Use of population viability analysis in conservation management in New Zealand

SCIENCE FOR CONSERVATION 243

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Published by
Department of Conservation
PO Box 10-420
Wellington, New Zealand

Science for Conservation is a scientific monograph series presenting research funded by New Zealand Department of Conservation (DOC). Manuscripts are internally and externally peer-reviewed; resulting publications are considered part of the formal international scientific literature.
Individual copies are printed, and are also available from the departmental website in pdf form. Titles are listed in the DOC Science Publishing catalogue on the website, refer http://www.doc.govt.nz under Publications, then Science and Research.

ISSN 1173-2946
ISBN 0-478-22591-1

In the interest of forest conservation, DOC Science Publishing supports paperless electronic publishing. When printing, recycled paper is used wherever possible.

This report was prepared for publication by DOC Science Publishing, Science & Research Unit; editing and layout by Geoff Gregory. Publication was approved by the Manager, Science & Research Unit, Science Technology and Information Services, Department of Conservation, Wellington.

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Use of population viability analysis in conservation management in New Zealand

1. Review of technique and software

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ABSTRACT

This review provides an introduction to what population viability analysis (PVA) is, how it works, and what situations it can be used for. PVA has become a commonly used tool in conservation biology and in the management of threatened or endangered species. The ready availability of generic computer packages for running PVA has increased its use. It is often used to gain a better understanding of the population biology of a threatened species, identify gaps in knowledge of its life history, and estimate the relative risks and conservation values of alternative management options. However, it can be used incorrectly, potentially to the detriment of the species being modelled, and some degree of guidance is needed to help users determine whether carrying out a PVA would be beneficial or whether they should pursue other alternatives. PVA is a useful tool provided that adequate data exist and the models and assumptions are carefully assessed. It is best suited for projecting population trends 10–50 years into the future to compare different management scenarios, but is less useful for predicting absolute measures of survival, such as probabilities of extinction. PVA is also most useful if continually updated and tested as new data are collected. Such an approach would be useful for species recovery groups in New Zealand. Case studies from New Zealand and elsewhere are given to highlight the different uses of PVA and to show the potential benefits. Also, different computer packages available for performing PVA are described, and a comprehensive list of references is included for further reading.

Keywords: population viability analysis, PVA, computer simulation, mathematical modelling, conservation management, threatened species, population trends, New Zealand.

Keedwell, R.J. 2004: Use of population viability analysis in conservation management in New Zealand. 1. Review of technique and software. *Science for Conservation 243*: 5–37.

or in full as:

Keedwell, R.J. 2004: Use of population viability analysis in conservation management in New Zealand. 1. Review of technique and software. Pp. 5–37 in: Keedwell, R.J. 2004: Use of population viability analysis in conservation management in New Zealand. *Science for Conservation 243*. 60 p.

1. Introduction

Population viability analysis (PVA) is widely used in conservation biology and in the management of threatened or endangered species. In its broadest sense, PVA is a collection of methods for evaluating the threats faced by populations or species, their risks of extinction or decline, and their chances of recovery. It is based on species-specific data and computer simulation models. PVA has been used for a range of species from large mammals to birds, reptiles, invertebrates, fish, and plants. One of the most important benefits from PVA is that it allows evaluation of different management options for a population or species, and can help assess how to use limited resources and money in the most effective way. It can also help identify future research needs.

PVA models were originally developed to assess minimum viable population sizes for endangered species, and often only considered one threat to the survival of the population. In contrast, PVA models in use today range from simple simulations of population trends to complex models involving spatial and temporal variation. These models can assess the effects of habitat quality, habitat patches, fragmented populations, rates of migration between sub-populations, and genetic effects such as inbreeding depression on population viability. They can also incorporate basic demographic parameters—size, age or other structure, and rates of birth, death, and migration. The usefulness of PVA has been recognised to the extent that the World Conservation Union (IUCN) uses PVA predictions as one of the main criteria for listing threatened and endangered species (Brook & Kikkawa 1998). To date, over 100 PVA have been published on a wide range of species. Many user-friendly computer packages are now available that enable people with little or no mathematical or computer expertise to run comprehensive simulations.

Although PVA is a useful technique, it can be used incorrectly, potentially to the detriment of the species being modelled. A quality PVA cannot be performed without sufficient data on the target species. Accordingly, some degree of guidance is needed to help users determine whether carrying out a PVA would be beneficial or whether they should pursue other alternatives.

This report is aimed specifically at Department of Conservation (DOC) managers to introduce how PVA can be used to help make quality decisions about management actions. Although it is not designed as a 'how-to' manual, and further training or reading would be necessary before formulating a PVA, the report outlines what a PVA is, and how it works, and describes the types of conservation applications to which it can be put. Case studies from New Zealand and overseas are given to highlight the different uses of PVA and to show the potential benefits. Different computer packages available for performing PVA are described. At present, PVA computer software is not available on the DOC computer network, but staff with stand-alone computers would be able to use it.

2. Defining PVA

Population viability analysis is the development of formal, qualitative and quantitative models representing the dynamics and ecology of species and the factors that affect them (Burgman 2000). PVA models begin essentially with the basic stock and population dynamics of the study species, such as birth and death rates, migration, sex ratio and age structure of the population. To this may be added effects of spatial structure (e.g. the amount, quality, and availability of suitable habitat), environmental and demographic uncertainty, dispersal, catastrophes, inbreeding and genetic effects, and external deterministic processes such as habitat loss or hunting that impinge on a species' chance of persistence (Burgman 2000). PVA simulation programmes use these input parameters to project forward through the years (or other unit of time) to determine the fate of each individual in the population at each stage of its life cycle.

Most life events modelled in a PVA are probabilistic events (i.e. the probability that an individual lives or dies, reproduces or fails to reproduce). The chance of each event occurring in the life of each simulated individual in the population is determined by probabilities entered by the user. The probabilities of different events happening are not always independent. For example, the survival or reproduction in each year may be directly related to the severity of simulated catastrophic events such as drought, flooding or severe food shortages. Alternatively, other models include genetic variation as affecting survival of an individual.

The results of PVA can be expressed in many different forms, but are usually based around the amount of population decline, the probability of decline, and the timeframe in which the decline is expected to take place. The fate of the population is simulated many times to give a frequency distribution of these measures of decline and survival. The results of PVA help in the process of identifying the viability requirements of a species and the threats faced by a species. It can also help in evaluating the likelihood that the population under study will persist for a given time into the future (Akcakaya & Sjögren-Gulve 2000).

PVA is often oriented towards management of rare and threatened species. The main objectives of conducting a PVA on such species are to identify threats to the population, identify missing data needs, and enhance management and decision-making processes. Ultimately, the aim is to help determine how to promote conditions in which species retain potential for evolutionary change without intensive management. PVA can help address many aspects of management of threatened species or populations, as listed below (modified from Akcakaya & Sjögren-Gulve 2000):

Planning research and data collection. PVA may reveal that population viability is relatively insensitive to particular parameters. For example, the model predictions may be more sensitive to changes in adult survival than to changes in the number of young produced. Research could then be focused on accurately determining adult survival, which may have the most important effect on probabilities of extinction or recovery.

Assessing vulnerability. PVA may be used to estimate the relative vulnerability of different species or populations to particular threats. Together with cultural priorities, economic constraints and taxonomic uniqueness, these results may be used to set policies and priorities for allocating scarce conservation resources.

Impact assessment. PVA may be used to assess the impact of human activities (e.g. exploitation of natural resources, damming of rivers, development, pollution) by comparing results of models with and without the population-level consequences of the human activity.

Ranking management options. PVA may be used to predict the likely responses of species to different management options such as: predator control, captive breeding, prescribed burning, weed control, habitat rehabilitation, or different designs for nature reserves or corridor networks.

In addition to the management-oriented objectives, PVA is a useful tool for organising the relevant information and assumptions about a species or a population. The process of organising available data for input into a PVA clearly highlights data deficiencies and forces explicit statement of all assumptions incorporated into the model.

PVA is generally only used in a single-species approach in which one or several populations of a single species are modelled. It is only rarely applied to multiple species within the same ecosystem because of the difficulties in accurately quantifying the complex interactions among all the organisms within the system being studied. However, some multi-species PVA models exist (Colding 1998; Blackwell et al. 2001) and the increase in computing power becoming available may help facilitate the multi-species approach in future.

3. When to use PVA

The first PVA models were built to address questions regarding the absolute risk of extinction. These models tried to estimate the minimum viable population size for a species or to predict the time to extinction, given a certain scenario. However, PVA is now used more often to address questions concerned with management options related to the relative risk of extinction: 'Which of these management plans would be most beneficial to this species?' (Ralls et al. 2002). It is widely accepted that assessing relative risk, and comparing the risks and benefits of different management strategies, rather than determining any absolute time to extinction, is one of the key benefits of doing PVA.

PVA model predictions can only be useful if there is a key objective that the model is designed to meet (see Section 4.1), and that there are enough data to support a model designed to meet that objective. Creating a PVA is worthwhile if available data are sufficient to show that a model could help either guide future data collection or provide a framework that highlights uncertainties and risks of certain management actions (Groom & Pascual 1998; Ralls et al. 2002).

Because most PVA are conducted on species that are threatened or endangered, seldom do enough data exist to meet all the parameter requirements of a PVA model. However, in some cases of scarce data a preliminary PVA may be worthwhile to consolidate existing information on the species, and highlight knowledge gaps to direct future research needs. If the data are extremely scarce (for example, basic life history of the species is not understood; no estimates of survival or reproduction exist), then going through the process of formally constructing a PVA is not necessary to identify the data needs, although it may be useful for prioritising data collection. Unknown parameters can be estimated using best guesses based on species knowledge or using data from similar taxa but if all parameters are estimated this way because no real data exist, then the model outputs are likely to be meaningless. An inaccurate PVA based on poor or incorrect data and assumptions may confuse issues, and may be a waste of scarce financial resources. Where data are scarce, basing conservation decisions on other information, such as presence/absence of a species in certain locations or knowledge of habitat requirements or key causes of decline, is a far better option. In some circumstances, an analytic approach using the broader area of matrix population modelling (Caswell 2000) and Leslie matrices can have advantages over the simulation approach emphasised in most PVA tools.

Although many complex PVA models exist, the benefits from using such complicated models when data are scarce are deceptive. Even though more complex models promise to yield viability assessments that are more accurate because they take into account a wider range of biological factors, these predictions will be worthless if too many critical components of the model must be 'guessed' at because reasonable data do not exist for some of the model parameters. There is a continuum of 'guesses' from well informed to downright speculative. The model structure should be detailed enough to use all the relevant data, but no more detailed.

3.1 SPECIES THAT CAN BE MODELLED WITH PVA

Although most PVA are applied to species that are already threatened or endangered, and for which urgent management action is required, they can also be used to get a better understanding of population dynamics for a species that is not yet in urgent need of assistance but may require assistance in the future.

Examples of species for which population models can be useful are:

- **Keystone species.** Species that are important to a number of other species such as top predators or seed dispersers. Understanding the population dynamics or changes to population trends for these species will have a flow-on effect to other species in the same ecosystem.
- **Indicator species.** Easily monitored species that are sensitive to changes in the environment and can provide indications of ecosystem health. Many invertebrate species fall into this category.

- **Threatened species.** Species that are restricted in distribution or limited in number, and particularly those species that may need intervention to prevent continuing population declines. PVA can be used to predict which management actions would be the most effective for attaining recovery.
- **Species of special cultural importance.** Species such as titi (sooty shearwaters *Puffinus griseus*) are culturally important to many iwi, and assessing titi population dynamics can help determine the current population trends and determine the effects of current or alternative levels of harvesting.
- **Well studied species.** The accuracy of the model predictions depends on the accuracy of the data used to run the model. Viability assessments for species that have been well studied will be more accurate and can be used to assess levels of confidence in such modelling approaches.

4. Key steps for building a PVA

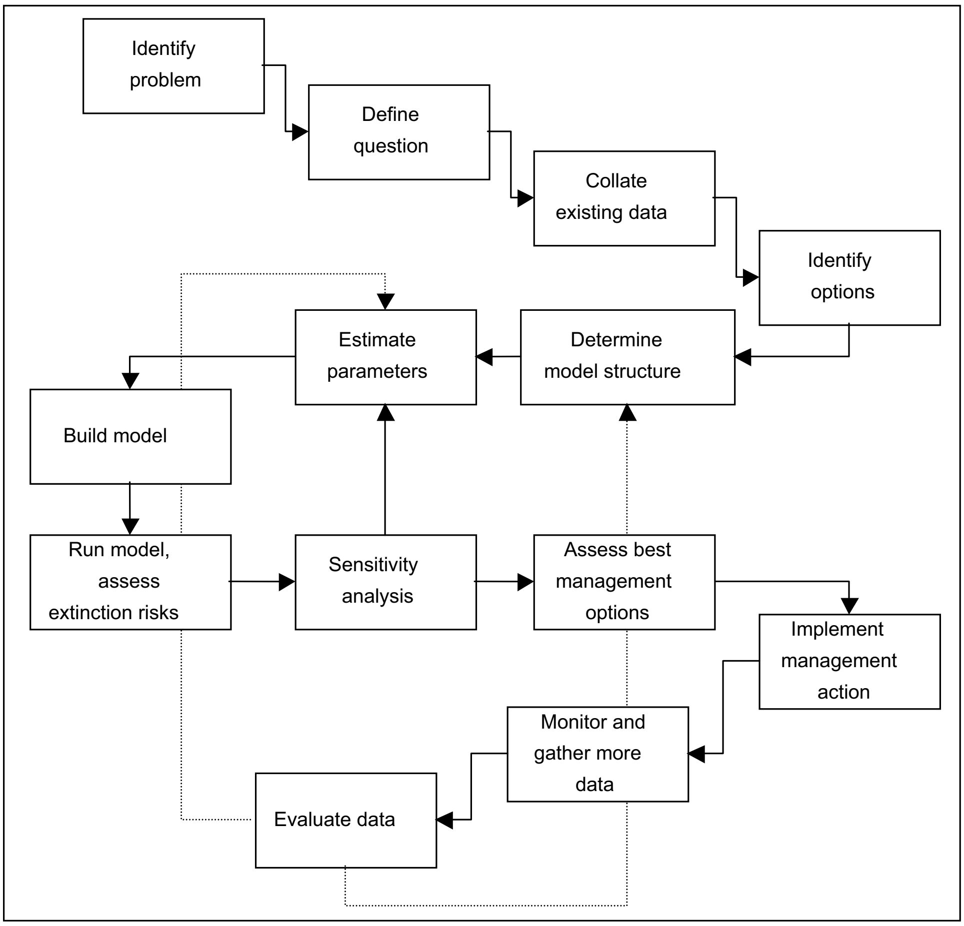
PVA is most useful when well targeted to answer a specific objective, and when the assumptions and limitations of the model are clearly stated. PVA is also better when used as an ongoing process than a one-off analysis. In most cases, PVA are based on existing data, rather than data specifically collected for them. Thus, using PVA predictions to direct future data collection, and continually refining and updating the model as more data are gathered, creates a stronger and more useful analysis. A Recovery Group that commissions PVA should view them as 'work in progress', or a tool to reassess management priorities at regular intervals. The series of steps below provides a guide as to how a PVA can be built and implemented (Fig. 1).

4.1 IDENTIFY THE QUESTION

Any scientific inquiry starts with a question, and PVA is no exception, although the question is likely to change during the course of the analysis. Initially, the question might be very general, such as, 'Is this species threatened, and if so, why?' The less known about the species, the more general the questions will be. At this step, a PVA should concentrate on the identification of factors (including natural factors and human impacts) that are important in dynamics of the specific populations under study, as well as conservation and management options. The methods to be used for this depend on the specific case at hand, and might include statistical analysis of historical data, comparison of populations that are declining with those that are stable, and correlating recent changes in the environment (climatic or habitat changes, introduced species, changing harvest patterns, etc.) with changes in the species.

After the available information about the ecology of the species and its recent history is collated and reviewed, the questions are likely to become more specific. Examples of such questions include:

Figure 1. Sequence of steps needed to perform a population viability analysis (figure adapted from Akcakaya et al. 1999).



- What is the chance of recovery of the wrybill (*Anarhynchus frontalis*) from its current threatened status?
- Which combinations of management options (e.g. predator control, reduced weed encroachment, improved river flows) will improve population viability in wrybills?
- What levels of fisheries by-catch pose unacceptable risks to populations of different species of albatross (*Diomedea* spp.)?
- Are current mitigation techniques on New Zealand fishing boats making a difference to viability of albatross populations?
- Is it better to provide more habitat or to carry out predator control in existing habitat for black-fronted terns (*Sterna albostriata*)?
- What level of predator control is required to ensure the survival of kokako (*Callaeas cinerea wilsoni*)?
- Is captive breeding and re-introduction to natural habitat patches a viable strategy for conserving kiwi (*Apteryx* spp.)?
- If so, is it better to re-introduce 20 kiwi to one habitat patch or 10 each to two habitat patches?
- Is it worthwhile to translocate endangered giant wetas (*Deinacrida* spp.) from their current populations to empty habitat patches to spread the risk of local extinctions?
- Is it better to preserve one large fragment of primary forest, or several smaller fragments of the same total area?

- Is it better to add another habitat patch to the nature reserve system, or enhance habitat corridors to increase dispersal among existing patches?

4.2 DETERMINE THE BASIC MODEL STRUCTURE

The most appropriate model structure for a population viability analysis depends on the availability of data, the essential features of the ecology of the species or population, and the kinds of questions that the managers of the population need to answer.

A wide range of models and viability analyses come under the heading of PVA (Ralls et al. 2002). However, most are based on matrix models and are either deterministic (vital rates such as survival and reproduction are constant or are determined in a predictable manner) or stochastic (vital rates vary unpredictably over time). Matrix models (Caswell 2000) are constructed with the population divided into age-, size- or stage-classes. Using the available vital rates for each class, the model is projected into the future to simulate population growth. PVA models with a basic matrix structure as the foundation can vary in complexity. Four types of models and the data requirements of each are outlined below in increasing order of complexity.

4.2.1 Single-population deterministic models

Deterministic matrix models predict an exact outcome and evaluate whether growth is increasing, stable or declining, given the current conditions (Fig. 2). A basic form of PVA practised by many population modellers is the estimation of lambda (λ): the finite rate of population increase.

When few data are available on how vital rates vary through time, or if the rates of environmental variation are low, deterministic models can provide a measure of growth rate (Table 1). To put together a model, the data must be divided into different classes. These classes can be age (e.g. 1-year olds, 2-year olds, etc.), size (e.g. <15 cm, 15–30 cm, etc.) or stage (e.g. seeds, seedlings, saplings, adults). The choice of class depends on the life history of the organism and the available data. Many populations of fish, invertebrates, and plants are modelled in stages, because growth is indeterminate and vital rates are more closely related to size or developmental stage than age. Often, only females from the population are modelled. See Morris et al. (1999) for a description of how to construct a single-species deterministic matrix model and calculations of λ. Although deterministic matrix models are widely used for modelling threatened species and some demographic stochasticity can be included, the lack of data on environmental variance and potential catastrophic environmental effects may lead to overestimates of population growth rates (Beissinger & Westphal 1998). Accordingly, stochastic models are often used to overcome this problem.

4.2.2 Single-population stochastic models

Single-population stochastic models are probably the most widely used form of PVA. Simulations usually model the fate of each individual, rather than cohort or stage, in the population. Simulated survival and reproductive rates are varied across individuals (demographic stochasticity) and through time

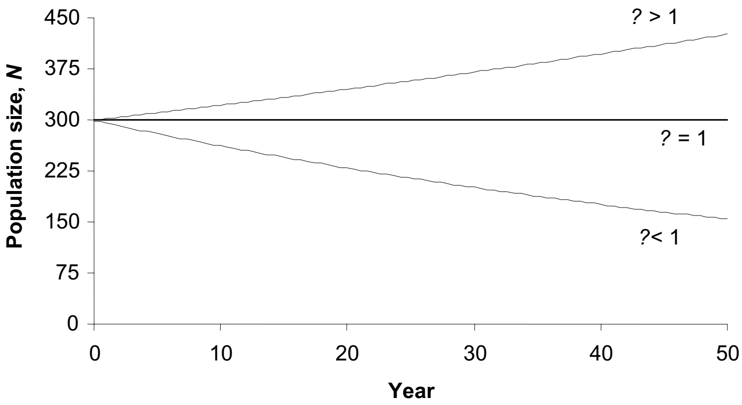


Figure 2. Sample population trajectories from a deterministic model, showing positive growth ($\lambda > 1$), stable population ($\lambda = 1$), and negative growth ($\lambda < 1$).

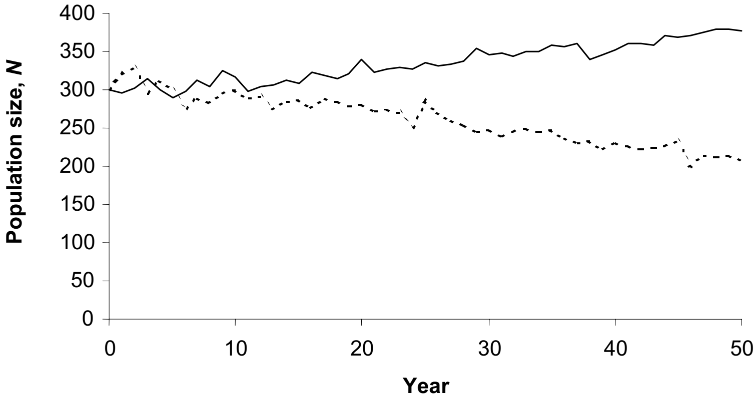
TABLE 1. DATA REQUIRED FOR THE DOMINANT TYPES OF DEMOGRAPHIC MODELS USED IN PVA.

DSP = deterministic single population, SSP = stochastic single population, Meta = metapopulation, and Space = spatially explicit. X indicates data are estimated for the population as a whole, and P that thay are estimated on a per 'patch' basis (i.e. data are estimated for each sub-population in the model). A gap indicates the model does not include those types of data (table adapted from Beissinger & Westphal 1998).

DATA TYPE	DATA NEEDS	DSP	SSP	Meta	Space
Demographic	Age or stage structure	X	X	X	X
	Age of first breeding	X	X	X	X
	Mean fecundity for each age or stage	X	X	P	P
	Mean survival for each age or stage	X	X	P	P
	Variance in fecundity		X	X	X
	Variance in survival		X	X	X
	Carrying capacity and density dependence		X	P	P
	Variance in carrying capacity		X	X	X
	Frequency and magnitude of catastrophes		X	X	X
	Covariance in demographic rates		X	X	X
	Spatial covariance in rates			P	P
Landscape	Patch types			X	X
	Distance between patches			X	X
	Area of patches			X	X
	Location of patches				X
	Transitions among patch types				X
	Matrix types				X
Dispersal	Number dispersing			P	P
	Age class and timing of dispersal			X	X
	Density dependent or independent dispersal			X	X
	Dispersal-related mortality			X	X
	Number immigrating			P	P
	Movement rules				X

(environmental stochasticity) and the amount of variability is based on observed or estimated probability distributions for variables such as survival, fecundity, and carrying capacity. Other factors such as catastrophic events or genetic effects may also be included. The projected trajectory of population growth in stochastic models changes each time the simulation is run (Fig. 3), giving a more realistic picture of what may happen in real populations.

Figure 3. Sample population trajectories from stochastic models, showing positive growth (solid line) and negative growth (dotted line).



However, some data requirements can be at least twice as great as for deterministic models (Table 1, Beissinger & Westphal 1998).

4.2.3 Metapopulation models

Metapopulation models are similar to single-population stochastic models, except that several interrelated populations of the same species are modelled. For example, several sub-populations of a bird species may be in unconnected forest fragments, but there is movement between the sub-populations (e.g. juvenile dispersal, source and sink dynamics). To run metapopulation models, data are required on the vital rates from each of the fragments, or habitat 'patches', and on the size, carrying capacity and dispersal rates of each of the patches in the model (Table 1).

4.2.4 Spatially explicit models

Spatially explicit models not only use data from population dynamics but also from the habitat the population occupies, such as the amount and quality of available habitat, the effects of changes to the habitat, or if there are spatial effects on the movements of a population with a metapopulation structure. Spatially explicit models are the most data-hungry models and are only worthwhile when there are extensive data available on survival and dispersal that are linked to detailed information on habitat type, size, location and suitability (Table 1). The use of these models in conservation has increased as awareness of landscape processes has expanded and tools for analysing landscape-scale phenomena have developed (e.g. geographic information systems, GIS) (Beissinger & Westphal 1998). Because the data requirements are so high for these models, readily available PVA packages are not always suitable, and much time and resources are often needed to develop a custom-built model, usually with the assistance of a statistician.

There are many commercially available PVA packages from which to choose when constructing a PVA (see Section 6).

4.3 EVALUATE EXISTING DATA AND ESTIMATE PARAMETERS

The next step is to estimate the model parameters with field studies (and sometimes experiments). The parameters that need to be estimated will depend on the model structure, and the type of data already available (see Table 1). The key questions (Section 4.1) may require a detailed model, whereas the available data can support only a simple model. Models that are overly complex can reduce the precision of predictions, but models that are overly simple are likely to have low accuracy. If the data available do not match data requirements, either more data must be collected or the question modified.

For most PVA studies, this is the limiting step, because data are often insufficient. However, if a decision on how to manage a population has to be made, it could be useful if the decision-maker has some input from a PVA, although it must be used responsibly. If a parameter is not well known, a range of numbers can be used for that parameter instead of a single number. For example, if the average annual mortality of a given species is 10%, but is not known accurately, we can use a range of 8–12%. Such estimates can be based on rates of similar species if known. These ranges can be used in a sensitivity analysis (Section 4.5).

4.4 CREATE AND RUN MODEL

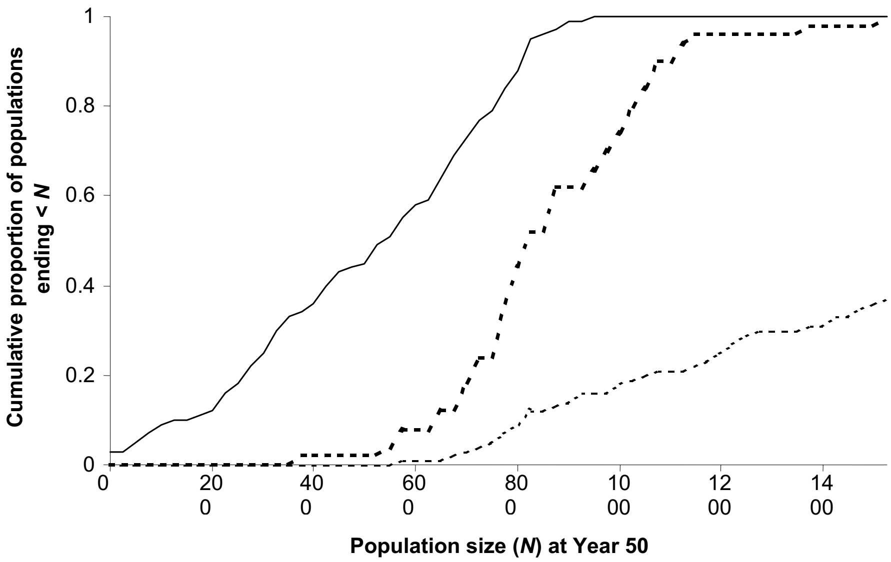
Building a model is a method of combining the existing information into predictions about the persistence of species under different assumptions of environmental conditions and under different management options. When doing this, it is important to keep a list of all assumptions made and report these along with any findings. This includes assumptions made in collating data or calculating vital rates and other parameters, as well assumptions built into the models.

Stochastic models need to be run for at least 50 and up to 10 000 simulations to ensure a consistent result is reached. The structure of the model and the questions addressed usually determine how the results will be presented. In most cases, the model will include random variation (stochasticity), which means that the results must be presented in probabilistic terms, i.e. in terms of risks, probabilities or likelihoods of events happening.

Often, PVA models were projected for a period of 100 years into the future, and a common measure of outcome was the proportion of populations going extinct within 100 years (i.e. extinction probability). However, given that models make the unrealistic assumption that conditions will remain as they are now for the next 100 years, it is more accurate to model the population for 10 to 20 years, or 50 years at the most. Calculations by Ludwig (1999) showed that extinction probabilities based on currently available data are often meaningless due to the large uncertainty accompanying the estimates. Fieberg & Ellner (2000) suggested that reliable predictions of extinction probabilities can be made only for 10–20% of the period over which the population has been monitored. Thus, if a population has been monitored for 10 years, a realistic prediction of the probability of extinction can be made only for the next 1–2 years. The probability of extinction over 20 to 50 years is better suited for comparative evaluation of different management scenarios than as an absolute prediction of population viability.

An alternative to extinction probabilities is the quasi-extinction function, i.e. the proportion of populations that are lower than a specified size within a given timeframe. For example, some population simulations may show no extinction after 50 years (so the probability of extinction is zero), but the population still shows a decline under the conditions modelled. These simulation results are more informative if presented as a quasi-extinction function. As an example, three hypothetical management scenarios have been compared through their quasi-extinction functions (Fig. 4). In Scenario A, 16% of simulations ended with a population size less than 1000; in Scenario B it was 74%; and in Scenario C all populations ended under 1000. The probability of extinction is shown where the function meets the y-axis; thus for Scenario C the probability of extinction within 50 years is 3%.

Figure 4. Quasi-extinction curves for a hypothetical population under three different management scenarios: Scenario A – dotted line, Scenario B – bold dotted line, Scenario C – solid line.



4.5 SENSITIVITY ANALYSIS

Often, a model must be run many times, with different combinations of the potential values of each parameter (for example, using the 95% confidence limits of each parameter) to make sure that all uncertainty in parameter values is accounted for. This provides a way to see how the model responds to inaccuracies in the parameters, changes in the model, and violations of assumptions (Drechsler 1998; Drechsler et al. 1998). Sensitivity analysis is useful for determining which parameters need to be estimated more carefully. If, for example, the risk of decline is very different with the low value and high value of the range in adult survival rate, then the results are sensitive to this parameter, and future field studies should concentrate on estimating adult survival more accurately to ensure the most accurate model predictions.

Model sensitivity to changes in parameters that could be achieved through management can also be examined. If adult survival had been comprehensively studied and the estimates of risk of decline were accurate, the sensitivity of the model to adult mortality suggests management should be aimed at increasing adult survival rates to have the best chance of increasing population viability. However, this may not be possible if adult survival is already very high and cannot be increased. Sensitivity analysis could show whether changes to more easily manipulated parameters (such as juvenile survival) would have a significant effect on population survival. Management action to reduce mortality for this group could then be implemented. Sensitivity analysis can also help determine which parameters are least important to the model.

The results of sensitivity analysis are often presented as a percentage change in growth rates or extinction rates after each individual parameter is varied from its original value. Table 2 shows the results of a sensitivity analysis from a PVA on black-fronted terns to help evaluate the efficacy of different management scenarios (Keedwell 2002). The model is most sensitive to adult survival rates, and least sensitive to parameters such as the proportion of 2- and 3-year olds breeding. Management of black-fronted terns that involved predator control would result in a decrease in mortality over a range of life stages. Sensitivity analysis where more than one parameter is varied at a time (e.g. mortalities of all life stages are varied at once) to simulate a management action would be the next step.

TABLE 2. SENSITIVITY ANALYSIS RESULTS FROM A BLACK-FRONTED TERN POPULATION MODEL.

Each parameter was varied by ±10% of its original value. Growth rate (λ) predicted by the population model when the parameters were unchanged was 0.974; the change in growth rate was calculated each time one parameter was varied (table adapted from Keedwell 2002).

PARAMETER	ORIGINAL VALUE	NEW VALUE	λ	CHANGE IN λ (%)
Decrease adult survival 10%	0.88	0.87	0.965	–0.93
Decrease survival to year 1	0.54	0.49	0.966	–0.85
Reduce percentage of adults breeding	1.0	0.9	0.966	–0.83
Decrease chick survival 10%	0.37	0.33	0.966	–0.81
Decrease renesting 10%	2.3	2.5	0.967	–0.70
Decrease egg survival 10%	0.60	0.56	0.969	–0.52
Decrease years 1 & 2 survival 10%	0.85	0.83	0.972	–0.18
Reduce adult age	26	24	0.973	–0.14
Decrease percentage of year 3 breeders 10%	0.75	0.73	0.974	–0.03
No change			0.974	0
Decrease percentage of year 2 breeders 10%	0.25	0.23	0.974	0.03
Increase percentage of year 3 breeders 10%	0.75	0.77	0.974	0.03
Increase percentage of year 2 breeders 10%	0.25	0.28	0.975	0.08
Increase years 1 & 2 survival 10%	0.85	0.86	0.975	0.13
Increase adult age	26	28	0.975	0.16
Increase egg survival 10%	0.60	0.64	0.978	0.41
Increase renesting 10%	2.3	2.7	0.980	0.64
Increase survival post-fledge to Y1	0.54	0.59	0.981	0.77
Increase chick survival 10%	0.37	0.40	0.982	0.84
Increase adult survival 10%	0.88	0.89	0.982	0.87

4.6 IMPLEMENTATION AND MODEL REFINEMENT

When the best management actions and/or the the most important data to collect purporting to improve estimates are identified, based on analysis using the model, the function of modelling is temporarily complete. The next step is to implement the management plan. It is important that the field studies continue during and after the implementation to monitor the species (Fig. 1). The results of monitoring can give valuable information about the response of the species to management, as well as provide more data to refine model parameters and improve the model. For example, evaluation of demographic data after the implementation of a management strategy might show that vital rates increase faster than predicted in response to removal of a predator in the system, but the carrying capacity responds more slowly than expected to the improvement of the habitat. Such a finding would definitely require modifying the model, refining its parameters, and re-estimating the extinction risks under different management options (Akcakaya et al. 1999).

5. Examples of PVA in conservation

PVA models have been used in New Zealand nature conservation for objectives ranging from exploratory preliminary models identifying management or data needs to comprehensive models that resulted in key management recommendations. Outlined below are a number of studies that used PVA for a variety of different reasons. Most of these are New Zealand examples, but two overseas examples are included to show a range of possibilities using PVA.

Accounting for uncertainty in risk assessment

Gillnetting by commercial fisheries is a primary cause of mortality for Hector's dolphins (*Cephalorhynchus hectori*). Although a sanctuary has been created at Bank's Peninsula, there is still uncertainty about whether this has benefited the dolphins. Because of this uncertainty, fisheries organisations are able to argue that gillnetting levels should be increased, while conservation groups argue that the sanctuary should be extended. Slooten et al. (2000) used PVA to explore how the levels of uncertainty affected survival of Hector's dolphins. They modelled the population for 20 years using an age-structured deterministic matrix model run in Excel. Input values for the model were chosen from a distribution that represented parameter uncertainty. They found that 94% of the time the population was predicted to decline, indicating that there is substantial risk of population decline, even when allowing for the uncertainty in the input parameters. They concluded that although there may be uncertainty about the actual rate of population decline over the timeframe modelled, there is a high risk of decline across all scenarios, and that uncertainty was no longer a reason to delay action. They also found that the model was most sensitive to survival rates, and survival could be increased by reducing the level of bycatch in gillnet fisheries. This study used PVA to clearly show that conservation decisions need not be delayed simply because of uncertainty in the data.

Effects of harvesting and predator control

Titi are harvested by Maori from large colonies on offshore islands but not from the smaller colonies on the mainland. Mainland colonies suffer high levels of predation by introduced mammals, and the size and extent of these colonies is thought to have decreased through time. Hamilton & Moller (1995) investigated if PVA could help to determine whether mainland populations are declining, assess the value of predator control, and determine whether harvesting on the mainland could be sustainable. They used VORTEX (5.1) to simulate colony survival for 100 years. Because most of the available data were fragmentary and many parameters relied on data from congeneric species, they modelled three different scenarios: optimistic (using highest estimated values for parameters), pessimistic (using lowest estimated values) and average (the mean of optimistic and pessimistic parameters). The model predicted that, if observed predation rates remained high, mainland colonies would decline unless there was high immigration from offshore colonies. The model also predicted that predator control would have its greatest effect if implemented at the start of the season when adults were most vulnerable. Only a few of the colonies were large enough to be able to withstand harvesting. Although this PVA was only a preliminary assessment, the authors showed that by selecting the most conservative scenario, management effort could be directed to where and when it is predicted to be most effective.

Survival prospects of populations under threat of predation

Mohua (*Mohoua ochrocephala*) populations are strongly affected by intermittent stoat irruptions in southern beech (*Nothofagus*) forests. Mohua are particularly vulnerable to stoats (*Mustela erminea*) because they are hole-nesters and also late breeders. Previous research has also shown that stoat predation had a much more dramatic effect on populations of mohua that raise only one brood in a year than on two-brood populations (Elliott & O'Donnell 1988). Elliott (1996) constructed a PVA computer model to examine the effects of frequency of predation episodes, predation of adults, the number of broods, and the carrying capacity on the extinction probabilities of mohua populations. He used data on mohua survival from a study where stoat abundance was low for three years and where both stoat abundance and predation were high in one year. Despite the weaknesses in the models (small sample size, only four years of data, no data on migration, actual occurrence of stoat irruptions unknown), the models provided empirical evidence that the predictions are approximately correct and that many small mohua populations appear to be approaching extinction. Based on the simulation results, Elliott suggested that stoat predation should be reduced to improve mohua survival. Furthermore, he suggested that stoat control only need be carried out in irruption years for two-brood populations but had to be carried out annually to ensure the survival of one-brood populations.

It should be noted that the results of the analyses would have been vastly different if data from only one or two irruptive or non-irruptive years had been used, or if the models had been based on data from only one-brood or only two-brood populations that might have been encountered by chance if the study area had been smaller. It is also worth noting that these particular mohua populations were effectively wiped out by rat irruptions, and that this might have followed as a consequence of carrying out the stoat control recommended following the PVA analysis, which highlights the complexity of the systems DOC may attempt to model.

Frequency and causes of mouse, rat, and stoat irruptions in a forest system

Feral house mice (*Mus musculus*) and ship rats (*Rattus rattus*) are common in New Zealand forest systems. Both these species show periodic population irruptions following beech mast seeding years. In response to mouse and rat population increases, stoat populations also increase, which can lead to increased predation on a number of rare or threatened native species. Blackwell et al. (2001) used the modelling package STELLA II to model the irruptive population dynamics of the three species and compared this against current knowledge of predator-prey cycles in New Zealand. The model included interdependent relationships among the three populations, for example, the number of mice in the simulation depended on the number of rats and stoats, and the reproductive rate of stoats depended on the number of rats and mice available. The model was calibrated with data from population dynamics from a beech forest system and was found to correctly predict the timing and amplitude of the species' responses to beech masting. The model highlighted gaps in current knowledge of predator and prey species biology and ecology. It also highlighted key areas where further field studies are needed to provide a better understanding of the factors driving small-mammal communities in New Zealand.

Effects of aerial poisoning of rodents on forest bird populations

Aerial poisoning with brodifacoum baits was widely used to eradicate rodents in New Zealand forests, but, because of the hazard of accumulation in the food chain, it is now used for eradication only on islands. Forest birds such as robins (*Petroica australis*) are known to peck at baits, showing potential for direct poisoning and may also suffer secondary poisoning from eating invertebrates that have fed on pellets. Armstrong & Ewen (2001a) used PVA to look at the short- and long-term effects poisoning had on a population of robins. They used VORTEX 8.3 to model six years of detailed data on survival, fecundity and dispersal rates, and carried out mark-recapture analysis to estimate survival rates after a poison drop. They concluded that 11% of the robin population died after the poison drop. They predicted that the drop in survival after poisoning set population growth back by about one year, but there were no long-term impacts.

Survival of a common and a threatened species in the same environment

Black-fronted terns and banded dotterels (*Charadrius bicinctus*) share similar breeding habitat in the braided rivers of the South Island but exhibit vastly different population trends. Black-fronted terns are threatened and in decline, whereas banded dotterels are common and the population is apparently stable. Keedwell (2002) used PVA to compare the life histories of the two species and to assess the potential benefits of implementing predator control. Simulations using STELLA 7.1 showed that the main difference in overall survival was because dotterels could raise more than one brood in a season and re-nested more frequently after predation, which resulted in higher productivity. Black-fronted tern productivity could be increased to stabilise population trends when predator control was simulated. The PVA showed that banded dotterels were better adapted to cope with the high predation levels that currently exist in the modified braided river habitat.

Value of follow-up translocations after population re-introduction

When re-introducing a population into an area, follow-up translocations may be necessary to ensure the new population persists. Population viability analysis can be used to help determine whether subsequent translocations are necessary and if so, what is the size and timing of follow-up translocations. Armstrong & Ewen (2001a, 2002) used PVA (VORTEX 8.3) to assess the value of follow-up translocations after a population of robins was re-introduced to Tiritiri Matangi Island. A follow-up translocation was completed 14 months after re-introduction because an initial PVA showed population growth rates were marginal. However, re-evaluation of this decision five years later showed the follow-up translocation was unnecessary because fecundity increased in the years following the initial translocation. Their simulations suggested that the follow-up translocation could have been delayed by up to nine years without reducing any benefits. They concluded that the best strategy would have been to wait for additional data, and to re-allocate the resources used for the follow-up translocation to research on the re-introduced population. It cannot be emphasised too strongly that too heavy a reliance on preliminary PVA could lead to poor conservation management decisions.

Timing and intensity of pest control

Research on kokako populations has shown that pest control does not have to be applied in all years to have a beneficial effect on kokako survival, but the frequency at which pest control is required has not been explored. Basse et al. (2003) developed matrix models to simulate the effects of different pest control regimes on kokako population growth and to determine how frequently pest control needed to be applied to achieve maximum benefits. Their model supported the empirical evidence that kokako populations do not need continuous pest control to maintain or greatly increase populations. The simulations provided key management recommendations on pest control frequency (pulses of 2–3 years' control were optimal) and on control strategies for kokako populations of varying sizes.

Vaccination against infectious diseases

The Ethiopian wolf (*Canis simensis*) is a critically endangered species that is adversely affected by epidemics of rabies and canine distemper triggered by contact with infected dogs. Haydon et al. (2002) developed one of the first PVA models that attempt to incorporate the effects of epidemiology. The models predicted that populations were stable in the absence of disease but when rabies was introduced, epidemics caused a rapid increase in extinction probabilities, particularly for smaller populations. The models suggested that vaccination of as few as 20%–40% of wolves against rabies might be sufficient to eliminate the largest epidemics and protect populations. From a management perspective, their results suggest that conservation action to protect even the smallest populations of wolves from rabies is both worthwhile and urgent.

Management scenarios for a critically endangered plant

Euphorbia clivicola is a threatened succulent, which is confined to two populations in South Africa and has shown a 91% decline in the past decade of monitoring. Pfab & Witkowski (2000) developed matrix models using Excel to assess four strategies for managing the populations. The models predicted that if management practices remained unchanged, the population had an 88% chance of extinction within the next 20 years. The population should recover under a management scenario involving a fire frequency of every three years, the exclusion of herbivores, and augmentation. Management practices were altered to reflect the model scenarios, and three years later, the model predictions were validated against the latest data. The authors suggest continued adaptive management in this style is the most effective strategy.

Hybridisation and management of an endangered species

The black stilt, or kaki (*Himantopus novaezelandiae*), is an endangered species, and critically low population sizes have resulted in widespread hybridisation with the closely related pied stilt (*H. himantopus*). Until recently, pure black stilts and dark hybrids were all managed as though they were black stilts, both in the wild and in the captive breeding programme. Genetic analysis showed that black stilts were genetically distinct from pied stilts and there were concerns about whether continued interbreeding with dark hybrids would destroy the black stilt gene pool. Wallis (1999) used a population genetics model, PopGen 2.0 (Wells 1992), to simulate the effects of different levels of hybridisation between the two species. The results showed that unless hybrids had reduced fitness, hybridisation had to be reduced to almost zero to maintain the integrity of the black stilt gene pool for 50 generations. As a result, only pure black stilts are now used in the management of the population.

6. Computer software for generic PVA models

Many computer simulation models are available for running PVA. Most generic models were built for a particular purpose and, as a result, are more suited for use on certain types of populations or problems. The selection of the most suitable programme is important because the features that may recommend a model's use in one study may make it unsuitable in others.

It should be noted that no custom-built models of PVA are currently supported by the DOC computer network, and none of the generic models outlined here can be downloaded to DOC computers except for stand-alones and some field centre computers. Although there are many custom-built models available, many excellent PVA models can be constructed using Microsoft Excel, which is readily available throughout DOC. Relatively sophisticated models can be built with Excel and the examples in Sections 5.1 and 5.10 provided important management information from PVA using Excel alone. Other applications such as S+, which is much more powerful and flexible to programme, can be used in a similar fashion. However, for these a good knowledge of Excel or S+ is required.

Many studies have examined the relationships between extinction risks predicted by different PVA programmes that were applied to the same dataset (Mills et al. 1996; Brook et al. 1997; Brook et al. 1999; Gerber & VanBlaricom 2001). In some cases, vastly different results have been predicted among models because of certain constraints within the model, such as how sex ratio within a population is modelled (Brook et al. 2000a). The quantitative predictions of different programmes can often be dissimilar because of differences in programme construction, but the qualitative rankings of different scenarios within each model are often more comparable across programmes. If time and resources are available, it is often worth running a PVA on more than one generic model to double-check the outputs. Alternatively, choosing the model that is most appropriate to the data and running a sensitivity analysis will provide an indication of model suitability.

This section provides a brief overview of eight main PVA programmes currently available (Tables 3 and 4). These programmes are frequently modified and updated, and the summary below is not specific to any one version of each programme. The basic features listed are available in most versions, but more recent versions of the software may have different attributes. More information on each programme can be found at the websites listed with each programme description.

6.1 ALEX

ALEX (Analysis of Likelihood of EXtinction, Possingham & Davies 1995) is suitable for modelling most vertebrate populations and some invertebrate and plant populations. ALEX was written to apply to most species that are under threat, not just populations that are extremely rare. The advantages of this programme are that it can model large populations quickly, it incorporates catastrophes and habitat dynamics, and it allows the user to specify a wide

TABLE 3. DATA CAPABILITIES OF EIGHT PVA PROGRAMMES.

PARAMETER	ALEX	GAPPS	INMAT	VORTEX	STELLA	RAMAS Stage	RAMAS Metapop	RAMAS GIS
Age structure	Limited	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Stage structure	No	No	No	No	Yes	Yes	Yes	Yes
Survival and fecundity	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Demographic stochasticity	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Environmental variation (EV)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Inbreeding depression	No	Yes	Yes	Yes	Yes	No	Limited	No
Catastrophes	Yes	Yes	No	Yes	Yes	Yes	Yes	Yes
Breeding structure	No	Yes	No	Yes	Yes	Yes	Yes	Yes
Correlation in EV*	Partial	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Metapopulation structure	Yes	No	No	Yes	Yes	No	Yes	Yes
Density dependence functions	Limited	Yes	Limited	Yes	Yes	Yes	Yes	Yes
Individual-based (I) or matrix-based (M)	M	I	M	I	I	M	M	M
Allows for harvesting	Yes	No	No	Yes	Yes	No	Yes	Yes
Allows for supplementation	Yes	No	No	Yes	Yes	No	Yes	Yes
Spatial/GIS data	No	No	No	No	No	No	No	Yes

* Temporal variation in survival corresponds to temporal variation in fecundity

TABLE 4. USER-FRIENDLINESS, AVAILABILITY, AND CAPABILITIES OF EIGHT PVA PROGRAMMES.

	ALEX*	GAPPS*	INMAT*	VORTEX	STELLA	RAMAS Stage	RAMAS Metapop	RAMAS GIS
Cost	Free	Free	Free	Free	$US699	$US495	$US595	$US1595
Availability	Internet	Author	Author	Internet	Internet	Internet	Internet	Internet
Operating system	MS-DOS or Windows	MS-DOS	MS-DOS	MS-DOS or Windows	Macintosh Windows	MS-DOS or Windows	Windows	Windows
Online help	No	No	No	Under development	Yes	Yes	Yes	Yes
Programme tutorial	No	No	No	Limited	Yes	Yes	Yes	Yes
Max. population size**	32 000	16 384	Unlimited	62 000	Unlimited	Unlimited	2.1 billion	2.1 billion
Model outputs:								
Mean ending population size	No	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Median ending population size	No	Yes	Yes	No	Yes	Yes	Yes	Yes
Extinction (%)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes
Quasi-extinction (%)	Yes	Yes	Yes	Yes	Yes	Yes	Yes	Yes

* These programmes are no longer updated

** These features may depend on computer memory size. Large populations or large numbers of metapopulations can take considerable time to run range of environmental processes. Its main application is for modelling of metapopulations. The main weaknesses are that the model does not include genetics, only one sex is modelled, and the age structure is very simple, with only three classes of individuals: newborn, juvenile, and adult. ALEX does have a user manual but users are advised to seek assistance from the programme author (Hugh Possingham) for complicated simulations. The programme is free, but cannot be used for generating income or writing scientific papers without the permission of the author. The programme is over 10 years old now and is no longer updated. It can be downloaded from: http://biology.anu.edu.au/research-groups/ecosys/Alex.

6.2 GAPPS

GAPPS (Generalised Animal Population Projection System, Harris et al. 1986; Downer 1993) originated from a specific model developed for grizzly bears (*Ursus arctos horribilus*) and is most suitable for large mammal population projections (Dixon et al. 1991; Dobson et al. 1992). The programme is an individual-based model and incorporates catastrophes, inbreeding depression, and environmental variation. It has a small range of density-dependence functions but cannot simulate metapopulations. GAPPS has a user manual (Downer 1993) and the software is available from the author, Richard Harris (rharris@montana.com).

6.3 INMAT

INMAT (INbreeding MATrix, Mills & Smouse 1994) is a matrix-based model developed to look at short-term inbreeding effects in stochastic environments. The programme has been used on mammals, birds, fish, and reptiles. The main disadvantages are that, although the model incorporates environmental stochasticity, it does not simulate catastrophes, only models one sex in the population, does not incorporate metapopulation dynamics, and has limited density-dependence functions. The programme has an accompanying manual and both the manual and software are available from the author Scott Mills (smills@forestry.umt.edu).

6.4 VORTEX

VORTEX (from the extinction vortex, Lacy 1993, 2000) is probably the most widely used generic PVA model currently available. It was originally designed for modelling mammal populations, but is also suitable for modelling birds and some populations of reptiles, invertebrates, and fish. VORTEX has been extensively applied to endangered species conservation. The programme is individual-based and incorporates environmental and demographic stochasticity, inbreeding depression, metapopulations, catastrophes, and some density-dependence functions. The programme also allows for simulation of harvesting from the population and supplementation (i.e. introducing translocated individuals to the population). The main disadvantages of the programme were that it did not have on-line help and the data outputs and graphing capabilities were somewhat limited, but recent upgrades have improved these limitations. The software is freely available and can be downloaded from: http://pw1.netcom.com/~rlacy/vortex.html.

6.5 STELLA

STELLA (High Performance Systems 2001) uses a different interface from most of the other PVA packages. It uses a pictorial approach in which the user builds a model map using icons on the screen, and the software converts the relationships among the variables to equations that are used in the simulations. As a result, the programme is highly adaptable and very user-friendly. This software is used in many disciplines besides biology and can be adapted to suit almost any species or population. STELLA can also be used for performing multi-species PVA where the relationship among several species can be simulated. STELLA has comprehensive online help and tutorials, and models can be built on sample populations to help new users learn how to use the programme. The software is used widely in education and has a range of graphical and numerical outputs. STELLA can be purchased and downloaded from: http://www.hps-inc.com/STELLAVPSR.htm.

6.6 RAMAS MODELLING SOFTWARE

RAMAS modelling software has been used for modelling a wide range of species including mammals, birds, reptiles, invertebrates, and plants. These programmes were originally used for teaching purposes but are also widely available for other uses. Because of the teaching focus, the programmes are all extremely user-friendly and have excellent online help and tutorials, helpful user manuals and a wide range of data outputs and graphic presentation options. The software for all RAMAS programmes can be purchased and downloaded from http://www.ramas.com/software.htm.

Three of the main RAMAS programmes are:

RAMAS Stage

RAMAS Stage (Ferson 1994) was originally developed for the US electric power industry. RAMAS Stage lets a user build, run, and analyse discrete time models for species with virtually any life history. It is useful for modelling species with complex life histories or other biologies in which stage membership (rather than age) determines the demographic characteristics of an individual. RAMAS Stage comes with templates for species from many taxa (such as mammals, insects, fish, birds, and plants), which are easy to customise. The matrix models on which the programme is based allow the user to include phenomena observed in some species that cause individuals to skip stages, revert to previous stages, or produce offspring of different status.

RAMAS Metapop

RAMAS Metapop (Akcakaya 1994) was developed from an earlier version of RAMAS Space (Akcakaya & Ferson 1990) and is primarily designed to incorporate metapopulation dynamics, although it can be used to model single populations. It incorporates the spatial aspects of metapopulation dynamics, such as the configuration of the populations, dispersal and recolonisation among patches and similarity of environmental patterns experienced by the populations. The programme can be used to predict extinction risks and explore management options such as reserve design, translocations, and re-introductions, and to assess human impact on fragmented populations.

RAMAS GIS

RAMAS GIS is designed to link GIS landscape data with a metapopulation model for population viability analysis. RAMAS GIS imports spatial data on ecological requirements of a species. These may include GIS-generated maps of vegetation cover, land-use, or any other map that contains information on some aspect of the habitat that is important for the species. RAMAS GIS combines the spatial information on the metapopulation with user-input ecological parameters of the species to complete the metapopulation model. RAMAS GIS contains RAMAS Metapop and the output options include the same results as for RAMAS Metapop. In addition, RAMAS GIS has a sensitivity analysis feature that allows multiple simulations with automatically changed input parameters.

7. Characteristics of a good PVA

Although the technique of PVA has been around for more than 15 years, the use of PVA in the past five years has increased dramatically. As a result, there is much debate about the usefulness of the technique and whether it is being applied appropriately (Beissinger & Westphal 1998). PVA is a process that gives a product (Ralls & Taylor 1997), but it is often the process (i.e. synthesising available data, identifying research gaps, etc.) that is more useful than the end product (i.e. predictions of extinction risk). The widely available generic computer programmes have made PVA a more accessible and easily used tool, which has led to increased dependence on the predictions of the model and less emphasis on carefully collating the data to run the model and ensuring the appropriateness of the model structure.

PVA have been criticised because they are a single-species technique, they omit risk sources that are difficult to estimate, and they project current conditions long into the future (Ralls & Taylor 1997). They have also been criticised for being used on endangered species when data are insufficient, or when the cause of decline is clear and easily acted on, so that performing the PVA was unnecessary. Despite these criticisms, PVA is still regarded as an extremely useful tool in conservation and threatened species management, and, *if used appropriately*, has many advantages over basing conservation management decisions on guesswork alone. Recent research that comprehensively tested the predictive powers of PVA, and tested the comparative predictions of different models, suggests that PVA is a valid and sufficiently accurate tool for managing endangered species (Brook et al. 2000a). Using PVA appropriately and ensuring the model is well constructed can provide useful, workable recommendations for conservation management. The guidelines below provide a summary of key issues to keep in mind when using PVA.

Define the question and key objectives

Clearly defined questions and objectives are essential to a good PVA (Section 4.1). Although PVA cannot always show why the population declined in the past, it can help answer questions about the best way to reverse or prevent ongoing decline. The model results should address the question, e.g. if the question concerns the risk of a 50% decline, the model should report such a result.

Ensure there are enough data, and use all available and relevant data

The way a PVA is constructed must be transparent and easily replicable. Thus, the data sources must be adequately described (for example, see Table 5) and the reasons for choosing particular datasets need to be explained and justified. The type of data required depends on what is likely to be important to the population at stake, and knowledge of the species and ecological theory are essential to ensure data are correctly used. Any data limitations also need to be discussed.

Parameters such as survival and reproductive rates must be estimated using robust methods. The proportion of marked individuals seen in subsequent years is not an estimate of survival rates because it combines the probability of an animal surviving with the probability of the animal being seen again. To get away from this problem, comprehensive mark-recapture analysis of resighting data is often used to estimate survival rates for use in PVA simulations (Armstrong & Ewen 2002; White et al. 2002), Kaplan–Meier estimates can be derived from radiotelemetry data, and Mayfield techniques used for nesting success. Estimates of variance in vital rates should be free of sampling variance, i.e. variation introduced by sampling or monitoring methods rather than variation in the actual vital rate itself (Brook 2000).

Another aspect of the data that needs consideration before undertaking a PVA is whether the number of years of study is sufficient to experience the full range of environmental conditions needed to develop accurate estimates of variance in vital rates. For example, a three-year study is unlikely to last as long as the long-term average return time of severe catastrophic events yet these events may be extremely important in determining whether small populations persist long-term. Long-term monitoring of mohua has shown catastrophic events occur in the form of severe winters and rat plagues, yet neither of these events was recorded during the initial monitoring study on which a PVA was based. As mentioned in Section 5.3, the efficient removal of stoats might have been an unforeseen influence on the magnitude of the rat catastrophe. Any uncertainties arising from inadequacies in the data need to be explored (see Section 7.5).

TABLE 5. DATA SOURCES AND PARAMETERS USED FOR A PVA ON BANDED DOTTERELS.

From Keedwell (2002). Value = value used in the model, Range = range of values reported in the literature.

PARAMETER	VALUE	RANGE	SOURCE
No. eggs laid per female	2.9	1–3	Keedwell (2002)
Egg hatch rate	0.57	0.52–0.65	Keedwell (2002)
Chick fledge rate	0.381	0.23–0.54	Based on detailed nesting studies (A. Rebergen unpubl. data; Sanders & Brown 2000, 2001; Keedwell & Sanders 2002)
Proportion renesting	Function proportional to egg and chick survival		Estimated based on accounts of productivity (A. Rebergen unpubl. data; Sanders & Brown 2000, 2001; Keedwell & Sanders 2002)
Survival from fledging to year 1	0.46	0.32–0.57	Estimated from other plovers (Larson et al. 2000)
Annual survival from year 1 to year 2	0.77		Estimated, based on assumption that survival would be slightly lower than that of adults
Annual adult survival (from year 2 onwards)	0.8	0.69–0.92	Estimated from other plovers (Marchant & Higgins 1993; Larson et al. 2000)
Maximum adult age	20		Estimated from other plovers (Marchant & Higgins 1993)
Proportion breeding at 1 year	0.75		Estimated from Pierce (1983) and other plover species (Marchant & Higgins 1993)
Proportion adults breeding	1		Estimated from other plover species (Marchant & Higgins 1993)
Starting population size (adults)	3300		Upper Waitaki Basin population size (Maloney et al. 1997)

Use appropriate model structure

In addition to being appropriate for the data and the objectives of the PVA, the model structure must be described in enough detail for someone else to replicate it. Some attempt should be made to validate the model or demonstrate why that structure is acceptable, and, if necessary, multiple model structures should be evaluated.

The model should have a parameter related to the question, e.g. if the question involves the effect of timber harvest, the model should include parameters that reflect such an effect realistically. The model should be projected over a short timeframe and have an adequate number of replicate simulations (Section 4.4).

State all assumptions explicitly

All assumptions made in collecting the data and building the model need to be clearly and explicitly stated. Always list all assumptions related to model structure, parameters and uncertainties, no matter how obvious they seem.

Discuss data uncertainties and implications of uncertain parameters

One benefit of PVA is that levels of uncertainty in different parameters can be tested. If data for a PVA are unavailable or uncertain, models with and without the unknown data can be constructed, or optimistic and pessimistic scenarios encompassing the range of uncertainty within a parameter can be modelled (see Section 6.2). Incorporating uncertainty into parameters provides a range of possible levels of extinction risk, which allows better understanding of the effect of the uncertain parameters on population survival. Uncertainties in the model or data must not be ignored, but need to be discussed and explained. For example, if genetic effects, catastrophic events, or density dependence are not modelled, the implications of this omission must be justified and discussed.

Factors leading to optimistic or pessimistic bias in the predictions need to be highlighted. Pessimistic bias can be introduced when variables (such as catastrophic events or environmental variation) are included as a parameter in the model, yet the effects of this variation are already incorporated into the vital rates being simulated. If the different sources of variation in the vital rates cannot be separated, this should be acknowledged and the model may be more appropriate without a separate parameter for environmental variation.

Analyse model outcomes and sensitivities to parameters

Adequate sensitivity analysis needs to be performed on PVA models that are intended to produce estimates of relative risks. Sensitivity analysis should be focused on identifying parameters that have the biggest impact on decreasing the uncertainty in model results. It is also useful in comparing the outcomes of different management scenarios.

State results in terms of relative risk, not absolute risk

Results such as risk of extinction and risk of population decline are more useful if they are relative ('Which management option gives higher probability of population increase?') rather than absolute ('What is the risk of extinction?')(Akcakaya & Sjögren-Gulve 2000).

State results in terms of risk of decline, not risk of extinction

Not all small populations will decline to extinction in the timeframe modelled. Therefore, the risk of a population declining is often more valuable information than the risk of extinction. Estimating and presenting λ indicates the risk of decline. Many populations are in trouble well before they become extinct, and this is often the crucial time for management.

Interpret and discuss model results

When interpreting the model, there needs to be discussion or recognition of the limitation in the data. For example, if uncertainty of some parameter estimates is not incorporated, does that bias the estimates of extinction probabilities? Does this also bias the conclusions that can be drawn from the modelling exercise? The results of the model should also be discussed in relation to other factors (such as behaviour or distribution of populations) that were not included in the model. If different management scenarios are modelled, the cost of implementing the different scenarios is just as important as the outcome of each scenario. Finally, the result should be presented as hypotheses to be tested in the field, and not presented as facts.

Validate model predictions and structure

A major criticism of PVA is that there are seldom enough data to validate the model, i.e. all available data are used in building the model. Where long-term datasets exist, part of the dataset can be used to build the model, and the model predictions can then be tested against the remaining data (Brook et al. 2000a). As more data are independently gathered, they should be tested against the model predictions, so that the model can be refined where necessary.

Seek expert statistical or modelling advice when necessary

Although generic computer packages have made PVA an accessible and easily used tool, the packages may not always be suitable to all datasets. In addition, many datasets will need analysis to extract the correct parameters for the models. Always seek expert advice on model suitability and how to proceed with analyses.

Peer-review all models

Other people not involved in developing the model should critique each PVA, and the data, model, and model assumptions should be carefully reviewed. PVA that can stand up to criticism by members of the scientific community are likely to be reliable models, and can be used in the political forum to further the cause of the species being modelled.

Use the model as a dynamic part of species management

PVA is not a tool to be used in isolation, nor should it be viewed as a static or one-off exercise. To gain the full benefit, PVA need to be used as a dynamic part of a manager's or researcher's toolbox. Instead of developing one model and using that to dictate management actions, the model (or a range of alternative models) should be constantly refined and updated every time more data are gathered.

8. Conclusions

PVA is a useful tool *if used correctly*. Using PVA in threatened species management can help take some of the guesswork out of management and formalise the decision making process. It has particular application for use by species recovery groups in New Zealand. Models that are specifically constructed to guide management actions, and that are continuously updated as more data are gathered, can provide an excellent framework on which to base and assess management decisions. PVA provides a method of assessing the relative risks and benefits of alternative management actions or combinations of actions. Formally weighing up the advantages of different management actions before implementing them provides a method for identifying the best use of money and resources.

The key strengths of PVA lie in their qualitative predictions, that is, the ability to weigh up the relative outcomes of different management scenarios. This is true even for models where datasets are incomplete because it can help focus attention on where further research is needed, and the process of carrying out the PVA aids in formalising existing knowledge of the species. Previous criticisms of PVA often focused on its use to make quantitative predictions such as risks of population decline and projected population sizes through time. Where datasets are incomplete, this criticism remains, but quantitative predictions are surprisingly precise for species where comprehensive long-term datasets exist (Brook et al. 2000a). It is important to conduct sensitivity analysis to highlight parameters that have greatest effect on the model outcomes and hence to identify parameters for which better data are needed.

Because PVA is a relatively new field, it is constantly changing as models and software are refined and updated, and new types of PVA models using Bayesian theory (Goodman 2002) and decision theory (Possingham et al. 2002) are becoming more widespread. Choosing the best approach for modelling any species is crucial and will ensure that management decisions based on model outcomes are the most appropriate.

9. Key references for further reading

This report provides an introductory overview of the use of PVA. Anyone wishing to integrate PVA into their management would need to do further reading and seek expert advice before embarking on any detailed analysis.

A general overview of PVA and discussion of its strengths and weaknesses is given in articles by Lindenmayer et al. (1993); Ralls & Taylot (1997); Reed et al. (1998, 2002); and Brook et al. (2000a, 2002), and books by Sjögren-Gulve & Ebenhard (2000); and Beissinger & McCullough (2002).

Many of the manuals accompanying the PVA packages outlined in Section 6 have useful background information on using PVA, and the websites given there for each programme are useful.

Detailed information on aspects of building a PVA is given by Morris et al. (1999). This handbook can be downloaded from the library at: www.conserveonline.org

Comparisons of the different generic PVA models are given by Lindenmayer et al. (1995); Mills et al. (1996); Brook et al. (1997, 1999, 2000a, 2000b); and Chapman et al. (2001).

10. Acknowledgements

Colin O'Donnell, Graeme Elliott, Doug Armstrong, and Scott Davidson provided valuable comments on earlier versions of this report.

This report was part of DOC research investigation no. 3581.

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12. Glossary

***Demographic stochasticity*:** Variation in demographic rates among individuals. In relatively small populations, demographic stochasticity can be an important factor influencing extinction probability. As population size increases, random demographic differences are averaged over larger and larger numbers of independent individuals. Impact of demographic stochasticity decreases substantially when N > 100.

Deterministic models: All parameters in the model are fixed to a specified value or vary through time by a predetermined amount. The population trajectories of multiple simulations from a deterministic model will be identical unless the parameters are manually varied.

***Environmental stochasticity*:** Usually refers to unpredictable events (e.g. changes in weather, food supply, or populations of competitors, predators, etc.) that affect all members of a population. Large population sizes do less to buffer against extinction in this case, in contrast to demographic stochasticity.

Mean time to extinction: An output from PVA models, the mean time to extinction is the average time at which non-surviving populations in the simulation went extinct.

Metapopulation: A population that is separated into smaller sub-populations, each of which may be linked to other sub-populations through migration. Each sub-population often has different vital rates and rates of migration.

***Natural catastrophes*:** Extreme cases of environmental uncertainty, such as hurricanes and large fires. Catastrophes are usually short in duration but widespread in their impact.

Parameter: Data variables that are put into the model, e.g. adult survival, frequency of catastrophes, environmental variation, migration rates between sub-populations.

Probability of extinction: An output from PVA models, the probability of extinction used to be widely quoted as the proportion of simulated populations that went extinct over a given period (usually 100 years). This output is most useful for comparing relative differences in projected scenarios over a 10- to 50-year period, and less useful for giving a quantitative risk of extinction.

Process variation: Actual variation in the parameter measured, e.g. annual survival to year 1 may have a mean of 0.24 but varies in nature by a standard deviation of 0.08. When building a stochastic model, it is important to separate out process variation from sampling variation wherever possible, to ensure the variation in the model reflects the real situation as closely as possible.

PVA: Population viability analysis—a broad term used to describe the process where data are used in a population model to estimate the risks of extinction.

Quasi-extinction: The proportion of simulated populations falling below some minimum threshold over a given period, i.e. 10–50 years. The threshold may be set by the user and either reflects a population that is functionally extinct (e.g. no breeding occurs if the population falls below the threshold) or a limit below which management action is imperative.

Sampling variation: Variation introduced into data measurements that is caused by sampling technique or is an effect of the sampling process. See process variation.

Sensitivity analysis: The process of testing which parameters the model is most sensitive to. This helps assess which parameters need to be estimated more carefully to ensure the most accurate model outputs. Sensitivity analysis also identifies which parameters are most likely to have the biggest effect on increasing population viability if increased or decreased through management actions.

Simulation: One 'run' of a population model for a specified period (usually 10–50 years). Most studies perform at least 50 and up to 10 000 simulations for a model and take a mean or median measure across all simulation results (such as growth rate, probability of extinction, etc.). Many simulations are needed to ensure the output is representative of all possible outcomes under that scenario.

Stochastic models: Models that incorporate variation in some parameters, such as birth or death rates, or incorporate a degree of environmental variation. These parameters are usually varied for each year of the simulation according to some probability distribution defined by the user. The population trajectories of multiple simulations from a stochastic model will all differ, and many simulations are run to provide some average measure of survival across all simulations.

Vital rates: Key demographic measures that limit the survival of a population such as birth rates, death rates, and migration rates.

USE OF POPULATION VIABILITY ANALYSIS IN CONSERVATION MANAGEMENT IN NEW ZEALAND 2. FEASIBILITY OF USING POPULATION VIABILITY ANALYSIS FOR MANAGEMENT OF BRAIDED RIVER SPECIES

R.J. Keedwell

Use of population viability analysis in conservation management in New Zealand

2. Feasibility of using population viability analysis for management of braided river species

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A B S T R A C T

Braided rivers have many threatened and endangered species, but no integrated approach exists for their management. Population viability analysis (PVA) and computer modelling form one approach that can be used to assess management options for a number of species. This report examines the feasibility of using multi-species PVA modelling of the braided river habitat, and provides evidence of a lack of data on, and understanding of, the complexities of the braided river system. Based on available data, a comprehensive multi-species approach was not suitable, but multiple single-species PVA on some taxa provided an opportunity to explore the approach. Adequate data were available for development of PVA models for banded dotterel (*Charadrius bicinctus*), black-fronted tern (*Sterna albostriata*), and Finsch's oystercatcher (*Haematopus finschi*). Simulations showed that predator control enhanced population growth in all three species, whereas scenarios simulating lowered food supplies or poor survival and reproduction in some years usually resulted in decreasing population. These models are preliminary and to be developed further require a large-scale collaborative research project to quantify the relationships in the braided river community among breeding birds, predators, rabbits, weed infestation, water abstraction, and seasonal effects. Such research would provide better understanding of the community dynamics and would enable increasingly efficient management of the braided river habitat and ensure ongoing survival of braided river taxa.

Keywords: population viability analysis, PVA, computer simulation, conservation management, community dynamics, braided river species, New Zealand.

Keedwell, R.J. 2004: Use of population viability analysis in conservation management in New Zealand. 2. Feasibility of using population viability analysis for management of braided river species. *Science for Conservation 243*: 39–60.

or in full as:

Keedwell, R.J. 2004: Use of population viability analysis in conservation management in New Zealand. 2. Feasibility of using population viability analysis for management of braided river species. Pp. 39–60 in: Keedwell, R.J. 2004: Use of population viability analysis in conservation management in New Zealand. *Science for Conservation 243*. 60 p.

1. Introduction

The wide gravel riverbeds of braided rivers of the South Island are a defining feature of the landscapes from Marlborough to Southland. These rivers and their catchments provide breeding and feeding habitat to a range of native and endemic species, many of which are entirely dependent on the braided river systems. These include invertebrates, freshwater fish, lizards, birds, and bats (Peat & Patrick 2001). The braided river habitat used to be more extensive than it is today, but hydroelectric development, irrigation, stop-banking, weed invasion, and gravel extraction have contributed to a decline in its quantity and quality (Wilson 2000). Many braided river species, such as the black stilt (*Himantopus novaezelandiae*), wrybill (*Anarhynchus frontalis*) and black-fronted tern (*Sterna albostriata*) are threatened or endangered because of declines in habitat availability and the impact of introduced mammalian predators on survival rates (BirdLife International 2000). The black stilt is intensively managed, and without this management would probably face rapid extinction. Although other braided river species are largely left unmanaged, there is increasing evidence that management will be necessary to halt ongoing decline in a number of species and degradation of the community as a whole (Dowding & Murphy 2001; Keedwell 2002; Sanders & Maloney 2002).

Because so many species face similar threats in these braided rivers, the most cost-effective means of managing numerous species may be to manage the threats faced by the whole community rather than by individual species. Key management issues in braided rivers include predator control, weed control, optimising water flows, minimising habitat loss resulting from abstraction and damming, mitigating impacts of surrounding land use, and optimising food availability (Hughey & Warren 1997; Maloney 1999; Keedwell et al. 2002). The most effective management actions that benefit all species have not been determined. In addition, the relative importance of management actions probably varies widely among rivers. For example, issues facing high-country rivers such as the Cass and Tasman Rivers in the upper Waitaki Basin are often different from those facing rivers near the coast such as lower reaches of the Waitaki and Ashburton Rivers because of different demands on water resources and differing impacts of threats within their catchments. Increased understanding of how different threats interact and impact across the range of braided river systems and the associated braided river species is urgently required. This knowledge would help in the exploration of different management actions required to recover threatened species and in determining which management actions have the greatest benefit for the widest range of species within threatened communities.

Population viability analysis (PVA) is one tool that is often used to explore viability of populations and the outcomes of various management actions (Akcakaya & Sjögren-Gulve 2000). PVA uses data from population dynamics of a species to simulate the fates of populations into the future. Insight into the relative importance of different management options can be obtained by varying the conditions of the PVA models and comparing the relative benefits of the outcomes (Hamilton & Moller 1995; Ralls et al. 2002). PVA is usually done for a single species because of the huge and complex data requirements for modelling several species and their interactions. However, a multi-species PVA approach has been used in the past to examine the interactions of populations of predators and prey within the same community (Blackwell et al. 2001) or the impacts of limiting certain populations of species within a community (Colding 1998). This approach is becoming more feasible with the ever-increasing capabilities of computers and in situations where intensive study provides adequate data.

Ideally, a comprehensive PVA model covering a range of species present in the braided rivers would provide opportunities to examine different management regimes for the braided rivers and to identify how the differing regimes affect the different taxa. However, data requirements for this are extensive and braided rivers are a poorly understood ecosystem. Accordingly, this report explores the feasibility of using PVA to aid in managing the braided river systems. The aims are to:

- Describe the interrelating factors influencing the long-term viability of some threatened braided river species.
- Assess the adequacy of data to undertake PVA for selected braided river species.
- Undertake a range of modelling scenarios looking at the relative impacts of predation and habitat loss on selected braided river species as a case study.
- Explore how these data might be used to develop a multi-species approach to managing braided river habitats in the future.
- Make recommendations about future management of and research on the braided river habitat and its species.

2. Modelling the braided river wildlife habitat

Braided river habitat and native species are directly and indirectly affected by a wide range of factors. Figure 1 provides a simplified version of the hypothesised links and interrelationships in the braided river system, and focuses on how these factors impact on native birds breeding on the riverbeds. Examples of direct relationships include predator abundance affecting predation rates at bird nests, and weed invasion affecting availability of bird breeding habitat. Indirect relationships include abundance of rabbits (*Oryctolagus cuniculus*) influencing predator abundance, which in turn influences predation rates at nests. Also, hydroelectric development indirectly affects habitat availability by lowering water flows and flood frequencies, which in turn allows further establishment of exotic weeds on the riverbeds (Balneaves & Hughey 1989; Hughey & Warren 1997).

Ideally, modelling this entire system would provide excellent information for assessing the effects of different actions, such as reducing predator numbers,

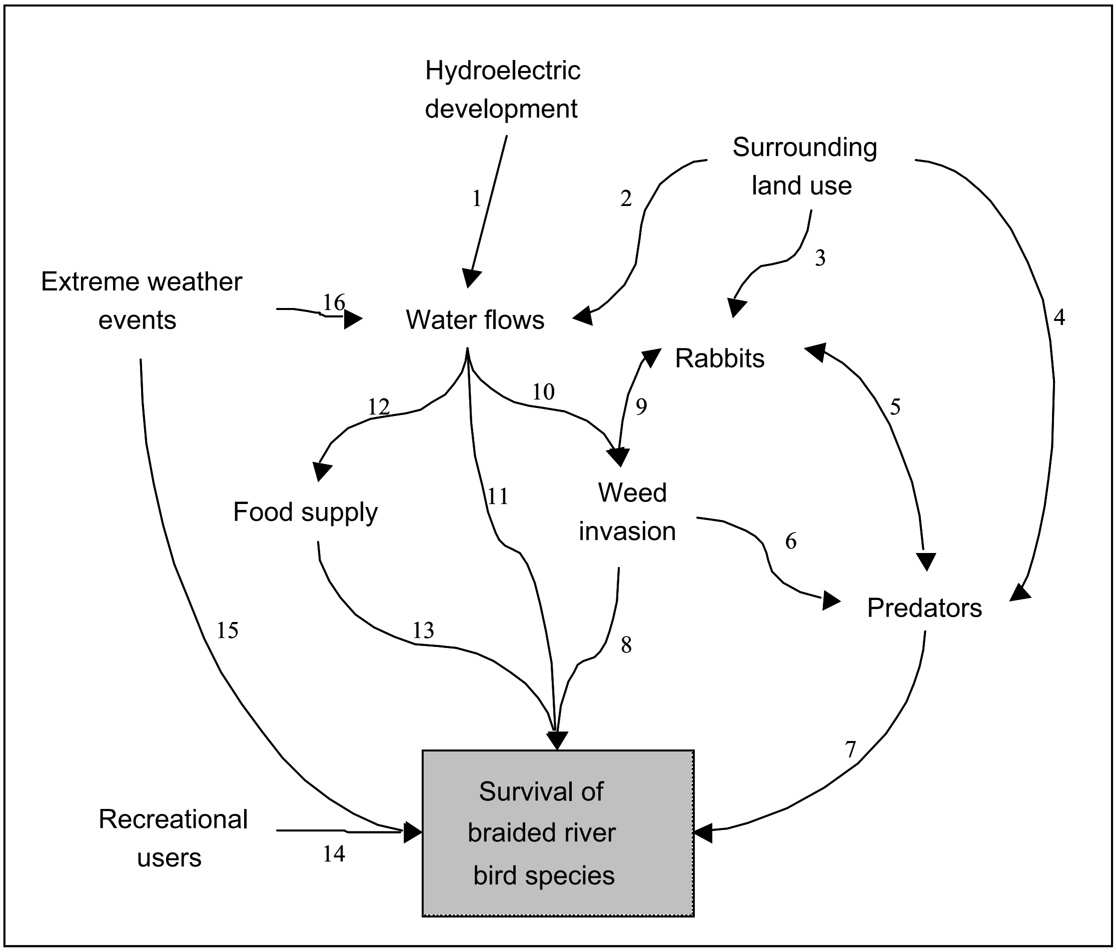

Figure 1. Interrelationships of some of the different species and factors occurring in the braided rivers of the South Island. Examples of hypothesised interactions between the different factors include: 1 – water is redirected into canals for power generation, lowering river flows and flood frequencies; 2 – water is abstracted for irrigation of farmland, lowering river flows; 3 – rabbit control on farmland lowers rabbit abundance; 4 – differing land use practices change habitat availability for predators; 5 – predator abundance is altered by changes to rabbit abundance but also helps control rabbit abundance; 6 – vegetation on riverbeds provides cover for predators; 7 – predators prey on eggs, chicks and adults; 8 – weeds clog up breeding habitat and alter feeding habitat; 9 – vegetation provides cover and food for rabbits, but some weed species are controlled by rabbit grazing; 10 – lowered water flows and floods allow vegetation to establish on riverbed; 11 – floods destroy nests; 12 – lowered water flows can alter abundance of aquatic insects; 13 – food abundance can influence survival of young or condition of breeding adults; 14 – fishers, campers, and 4WD drivers can destroy nests or disturb breeding birds; 15 – extreme cold spells can kill eggs and chicks; 16 – high rainfalls can cause floods.

changing water flows or clearing weeds. However, although some of these relationships have been described and are understood on a gross scale (e.g. Rebergen et al. 1998), very few have been quantified and each is likely to affect each wildlife species differently. For example, sufficient evidence exists to suggest a relationship between rabbit abundance, predator abundance, and predation rates at nests, but exactly how the three interact has not been quantified (Rebergen et al. 1998; Norbury 2000; Norbury 2001). How much of a decrease in rabbit abundance is needed to affect predator abundance and predation rates? How are changes in predation rates linked to predator abundance, and how does this change through time in response to sudden declines in rabbit abundance? To model individual species and the interactions between those species in the braided river habitat, the relationships in Fig. 1 need to be quantified.

These relationships also differ among the various species that are at risk. For example, banded dotterels (*Charadrius bicinctus*) appear to survive better under high predation rates than do black stilts or black-fronted terns (Keedwell 2002); wrybills are more affected by flooding than most other nesting species (Hughey 1985); black-backed gull (*Larus dominicanus*) colonies tend to increase in size as a result of some land uses (e.g. rubbish dumps and food availability) and large colonies will impact detrimentally on other native species (Marchant & Higgins 1993). Thus, the relationship between each native species and the factors in Fig. 1 needs to be understood. Also, the relative importance of the different relationships will differ geographically both within and between rivers.

3. Modelling braided river species

3.1 ADEQUACY OF DATA

One option for a preliminary investigation into the use of PVA for assessing relative impacts of different threats is to assess the availability of appropriate data for a variety of species. Where adequate data exist, multiple single-species PVA models can be run but with each model subjected to the same set of scenarios that simulate different management actions (Keedwell 2004).

Over 20 species of wetland birds use the braided rivers for feeding and breeding (Maloney et al. 1997). However, the main animal species of interest are the endemic and obligate river birds, and invertebrates such as the endangered robust grasshopper *Brachaspis robustus* (White 1994). Listed below is the status of each of the main braided river species and a summary of data availability and suitability for a PVA based on the braided river population.

Banded dotterel

Population status: Endemic, Gradual Decline (Hitchmough 2002)

Data availability: This is a common and widely studied bird in the braided river systems. Predation rates are high and predation rates at banded dotterel nests on braided rivers have been frequently studied (Rebergen et al. 1998). However, the potential impacts of river flow changes and weed encroachment on population dynamics have not been studied. The population size is estimated at over 12 000 individuals, but they breed on river terraces and coastal areas as well as on braided rivers (Marchant & Higgins 1993). Data exist on survival rates for eggs and chicks but not for adult or juvenile survival (Keedwell 2002). Natural history is well documented.

PVA suitability: Adequate data for modelling

Black-fronted tern

Population status: Endemic, Serious Decline HI* (Hitchmough 2002)

Data availability: Population is probably less than 10 000 and in decline (Keedwell 2002). Black-fronted terns suffer high predation rates at all life stages during the breeding season. One comprehensive study provides data on survival rates across all ages (except juveniles) and provides basic natural history information (Keedwell 2002). Black-fronted terns feed primarily over water on invertebrates and small fish, but how changes to water flow affect diet or survival are not understood.

PVA suitability: Adequate data for modelling

Finsch's oystercatcher (*Haematopus finschi*)

Population status: Endemic, not threatened (Hitchmough 2002)

Data availability: Finsch's oystercatcher populations have increased to over 100 000 individuals in the past 50 years (Sagar et al. 2002). Extension of the oystercatcher's breeding range from braided rivers to agricultural land and grasslands has led to increased breeding success. Comprehensive data exist on survival rates of adults and breeding success rates from long-term studies (Sagar et al. 2000; Sagar et al. 2002).

PVA suitability: Adequate data for modelling, but most available data are from studies on farmland rather than on riverbeds.

Wrybill

Population status: Endemic, Nationally Vulnerable (Hitchmough 2002)

Data availability: Fewer than 5000 individuals and probably in decline (Veitch & Habraken 1999). Two comprehensive studies on breeding success and survival in Canterbury braided rivers are now almost 20 years old, and the only data recently collected have not been analysed (E. Murphy, pers. comm.). No good estimates of adult or juvenile survival or rates of reproductive success per female exist. Because of the small population size and vulnerable status, accurate estimates are required for building an adequate PVA model.

PVA suitability: Insufficient data until further analysis is carried out.

Black-billed gull (*Larus bulleri*)

Population status: Endemic, Serious Decline (Hitchmough 2002)

Data availability: The population size is probably less than 100 000 individuals and in decline (Taylor 2000). Most studies of black-billed gulls have focused on movements and distributions, and few have detailed information on breeding success or breeding biology (Higgins & Davies 1996). Currently there are no data on breeding success, effects of predators, population dynamics (e.g. age of first breeding, longevity), or survival rates.

PVA suitability: No adequate data for modelling. Data could be borrowed from the related red-billed gull (*Larus novaehollandiae*), but would result in a model based largely on educated guesses for parameters.

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* Qualifiers: HI = Human I nduced

Black stilt

Population status: Endemic, Nationally Critical CD, ST, HI, OL* (Hitchmough 2002)

Data availability: This species has been intensively managed since the 1980s (Pierce 1996). The population is fewer than 200 individuals and they are only found in the rivers of the upper Waitaki Basin. Comprehensive data exist on survival rates, breeding success in captivity, and natural history, but the survival of the population currently relies on the captive breeding programme.

PVA suitability: Not suitable for modelling because survival of the species currently depends entirely on success in captivity, rather than management in the wild.

Robust grasshopper

Population status: Endemic, Nationally Endangered HI*(Hitchmough 2002).

Data availability: This species is known from only 10 sites along rivers of the Mackenzie Basin. Population size is largely unknown but is conservatively estimated at around 800 individuals (White 1994). The species is found only in association with braided river systems, but most natural history characteristics are unknown. For example, the age of female at oviposition, the number of eggs laid per female in a season, whether the eggs overwinter before hatching, and survival rates across all age classes are unknown.

PVA suitability: Insufficient data for modelling.

3.2 PVA METHODS

VORTEX (v8.42) was used to construct a separate population model for each of the three species that had adequate data (banded dotterel, black-fronted tern, and Finsch's oystercatcher). Each population model was then subjected to different scenarios (see below) that examined the relative impacts of predation, weed encroachment, and loss of water flows. VORTEX is the most widely available computer programme used for PVA and was originally designed to model bird and mammal populations (Lacy 1993, 2000). The programme models individuals within a population and incorporates environmental and demographic stochasticity, inbreeding depression, metapopulations, catastrophes and some density-dependence functions (Lacy 1993, 2000). It also allows for simulation of harvesting from the population and supplementation (i.e. introducing translocated individuals to the population).

Only one population of each species was modelled: a hypothetical population comprising all rivers of the Mackenzie Basin. Starting population size was based on surveys of rivers in the upper Waitaki Basin (Maloney et al. 1997). Inbreeding was not incorporated, survival and reproduction were assumed to be correlated with environmental variation, and density-independence was assumed because of the low populations. For simplicity, all adult males and females were assumed to be in the breeding pool each year, sex ratio was 50:50

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* Qualifiers: CD = Conservation Dependent; ST = Stable; HI = Human Induced; OL = One Location

and the populations started from stable age distributions. Carrying capacity was set at five times the starting population size and remained unchanged throughout the length of each simulation. Catastrophic events, such as extreme weather conditions or floods, were not included in the initial models.

Braided river species can re-nest more than once after loss of eggs or chicks, but the structure of VORTEX does not explicitly allow this to be modelled. To take re-nesting into account, the parameter for the percentage of females breeding was instead used to represent the percentage of females successfully fledging one or more young. This percentage (B) was derived from: $B = S^*[(1\text{-}S)^*S^*R]$, where S is the probability of fledging success and R is the probability of re-nesting if the first nesting attempt fails. Multiple re-nesting could also be incorporated into the equation by including the proportion of birds having failed re-nests that went on to nest again. The standard deviation for the proportion of females breeding was arbitrarily set at 10%. Mortality from age 0–1 was then changed to include only the mortality from fledging to year 1, i.e. it did not include egg and chick mortality. The number of young produced by each female was set using the mean (± SD) number of young fledged per successful female per year (hereafter, mean brood size).

Data were gathered from all available sources (listed below) to construct parameters for each species and represent the best data currently available. Table 1 lists the parameters used in the model, and described below are the sources and assumptions involved in estimating some of the parameters.

TABLE 1. DATA USED IN PVA MODELS FOR BLACK-FRONTED TERN, BANDED DOTTEREL, AND FINSCH'S OYSTERCATCHER.

PARAMETER	BANDED DOTTEREL	BLACK-FRONTED TERN	FINSCH'S OYSTERCATCHER
Breeding system	Monogamous	Monogamous	Monogamous
Age of first breeding	1	2	4
Maximum age	20	25	30
Sex ratio at birth	50:50	50:50	50:50
Percentage of females successfully breeding annually	56	32.8	61.1
SD breeding females	10	10	10
Mean brood size	1.65	1.5	1.59
SD young/year	0.44	0.25	0.15
Mortality age 0–1	54	53	60
SD mortality 0–1	10	10	10
Mortality age 1–2	-	15	20
SD mortality 1–2	-	3	3
Mortality age 2–3	-	-	10.8
SD mortality 2–3	-	-	3.4
Mortality age 3–4	-	-	10.8
SD mortality 3–4	-	-	3.4
Adult mortality	20	12	10.8
SD adult mortality	3	3	3.4
Starting population size	3300	2100	1000

SD = standard deviation

Banded dotterel

Egg survival (0.57) and chick survival (0.38) reported in Keedwell (2002) were used to calculate the proportion of females successfully breeding. Ninety five percent of females were assumed to re-nest after the first and second nest failures and 50% after the third nest failure. Banded dotterels have a long breeding season and regularly re-nest twice or more in a season. They are also capable of raising more than one brood in a season. Mean brood size and standard deviation was calculated from intensive studies of banded dotterel breeding success over several seasons on the Ahuriri River (Project River Recovery, unpubl. data) and at Ruataniwha Wetlands (Sanders & Brown 2000, 2001; Keedwell & Sanders 2002). Mortality rates were based on the figures presented in Keedwell (2002).

Black-fronted tern

The percentage of females successfully breeding was based on egg survival of 0.6 and chick survival of 0.35 as presented in Keedwell (2002). These estimates are from the upper end of the range reported because using the mean or lower range resulted in extremely rapid population decline. Black-fronted terns were assumed to re-nest only once in a season and the re-nesting rate was estimated at 70%. Mean brood size was optimistically estimated at 1.5 ± 0.25. The only available data on brood size was from two seasons and was closer to 1.2 (R. Keedwell, unpubl. data). This figure was too low and resulted in unrealistically negative population growth. Mortality rates were also taken from Keedwell (2002).

Finsch's oystercatcher

Average survival from egg laying to fledging (0.425) was calculated from values presented in Sagar et al. (2000) and from four years' data on the Ahuriri River (Project River Recovery, unpubl. data). Re-nesting rates for the first and second re-nests were set at 0.45 and 0.2 respectively (based on data from Sagar et al. 2000). Mean brood size was also derived from Sagar et al. (2000). Mortality from fledging to one year was estimated from Kersten & Brenninkmeijer (1995), and annual mortality from 2 years to adult was from Sagar et al. (2002). Mortality from 1 to 2 years was estimated, but was assumed closer to sub-adult mortality than juvenile mortality rates.

3.3 SCENARIOS MODELLED

For each species, the models were set to run 250 iterations over 25 years. The mean population growth rate across all 250 simulations, and the probability of quasi-extinction (i.e. the proportion of simulations that fell below 25% of the starting population size) were compared across seven different scenarios. The current situation (the 'base model') was modelled using the most realistic data possible (listed in Table 1). Six additional scenarios modelled were based on assessment of realistic management options or potential threats. Each scenario was defined as a change in the environment or management and the changes made were based on existing knowledge. The scenarios included implementing predator control, lowering the food supply (reflecting water abstraction or other severe changes to habitat), and increasing the severity and frequency of poor years (i.e. high predation or extreme climatic events).

Scenario 1: Implement predator control

This scenario simulated the effects of predator control implemented over the breeding season. Rates of adult mortality were lowered by one percentage point (e.g. for banded dotterels from 20% mortality to 19% mortality), and the proportion of females successfully breeding was altered to reflect an increase in the survival of eggs and chicks. For banded dotterels, survival of eggs was increased to 0.66 and chicks to 0.45 (from the upper end of data reported in Keedwell 2002), which increased the percentage of females successfully breeding to 69%. Black-fronted tern egg and chick survival in the absence of predation at one colony on the Ohau River was 0.74 and 0.5, respectively (Keedwell 2002), and the percentage of females successfully breeding was accordingly raised to 53.3%. Survival of oystercatchers to fledging was increased to 0.55 (upper end of data recorded, unpubl. data, Project River Recovery), which gave 69.9% of females successfully breeding.

Scenario 2: Decrease food supply

This scenario assumed that access to food supply became severely limited because of changes to the habitat such as weed encroachment or decreases in water flows. This scenario was hypothetical only and was designed to compare the effects of severe limitations on reproductive success and survival among the three species. For all three species, re-nesting rates were reduced by 20%, chick mortality increased 20%, year 0–1 mortality increased 5%, and adult mortality increased by one percentage point.

Scenarios 3a–3d: Frequency and severity of poor years

Four scenarios were run to reflect differing frequency and severity of poor years caused by factors such as extreme weather conditions, food failure, and flooding. Firstly, catastrophic events were simulated with high frequency (one year in every five on average) and high severity (reproduction and survival were decreased by 25% and 10% respectively in a catastrophe year). This catastrophe simulation was repeated, but with low frequency (1 year in every 10). The third and fourth catastrophe scenarios were simulated with high and low frequency, but with low severity (reproduction and survival were both decreased by 10% in a catastrophe year). The data used in these scenarios were also hypothetical but designed to test each species' ability to withstand the occurrence of poor years.

3.4 SENSITIVITY ANALYSIS

All parameters within each model were varied one at a time to assess which parameters had the biggest effect on model predictions. Mortality rates, percentage of successful females, and brood size were increased and also decreased by 10% (if the base parameter was greater than 0.5, it was first subtracted from 1 before the 10% variation was calculated). Maximum age was increased by 10% and the percentage of males in the breeding pool was decreased to 90%. The age of first breeding was increased by 1 year because first breeding age in the models was set at the age new adults were commonly observed breeding, but it did not necessarily reflect the age all new adults began breeding. The model was also run assuming no correlation between environmental variation and survival or reproductive success. The percentage change in mean growth rates between each sensitivity run and the base-model growth rate were compared.

4. Simulation results

4.1 PREDICTED POPULATION TRENDS

The base-model simulations predicted stable or slightly increasing growth rates over 25 years for both banded dotterels and oystercatchers. The mean growth rate across all 250 simulations for banded dotterels was 0.014 and for Finsch's oystercatchers was 0.009, and the probability of quasi-extinction for both species was zero (Figs 2 and 3). Some of the banded dotterel simulations had such strong population growth that population size reached carrying capacity.

The black-fronted tern population was predicted to decline over a 25-year period, with a mean growth rate of –0.025 and a quasi-extinction probability of 0.01, i.e. 1% of all simulated populations fell to below a quarter of the starting population size within 25 years (Fig. 4).

4.2 SCENARIO 1: IMPLEMENT PREDATOR CONTROL

Simulations imitating the potential effect of predator control during the breeding season resulted in substantial increases in growth rate for all three species, with the biggest proportional increase seen for black-fronted terns (Fig. 4). Mean growth rate for black-fronted terns increased to 0.041 and quasi-extinction probability reduced to zero. Growth rate increased to 0.072 for banded dotterels (Fig. 2) and 0.024 for Finsch's oystercatchers (Fig. 3).

4.3 SCENARIO 2: DECREASE FOOD SUPPLY

This simulation reduced both reproductive output and survival and resulted in negative growth rates for all three species. Growth rate and quasi-extinction probabilities for each species dropped to: banded dotterels –0.057 and 0.58, black-fronted terns –0.065 and 0.75, and Finsch's oystercatchers –0.016 and a zero probability of quasi-extinction, respectively (Figs 2–4).

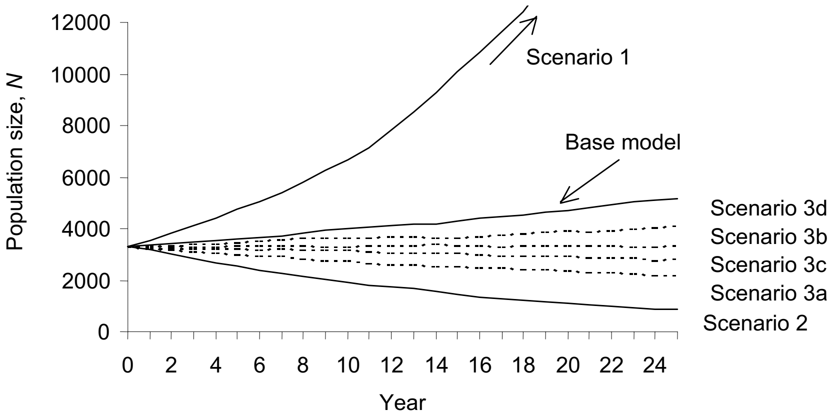

Figure 2. Simulated population growth of banded dotterels under different scenarios: Base model = the starting model upon which the scenarios are based; Scenario 1 = predator control implemented; Scenario 2 = severe decrease in food supply; Scenarios 3a–3d = catastrophic events of differing severity and frequency.

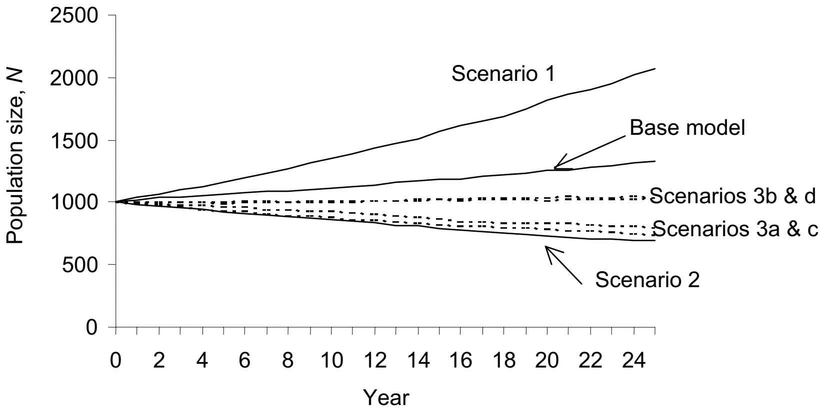

Figure 3. Simulated population growth of Finsch's oystercatchers under different scenarios: Base model = the starting model upon which the scenarios are based; Scenario 1 = predator control implemented; Scenario 2 = severe decrease in food supply; Scenarios 3a–3d = catastrophic events of differing severity and frequency.

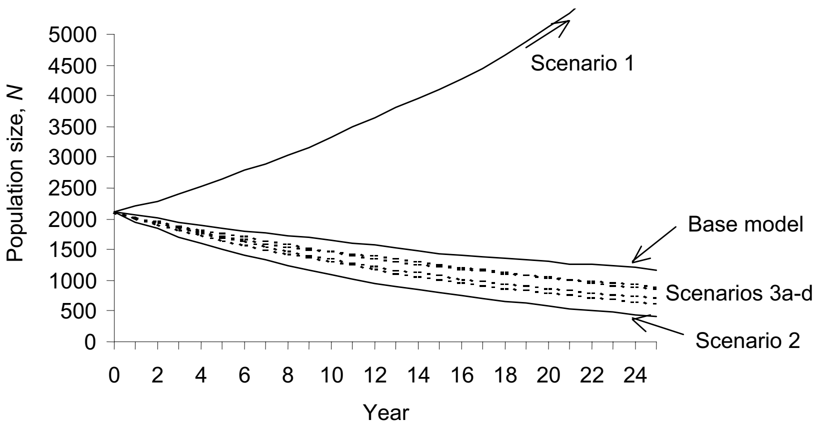

Figure 4. Simulated population growth of black-fronted terns under different scenarios: Base model = the starting model upon which the scenarios are based; Scenario 1 = predator control implemented; Scenario 2 = severe decrease in food supply; Scenarios 3a–3d = catastrophic events of differing severity and frequency.

4.4 SCENARIO 3A-3D: FREQUENCY AND SEVERITY OF POOR YEARS

Table 2 shows the effects of catastrophic events on mean growth rate (*r*) and probability of quasi-extinction *P(E)* for banded dotterel, black-fronted tern, and Finsch's oystercatcher simulation models. Starting model values for growth rate and quasi-extinction for each species were: banded dotterel 0.014 and 0; black-fronted tern −0.025 and 1%; Finsch's oystercatcher 0.009 and 0. All catastrophes simulated had a negative effect on population growth rate for the three species (Table 2). Black-fronted terns were the most sensitive to the effects of catastrophic events and quasi-extinction probabilities increased to 0.38 under the most severe scenario. Although banded dotterel growth rates decreased under all four scenarios, they remained positive when catastrophes were of low frequency and severity (Figs 2–4).

TABLE 2. EFFECTS OF CATASTROPHIC EVENTS ON MEAN GROWTH RATE (*r*) AND PROBABILITY OF QUASI-EXTINCTION *P(E)* FOR BANDED DOTTEREL, BLACK-FRONTED TERN, AND FINSCH'S OYSTERCATCHER SIMULATION MODELS.

CATASTROPHE TYPE	DOTTEREL *r*	DOTTEREL *P(E)*	TERN *r*	TERN *P(E)*	FINSCH'S *r*	FINSCH'S *P(E)*
High frequency, high severity	−0.021	0.10	−0.049	0.38	−0.015	0.01
Low frequency, high severity	−0.006	0.03	−0.037	0.15	−0.003	0
High frequency, low severity	−0.012	0.04	−0.048	0.32	−0.014	0.01
Low frequency, low severity	0.002	0.02	−0.036	0.12	−0.003	0

Note: positive values for *r* denote growth in the populations, negative values denote population declines.

4.5 SENSITIVITY ANALYSIS

Table 3 shows sensitivity analysis results for banded dotterel, black-fronted tern, and Finsch's oystercatcher simulation models. Base model values for mean growth rate (*r*) were: banded dotterel 0.014; black-fronted tern −0.025; Finsch's oystercatcher 0.009. The banded dotterel and oystercatcher models used slightly higher survival rates of young (i.e. fledging success) than black-fronted tern models and consequently both models were most sensitive to an increase in the age of first breeding (Table 3). This was followed by sensitivity to sex ratio, brood size, and adult and juvenile mortality. In contrast, the black-fronted tern model had lower fledging success and the model was most sensitive to the percentage of females successfully breeding, and the sex ratio, followed by adult and juvenile mortality, brood size, and increasing the age of first breeding (Table 3).

TABLE 3. SENSITIVITY ANALYSIS RESULTS FOR BANDED DOTTEREL, BLACK-FRONTED TERN, AND FINSCH'S OYSTERCATCHER SIMULATION MODELS.

Base model values for mean growth rate (r) were: banded dotterel 0.014; black-fronted tern –0.025; Finsch's oystercatcher 0.009. Percentage changes in r from the base model are presented.

PARAMETER	CHANGE IN r, %		
	DOTTEREL	TERN	OYSTERCATCHER
Age 1st breed < 1 year	–286	–44	–133
Percentage females breed > 10%	–114	–48	–56
Percentage females breed < 10%	114	44	67
Sex ratio 45% males	143	36	11
Sex ratio 55% males	–171	–48	–100
Mean clutch size > 10%	–164	–44	–111
Mean clutch size < 10%	150	40	111
Fledge to yr 1 mortality > 10%	143	32	89
Fledge to yr 1 mortality < 10%	–157	–44	–111
Adult mortality > 10%	143	40	100
Adult mortality < 10%	–143	–44	–100
EV* not correlated	–57	–28	–33
Maximum age > 10%	–29	–12	–22
Maximum age < 10%	14	12	11
90% males breed	–7	0	–11
Year 1–2 mortality > 10%		4	22
Year 1–2 mortality < 10%		–4	–44
Year 2–3 mortality > 10%			11
Year 2–3 mortality < 10%			–11
Year 3–4 mortality > 10%			22
Year 3–4 mortality < 10%			0

* Environmental variation not correlated with survival or reproduction

5. Discussion

5.1 SIMULATION RESULTS

All three of the base models provide predictions that broadly agree with the current conservation status and observed population trends of each species, but the many assumptions and guessed parameters make the models preliminary at best. The models and data from adaptive management can give broad indications of the effects of different management actions such as the benefits of predator control but until the models are refined and the data improved, specific or fine-scale predictions or recommendations cannot be made using the models alone.

Many assumptions were made to simplify the models in the absence of other data. The models for all three species assumed that all females and males of breeding age were in the breeding pool each year. They also assumed that all new adults began breeding as soon as they reached the minimum breeding age, rather than new adults entering the breeding pool over a range of ages.

Sensitivity analyses showed that the models were very sensitive to uncertainty in some of the parameters that were assumed. The models also omitted factors such as density-dependence, which would impact on the populations if predator control increased population growth rates.

In addition, the potential effects of the scenarios modelled above need verifying on real populations. No data exist to quantify exactly how predator control increases survival, or what the effects are of poor food years and catastrophic weather events. Without these data, estimating how these scenarios interact is difficult. For example, what growth rates result if predator control is implemented during a poor food year? Despite these limitations, the strengths of the models lie in the ability to make comparisons between the relative outcomes of each of potential management scenarios and for the different species.

Banded dotterel

The base model predicted positive growth rates for banded dotterels, but the conservation status of this species is 'gradual decline'. However, the sensitivity analysis showed that the population trend for banded dotterels using this model could easily be sent into strong decline with only minor changes to one of a range of parameters. Because the model had several estimated parameters (e.g. adult and juvenile mortality rates, re-nesting rate), real population growth could be quite different from the model predictions. The banded dotterel was probably the most sensitive model out of the three species because their shorter life cycle and shorter generation time meant changes to vital rates quickly showed up in population size and growth. Predator control would clearly lower the risks of population decrease. The model also suggests the banded dotterel population could only withstand infrequent, low-level catastrophe years. If years of poor breeding or survival that result from factors such as food limitation were too frequent, the population would decline.

Although some parameters in the banded dotterel model were estimated, the values used for egg, chick and adult survival were in the lower range of those reported elsewhere (Keedwell 2002), thus survival could feasibly be higher than the model predicts. The model was most sensitive to increasing the age of first breeding by one year. VORTEX sets the age of first breeding at one specified year only, and although banded dotterels can breed at one year, there is probably a proportion that does not breed until the second year, which would strongly influence model outcomes.

Mean brood size, sex ratio, and the proportion of females successfully breeding all need to be better estimated to ensure more accurate model outputs. Sex ratio is limiting on the population if the proportion of males increases, but, given that male banded dotterels incubate overnight—the most vulnerable time for predation—the sex ratio is more likely to be biased towards females. Banded dotterels can nest outside of the riverbed areas and it is unknown whether breeding success and survival is better on river terraces or along coasts. If survival rates are different, there may be migration between populations in different habitats.

Black-fronted tern

This model predicted strong population declines despite using the most optimistic parameters for the majority of vital rates. The data used in this model are almost solely from research in the Ohau River and it is not clear whether the results from this river reflect survival rates for the whole population. However, anecdotal observations from Canterbury and counts from the Ashburton River suggest the inference is a valid one (C. O'Donnell, pers. comm.). Further research is necessary to verify whether these low breeding success rates are accurate. The model suggests that all catastrophe years are severely detrimental to the population and that predator control provides an option for reversing population decline. As with the other models, the proportion of males and females breeding was assumed, and clutch size and re-nest rate were estimated. Despite the assumptions in the model, the outcomes are similar to those projected in Keedwell (2002), which were based on a differently constructed model and input parameters.

Finsch's oystercatcher

The longer life span and generation time of this species relative to the 25-year simulation timeframe meant the model was less responsive to changes in parameters than for the other two species. This was reflected in the very low quasi-extinction probabilities even in the most negative scenarios. The Finsch's oystercatcher population is expanding (Sagar et al. 2002), but this is primarily due to the benefits provided by increased access to agricultural land. The model relies heavily on data collected from long-term studies on farmland, where survival may differ to that on riverbeds. As for banded dotterels, it is not clear how migration between the different habitats may affect the survival of populations breeding on the riverbeds. There were fewer assumptions made in these data because better data exist on all the vital rates except for survival between fledging and breeding age.

5.2 CURRENT BRAIDED RIVER PROJECTS

These models illustrate that many aspects of the ecology of bird species on braided rivers remain unknown or are not clearly quantified. Currently, adequate data do not exist to allow comprehensive PVA to be constructed to properly understand the dynamics of each species within the braided river habitat (e.g. Fig. 1). For those species where some data exist, much of this is incomplete or from small sample sizes. However, these preliminary results do show that predator control is essential for the ongoing survival of black-fronted terns. Although only three braided river species were modelled, they all responded similarly to simulations of management such as predator control, and to simulated threats such as lowered food supply or years of poor reproduction or survival. These models are far from comprehensive enough to predict what the best management strategies are, or to extrapolate results to the entire braided river community. However, they do provide further evidence about the likely beneficial effects of management of the braided river system.

Further research is needed to refine the models to make more accurate management predictions and to determine management regimes that are beneficial for the widest range of braided river species. Better data on a range of species and their interactions would enable the development of multi-species PVA models and provide information for management that is currently unattainable, e.g. guidelines for the intensity and frequency of predator control. Intensive adaptive management and research in forest systems determined the optimum pest control regimes that used minimum resources to have maximum effect on the target species, kokako (*Callaeas cinerea*) and other forest birds (Innes et al. 1999). A similar approach is necessary in the braided rivers. In addition to determining the best predator control regime, any braided river research also needs to incorporate management of factors such as weed encroachment and water loss, and to examine whether these management actions have differing impacts on the different taxa in the braided river community.

Currently, the majority of management and research projects carried out in the braided rivers are targeted at managing or researching individual species, rather than managing the habitat to enhance the survival of the species living within it. Examples of ongoing or recent braided river projects include:

- Department of Conservation. Black stilt captive management; trials of different predator control regimes; wrybill research examining survival and breeding success; and stoat research (Cook & Maloney 2001; Dowding & Elliott 2003; E. Murphy pers. comm.).
- Project River Recovery (DOC). Habitat preservation and restoration through weed removal; predator research projects; predator-proof fence studies; and wetland creation (Maloney et al. 1999; Keedwell & Sanders 2002; Sanders & Maloney 2002).
- Landcare Research. Dynamics between rabbits and predators in the grassland habitat surrounding riverbeds (Norbury & Heyward 1997; Norbury 2000; Norbury 2001).
- Universities. Student projects investigating aspects of the biology of predator and bird species (Pascoe 1995; Moss 1999; Wilson 2001; Keedwell 2002).
- Canterbury Regional Council. Willow planting and riverbed management.
- Investigations into potential effects of water abstraction for irrigation and damming in the lower Waitaki and the Rangitata (Boffa Miskell Ltd 2002).
- Development of a draft Braided River Recovery Plan by DOC (K. Brown, pers. comm.).

Many of these projects focus on the ecology and survival of one species only. In addition, some projects have been in conflict, for example, until recently in the Mackenzie Basin the Regional Council was actively planting willows while Project River Recovery was removing them. An integrated plan managing the whole braided river system as a habitat would be more effective than numerous plans managing the individual species within that habitat. There are numerous species at risk in braided rivers and most of them are facing the same threats. Pooling resources to manage the habitat collectively will provide greater benefits than a series of unconnected projects all focusing on different or conflicting aspects of braided river habitat and species.

5.3 INTEGRATED APPROACH TO MANAGING THREATENED BRAIDED RIVER COMMUNITIES

To ensure the survival of braided river species and their habitat, a collaborative research project is required. This will ensure that all research is working towards the same goal and will provide a better understanding of the braided river system for future management. The key objectives of such a project would be to increase current understanding of braided river community dynamics (see Fig. 1), to develop efficient predator control methods, and to develop habitat management to maximise survival of braided river species. I envisage a project that is jointly run by DOC (including the Black Stilt Team, Project River Recovery, and Science & Research Unit), NIWA, and Landcare Research, but includes substantial input from university researchers, post-doctoral students, and regional councils. The project would need to be long-term (i.e. a minimum of 8–10 years) and to seek outside funding from organisations such as the Foundation for Research, Science and Technology.

The project could be based primarily in the rivers of the Mackenzie Basin, but should include at least one lowland braided river in mid- or northern Canterbury. The research would need to be replicated at several rivers at each location and the following aspects should be monitored:

- Breeding success of a sample of the key animal species found at each location, e.g. banded dotterels, black-fronted terns, wrybills, stilts, robust grasshoppers, and lizards.
- Rabbit abundance.
- Predator abundance and guild composition.
- Food availability and water flows.

In addition, aspects of ecology that are currently unknown should be incorporated, e.g. increasing available knowledge of the ecology of the robust grasshopper, and filling in knowledge gaps on survival rates of river bird species like those identified in the preliminary models described earlier.

If the project is well replicated, the use of perturbations across sites and through time will provide crucial information to help both qualify and quantify the key relationships shown in Fig. 1. Examples of perturbations and research objectives include:

- Develop effective predator control systems.
- Determine what level and frequency of predator control is necessary to increase breeding success of a range of bird species.
- Manipulate predator abundance to determine effects on rabbit abundance and bird breeding success.
- Manipulate rabbit population levels and examine effects on predator abundance and bird breeding success.
- Determine whether food supply is a limiting factor for breeding birds in both controlled and uncontrolled rivers.
- Monitor long-term changes in abundance of all species to assess the effects of climate and season on population dynamics.
- Determine whether weed control is beneficial to bird populations.

The data collected throughout the project could be used in developing and refining PVA models, and the model outputs would provide constant feedback and evaluation of objectives. Ultimately, the research would lead to development of a comprehensive management plan for the braided rivers that clearly outlines best management practice for ensuring ongoing survival of braided river species.

Until a large-scale research project like this is under way, multi-species modelling of the braided river system will not be feasible. Current attempts at multi-species modelling will be guesstimating such a large range of parameters that the outputs will be unusable for any management purpose. The priority is to focus on implementing a large-scale research project that aims to fill in the knowledge gaps in the relationships demonstrated in Fig. 1 and to determine which are the key relationships that can be managed.

It is feasible to continue with the current system of single-species management and modelling in the braided rivers. However, the status of several species is becoming critical, and they will need intensive management similar to current management of the black stilt. For example, recent work suggests black-fronted terns urgently require management to prevent strong and continued decline (Keedwell 2002), and even common species such as banded dotterels are suspected of being in gradual decline (Hitchmough 2002) and may one day be in the same position as the threatened species of today. Resources are too scarce to enable intensive management projects focused on an array of individual species. A collaborative approach is the only way to ensure the habitat is managed to reduce the threat to all species and prevent further threatened braided river species from becoming endangered.

6. Conclusions and recommendations

This case study illustrates the incredible complexity of the braided river wildlife habitat and how further research is needed to begin to understand this complexity. Although the braided river habitat is fundamentally too complex to model completely and there are too many different taxa that are of concern, using modelling provides one tool for gaining an understanding of the relative impacts of threats, crucial gaps in knowledge (from the reviews and sensitivity analysis) and how they might vary among taxa. Better understanding of the system will enable better management and enhanced survival. Scenario modelling can help us to understand the relative impacts of threats and their interactions and to develop management recommendations, but caution is needed to ensure PVA does not over-simplify the system.

These models show that predator control is important for ongoing survival of threatened braided river species, and they also suggest that detrimental effects will occur if large-scale water abstraction or weed infestation leads to a loss of feeding and breeding habitat. Further research is essential for both determining the best management actions and also for understanding the effects and interactions of current and potential management. There is an urgent requirement for the implementation of a large scale research project to help understand the complexities of the braided river system. Development of an adaptive management research project with constant redefining of population models for a range of braided river taxa will go some way toward understanding braided river population dynamics and ensuring ongoing survival of both the taxa and habitat.

I recommend that a meeting is organised for relevant parties to discuss the potential for a collaborative research project. The meeting should consist of representatives from: DOC Science & Research Unit, Project River Recovery, Kaki Project, Landcare Research, NIWA, Canterbury Regional Council, and relevant university representatives. The key objective of the meeting would be to establish a committee to develop research objectives and to investigate funding sources for the research project.

7. Acknowledgements

Thanks to Colin O'Donnell, Doug Armstrong, Mark Sanders, Andy Grant and Brenda Greene for helpful comments on earlier versions of this report.

This report was part of DOC research investigation no. 3581.

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