs presently available for viability analysis including GAPPS (Harris et al., 1986), VORTEX (Lacy,1993),RAMAS/age (Ferson and Akçakaya, 1990), RAMAS/stage (Ferson, 1990), RAMAS/space (Akçakaya and Ferson, 1992), and ALEX (Possingham et al., 1992). The selection of the most appropriate program for a given task is important because the features that may recommend its use in one study may make it unsuitable for others. For example, Samson (in Simberloff, 1988) noted that the structure of the model POPDYN which was applied to the Gopher Tortoise, *Gopherus polyphemus (Cox,* 1988), would preclude its use in studies of species that do not breed annually such as the Northern Spotted Owl, *Strix occidentalis caurina.* As a result, a potential problem for many conservation biologists may be the selection of the program that is best suited to answer specific management questions and the attributes of the target species.

Table 1
Selected examples of applications of ALEX, RAMAS/space and VORTEX

Program	Species	Reference
ALEX	Powerful owl (*Ninox strenua*)	Possingham and Noble, 1991; Possingham et al., 1992
	Greater glider (*Petauroides volans*)	Possingham et al., 1992,1994; Lindenmayer et al., 1993c
	Leadbeater's possum (*Gymnobelideus leadbeateri*)	Lindenmayer and Possingham, 1995a
RAMAS/space	California spotted owl (*Strix o. occidentalis*)	LaHaye et al., 1994
	Waved albatross (*Diomedea irrorata*)	Buckley and Downer, 1992
	Californian gnatcatcher (*Polioptila c. californica*)	Ogden Environmental and Energy Services, 1992
VORTEX	Puerto Rican parrot (*Amazona vittata*)	Lacy et al., 1989
	Eastern barred bandicoot (*Perameles gunnii*)	Lacy and Clark, 1990
	Leadbeater's possum (*Gymnobelideus leadbeateri*)	Lindenmayer et al., 1993b; Lindenmayer and Lacy, 1995;

Programs for metapopulation viability analysis typically focus on species in which populations are restricted to more or less isolated patches of habitat of differing quality that are interconnected by dispersing individuals (Levins, 1970; Den Boer, 1990). Modelling metapopulations is complex (e.g. Hanski and Gilpin, 1991; Howe et al., 1991), and there is a lack of consensus amongst the proponents of different models about what factors are, and are not important in estimating extinction risks for natural populations. Moreover, many users of generic models for metapopulation viability analysis are often perplexed as to why more than one program exists. Here, we review three generic computer simulation pro-grams that are used for the analysis of metapopulation dynamics: ALEX (Analysis of the Likelihood of EXtinction, Possingham and Noble, 1991; Possingham et al., 1992), VORTEX (from the "extinction vortex" of Gilpin and Soule, 1986; Lacy, 1993), and RAMAS/space (Risk Assessment and Management Alternatives System; Akçakaya and Ferson, 1992). All three programs are widely available and have been applied in many studies of threatened species (Table 1). This investigation aims to review the strengths, limitations and assumptions of each model, and more generally to evaluate the usefulness of pro-grams of this kind in metapopulation viability analysis.

2. Methods

Because ALEX, VORTEX and RAMAS/space are regularly modified and upgraded, a specified review date was set at 1 January 1992. The programs and accompanying documentation that were assessed in this investigation were ALEX Version 2.2b, RAMAS/space Version 1.3, and VORTEX Version 5.1. A questionnaire was used as a guide for the reviews. The questions covered cost and availability, "user-friendliness" and the range of sub-models within the packages. Each package was reviewed by its architect as well as the four other participants in the project. The reviews were synthesized by the two participants who were *not* associated with the development of any of the programs (DBL and MAB).

Table 2
Key attributes of three computer packages used in the analysis of metapopulation viability

Attributes	Program		
	ALEX	RAMAS/space	VORTEX
Architect(s) of program	H. Possingham I. Davies I. Noble	R. Akçakaya S. Ferson	R. Lacy
Availability	H. Possingham, Dept. Applied Mathematics, University of Adelaide, Adelaide, S.A. 5005, Australia	Applied Biomathematics, 100 North Country Rd., Setauket, NY 11733, USA	Captive Breeding, Specialist Group, 12101 Johnny Cake Ridge Rd., Apple Valley, MN 55124, USA
Copyright	Yes	Yes	Yes
Cost	$A20 [a]	Free	$US25
Program language	Turbo-Pascal	Turbo-Pascal	C
Source code availability	No	No	No (can be released by author)
Types of operating system	MS-DOS	MS-DOS	MS-DOS
Max. population size	32000	2 billion	> 1000 [b]
Max. number of populations	45	160	20
Max. number of replications	1000	10000	32000
Random number generator	Limited adjustment	Can be adjusted (but is discouraged)	Fixed and cannot be be adjusted
Age structure	Yes (limited)	No [c]	Yes (limited)
Stage structure	No	No [c]	No
Graphical view of input parameters	Yes (limited)	Yes	No

[a] The package may not be used to generate income or scientific papers without permission of the architect (HPP).
[b] Complex models for > 1000 individuals may take several days to run on a 80386 machine.
[c] Accessed via sister programs RAMAS/age or RAMAS/stage.

Table 3
Key factors of metapopulation dynamics incorporated in ALEX, RAMAS/space and VORTEX

Attributes	Program		
	ALEX	RAMAS/space	VORTEX
Environmental variation	Yes	Yes	Yes
Genetic variability	No	No	Yes
Correlation of environmental variation among patches	Partial	Yes	No
Demographic variation	Yes	Yes	Yes
Density dependence	No (Limited)	Yes	No (Limited)
Allee effects	No	Yes	Yes [a]
Catastrophes	Yes	No	Yes
Density-dependent migration	Yes	Yes	No
Distance-dependent migration	Yes	Yes	No
Harvesting and supplementation	Yes [b]	Yes [b]	Yes (Limited)
Explicit social structures	No	No	Yes
Temporal variation in carrying capacity	Yes (only stochastic changes)	Yes	Limited (linear + stochastic changes)

[a] Allee effects are modelled in VORTEX by selection of an appropriate polynomial model of density dependence.
[b] Through the use of dummy sub-populations.

Table 4
A summary of features of ALEX, RAMAS/space and VORTEX describing the user-friendliness of the various computer simulation programs

Feature	ALEX	RAMAS\space	VORTEX
Automatic check of input parameters	Yes (warning message)	Yes (warning message)	No
Example datasets	Yes	Yes	No
On-line help	No	Yes	No
Program tutorial	No	Yes	Yes (Partial)
Keyboard input	Yes	Yes	Yes
Save and/or edit batch files	Yes	Yes	Yes [a]
Interactive menu system	Yes	Yes	Limited
Help from architect when modelling	useful [b]	useful (not essential)	useful (not essential)
Description of numerical procedures	No	Yes (limited)	Yes
Graphical view of results on screen	Yes	Yes	No
Assistance in deriving input parameters	Limited	Limited	Limited
Documentation on user errors and solutions	No	Yes	No
Printing of graphical results	No	Yes	No [c]
Export of results to other software	No	Yes (limited)	Yes
Assistance with program from manual	Limited	Excellent	Moderate
Background information on extinction and PVA in manual	No (limited)	Yes	Yes
Background information on population dynamics in manual	No (limited)	Yes	Yes
Planned modifications	On-line help; Catastrophe spread; Harvesting and translocation	GIS interface; Stage structure; Sensitivity analysis	Age/sex- specific migration rates; Graphics interface

[a] The format of the batch file is not easy to create.
[b] The architect prefers consultation with program user.
[c] Through sister program VORPLOTS.

3. Results

The information presented in Tables 2, 3 and 4 is a summary of the features of the various programs. Some attributes of the packages needed a more detailed explanation than could be included in the tables and these have been outlined below.

3.1. Demographic structure

ALEX
Only the fate of one sex, the sex that limits reproductive capacity (normally females), is followed. There are three life-history stages: individuals are classed as newborn in the first year, become juveniles for a period of 0-5 years, and are categorised as adults for the remainder of their lives and are capable of breeding until they die. The probability of survival may vary between the different classes. No provision is made for differences in mating systems and social structure. All populations in the metapopulation have the same demographic parameters. The populations are assumed to be at the stable age distribution at the beginning of a simulation.

RAMAS /space
RAMAS/space is not age- or stage-structured. However, such data can be included by first running the sister programs RAMAS/age or RAMAS/stage. Different sub-populations may have different demographic parameters such as mean and standard deviation of growth rate, carrying capacity and survivorship. No provision is made for differences in mating systems and social structure.

VORTEX
Birth and death rates are age- and sex-specific but they are constant from the age of first breeding until an organism reaches the maximum longevity specified by the user. VORTEX can model some kinds of monogamous and polygamous mating systems. The monogamous mating system assumes a random recombination of pairs at the end of each year, and it would not be entirely appropriate for species that form monogamous pairs that persist for more than one year (e.g. some species of birds). The user can

specify the proportion of the adult males in the breeding pool and these animals are assumed to have an equal chance of siring offspring.

3.2. Environmental variation

ALEX
Environmental variation is modelled by sampling a random number from a normal distribution with a specified mean and standard deviation. This variation influences the probability of reproduction in any given year through a user-defined response function. Death rates are not subject to environmental variation. Patch quality and environmental variation affect only the population birth rates and not mortality.

RAMAS /space
Environmental variation is modelled by sampling the annual rate of population growth from a random (log normal) distribution with a specified mean and standard deviation. These parameters may vary between sub-populations. The carrying capacities of the patches are not affected by environmental variation.

VORTEX
Environmental variation in birth and death rates for each sex and age class is modelled by sampling the annual probabilities from binomial distributions with specified means and standard deviations. The effects of environmental variation impact simultaneously upon all individuals in the population. The specified standard deviation reflects the impacts of environmental variability by increasing the variability of binomial trials for births and deaths. Environmental variation in the carrying capacity of each patch is modelled by sampling the normal distribution with a specified mean and standard deviation.

3.3. Correlations between environmental variation, patch quality and demographic structure

ALEX
As only adult organisms are capable of reproducing in ALEX and environmental variation affects only the birth rate, there is no correlation between environmental variability and age class. The level of correlation between patches for the single environmental parameter (see above) can be varied by the user between 0 (completely independent) and 1 (completely correlated). The first patch in any given scenario must be assigned a correlation value of 1 and other patches are assigned a correlation with reference to patch one. Thus, the correlation structure is limited to a single value between each patch and the reference patch. This does not allow for all possible correlation structures.

RAMAS */space*
Correlations between sub-populations are modelled by sampling population growth rates from correlated random distributions. The level of correlation can be either specified, or a suite of default values can be generated from a function that relates the level of similarity in environmental variability with the distance between two sub-populations. The level of correlation between patches can be varied by the user between zero (completely independent) and one (completely correlated).

VORTEX
Environmental variation in reproduction, mortality and carrying capacity is completely correlated between age-sex classes. Environmental variation is independent among sub-populations. Within sub-populations, the three types of environmental variation are either assumed to be completely correlated or completely independent. VORTEX makes no provision for partial correlations between environmental variability in reproduction, mortality and carrying capacity.

3.4. Demographic variability

ALEX
ALEX models demographic variability by drawing random numbers from a binomial distribution to represent the numbers of births and deaths.

RAMAS */space*

Demographic variability is modelled by selecting the number of survivors from a binomial distribution and the number of offspring from a Poisson distribution. In both ALEX and RAMAS/space, this approach gives the same result as simulating the fate of each individual (Akçakaya, 1991).

VORTEX

Demographic variation is modelled by tracking the fate of each individual and each of its major life history events, i.e. sex determination, birth, migration and death. Each individual trial represents a binomial sampling process.

3.5. Density dependence

ALEX

A density-dependence model applies only when the population exceeds a specified carrying capacity (termed a "ceiling exponential" model). When the ceiling is exceeded, animals are re-moved from the population beginning with those from the youngest age classes until the ceiling is reached.

RAMAS */space*

The program incorporates four density-dependence models viz: logistic growth; the Ricker function; Allee effects and Malthusian or density-independent growth. It is also possible to specify the density-dependence function so that it can incorporates both overcrowding (e.g. a logistic function) and undercrowding (Allee effects). Therefore, the growth rate may decrease as the population increases or declines with a maximum value attained at intermediate densities. A different density-dependence model may be specified for any given population.

VORTEX

VORTEX also uses a "ceiling model" in which density dependence in survival is invoked only when the size of the population becomes larger than the pre-determined carrying capacity. VORTEX imposes the carrying capacity via a probabilistic truncation of each age class whenever the population exceeds the specified size. Each animal in the population has an equal probability of being removed during this truncation. The impacts of density dependence on reproduction can also be modelled using a fourth order polynomial that gives the relationship between population size and the probability of breeding. The reduction in breeding potential acts equally on each adult in the population.

3.6. Catastrophes

ALEX

Up to three types of catastrophes can be modelled in ALEX. These have impact on the population size only in the year in which they occur, but influence habitat suitability and breeding success in subsequent years. The frequency of catastrophes can be specified as an annual probability of occurrence that may be either density dependent (e.g disease) or habitat quality dependent (e.g. fire). Catastrophes may act independently in each patch or simultaneously in all patches.

RAMAS /space

Catastrophes cannot be modelled explicitly in RAMAS/space. The program assumes that catastrophes are represented as the left tails of the distributions of population growth rates.

VORTEX

Any number of catastrophes can be modelled in VORTEX. Catastrophes are modelled as inde-pendent events that are uncorrelated amongst populations. They have an impact on reproduction and survival only in the year that they occur. The probability of occurrence of a catastrophe in any given year and its impact on reproduction and survival can be specified by the user.

3.7. Migration

For the purposes of this review, the term "migration" refers to the movement of organisms between patches of habitat and it includes processes such as dispersal.

ALEX

Two types of movement can be simulated in ALEX. These are called migration and diffusion and their probability of occurrence varies between age classes and the density of animals in any given patch that is a "source" of dispersalists.

(1) *Migration.* Each individual has a specified probability of migrating when the density of individuals in a particular patch exceeds a given proportion of its carrying capacity. This enables the rate of movement to vary according to temporal changes in the abundance of animals in a source area. The mean distance an organism can move before it dies is specified by the user. Each emigrant moves in a randomly chosen direction from its source patch. The organism dies if the direction of movement does not result in it contacting another habitat patch. If the direction of movement intersects with another patch, then the probability that the organism reaches that area declines exponentially with increasing inter-patch distance. For scenarios with only one habitat patch, all emigrating animals die.

(2) *Diffusion.* Diffusion simulates the movement of animals between adjacent or connected patches and it can be invoked only when there are two or more sub-populations. The maximum number of animals that can diffuse between patches is a function of the common length of the boundary. Hence, diffusion is likely to be more prevalent when there is an extensive common area that is shared by neighbouring patches. There is no probability of mortality associated with the process of diffusion. The preferential movement of animals to areas of better quality habitat also can be specified by the user.

RAMAS /space

Migration is modelled in RAMAS/space by specifying a probability of movement between pairs of sub-populations. The migration rates are specified as a matrix. This can be filled automatically by calculating the rates from a user-specified function of the distance between sub-populations. The matrix can subsequently be modified to ac-count for corridors (an increase in the migration rate between pairs of sub-populations) and barriers (a decrease in inter-population migration). Migration rates can be density-dependent and the nature of density-dependence can be specified for each sub-population. This, in turn, allows factors such as the abundance of animals in given habitat patches, to result in temporal variations in the rate of migration. A parameter for the direction of a migration can be specified to reflect circumstances where it is more difficult to move from patch B to patch A than it is to move from patch A to patch B (such as a stream environment).

VORTEX

The rate of migration between any pair of populations is specified by the user. They are independent of age and sex and modelled as an annual probability that a given individual will migrate from one sub-population to another. There is no provision for incorporating temporal changes in the rate of migration.

3.8. Genetics

Only VORTEX models the impacts of changes of genetic variation. At the beginning of the simulation, each animal is assigned two unique alleles at a hypothetical locus. The alleles are transmitted in a random, Mendelian fashion. Thus, an infinite alleles model is used in which the number of distinct alleles at the hypothetical locus is initially twice the number of animals. Because the proportional loss of gene diversity (also termed "expected heterozygosity") due to genetic drift and inbreeding is independent of the starting allele frequencies (Crow and Kimura, 1970), the infinite alleles model is quite general and it is commonly employed in simulation studies (e.g. MacCluer et al., 1986). The user specifies the severity of inbreeding depression which is reflected as a loss of viability amongst inbred animals. Inbreeding depression can be simulated using one of two possible models available within VORTEX: (a) the heterosis model, and, (b) the recessive lethals model. All animals of reproductive age have an equal probability of breeding and the impacts of inbreeding depression effects only one component of fitness - the survival of young that are < one year old.

(1) *Heterosis model.* Here, selection against homozygotes does not remove the genetic load but allows for a user-defined number of "lethal equivalents" or a measure of the severity of selection against homozygotes. As a result, homozygotes have reduced fitness compared with heterozygotes.

(2) *Recessive lethals model.* In this subroutine each founder starts with one unique recessive lethal allele and a unique, dominant non-lethal allele. Thus, there are initially N distinct, dominant, non-lethal alleles and N distinct, complementary, recessive, lethal alleles at the hypothetical locus in a population of N animals. There is selection against homozygotes for lethal alleles in future generations and this

removes deleterious alleles from the population. The presence of one recessive lethal per founder models a relatively weak effect of inbreeding. This is based on empirical studies which have found that mammal populations more typically contain two to four recessive lethal alleles per individual (Rails et al., 1988). The effect of modelling all recessive lethal alleles at the same locus, rather than the more realistic case of recessive lethals being spread across many loci, is quite small. The likelihood of death due to inbreeding would be slightly lower if the lethal alleles were spread amongst many loci. This is because there would be a small probability that such animals would be homozygous simultaneously for lethal alleles at more than one locus. For example, for full-sib matings, the probability of genetic death would be 0.125 using the single locus model in VORTEX, but 0.118 if the lethal alleles were distributed amongst a large number of loci. When a lesser effect of inbreeding is modelled (e.g. inbreeding coefficients < 0.10), the number of loci that are simulated has virtually no impact on the probability of genetic death amongst inbred animals.

3.9. Output

ALEX
Output from ALEX includes: the probability of quasi-extinction (threshold target for population size; see Ginzburg et al., 1982; Burgman et al., 1993), the mean, median, first and third quartile time to extinction, and the number of simulation time steps during which each habitat patch was unoccupied.

RAMAS */ space*
Output from RAMAS/space includes: the probability of quasi-extinction, the mean, standard deviation, minimum and maximum population size for the metapopulation and each population, metapopulation occupancy through time, risk of population explosion, distribution of time to extinction (with median time indicated), cumulative time to extinction, and risk of population decline during the simulation or at the end of the simulation.

VORTEX
Output from VORTEX includes: deterministic rate of growth, the stable age distribution, the observed rate of growth, mean population size, probability of extinction, mean and median time to extinction for the metapopulation and for each sub-population, observed and expected heterozygosity, and the number of founder alleles remaining. Where appropriate standard deviations and standard errors are given for each variable.

3.10. Special features

ALEX
The most important features of ALEX are: (i) a built-in capability for sensitivity analyses, (ii) the movement of organisms to areas of greater habitat quality, and, (iii) relatively flexible mecha-nisms for the representation of different kinds of catastrophes, in particular those that may depend on biomass (e.g. fires) or influence habitat quality and population size. This enables species that prefer particular stages of vegetation succession to be modelled.

RAMAS /space
RAMAS/space is the only program to include a range of density-dependence mechanisms, including Allee effects. RAMAS/space has several special features, the most striking of which is a user interface that is superior to those provided in the other two packages. It includes, for example, spatially-orientated graphics that include an option for adding geographic or map-based data to information on metapopulations.

VORTEX
VORTEX is the only one of the programs that tracks individuals and as a result it has the capability of including some detail on behaviour and mating systems. The program also models the impacts of genetic factors.

3.11. Values for teaching

ALEX
ALEX has a demonstration option that provides a graphical display of the dynamics of each population. However, a considerable body of assumed prior knowledge is required to operate the package. A more user-friendly interface together with enhanced documentation that better out-lines the parameters input to, and procedures followed in, the program would be needed to facilitate its use as a teaching tool. Indeed, the manual that accompanies the program states that ALEX is designed to be used with the assistance and input of its principal architect.

RAMAS /space
RAMAS/space is a valuable instrument for teaching because of its user-friendliness (Table 4), graphical data displays, tutorial and on-line help menus, array of other support functions and comprehensive documentation. The program is the most easily used of the three and it can be run with a limited initial understanding of population dynamics. It has been used in graduate and undergraduate classes and in several workshops involving people from conservation and land management agencies (e.g. Akçakaya et al., 1992).

VORTEX
The manual provides background for viability analyses. The program has no help functions and the documentation does not provide a clear indication of the capabilities or limitations of the program. VORTEX has been used extensively in teaching post-graduate and advanced under-graduate students. The program has also been applied in several workshops with officers from conservation and land management agencies (e.g. Clark et al., 1991). The effective use of VORTEX requires an understanding of population dynamics, particularly for the assembly of input data. The lack of a graphical interface limits its class-room utility.

4. Discussion

Comprehensive knowledge and data are usually unavailable or incomplete for most species. For any given application of any one of the pro-grams reviewed, it is likely that some of the information required by the program will be missing. Users are bound to confront the question of how the programs will behave in the absence of key data. All of the programs may be run by omitting values for some factors such as environmental variation and catastrophes. ALEX and VORTEX provide default values for most parameters. For example, when a new population is added to ALEX, it is allocated an initial size and the patch has an initial (non-zero) carrying capacity. In contrast, RAMAS/space provides default values for a number of parameters but there are far fewer non-zero defaults than in VORTEX or ALEX.

The differences in the way defaults are handled reflect an important difference in the philosophies and intentions of the architects. ALEX, and to a lesser extent, VORTEX, are designed to be used with the direct assistance of their architects (HPP and RCL respectively). Indeed, in ALEX the user manual states that the program should not be used to generate income or produce scientific papers without the permission of the author. This position is reinforced by the user manual. Defaults are allocated for convenience because it is assumed that the architect of the program will be near at hand for most applications. RAMAS/space, on the other hand, is designed to be used without the direct assistance of the architects. The completeness of the documentation and the general user-friendliness of the software reflect this orientation. Non-zero defaults are not provided because the architects want the users to specify population-specific parameters. However, the program RAMAS/space also has 13 sample data files that illustrate various ways of parameterising the model.

The information presented in Tables 2, 3 and 4 provides a guide to the utility of the programs. For example, the number of sub-populations (e.g. > 100) may favour the selection of a particular program (see Table 2). An alternative package may be required where the impacts of catastrophes on population dynamics are considered to be important. There are additional limitations that may not be clear from the summaries in Tables 2, 3 and 4. As ALEX tracks only the fate of one sex in a metapopulation, it may not be suitable for those species where the number of both sexes is a potentially limiting factor. RAMAS/space would not be suited to the analysis of very small populations (e.g. those held in captivity) or where catastrophes are important. VORTEX, in common with ALEX, is likely to have difficulties modelling highly fecund taxa including many plants, invertebrates, amphibians and fish where thirty or more young are produced in a single reproductive event.

There are species for which all of the pro-grams will be inadequate. For example, if there is a need to model explicitly the effects of catastrophes on a species for which exponential growth to a ceiling is not appropriate, then none of the programs will be adequate. None of the packages appear to be suitable for modelling some stage-structured species (e.g. insects; see Murphy et al., 1990) or organisms that reproduce sporadically in response to unusual climatic conditions such as plants that inhabit semi-arid or arid environments (e.g. Burgman and Lamont, 1992). Analyses would be difficult to complete for species with multi-annual population cycles (Burgman et al., 1992) such as small mammals that inhabit deserts or high latitude environments in the Northern Hemisphere.

The choice of the most appropriate program for a given investigation should be dependent on the objectives of the study together with an understanding of the strengths, limitations and assumptions which are implicit and explicit in each (Simberloff, 1988; Boyce, 1992). This may require an intimate understanding of the various packages.

The results of our study make it apparent that a different program may be required to address different questions, even for the same species. This is highlighted by a suite of investigations of Leadbeater's Possum *Gymnobelideus leadbeateri* which is an endangered species that inhabits the forests of south-eastern Australia. VORTEX was used in an examination of the interacting effects of genetic factors and population demography on the extinction of the species (Lindenmayer et al., 1991,1993a; Lindenmayer and Lacy, 1994). Conversely, RAMAS was applied in a study of the efficacy of various strategies for the reintroduc-tion and translocation of *G. leadbeateri* (Burgman et al., 1995). Finally, a detailed investigation of the impacts of timber harvesting operations on G. *leadbeateri* where logged and regenerated forest patches display marked variations in habitat suit-ability has recently been completed using ALEX (Lindenmayer and Possingham, 1995a,b).

In some cases it will be necessary to modify a generic package, or to develop a new program, to reflect the biology of a particular species (Star-field and Bleloch, 1992; Burgman et al., 1993). This approach was adopted for viability analyses of, for example, the white-footed mouse *(Peromyscus leucopus,* Fahrig and Merriam, 1985), giant kelp *(Macrocystis pyrifera,* Burgman and Gerard, 1990), Furbish's lousewort *(Pedicularis furbishiae,* Menges, 1990), the helmeted hon-eyeater *(Lichenostomus melanops cassidix, Mc-*Carthy et al., 1994), and the matchstick banksia *(Banksia cuneata,* Burgman and Lamont, 1992). The wide range of species, diversity of life history strategies and the plethora of applied conservation issues highlights the need for a wide range of packages as well as the development of new ones for metapopulation viability analysis. However, widely available generic packages have several major advantages. For example, thoroughly tested packages will be relatively error free, preventing potentially inconsistent interactions between in-put parameters that may, in turn, significantly influence the results of viability analyses. This can facilitate routine procedures such as sensitivity analysis that are used to determine the impacts of critical factors affecting population behaviour (Possingham et al., 1993).

The software and documentation of ALEX, RAMAS/space and VORTEX are regularly assessed and upgraded. This is a key procedure in the evolution of computer simulation programs and it enables new information and features to be incorporated. Indeed, there will be updated versions of the all programs in the near future (Table 4) with new features such as a G.I.S. interface (e.g. Akçakaya et al., 1994). Notably, each of the three packages that were examined in this study were sufficiently general to have been used in studies of a wide variety of taxa and applied management issues (Table 1; Lindenmayer et al., 1993a). The extra features that will be added to the various programs will make them more generic and increase the range of aspects of metapopulation dynamics that can be modelled. However, whilst it will be theoretically possible to continue to extend further the generality of the various packages, the need to do this may have to be considered alongside other factors. These include the time required to run more extensive models and the difficulties in parameterising numerous additional input variables.

This review was designed to assist potential users to assess the various programs and deter-mine which one of the three, if any, is best suited to a particular case study or target species. It focused on only three of a number of packages presently available for metapopulation viability analysis. Other valuable and widely available programs such as GAPPS (Harris et al., 1986) were not evaluated. However, it is likely that these will have features that make them inappropriate for particular case studies.

Any computer program, including those re-viewed here, necessarily contains a large number of assumptions and simplistically models the behaviour of organisms. Thus, the results of viability analyses can only be estimations of the actual dynamics of wild populations. As a result, caution should be used when interpreting and applying the results of any such analysis, even when the package has features that make it suitable for the problem at hand. The results of analyses should reflect general trends in population behaviour (Soulé, 1987) that are useful for management (Shaffer, 1990). Viability analysis typically does not consider aspects of community ecology such as interactions between, and the inter-dependence of, organisms in ecosystems or their "functional role" (Conner, 1988). For example, a reduction in population size may influence important biological processes in ecosystems such as pollination and/or the dispersal of propagules (e.g. Claridge et al., 1992).

5. Conclusions

(1) The programs examined in this study are structured differently and model key aspects of population dynamics in different ways. To some extent these variations represent differences in what the architects of the programs consider to be the most important factors influencing the dynamics of metapopulations.

(2) The three programs examined in this study are relatively free from numerical errors and can be used in a wide range of cases. Each program has particular features not common to the others. Some programs will be better suited to studies of particular species and tasks than others. The choice of the most appropriate program must be guided by the features of the package and how these correspond to the objectives of the project and the attributes of the target taxon.

Acknowledgements
Criticisms by K. Viggers, R. Downer and M. McCarthy improved earlier drafts of the manuscript. D.B. Lindenmayer is supported by an Australian Research Council Post Doctoral Fellowship.

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