Population Viability Analysis as a Tool in Wildlife Conservation Policy: With Reference to Australia

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ABSTRACT / Wildlife conservation policy for endangered species restoration follows a six-phase process. Population viability analysis (PVA) can play a major contributing role in four of these. PVA, as discussed here, is a technique where extinction vulnerabilities of small populations are estimated using computer simulation modeling. The benefits and limitations of using PVA in wildlife decision and policy processes are reviewed based on our direct experience. PVA permits decision makers to set time frames for management, estimate the required magnitude of restoration efforts, identify quantitative targets for species recovery, and select, implement, monitor, and evaluate management strategies. PVA is of greatest value for rare species policy and management. However, a limitation of PVA simulation models is that they are constrained by the amount of biological data available, and such data are difficult to obtain from small populations that are at immediate risk of extinction. These problems may be overcome with improved models and more data. Our experience shows benefits of PVA far outweigh its limitations, and applications of the approach are most useful when integrated with decision analysis and completed within an adaptive management philosophy. PVAs have been carried out for 14 Victorian species and less used elsewhere in Australia. Management and recovery plans are developed from these PVAs. We recommend that PVA be used to guide research programs, develop conservation strategies, and inform decision and policy making for both endangered and nonendangered species because it can significantly improve many aspects of natural resource policy and management.

The rapid and ongoing global loss of biodiversity is unprecedented (Wilson 1988). Nowhere is this loss more evident than in Australia (Kennedy 1990), one of the world's seven "megadiversity" countries (Economist 1988). Since the European settlement of Australia in 1788, there has been an extraordinary rate of extinction (Recher and Lim 1990) and ecosystem destruction (Saunders and others 1987). In Australia, biodiversity conservation is recognized as an integral element of sustainable development (Ecologically Sustainable Working Group 1991), and federal and state government policies embody biodiversity conservation language and aspirations [e.g., The National Conservation Strategy (Anon. 1982), State Conservation Strategy (Victorian Government 1987) and The Flora and Fauna Guarantee (Victorian Government 1988)].

If biodiversity conservation is to be achieved among growing and competing demands for natural resources in Australia and elsewhere, the sizes of viable populations and viable ecosystems must be estimated and policy prescriptions and management programs successfully instituted. Population viability analysis (PVA), a relatively new concept and technique, is a useful tool in meeting biodiversity conservation policy goals. Clark and others (1991, p. 1) define PVA, as we use it in this paper, as "a procedure that allows wildlife managers to simulate, using computer models, extinction processes that act on small populations of organisms, and therefore to assess their long term viability." Other PVA methods were

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listed by Shaffer (1981) and are discussed later. Computer simulation models employed in PVA use a range of input data including: (1) demographic attributes (e.g., age and sex-specific birth and death rates), (2) type of breeding system (e.g., monogamy, polygyny), (3) ecology (e.g., the amount, spatial distribution, and changes in the availability of habitat), and (4) genetics (e.g., the response of the population to inbreeding, which is typically determined by the genetic load of deleterious alleles). PVA simulation programs (e.g., VORTEX) then project forward through years, or other time increments, to determine the fate of each individual in the population at each stage of its life cycle (birth, dispersal, reproduction, migration, disease, death, etc.). Most life events, except aging, are probabilistic phenomena and the occurrence of events in the life of the simulated organism are determined by random sampling from probability distributions describing such events. These probabilities can be interdependent. For example, the probability of death can be a function of the genes inherited from the parents. PVA simulations track the fate of individuals through generations and provide an array of population statistics such as population size, sex ratio, age distribution, and genetic variation. The fate of the population is simulated many times to give a frequency distribution of extinction or survival. We have used PVA in a wide variety of cases. It is not a panacea, but it is highly useful in many instances to organize data and as a forecasting tool. Our direct experience over eight years has consistently shown that it has helped biologists, managers, and administrators looking at important parameters for small populations and appreciating the gravity of extinction threats. When PVAs are applied to situations where we have a lot of data over many years, their predictive capacity can be checked.

In this paper we: (1) review the concept of PVA and the methods to apply it, (2) introduce the wildlife conservation policy process and examine how it can be improved using PVA, and (3) assess the potential of PVA to improve wildlife and land-use policy, programs, and management, including a review of its strengths and limitations with reference to Australian examples. We seek to put PVA in the context of the policy process in a more comprehensive and innovative treatment than has thus far been published.

Population Viability Analysis: A Review

Estimating Viability of Populations

Modern conservation biology focuses on managing small populations, and this requires estimating their viability (or vulnerability to extinction) so that appropriate management action can be taken. Shaffer (1981) noted that a range of factors make populations vulnerable to extinction. These do not operate in isolation (Burgman and Neet 1989, Gilpin 1989). A classic example of the extinction process is the heath hen (*Tympanuchus cupido cupido*) in the northeastern United States. Initially, hunting and human-induced habitat degradation dramatically reduced the species' distribution and abundance. This decline continued because of fires, windstorms, and unfavorable seasonal conditions. Later a combination of disease, inbreeding depression, reduced sexual vigor, and an imbalanced sex ratio led to extinction (Simberloff 1986a). This example illustrates the complex interaction of both deterministic and stochastic (e.g., random) forces in the extinction of a species population. Further, it shows that demographic, environmental, genetic, and episodic catastrophes are important in extinction processes. Another factor, social dysfunction, may also contribute to the vulnerability of small populations (Allee 1949, Soulé 1983, Ferson and Burgman 1990).

Shaffer (1981) has listed five approaches to estimate the cumulative impacts of various chance events on small populations:

1. Experimentation, where isolated populations are monitored over time, and the fate of each population is documented.
2. Biogeographic analyses, including studies of island biogeography (e.g., MacArthur and Wilson 1967, see Shafer 1991 for a comprehensive review) and patch dynamics (Levin 1976, Pickett and Thompson 1978).
3. Theoretical and analytical models, including models of population growth and change (e.g., Richter-Dyn and Goel 1972, Keiding 1975, Wright and Hubbell 1983, Reed and others 1986, Ewens and others 1987, Phillippi and others 1987). For example, Goodman (1987) developed a model that estimated the likelihood of persistence of populations based on their size and fluctuations in growth rate (e.g., Belovsky 1987, Kinniard and O'Brien 1991).
4. Genetic principles, where the size of a population required to retain genetic diversity (i.e., fitness) is estimated (Lehmkuhl 1984, Davey 1989).
5. Simulation models, in which the fates of hypothetical populations are tracked in response to a suite of parameters (e.g., Salwasser and others 1984, Harris and others 1986, Marcot and Holthausen 1987, Grier and Barclay 1988, Doak 1989,

Lacy and others 1989, Seal and Lacy 1989, Seal and others 1989, Burgman and Gerard 1990, Ginzburg and others 1990, Lacy and Clark 1990).

Our discussion of PVA is limited to those techniques that employ computer simulation models.

There are advantages and disadvantages of each approach (Shaffer 1981, Simberloff 1988), although Burgman and others (1988) consider that island biogeography has little or no practical application to wildlife conservation mainly because theory tells us nothing about the fates of individual species. However, Shafer (1991) provides an alternative view of the value of island biogeography, showing its utility in the design of reserves. Thus, most or all of these approaches have the potential to improve the understanding of the biological processes leading to extinction and to help identify appropriate conservation strategies (Clark and others 1990, Shaffer 1990). For example, these five methods were applied to the endangered black-footed ferret (*Mustela nigripes*) by Groves and Clark (1986), Harris and others (1989), and Lacy and Clark (1989) to estimate population viability following three years of field data collection. Results of these analyses were used to set recovery targets and management needs.

Minimum Viable Populations (MVP) and Population Viability Analysis

Shaffer (1981) noted that the probability of survival of a population was high if its numbers could be maintained above a certain size. This was termed a "minimum viable population" (MVP). Shaffer (1981, p. 132) arbitrarily defined a MVP for any given species as one "having a 99% chance of remaining extant for 1000 years despite the foreseeable effects of demographic, environmental and genetic stochasticity, and natural catastrophes." Originally, it was implied that a population's MVP could be determined using PVA (Shaffer 1981). Today, it is understood there is no such thing as an MVP *per se*. Instead, populations become increasingly vulnerable to extinction the smaller they are (Shaffer 1990, Ferson and Burgman 1990).

Conceptually, MVP and PVA are intimately linked. PVA was developed to investigate the relative and cumulative impacts of various deterministic and stochastic influences on a given population (Lacy and others 1989). For example, a lack of genetic diversity, inbreeding depression, and reduced adaptability can lead to a decline in population size, a lower probability of finding a mate, and increased inbreeding and reduced genetic variability (Marcot and Holthausen 1987). Such a population will usually spiral toward extirpation in an "extinction vortex." Gilpin and Soulé (1986) described several types of vortices that reflect the different forms of interactions between stochastic factors. Brussard (1985), Seal and others (1989), and Thomas (1990) noted that the threshold size of a population needed for a species to remain above an extinction vortex would be an MVP.

Through the development of PVA techniques, it became apparent that the size of a viable population is not static (Usher 1987, Menges 1990) but will differ according to the particular species (Gilpin and Soulé 1986) and the circumstances impinging on that organism at any given time (Fowler and MacMahan 1982) and place (Grumbine 1990). This is because vulnerability to extinction will be, in part, related to demographic attributes and other characteristics (Howe and others 1991) and some of these will vary with environmental parameters that vary over time and space. For example, a changed disturbance regime such as forest logging will dictate a different population size necessary to ensure a given chance of persistence relative to an undisturbed forest. This was recognized by Belovsky (1987), who noted that his application of the model developed by Goodman (1987) did not determine an MVP but emphasized that the probability of persistence would increase with population size. PVA may indicate that a particular population is not viable, although this does not imply that attempts to conserve it should be abandoned (Soulé 1987, Thomas 1990). For example, Lacy and Clark (1990) used PVA to examine the vulnerability of a small population of the eastern barred bandicoot (*Perameles gunnii*) in western Victoria, Australia, and concluded that it had a 91% probability of extinction within 15 years unless active management were undertaken. A nonviable population is one in urgent need of management to reduce its vulnerability to extinction (Kinniard and O'Brien 1991).

In summary, an application of PVA may allow the identification of the population size necessary for the survival of a given species, with a given probability, over a particular time span (e.g., 100 years), in a particular place, and under certain conditions (Ginzburg and others 1990).

Examples When PVA Has Been Used

PVA has been applied in North America, Australia, Asia, Africa, and Europe (Table 1). Researchers, managers, and administrators are coming to appreciate the method and use it (Mace and Lande 1991). In North America, PVA has been used in studies of a wide range of species. Some of the most notable have

Table 1. Examples of the use of population viability assessment

Species	Geographic range	Primary cause of risk	References
Grizzly bear *Ursus arctos horribilis*	NW No. America	Human mortality, habitat loss	Schaffer 1983, Suchy and others 1985
Red-cockaded woodpecker *Picoides borealis*	SE USA	Habitat loss due to logging	US Fish and Wildlife Service 1985
Florida panther *Felis concolor coryi*	So. Florida, USA	Road kills, inbreeding, lack of habitat	Seal and Lacy 1989
Puerto Rican parrot *Amazona vittata*	Puerto Rico, USA	Low fecundity, hurricanes	Lacy and others, 1989
Sumatran rhino *Dicerorhinus sumatrensis*	Southeast Asia	Timber harvesting	Maguire and others, 1987
Javin rhino *Rhinoceros sondaicus*	Java, Indonesia Viet Nam	Poaching, disease, inbreeding	Seal and Foose 1989
Eastern barred bandicoot *Perameles gunnii*	Victoria, Australia	Road kills, cat kills	Lacy and Clark 1990, Maguire and others 1990
Northern spotted owl *Strix occidentalis caurina*	NW USA	Habitat loss	Lande 1988, Marcot and Holthausen 1987, Doak 1989, Thomas and others 1990
Bay checkerspot butterfly *Euphydryas editha bayensis*	California, USA	Habitat loss	Murphy and others 1990
Key deer *Odocoileus virginianus clavium*	Florida Keys, USA	Road kills, hurricanes, habitat loss	Seal and Lacy 1990
Black-footed ferret *Mustela nigripes*	Central USA	Loss of prey	Harris and others 1989
Bighorn sheep *Ovis canadensis*	Western USA	Habitat loss, grazing competition	Berger 1990
Furbish's lousewort *Pedicularis furbishae*	NE USA, SE Canada	Habitat loss, land-use problems in watersheds	Merges 1990
Gopher tortoise *Gopherus polyphemus*	SE USA	Habitat loss	Cox 1988
Leadbeater's possum *Gymnobelideus leadbeateri*	Central Victoria, Australia	Logging, habitat loss	Thomas and Lindenmayer 1990, Lindenmayer and others 1991
Orange-bellied parrot *Neophema chrysogaster*	Victoria Tasmania	Habitat loss, coastal development	Brown and others 1990[a]
Long footed potoroo *Potorous longipes*	NE Victoria, Australia	Prescribed burning, logging, fragmentation	Saxon and others 1990[a]
Helmeted honeyeater *Lichenostomus melanops cassidix*	Central Victoria Australia	Habitat loss, competition	Menkhorst and others 1990[a]
Mountain pygmy possum *Burramys parvus*	Central Victoria No. NSW Australia	Ski resort development	Mansergh and Scotts 1990[a]
Cod *Gadus morhua*	Atlantic Ocean	Overexploitation	Ginzburg and others 1990
Tana River crested mangabey *Cercocebus galeritus galeritus*	Kenya, Africa	Habitat loss, agricultural development	Kinnaird and O'Brien 1991

[a](In Clark and others 1991).

been the grizzly bear (*Ursus arctos horribilis;* Shaffer 1981, 1983, Shaffer and Samson 1985, Suchy and others 1985) and the northern spotted owl (*Strix occidentalis caurina;* Marcot and Holthausen 1987, Lande 1988, Doak 1989, Thomas and others 1990). Other North American studies include PVA of plants, invertebrates, and representative species of all major vertebrate groups (Table 1).

PVA has been used only recently in Australia on the eastern barred bandicoot (Lacy and Clark 1990), greater glider (*Petauroides volans;* Possingham and others 1991), powerful owl (*Ninox strenua;* Possingham and others 1991), Leadbeater's possum (*Gymnobelideus leadbeateri;* Lindenmayer and others 1991), brush-tailed rock wallaby (*Petrogale pencilliata;* Hill 1991), orange-bellied parrot (*Neophema chrysogaster*),

long-footed potoroo (*Potorous longipes*), helmeted honeyeater (*Lichenostomus melanops cassidix*), and mountain pygmy possum (*Burramys parvus;* Clark and others 1991). Other Australian studies were described by Burgman and Lamont (1992).

Wildlife Conservation Policy and Management

Biodiversity and endangered species conservation are both technical and policy challenges. The present biodiversity crisis stems from the failure of past natural resource, economic, and human population policies. All natural resource and endangered species conservation policies undergo predictable sequential phases (Kellert and Clark 1991). PVA is directly relevant to several of these phases and can improve the overall policy process if utilized in appropriate ways and within pertinent phases.

The theoretical perspective of the policy process used here follows Lasswell (1971), Brewer and deLeon (1983), and Clark (1992). Policy processes, whether in the management of biodiversity or other problems, are dynamic, including many actions by many actors, each with potentially different interests, roles, information, and perspectives. The policy process is marked by predictable phases that are populated by somewhat different agencies and interest groups with different analytical and political agendas. The policy process is often not optimized for the system as a whole, because no one is in control of the overall system and because it is not always possible to determine optimality in any specific application (Ascher and Healy 1990).

The policy process can be divided into six phases (Brewer and deLeon 1983) and these can be seen clearly in attempts to manage biodiversity, endangered species, and natural resources. The phases are:

1. initiation: a problem is perceived, identified, and placed on the public agenda,
2. estimation: the problem is defined in more detail using expert analysis and technical considerations,
3. selection: a policy response to the problem is formulated, debated, and authorized by a legitimate source,
4. implementation: a program is developed and applied to the problem,
5. evaluation: ex post appraisal of the implementation effort and the original policy formulation, and
6. termination: discontinuation, revision, or succession of policy.

PVA can be used to improve all phases of the policy process, especially estimation, selection, implementation, and evaluation. The technique permits policy makers to understand extinction as the result of a complex sequence of deterministic and stochastic events that may be prevented through the application of appropriate policy and management. Since rare, vulnerable, and endangered species occur in many habitats and ecosystems, PVA can be useful to foresters, park managers, and a wide range of other people.

PVA is integral to the estimation phase, because it enables estimation of the likelihood of extinction and provides a basis for setting quantitative targets for species restoration. A host of management options and their expected costs and benefits can then be explored. PVA produces numerical targets in terms of numbers of the individuals and populations needed to prevent significant population decline or even extinction. These targets are usually given in terms of a probability statement over 25, 50, 100, or more years.

PVA is central to the selection phase because this is where the relative merits of various programs can be compared and a decision is taken on a specific management course. Decision making can be made much easier by relying on PVA.

PVA is essential to the implementation phase because once a recovery target has been set, the size, resource, and organizational requirements of the program can be estimated and instigated. PVA encourages a realistic assessment of the personnel, financial, technical, and institutional commitments required to restore and maintain a population.

PVA can be used in the evaluation phase to measure the performance of the restoration program and determine if policies, programs, and recovery targets have been met. This is possible because PVA estimates numerical targets in terms of population sizes and numbers of populations needed to prevent extinction. If these targets are met, the program can be evaluated as successful. For example, Clark and Harvey (1988) evaluated an endangered species recovery program where a host of organizational problems significantly constrained the restoration effort, in part because PVA was not used early on in estimation and selection.

In summary, PVA can be crucial in the process of policy formulation, implementation, and appraisal for endangered species restoration and biodiversity conservation. Management can be significantly improved if PVA is explicitly used in these policy and programmatic processes.

Merits and Limitations of PVA

The following discussion focuses on the relative strengths and weaknesses of PVA as a method for improving natural resource management and policy. These strengths and limitations will have different ramifications according to the policy phase in which PVA is applied and the purpose for which it is applied.

Strengths of Population Viability Analysis

It produces an explicit statement of the ecology of the species and identifies missing data. PVA requires a review of the ecology of the species including demographics, environmental conditions, genetics, and catastrophes. This leads to explicit statements about what is known about a species and reveals those attributes for which values must be estimated. It also forces biologists and decision makers to interpret their decision making styles rigorously using a formal framework. This assessment is an important first step in formulating strategies and objectives for research, conservation, and management. Once weaknesses and gaps in the data are identified, research can be planned to acquire key information so that subsequent PVAs can be based on a more complete data set.

It synthesizes interacting factors and identifies trends in population behavior. PVA produces an estimate of the relative impacts of a number of interacting factors on extinction. Estimates of the impacts of these factors would be difficult or impossible without PVA. These estimates are important because: (1) the dynamics of populations may change according to size and circumstance (Seal and others 1989, Berger 1990, Lindenmayer and others 1991), and (2) a plethora of factors influence population dynamics and behavior.

PVA allows trends in population behavior to be identified and quantified. Factors that may exert influence on such trends can be determined. Key factors can be addressed, such as: (1) the relationship between population size and population stability, and (2) the population size at which stochastic events become important and those factors that are most critical. An understanding of the processes leading to extinction can also have an important instructional role to both biologists and policymakers (Simberloff 1986a, Seal and others 1989, Clark and others 1990).

Trends for declining populations can be identified early and the application of PVA may allow a preventive management philosophy, under which species are managed before they become endangered. This is useful because attempts to conserve small and declining populations can be expensive (Clark and Harvey 1988), difficult to organize (Clark and Westrum 1989), and prone to failure (Griffith and others 1989, Clark and Cragun 1991).

It identifies processes threatening to the species. PVA may identify previously unknown factors or anticipate the effects of known factors that threaten population viability (Lacy and Clark 1990). For example, a PVA of the Puerto Rican parrot (*Amazona vitatta*) illustrated that a catastrophe could decimate wild populations of the species (Lacy and others 1989). A hurricane struck Puerto Rico soon after the PVA was completed, killing approximately half the birds in the wild flock, but the hurricane hit before management changes were made that reflected the new understanding of catastrophic risks.

The State Conservation Strategy of Victoria (Victorian Government 1987, p. 31) states that it "will control and manage any activities threatening terrestrial plants and animals." Thus, the application of PVA can qualify and quantify the impact of any particular threatening process and assist governments in meeting their aims to preserve biodiversity. PVA can also reveal if current policy and programs are meeting stated aims.

It can be used in defining "minimum critical area" and designing reserves. PVA has implications for determining the "minimum critical area," i.e., the size of an area needed to support a viable population of a given species (Soulé and Simberloff 1986, Conner 1988, Davey 1989). Wilcox (1984) in Shafer (1991, p. 104) proposed a sequence of steps for defining such critical areas, *viz.*: (1) target taxon, (2) minimum viable population, (3) habitat requirements, and (4) minimum critical area requirements. These important links between PVA and minimum critical areas are predicated on an understanding of several factors, including: (1) the habitat and area requirements of the species, (2) the spatial and temporal availability of suitable habitat, and (3) the effectiveness of remaining habitats (e.g., wildlife corridors) in contributing to minimum critical areas (Lindenmayer and others 1991). Currently, the habitat requirements of most species are poorly understood (Simberloff 1986b), as are the area requirements for viable populations (Diamond 1978, Usher 1986), but PVA can aid in highlighting the need for such information. PVA may also be used in tandem with a range of other procedures to design and assess the adequacy of nature reserves (Wright and Hubbell 1983, Grumbine 1990, Ecologically Sustainable Development Working Group 1991) and to determine the impacts of various land uses on conservation values (Shaffer 1981, Reed and others 1988, Thomas 1990).

It can clarify management needs. PVA may play a central role in management planning, aid the implementation of existing policy, and indicate that new policy and management are needed. The use of PVA as a preventive management tool is being considered in Australia by the Resource Assessment Commission (1991), Australian National Parks and Wildlife Service (Hill 1991), and Ecologically Sustainable Working Group (1991). In this context, the Resource Assessment Commission (1991, p. N11) states that "estimates of the size of viable populations and the risks of extinction under multiple-use forestry practices ought to be an essential part of conservation planning." Similarly, Mace and Lande (1991) recommended using PVA to classify threatened species into "risk" categories.

It can enhance on-ground management and decision making. PVA must be integrated with, and not substituted for, other approaches to wildlife management and natural resource conservation. The technique should be an adjunct to detailed studies of key taxa including those potentially threatened by the exploitation of natural resources (Murphy and others 1990). These studies need to be carefully targeted to test hypotheses and quantify results. Simberloff (1988, p. 50) correctly noted that "sound conservation science must be founded on autecological studies of individual systems." This view was supported by Burgman and others (1988) in a detailed review of the use of extinction models. Such an approach is presently being used in several Australian endangered species restoration efforts (e.g., eastern barred bandicoot; Clark and Seebeck 1990).

The use of PVA, data collection, and monitoring and evaluation of management actions are closely interlinked (see Arnold and others 1990). These tasks need to be integrated, maintained, and regularly updated in an adaptive management approach or management by experiment and feedback (Holling 1973, 1978, Clark and Seebeck 1990, Clark and others 1990), with each facet of such a framework providing feedback to the others (Clark 1989, Clark and Harvey 1988). This will allow more responsive and more effective conservation and management (Casey and others 1990). The needs for such management were highlighted by Holling (1973, p. 21), who recognized a need to "devise systems that can absorb and accommodate future events in whatever unexpected form they may take."

Such adaptive management is presently being applied in efforts to conserve the eastern barred bandicoot in western Victoria (Arnold and others 1990). Marcot and Holthausen (1987) recommended adoption of regularly reevaluated management procedures for the conservation of the northern spotted owl (see Holling 1978). Clark and Harvey (1988) noted the value of a similar approach for the management of the remaining populations of the black-footed ferret. Adaptive management could also be accompanied by attempts to develop a standardized procedure for the use of PVA (Salwasser and others 1984, Mace and Lande 1991).

The likely consequences of management actions can be estimated using PVA (Shaffer 1990, Maguire and others 1990), and these estimates can be made available to land managers. A useful example is provided by Thomas and others (1990) in an investigation of the probability of extinction of the northern spotted owl. They demonstrated that proposed management strategies were inadequate to conserve the species and recommended new ones more likely to improve the probability of survival. Furthermore, the study identified a need for further studies of the dispersal behavior of the northern spotted owl.

PVA should be coupled with decision theory (see Maguire 1991) to assist land managers in choosing among numerous options (Salwasser and others 1984, Maguire 1986, 1989, Maguire and others 1987, 1990, Gilpin 1989, Soulé 1989, Marcot in press). Several examples illustrate the value of combining PVA and decision analysis. Decision analysis is a technique that lays out management options in a branching treelike arrangement. This approach permits systematic examination and comparison of expected benefits and costs among all management options. Maguire and others (1987) integrated PVA and decision analysis to explore management options for Sumatran rhino (*Dicerorhinus sumatrensis*) conservation. Similar analyses have been completed for the black-footed ferret (Maguire 1989), the eastern barred bandicoot (Maguire and others 1990), and the Concho water snake (*Nerodia harteri paucimaculoota*) (Soulé 1989). Maguire and Lacy (1990) used decision analysis in studies of the captive management of tigers (*Panthera tigris*).

Both PVA and decision analysis can be useful in planning conservation strategies. This can be important, particularly given the cost and logistic requirements for species recovery programs (Clark and Harvey 1988, Clark and others 1989, Clark and Westrum 1989, Murphy and others 1990) and the limited resources typically allocated for nature conservation. Thus PVA, in tandem with decision analysis, can assist in ranking tasks and allocating scarce resources (Soulé 1989, Maguire and others 1990). Without PVA, decision and policy makers and managers have few conceptual, explicit, and data-based frameworks by which

to assess the impacts of land-use decisions on the risks of extinction (Murphy and others 1990). Therefore, the use of PVA may reduce the potential for inappropriate, subjective, or partisan assessments of population vulnerability (Mace and Lande 1991).

It has application in species recovery, reintroduction, and captive breeding programs. PVA can be used to define a target number of animals for species recovery (Hill 1991), reintroduction, and captive breeding (Clark and others 1991). Lacy and Clark (1990) and Maguire and others (1990) illustrated this for the eastern barred bandicoot in western Victoria. In other cases, Seal and Lacy (1989), Lacy and others (1989), and Maguire and Lacy (1990) used PVA and decision analysis to explore the effectiveness of reintroduction and captive breeding programs for various endangered species. Thus, applications of PVA may be important in developing endangered species recovery programs, such as those required under the Australian National Strategy for the conservation of species and habitats threatened with extinction (Australian National Parks and Wildlife Service 1989) and the Flora and Fauna Guarantee (Victorian Government 1988). For example, PVA has been applied in the development of a species recovery program for the brush-tailed rock wallaby, *Petrogale pencilliata* (Hill 1991).

In summary, application of PVA can provide a suite of potential advantages for endangered species and natural resource management. Among these are an improved approach for research, species recovery and management, identifying endangering processes, setting and monitoring policy, making decisions, and taking management actions. PVA is most effective when coupled with decision analysis and applied within an adaptive management framework.

Limitations of Population Viability Analysis

It is a data-intensive technique. The more data the better for PVAs. Often such data are unavailable or incomplete (Grumbine 1990), in particular those for rare and endangered organisms that may urgently require PVA. Estimation of the values for modeled parameters requires experience and must be based on a detailed knowledge of the biology of a species or attributes of related taxa (Simberloff 1988). PVA may be very time consuming, as there may be a myriad of parameters and many values within each parameter that need to be tested. It may take time to identify those factors that are important and therefore warrant thorough and further investigation.

Some people view the paucity of detailed biological, ecological, and genetic data for many taxa as a limitation of the technique (e.g., Davey and Norton 1990). More accurate estimates will be predicated on the collection of more comprehensive basic biological data.

It does not examine the functional role of taxa. PVAs focus on the probability of extinction of a species but they do not consider the functional role of species, or the interdependence of organisms, in ecosystems (Conner 1988). Population reduction or loss can have major implications for important biological and ecological functions in ecosystems, such as pollination, seed dispersal, and nutrient cycling. On this basis, Conner (1988, p. 82) believed that populations of organisms must be conserved in "sufficient abundance to be ecologically functional in their community."

However, the estimation of ecologically functional populations is presently not possible (Conner 1988). PVA is typically a single species approach to wildlife conservation (Soulé 1987, Shafer 1991). Ecosystem viability may be indicated by the viability of bioindicator, keystone, umbrella, or mobile-link species (see Kohm 1991). Therefore, PVA may be most effective if focused on these species (Soulé 1987, Thomas 1990), but few data exist on such organisms (Ecologically Sustainable Development Working Group 1991). This approach assumes that the conservation of such organisms will also result in the conservation of a significant proportion of other species. Soulé (1987), Soulé and Kohm (1989), and Norton and Lindenmayer (1991) further discuss the value of using various types of indicator species to conserve biodiversity.

It simplifies all the interactions between parameters. PVA may not be able to incorporate all the potentially synergistic impacts of factors that influence actual populations (Soulé 1987, Lande 1988, Mace and Lande 1991). For example, changes in carrying capacity resulting from the loss of trees with hollows will reduce the area of suitable habitat available for Leadbeater's possum (Lindenmayer and others 1990). This will, in turn, increase mortality among dispersing animals and further isolate remaining subpopulations (Lindenmayer and others 1990). The incorporation of such synergistic interactions between parameters would provide more accurate estimates of the vulnerability of populations. This could be achieved by modifying the computer programs used in PVA. For example, a new version of the simulation model VORTEX (Lacy unpublished) as well as the programs FORPOP (Possingham and others 1991), ALEX (Lindenmayer and Possingham 1991), and RAMAS/space (Akcakaya and Ferson 1990) can be used to investigate the validity of metapopulations and subpopula-

tions and the importance of exchanges of individuals between such groups.

It is a simplification of population dynamics. Population dynamics are more complex than can be simulated by computers. Computer programs necessarily include a large number of assumptions (Lindenmayer and others 1991) and simplistically model the responses of organisms to catastrophes and environmental variation. Thus, PVA can provide only a relatively simple estimation of the actual dynamics of wild populations, and caution should be used when interpreting and applying the results of PVA. PVA will, however, usually reflect general trends in population behavior (Soulé 1987).

More reliable estimates of population viability may be obtained with new, more detailed and comprehensive models together with better input data (Soulé 1987). Thus, it will be appropriate to repeat and upgrade a PVA for a particular taxon when new data and models become available. This is part of the adaptive management process described above.

It is not a generic model applicable for all species. A suite of PVA programs exist. Some of these include: GRIER (Grier 1980a), SPGPC (Grier 1980a,b, Grier and Barclay 1988), GAPPS (Harris and others 1986), POPDYN (Cox 1988), SIMPOP (Lacy and others 1989, Seal and Lacy 1989, Lacy and Clark 1990), VORTEX (Seal and Lacy 1990, Clark and others 1991), RAMAS (Ferson and others 1988 in Ginzburg and others 1990, p. 65), RAMAS/age (Ferson and Akcakaya 1990), RAMAS/space (Akcakaya and Ferson 1990), FORPOP (Possingham and others 1991), and ALEX (Lindenmayer and Possingham 1991).

Each of these models has inherent strengths and limitations, some have unique features, and some are better suited to PVA analysis of particular taxa than others. For example, Samson (in Simberloff 1988, p. 494) noted that the structure of the model POPDYN, which was applied in a PVA of the gopher tortoise (*Gopherus polyphemus*) (Cox 1988), would preclude its use from studies of species such as the northern spotted owl that do not breed annually. In other examples, the models FORPOP (Possingham and others 1991), ALEX (Lindenmayer and Possingham 1991), and the RAMAS family of programs simulate population dynamics within and between various patches of suitable habitat but take no account of genetics as a factor contributing to extinction.

Values for many parameters that influence population dynamics, particularly life-history and demographic attributes, are species-specific (Thomas 1990). Thus, estimates of vulnerability and viable population size will differ for each species and each location (Newmark 1986 in Soulé 1987, p. 175, Belovsky 1987, Soulé 1987) and the modeling procedure used (Kinniard and O'Brien 1991). This was shown by Belovsky (1987), who demonstrated that the probability of extinction of mammals in residual montane environments varied according to a range of factors, including body size. These findings also indicate that not all species in a given area face that same probability of extinction (Burgman and others 1988) and that strategies appropriate for the conservation of one species may be inadequate for others (Doak 1989). Hence, PVAs will need to be completed for each species of concern (Soulé 1987), although some of the work required may be reduced by completing PVAs for bio-indicators, keystone species, and umbrella species.

Most models for PVA will need to be modified to meet the particular requirements of a given case study. For some studies, new models may need to be developed, whereas in others several models may be used simultaneously. The choice of a program is dependent on the objectives of the study together with an understanding of the strengths, limitations, and assumptions of the model (Simberloff 1988). Because of the unique problems inherent in many cases, we consider that it is unlikely that a generic model can be developed (Lindenmayer and others 1991). However, this does not detract from the value of PVA or the concepts and theory which underpin the approach.

Conclusions

Improving wildlife conservation and policy is, in part, dependent on using appropriate concepts and applied tools, which permit: (1) early recognition of problems (initiation of the wildlife policy process), (2) accurate estimation of the size or extent of those problems, (3) selection of an appropriate solution, (4) successful implementation of solutions through various programs, and (5) continuous evaluation of the original problem as well as the effectiveness and adequacy of implementation efforts. PVA can aid in all these phases of the restoration of endangered populations and in preventing currently somewhat larger populations from being reduced and eventually endangered. In turn, PVA can help decision and policy makers understand the extinction process in general and, it is hoped, conclude that large-scale biodiversity conservation is the best policy for conserving a nation's biological wealth (see Kohm 1991).

PVA adds a new and important dimension to the study, utilization, and management of natural resources. Applications of the technique can: (1) yield

information on trends in population behavior, (2) identify and assess the impacts of factors that influence the viability of populations, and (3) provide an objective and explicit framework for assessing extinction risks, research, decision making, and wildlife and land use management. PVA will be most effective if applied within an adaptive management framework.

PVA has a number of weaknesses. In particular, an array of assumptions underpin its use (Lindenmayer and others 1991). These problems are often exacerbated by a lack of detailed biological information for target species, although this is not a weakness of the technique *per se*. Many of these apparent limitations can be overcome with more detailed biological research together with efforts to improve and further refine computer simulation models. There is merit in future attempts to upgrade models for use in PVA because it is one of the few techniques capable of assessing the combined effects of various factors and management options on population viability. This is important given the anticipated rise in the number of species facing extinction (Recher and Lim 1990) and growing pressure to exploit natural resources (Davey and Norton 1990).

In summary, we consider that the benefits of PVA far outweigh the limitations of the technique and recommend that the approach be used in improving policies and programs aimed at managing natural environments and their biota.

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