This is a preprint of **Akçakaya H.R. and P. Sjögren-Gulve. 2000. Population viability analysis in conservation planning: an overview.** ***Ecological Bulletins*** **48:9-21.**

Population viability analyses in conservation planning: an overview

H. Reşit Akçakaya and Per Sjögren-Gulve

Population viability analysis (PVA) is a collection of methods for evaluating the threats faced by populations of species, their risks of extinction or decline, and their chances for recovery, based on species-specific data and models. Compared to other alternatives for making conservation decisions, PVA provides a rigorous methodology that can use different types of data, a way to incorporate uncertainties and natural variabilities, and products or predictions that are relevant to conservation goals. The disadvantages of PVA include its single-species focus and requirements for data that may not be available for many species. PVAs are most useful when they address a specific question involving a focal (e.g., threatened, indicator, sensitive, or umbrella) species, when their level of detail is consistent with the available data, and when they focus on relative (i.e., comparative) rather than absolute results, and risks of decline rather than extinction. This overview provides guidelines for choosing a PVA model among three categories, from data-intensive individual-based population models to simple occupancy metapopulation models.

H. R. Akçakaya (resit@ramas.com), Applied Biomathematics, 100 North Country Road, Setauket, NY 11733, USA. — Per Sjögren-Gulve (per.sjogren-gulve@environ.se), Dept of Conservation Biology and Genetics, Evolutionary Biology Centre, Uppsala Univ., Norbyvägen 18D, SE-752 36 Uppsala, Sweden (present address: Swedish Environmental Protection Agency, SE-106 48 Stockholm, Sweden)

Practical problems in conservation planning and wildlife management are increasingly phrased in terms of questions about the viability of threatened or indicator species. Because of the nature of these questions, and the natural variation and uncertainty inherent in ecological data, risk-based methods are appropriate for population viability analyses (PVAs). Viability of a species in a given geographic region is often expressed as its risk of extinction or decline, expected time to extinction, or chance of recovery. PVA models attempt to predict such measures of viability based on demographic data (such as censuses, mark-recapture studies, surveys and observations of reproduction and dispersal events, presence/absence data) and habitat data.

Although conservation planning is often done at the ecosystem or landscape level (see *Alternative methods* below), several factors highlight PVA as a central tool for conservation assessments. These factors include the needs of threatened species, recent developments in the use of indicator species (Fleishman et al. 2000), and the potential for rigorous risk assessments using a variety of data types. The aim of this paper is to give a short description of population viability analysis, discuss its advantages and limitations in conservation planning, compare it with other methods of assessment, and discuss the most useful approaches to PVA. We begin by reviewing a number of alternative methods for conservation assessments that provide a context for evaluation of the PVA approaches. We then present a short introduction to PVA and its three main categories of models, and some guidelines for choosing a model. Subsequently we discuss the limitations and advantages of PVA, and end with some recommendations of how to make the method most useful.

Alternative methods for conservation assessments

A number of quantitative methods for assessment are used in conservation planning. These methods form the context in which we evaluate the PVA approach.

Reserve selection algorithms

These methods are designed to select nature reserves, i.e., choose a subset of available habitat patches for protection (e.g., Margules et al. 1988, Pressey et al. 1993, 1996, Pimm and Lawton 1998, Possingham et al. 2000), often using criteria that maximize the number of species included in the reserves. The algorithms are usually based on the presence/absence of species in each habitat patch, and do not explicitly consider the viability of species in habitat patches, or the interaction among populations in different habitat patches (e.g., metapopulation dynamics). The presence of a species in a particular patch does not necessarily indicate that the patch can support a viable population, or that the population will persist even if the neighboring habitat patches are not included in the reserve system. Nevertheless, these methods are useful if the only available data are occurrences.

Habitat suitability models

The aim of habitat suitability (HS) models is to predict a species' response to its environment. The response is usually the occurrence or abundance of the species at a certain locality or the carrying capacity of the habitat. The statistical procedures to obtain the HS model (such as multiple logistic regression) use species occurrence or abundance at each location as the dependent variable and the habitat characteristics as the set of predictive variables (see several chapters of Verner et al. 1986; Straw et al. 1986, Mills et al. 1993, Pearce et al. 1994, Sjögren-Gulve 1994, Fleishman et al. 2000). Most statistical methods require both presence and absence data, while others (such as "climatic envelopes") require only presence data (Elith 2000).

One advantage of habitat suitability models is that they are statistically rigorous and can be validated. They can also be used to explore effects of environmental changes on habitat patch suitability, and to calculate probabilities of species occurrence (see Sjögren-Gulve and Hanski 2000). Another advantage is that they can use all the available habitat data (including point observations, GIS data of various types, satellite images, digital elevation maps, etc.), and incorporate nonlinearities of, and interactions among habitat variables. The main disadvantage of habitat suitability models is that suitability is only one component of viability, which also depends on demographic factors. However, habitat suitability models can be integrated with PVA models to identify habitat patches and characterize the spatial structure of metapopulations (e.g., Akçakaya and Atwood 1997).

Gap analysis

A "gap" is the lack of representation or inadequate representation of a plant community or animal species in areas managed primarily for natural values. Identification of a gap indicates potential risk of extinction or extirpation unless changes are made by land stewards in the management status of the element. Gap Analysis Program (GAP) is a process widely used by state agencies in the USA to identify such gaps. The process involves overlaying (intersecting) land cover and species distribution (element occurrence) coverages with the coverage of areas protected or managed primarily for natural values (Scott et al. 1993, Kiester et al. 1996).

The advantages of gap analysis are its widespread use, and its use of all available geographic information. The major disadvantage of gap analysis is that it is not based on population dynamics, and does not utilize available demographic information. Hence, it does not provide a direct measure of viability. Another disadvantage is that it often relies on species-habitat associations and species distribution patterns that are not rigorously determined.

Rule-based and score-based methods for prioritization

These are algorithms for categorizing species in terms of the threat they face (IUCN 1994, Millsap et al. 1990, Master 1991). For example, IUCN (1994) rules assign species to categories of "Critically endangered", "Endangered", "Vulnerable" and "Lower risk", based on information available on abundance, distribution, population trends, population fragmentation, and extinction risk estimates. They are used widely by international conservation organizations. This method works as a way of classifying threatened species by the risks they face, even if there is little information. For example, IUCN rules are based on many aspects of habitat and demography, but the method is not dependent on a full set of information. Species can often be classified even if information is available only on one aspect (e.g., abundance). IUCN rules can also use PVA results and can explicitly incorporate uncertainties in data (see Akçakaya et al. 2000). One disadvantage of these methods is that the rules and thresholds are necessarily arbitrary. As a result, ranks or classifications of the same set of species with different rule sets may have low correlation (Burgman et al. 1999).

Estimating extinction probability from sighting data

These methods also try to estimate probabilities of extinction, but they work from a record of sightings, rather than the more detailed demographic information that PVA uses (Solow 1993). The quantity estimated with these methods is the probability that the species is already extinct, rather than the probability that it will become extinct by a given future date. Although the meaning of the estimated probability does not exactly coincide with future viability, these methods are useful when the only available data are sightings.

Landscape indices

These include metrics such as patch size distribution, fractal dimension, shape index, and other descriptions of spatial structure, which are calculated from digital raster maps of habitat types in the landscape (for example, the FragStats program; McGarigal and Marks 1995). Although many of these indices may be informative in particular situations, there are three major problems with their general application to conservation issues. First, the objects that form the structure (e.g., patches of forest habitat) are often arbitrarily defined. Second, the spatial scale is often arbitrarily selected. Both the definition of "patch" and the selection of spatial scale require a specific phenomenon or focal species. Third, and most important, the relationship between these metrics and conservation goals may be weak or very restricted (applying to specific populations in specific landscapes).

Other types of landscape indices involve connectivity and dispersal, which are also part of the metapopulation approach. However, these metrics alone may also be ambiguous as conservation goals. For instance, increased dispersal usually increases viability, but not always (see Stacey et al. [1997] and Beier and Noss [1998] for reviews). Even when it does, increasing dispersal may not be the best option (cost may be too high and/or increase in viability may be too low, compared to options related to other aspects such as carrying capacity, fecundity, or survival). The best way to make such metrics relevant to conservation is to use them in metapopulation models and estimate the dispersal parameters of these models.

Ecosystem-based methods

These methods deal with more than target or focal species. Some attempt to consider multiple criteria, dealing with a vast array of issues and factors from fungi species, prescribed fires, tribal rights and tourism, to endangered species and jobs. The assessments are based on various methods, including point scoring sheets, expert opinion, rating systems, etc. Others focus on "emergent" properties such as nutrient cycling or various measures of species diversity.

The clear advantage and appeal of the ecosystem approach is its comprehensiveness. The ultimate goal of most conservation efforts is the preservation of well-functioning, representative, natural ecosystems. Even species-specific methods such as PVA are often used as parts of this overall goal (e.g., by focusing on indicator, sensitive, or umbrella species).

The main disadvantage of the ecosystem approach is the complexity of interactions among species and our lack of understanding of community and ecosystem dynamics. As our understanding increases, conservation practices will hopefully become more ecosystem-based. However, the contingencies and complexities involved may make it impossible to find general laws in ecosystem ecology (Lawton 1999). Currently, ecosystem-based approaches to practical problems in conservation suffer from vagueness and circularity (Goldstein 1999). At their worst, the vagueness of these approaches makes it possible to get almost any answer to practical questions related to management decisions, often to support entrenched views. At their best, they provide a forum for helping stakeholders understand management trade-offs. They are most valuable if the criteria for decision-making can be agreed upon by all interested parties before the assessment is made.

A short introduction to Population Viability Analysis

Population viability analysis is a process of identifying the viability requirements of, and threats faced by, a species and evaluating the likelihood that the population(s) under study will persist for a given time into the future. Population viability analysis is often oriented towards the management of rare and threatened species, with two broad objectives. The short-term objective is to minimize the risk of extinction. The longer-term objective is to promote conditions in which species retain their potential for evolutionary change without intensive management (see also Beissinger and McCullough 2001). Within this context, Box 1 outlines management questions that may be addressed with a PVA.

Box 1. Population viability analysis (PVA) may be used to address the following aspects of management for threatened species and/or focal species, indicative for larger species groups:

(1) *Planning research and data collection.* PVA may reveal that population viability is insensitive to particular parameters. Research may be guided by targeting factors that may have an important effect on probabilities of extinction or recovery.

(2) *Assessing vulnerability.* PVA may be used to estimate the relative vulnerability of populations to extinction. Together with cultural priorities, economic imperatives and taxonomic uniqueness, these results may be used to set policies and priorities for allocating scarce conservation resources.

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

(4) *Ranking management options.* PVA may be used to predict the likely responses of species to reintroduction, captive breeding, prescribed burning, weed control, habitat rehabilitation, or different designs for nature reserves or corridor networks.

In addition to the management-oriented objectives in Box 1, PVA is also an excellent tool for organizing the relevant information and assumptions about a species or a population. By making the assumptions explicit, and highlighting the data deficiencies, it serves as a structured working and learning process. If the PVA focuses on species that are indicative for entire species groups (see Fleishman et al. 2000), its implications for habitat management have wider taxonomic relevance.

The result of a PVA can be expressed in many different forms (see examples in Fig. 1, Akçakaya [2000] and Beissinger and McCullough [2001]). These include extinction risk, time to decline, chance for recovery, persistence time, and local and regional occupancy rate. Which measure is used depends on the question. Most outputs from demographic PVAs are based on three variables: the amount of decline (e.g., 100% or total extinction or partial decline), the probability of decline, and the time frame in which the decline is expected to take place (Akçakaya 1992, 2000). Measures of occupancy model PVAs (see below) include risk of regional extinction, the number or proportion of occupied habitat patches (regional occupancy) projected over time, and extinction and colonization probabilities for individual patches under current environmental conditions (see Sjögren-Gulve and Hanski 2000).

There is no single recipe to follow when doing a PVA, because each case is different in so many respects. Main components of a PVA may include identification of the question (i.e., what issue the PVA is trying to address), data collection, data analysis and parameter estimation, modeling and risk assessment, sensitivity analysis and refinement of the model, monitoring and evaluation (Akçakaya et al. 1999).

Methods of PVA

Various types of models are used in PVAs, each type requires different data, and may answer different questions. The three types of models discussed below range from simple to complex, and demonstrate the trade-off between flexibility (realism) and practicality (data requirements). Simple occupancy models are applicable only to species in metapopulations, either with unoccupied and occupied patches observed at the same time, or with population turnover (i.e., observed local extinctions and recolonizations; see Sjögren-Gulve and Hanski 2000). In the more complex structured (Akçakaya 2000) or individual-based models (Lacy 2000a), single-population models can be considered as a special case of metapopulation models. For a more detailed discussion of single-population models, see Burgman et al. (1988, 1993), Caswell (1989), and Akçakaya et al. (1999).

(1) Occupancy models for metapopulations

The simplest metapopulation approach models the occupancy status of habitat patches in a geographic region (i.e., the presence or absence of the species in these patches). This approach dates back to a model that was originally developed by Levins (1969) and that has been modified and expanded by several authors. The two specific approaches described below are based on this model. For examples of applications of occupancy models, see Sjögren-Gulve and Hanski (2000).

Occupancy models are parameterized using data on the presence or absence of a species in habitat patches from one or more regional inventories. They may be advantageous to demographic models when demographic data are difficult to obtain. However, the management question and the ecology of the species, and not just data availability, should dictate the model used (see *Data needs and choosing a model*). Occupancy models require that the species has local populations confined to a clearly delimited habitat in a landscape. They ignore local population dynamics, and do not model fluctuations in size or composition of the local populations (sex, age, stage; see Akçakaya 2000). This may be disadvantageous, for instance when population processes not tightly correlated with habitat characteristics are important for local extinctions. Since they model future changes in patch occupancy based on observed instantaneous occupancy or correlates of observed population turnover, their predictions of local extinctions may be considered a less independent assessment than that of demographic models, which are based on survival and fecundity rates among individuals in the populations. An example where occupancy models and a demographic model are compared is provided by Kindvall (2000). Two general types of occupancy models, which are presented in greater detail by Sjögren-Gulve and Hanski (2000), are briefly described in Boxes 2 and 3.

Box 2. Occupancy models (I)

Incidence function models (IFM; Hanski 1994, 1999) require data on the areas and geographic locations of suitable habitat patches and the presence/absence of the species in these patches from at least one complete inventory. A habitat-suitability analysis (see above) of the species presence/absence pattern may be required for reliable habitat patch identification and delimitation. Based on these data, colonization and extinction probabilities are estimated for each patch using regression. These estimated probabilities are then used in simulations to predict metapopulation persistence and patch occupancy (e.g. Kindvall 2000, Vos et al. 2000).

Box 3. Occupancy models (II)

State transition models (e.g., Verboom et al. 1991, Sjögren-Gulve and Ray 1996) are conceptually related to the incidence function models discussed above. They require presence/absence data, but from two or more yearly inventories. Instead of relying on patch occupancy patterns, these models use patterns of patch state transitions. They predict state transitions (vacant to occupied as a result of colonization; and occupied to extinct, as a result of local extinction) from correlated environmental variables. Similar to habitat-suitability models, the patch transitions are modeled using predictive environmental variables discerned by multiple logistic regression (see Sjögren-Gulve and Hanski [2000] and Kindvall [2000]).

(2) Structured (meta)population models

Structured population models consider factors that may be important for the persistence of local populations by modeling the dynamics of each population occupying a habitat patch. As in the occupancy models discussed above, they also incorporate the spatial structure of the habitat patches (Burgman et al. 1993). In addition, they incorporate internal dynamics of each population (e.g., variation in age structure, immigration, emigration, density dependence, and environmental fluctuations), which often are important determinants of metapopulation persistence (Gilpin 1988, Burgman et al. 1993, LaHaye et al. 1994).

The main advantage of structured population models compared to occupancy models is their flexibility. In modeling the local population dynamics, they can incorporate several biological factors and can represent spatial structure in various ways; they have been applied to a variety of organisms (see Akçakaya [2000] and Menges [2000] for reviews, and Berglind [2000] and Lennartsson [2000] for examples). Since they model demographic processes, the populations are the focal object rather than the habitat patches. Consequently, the species-habitat association need not be as strong as in occupancy models. Another advantage is that, despite their realism, structured models are based on a number of common techniques or frameworks that allow their implementation as generic programs (such as RAMAS; see Akçakaya 1998). This common framework becomes advantageous when models and viability analyses are needed for a large number of species, and time and resources limitations preclude detailed programming for each species. A third advantage is that structured demographic modeling allows careful risk assessment for species with very few local populations (occupancy models require a larger number), and under circumstances in which no extinctions have occurred and habitat patches are not easily identified.

The main disadvantage of structured models is that they require more data than occupancy models, including stage-specific survival and fecundity rates, and the temporal and spatial variation in these rates. However, for species with weak habitat association, such data may be more easily obtained than observations of population turnover. Another difficulty lies in the estimation of local vital rates for populations that may, in the future, colonize currently vacant patches. In such cases, vital rates are usually estimated as functions of habitat characteristics, based on relationships obtained from occupied patches.

(3) Individual-based (meta)population models

There are various types of individual-based models. In a commonly used approach, the behavior and fate of each individual is modeled in a simulation (DeAngelis and Gross 1992). The behavior and fate (e.g., dispersal, survival, reproduction) of individuals depend on their location, age, size, sex, physiological stage, social status and other characteristics.

The advantage of individual-based models is that they are even more flexible than structured models, and can incorporate such factors as genetics, social structure, and mating systems more easily than other types of models (see Lacy [2000a] and Ebenhard [2000] for examples). One disadvantage of individual-based models is that they are very data-intensive. Only a few species have been studied well enough to use all the power of individual-based modeling. Another disadvantage is that the structure (as well as the parameters) of the models depend on the ecology and behavior of the particular species modeled. Thus, unlike structured models with a common framework, each individual-based model must be designed and implemented separately, making this approach impractical for most species. However, there are generic programs (such as VORTEX; see Lacy 1993, 2000b) that are based on individual-based modeling techniques but with a fixed, age-based structure.

Data needs and choosing a model

The amount of data needed to build a PVA model depends mostly on the question addressed and on the ecology of the species.

The types of data that can be used in a PVA include distributions of suitable habitat, local populations or individuals, patterns of occupancy and extinction in habitat patches, abundances, vital rates (fecundity and survival), as well as temporal variation and spatial covariation in these parameters. Not all of these types of data are required for any one model. For more information about data needs of particular types of PVA models, see Sjögren-Gulve and Hanski (2000), Akçakaya (2000) and Lacy (2000a).

The more data one has, the more detailed models one can build. Including more details makes a model more realistic, and allows addressing more specific questions. However, in most practical cases, available data permit only the simplest models. Attempts to include more details than can be justified by the quality of the available data may result in decreased predictive power and understanding.

The trade-off between realism and functionality depends on the characteristics of the system under study (e.g., the ecology of the species), what you know of the system (the availability of data), and what you want to know or predict about the system (the questions addressed). Even when detailed data are available, models intended to analyze long-term metapopulation persistence may include less detail than those intended to predict next year's distribution of breeding pairs within a local population. In cases where data are available and the ecology of the species implies that more than one type of PVA modeling is appropriate, comparative modeling (e.g., Kindvall 2000, Brook et al. 2000) may shed additional light on management options and strengthen the PVA process and conclusions. It is important to note that there are cases in which exploratory modeling is valuable for its own sake, even in the absence of sufficient data (see *Data needs* below).

Box 4 lists aspects that should be considered in determining the appropriate model. Different considerations may point to models of different complexity. For instance, the question addressed may require a detailed model whereas the available data can support only a simple model. In such cases, either more data must be collected or the question modified.

Box 4. The following should be considered in determining the appropriate PVA model:

- Model **structure** should be detailed enough to use all the relevant data, but no more detailed.
- Model **results** should address the question at hand (e.g., if the question concerns risk of a 50% decline, the model should report such a result).
- 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).
- Model **assumptions** should be realistic with respect to the ecology of the species and the observed spatial structure (e.g., if there is population subdivision, a metapopulation model should be considered).
- For occupancy modeling, the species must occur as geographically distinct local populations in a landscape or region, and species occurrence or turnover patterns (extinction/colonization) need to correlate significantly with measurable habitat variables (see Boxes 2, 3 and 5).

Occupancy models may be more advantageous than demographic models in situations where demographic data are not available, and the species occurs in a large number of local populations confined to a distinct type of habitat in the region of concern. In order to do the PVA with an incidence function model, inventory data are needed, including presence/absence of the species and measurements of individual habitat patch characteristics (environmental variables) that may explain its presence/absence pattern. For state transition modeling, a sufficient number of local extinctions (> 5) and colonizations (>5) must have occurred between repeated inventories (in different years) that correlate significantly with local patch characteristics (see Sjögren-Gulve and Hanski 2000).

Box 5 presents some further guidelines on conditions under which demographic (structured or individual-based) models are more advantageous than occupancy models. The choice between structured and individual-based models depends on the size of the population(s), the importance of genetics and social interactions, and availability of data (see Akçakaya 2000).

Box 5. Guidelines for selecting a model: Conditions under which demographic models that incorporate internal dynamics (such as structured models or individual-based models) are more advantageous than occupancy models. Note that these are only general guidelines; there may be exceptions to most of them.

i. demographic data for building a structured or individual-based model already exist

ii. there are reasons to believe that demographic, behavioral or genetic processes are important for local extinction, or the ecology of the species indicates that internal population dynamics are important

iii. the species occurs in a small number of populations

iv. suitable but unoccupied habitat patches cannot be easily identified

v. species occurrence or turnover (extinction/colonization) patterns do not correlate significantly with measurable habitat characteristics (or such data are harder to collect than demographic data)

vi. the management question addressed involves a factor related to within-population dynamics (e.g., questions about impacts on different age classes or questions regarding management and conservation actions that affect different life history stages differently)

vii. the required answer is in terms of abundance rather than occupancy (e.g., risk of a population decline, or expected time until the population falls below a given threshold abundance)

Limitations of Population Viability Analysis

As any other method, PVA has certain limitations, both practical and philosophical.

Single species focus

The focus of a PVA is generally a population or multiple populations of a single species. Its focus on single species is a limitation in cases where the goal is the management and conservation of an ecosystem. In other cases, the single species focus is the strength of PVA: the dynamics of single species are much simpler (and thus better understood) than the dynamics of communities or ecosystems (Lawton 1999). Uncertainties in structure and parameters of single-species models (see below) are magnified when multiple species and their interactions are considered.

One way to deal with the single-species limitation is to select target species that are representative of the community, that are sensitive to potential human impact, and whose conservation is likely to protect other species as well (umbrella species). Such species are sometimes called "indicator" species (see Fleishman et al. 2000). However, it is important not to make the mistake of managing the landscape specifically for the indicator species without ascertaining that the enhancements benefit other species as well (Simberloff 1998). For example, the proverbial "miner's canaries" would be useless as "indicators" if they were given little oxygen masks so that they survive!

Data needs

PVAs may need more data than some of the other methods discussed. However, incomplete information does not necessarily preclude meaningful results. First, PVAs can incorporate uncertainties in the data, and in some cases, these uncertainties do not effect the overall conclusion (see below). Second, uncertainties in the data may not affect results when the goal of PVA is comparative, as in ranking management options (Akçakaya and Raphael 1998). Third, there is very significant

significant value in building a model for its own sake. It clarifies assumptions, integrates knowledge from all available sources, and forces us to be explicit and rigorous in our reasoning. It allows us to identify, through sensitivity analyses, which model structures and parameters matter, and which do not (Akçakaya and Burgman 1995). In fact, this modeling process is necessary for determining whether or not there *are* sufficient data for reaching management decisions. It allows identification of the parameter(s) which deserve highest priority in terms of obtaining more precise estimates. This identification does not refer to the *types* of data needed for models with different structures, but to the numerical values of the parameters, and to the contribution of each particular parameter to the uncertainty in model results.

Risk criteria

Some uses of PVA involve determining whether the risk faced by a particular species is acceptable. Such questions require a benchmark for "an acceptable level of risk" for the extinction of species. There are some benchmarks used (e.g., IUCN categories; see Gärdenfors 2000), but none is accepted universally. Obviously, the determination of such benchmarks is a societal issue, outside the scope of PVA.

Identifying causes of decline

Caughley (1994) contrasted two paradigms in conservation biology: "small population" and "declining population". Under the "small population paradigm", factors threatening species with extinction include stochasticity, catastrophes and genetic degradation; under the "declining population paradigm," they include overkill, habitat loss and fragmentation. In this scheme, PVA and modeling are included under the "small population paradigm". This separation is now seen as artificial (Hendrick et al. 1996, Akçakaya and Burgman 1995, Beissinger and McCullough 2001) because PVAs can and do incorporate systemic pressure (i.e., deterministic decline; e.g., LaHaye et al. 1994), effects of habitat loss (e.g., Akçakaya and Raphael 1998), and overkill (or overharvest; e.g., Ebenhard 2000). It is important to remember that, as Caughley (1994) emphasized, no modeling effort by itself can determine why a population is declining or why it has declined in the past. This is rather obvious, but it is often forgotten and models are expected to provide answers to questions they were not designed to address. For modeling to be used successfully to evaluate options for management of species, it must be part of a larger process and incorporate other methods, including study of natural history, field observations and experiments, analysis of historical and current data and long-term monitoring. The challenge that PVA modelers take is to incorporate all the relevant factors and impacts in their model.

Advantages of Population Viability Analysis

PVA is one of the central tools for conservation planning and evaluation of management options. Compared to other methods reviewed above, PVA has several advantages.

Relevance to conservation of biodiversity

PVA has direct relevance to biodiversity conservation. An increasing number of species are presently threatened or endangered, and PVA results directly relate to the mandates of such laws as the Endangered Species Act. In addition, PVA can be applied to validated focal or umbrella species (Fleishman et al. 2000) to guide conservation efforts for entire nested species groups. Thus, PVAs of selected threatened species and sets of indicative species will be central for efficient conservation planning at local or regional levels, and for measures taken to comply with international treaties such as the UN Convention Biological Diversity (UNCED 1992). By focusing on species viability, instead of relying only on subjective rules-of-thumb or opinions, or only habitat data, the risk assessment approach directly relates to the maintenance of viable and well-distributed populations of native species.

Rigor

Unlike some of the other methods, PVA is rigorous and quantitative. Its results can be replicated by different researchers. The assumptions of a PVA can be (and should be) explicitly stated and enumerated; they can also be validated given sufficient data. Validation of stochastic results (such as risk of decline or extinction) requires data for several independent populations, as well as observed trajectories or extinctions for comparison. For example, in a collective comparison of the historic trajectories of 21 populations with the results of the PVAs for these populations, Brook et al. (2000) validated PVAs in terms of their predictions of abundance and risks of decline. In this comprehensive and replicated evaluation, they estimated the parameters from the first half of each data set and used the second half to evaluate model performance. They found that PVA predictions were accurate: the risk of population decline closely matched observed outcomes, there was no significant bias, and population size projections did not differ significantly from reality. Further, the predictions of five PVA software packages they tested were highly concordant. They concluded that PVA is a valid and sufficiently accurate tool for categorising and managing endangered species. Although validation of stochastic results may not be possible in every case, components of a PVA can be validated. For example, the density dependence function can be validated by experimental manipulation of densities, or the habitat relationships that form the basis of the spatial structure of a metapopulation PVA can be validated by using half of the available data to predict the other half (e.g., see Akçakaya and Atwood 1997). In addition, some model results can be validated by comparing predicted values with those observed/measured in the field (e.g., Sjögren-Gulve and Ray 1996, McCarthy and Broome 2000, McCarthy et al. 2000, Kindvall 2000, Vos et al. 2000).

Ability to use all available data and multiple data types

A PVA can use various types of data sets, including presence-absence data, habitat relationships, GIS data on landscape characteristics, mark-recapture data, surveys and censuses. Thus, it is possible to incorporate all available data into the assessment. Such an assessment is more reliable than one that ignores part of the available information. Most of the alternative methods discussed above use a limited range of data types. For example, reserve selection, habitat suitability or gap analysis methods cannot use available demographic data.

Incorporating uncertainty

Uncertainty is a prevalent feature of ecological data that is ignored by most methods of assessment. If data for a PVA are unavailable or uncertain, ranges (lower and upper bounds, instead of point estimates) of parameters are used. In addition, uncertainties in structure of the model can be incorporated by building multiple models (e.g., with different types of density dependence). There are various methods of propagating such uncertainties in calculations and simulations (Ferson et al. 1998). One of the simplest methods is to build best-case and worst-case models (e.g., Akçakaya and Raphael 1998). A best-case (or optimistic) model includes a combination of the lower bounds of parameters that have a negative effect of viability (such as variation in survival rate), and upper bounds of those that have a positive effect (such as average survival rate). A worst-case or pessimistic model includes the reverse bounds. Combining the results of these two models gives a range of estimates of extinction risk and other assessment endpoints. This allows the users of the PVA results (managers, conservationists) to understand the effect of uncertain input, and to make decisions with full knowledge of the uncertainties.

The uncertainties can also be used in a sensitivity analysis. Results of sensitivity analyses are used to identify important parameters and help guide future fieldwork. For example, PVA models can also be analyzed with respect to their sensitivity to uncertain parameters. Such analyses guide fieldwork by quantifying the expected decrease in the uncertainty of the results with narrower ranges for each parameter (see Akçakaya 2000).

Conservation planning with multiple objectives

Conservation and landscape management decisions often involve multiple objectives such as ecological and economic goals. Population viability analyses do not explicitly incorporate economic factors, because it is often counterproductive (and usually impossible) to assign monetary value to the viability or persistence of a species. However, because of the quantitative nature of PVA results, it is possible to jointly consider ecological and economic objectives, for risk-based (and risk-weighted) decision-making. This can be done by keeping ecological and economical values separate, and presenting the results of the analysis in two dimensions, instead of only one (Fig. 2). Thus, the resulting graph has an x-axis in monetary units (e.g., the cost of implementing a certain management or conservation option), and a y-axis in biological units (e.g., reduction in the risk of extinction of the species). As more money is spent, the viability (chance of long-term survival) increases (possibly reaching an asymptote, depending on the problem). However, different management options have different curves, which may cross. This means that depending on the amount of resources available, one or the other option may be preferable. Such a graph may be used in several ways: selecting the optimal management given the fixed resource; or estimating resources necessary for a certain level of viability (e.g., moving from "endangered" to "vulnerable"). If there are monetary benefits of conservation, these can either be shown as a different curve, or (better yet) subtracted from the cost beforehand.

When are population viability analyses most useful?

The preceding discussion highlights the conditions under which PVAs are most appropriate and most predictive. We conclude this paper with a summarized check-list of how to optimize the PVA as a conservation tool and design the analysis to get reliable qualitative answers.

Address a specific question involving focal/target species

General mandates such as “Manage this landscape so that everyone benefits” or general questions such as “Why are neo-tropical migrants declining?” are not very suitable to a direct PVA. To address such issues with a PVA, they must be reduced to a set of more specific questions, such as “Which management option would result in the highest chance of recovery of threatened species?” (e.g. Berglind 2000) or “Which set of reserves is best for the persistence of one or several focal (umbrella, indicator) species?” or “What are the long-term implications of an observed population decline for the viability of a neo-tropical migrant?”

Focus on a case with sufficient data

When data are scarce, it is risky to make assessment with any method, including PVA. In these cases, PVAs are most appropriate as exploratory tools, used to identify important assumptions and parameters, and to guide fieldwork.

Use all the available and relevant data

Assessments that use all the available and relevant data, including spatial (GIS) data, presence-absence data, habitat relationships, and demographic data from mark-recapture studies, surveys and censuses, are more reliable than those that ignore part of the relevant information.

Use the appropriate model

Model choice should be based on the availability of data, the question addressed and the ecology of the species (see *Data needs and choosing a model* above).

State all assumptions explicitly

Modelers usually know the assumptions of their models, but often forget that these assumptions may not be transparent to others. An assessment should explicitly list all the assumptions (even the most obvious ones) related to model structure, parameters and uncertainties.

Validate assumptions and results where possible

Model accuracy (about model precision, see below) can be validated by using data from one half of the study system and making predictions for the other half that are compared to observed values (Kindvall 2000). Alternatively, data from a previous time period can be used for model predictions of the current (observed) situation (e.g. Sjögren-Gulve and Ray 1996, Brook et al. 2000, Vos et al. 2000). Validating assumptions of a model is often difficult; after all, when assumptions can be validated, they become parameters. However, the model should point out to the types of data that may be useful to validate or reject assumptions.

Incorporate data uncertainties, and discuss the implications

All parameters should be specified as ranges that reflect uncertainties (lack of knowledge, measurement errors). See *Incorporating uncertainty* above.

Analyze the sensitivity of results to assumptions and parameters

Sensitivity analysis identifies important parameters and assumptions. Sensitivity analysis should be geared towards identifying parameters that, if known with a higher precision, would decrease the uncertainty in model results to the largest extent. The importance of a parameter in determining viability depends on both the range of plausible values (its current uncertainty), and practical limitations (such as cost considerations).

Another use of sensitivity analysis is determining the most effective management action (e.g., Crowder et al. 1994, Berglind 2000, Lennartsson 2000). This is often done by evaluating the sensitivity of the model results to each parameter. However, most management actions cause changes in more than one parameter. For example, an effort to increase the survival of newborns affects both the first survival rate and the fecundity in a matrix model based on pre-reproductive census. It most likely affects the survival of other age classes as well. In such cases, it is better to evaluate “whole-model” sensitivity (with respect to management actions) instead of parameter-by-parameter sensitivities (see Akçakaya et al. 1999, Akçakaya 2000).

Report viability results

Results are more reliable and relevant if they are expressed in probabilistic terms (risk of decline) rather than deterministic terms (abundance 10 years from now) (e.g. Berglind 2000, Ebenhard 2000). When probabilistic results are based on simulations, the number of replications or iterations determines the precision of these results. In most cases, the randomly sampled model parameters are statistically representative if the number of replications is in the 1000 to 10000 range.

Use relative risks (instead of absolute risks)

Risk of extinction, and risk of decline to an unacceptably small population size (quasi-extinction probability results from demographic models; Burgman et al. 1993, Akçakaya 2000), is a frequently reported PVA result. Here, it should be remembered that such results are usually more reliable if they are relative (which option gives higher viability?), rather than absolute (what is the risk of extinction?). As discussed above, relative results may not be as sensitive to uncertainties in the data, even in cases where the uncertainties in the data result in uncertainties in absolute results (e.g., Akçakaya and Raphael 1998).

Focus on risk of decline (instead of risk of extinction)

Because of uncertainties in modeling very small populations, the results are more reliable if risk of decline (rather than total extinction) is used. Thus, results should be expressed as the probability that the population size falls to or below a critical population level for social dysfunction or other severe effects, say, 20 or 50 individuals.

Project population dynamics for short time horizons

Short-term results are more reliable, because uncertainties are compounded with time. If a model is based on 5 years of data, running simulations for 100 years makes a lot of assumptions about the average and variation of model parameters. Even if long-term results may be warranted because land-use allocations are irreversible, these assumptions must be kept in mind. Furthermore, if PVA is used for impact assessment, it is important to remember that both very long and very short time horizons may mask the effects of the simulated human impact. This is because in the very near future (say, next year), it is unlikely that the population will fall to very low levels, with or without impact. Over very long time horizons, the risk will be close to one, even without the impact. Thus the difference between the two simulations (with and without impact) will be very small or zero, for very short or very long time horizons. One solution is to select the time horizon that gives the largest difference between impact and no-impact scenarios (i.e., the time horizon for which the model is most sensitive to the simulated impact). PVA models (especially those with long time horizons) should consider the possibility of a trend in average vital rates (e.g., in addition to random fluctuations, fecundity may also have a decreasing trend in its average).

Provide a feedback between fieldwork, modeling and monitoring

It is important that a PVA model, once used to make conservation decisions, is not abandoned. Additional fieldwork should provide data to refine model parameters, and monitoring should check the realism of the model. The revised model should guide further fieldwork (identify important parameters), and monitoring (identify important variables/outcomes).

Allow for adaptive management

Just as a PVA model should evolve as more data become available, the management decisions should also adapt to new PVA results. In some cases, this is not possible. For example in the case of reserve design questions, it may not be possible to change a decision. However, in the case of long-term management actions (for example, translocations, habitat restoration, harvest limits, etc.), the recommendations from a PVA should be revisited whenever new data are used to refine a model.

Acknowledgements – We thank Mark Burgman, Erica Fleishman, Linda Hedlund, Oskar Kindvall, Mark Shaffer, and two anonymous referees for constructive comments on the manuscript.

References

Akçakaya, H. R. 1992. Population viability analysis and risk assessment. – In: McCullough, D. R. and Barrett, R. H. (eds), Wildlife 2001: Populations. Elsevier Publishers, London, pp. 148-157.

Akçakaya, H. R. 1998. RAMAS GIS: Linking Landscape Data with Population Viability Analysis (ver 3.0). – Applied Biomathematics, Setauket, New York.

Akçakaya, H. R. 2000. Population viability analyses with demographically and spatially structured models. – Ecol. Bull. 48: 000-000.

Akçakaya, H. R. and Atwood, J. L. 1997. A habitat-based metapopulation model of the California Gnatcatcher. – Conserv. Biol. 11: 422-434.

Akçakaya, H. R. and Burgman, M. 1995. PVA in theory and practice (letter). – Conserv. Biol. 9: 705-707.

Akçakaya, H. R. and Raphael, M. G. 1998. Assessing human impact despite uncertainty: viability of the northern spotted owl metapopulation in the northwestern USA. – Biodiv. Conserv. 7: 875-894.

Akçakaya, H. R., et al. 2000. Making consistent IUCN classifications under uncertainty. – Conserv. Biol. 14, in press

Akçakaya, H. R., Burgman, M. A. and Ginzburg, L. R. 1999. Applied Population Ecology: principles and computer exercises using RAMAS EcoLab 2.0. Second edition. – Sinauer, Sunderland, Massachusetts.

Beier, P. and Noss, R. F. 1998. Do habitat corridors provide connectivity? – Conserv. Biol. 12: 1241-1252.

Beissinger, S. R. and McCullough, D. R. (eds). 2001. Population viability analysis. – The University of Chicago Press. (in press)

Berglind, S-Å. 2000. Demography and management of relict sand lizard (*Lacerta agilis*) populations on the edge of extinction. – Ecol. Bull. 48: 000-000.

Boyce, M. S. 1992. Population viability analysis. – Ann. Rev. Ecol. Syst. 23: 481-506.

Brook, B. W., et al. 2000. Predictive accuracy of population viability analysis in conservation biology. – *Nature* 404:385-387.

Burgman, M., Akçakaya, H. R. and Loew, S. S. 1988. The use of extinction models in species conservation. – Biol. Conserv. 43: 9-25.

Burgman, M. A., Ferson, S. and Akçakaya, H. R. 1993. Risk assessment in conservation biology. – Chapman and Hall, London.

Burgman, M. A., Keith, D. A. and Walshe, T. V. 1999. Uncertainty in comparative risk analysis of threatened Australian plant species. – Risk Analysis 19: 585-598.

Caswell, H. 1989. Matrix Population Models: Construction, Analysis, and Interpretation. – Sinauer Associates, Sunderland, Massachusetts.

Caughley, G. 1994. Directions in conservation biology. – J. Anim. Ecol. 63: 215-244.

Crowder, L. B., Crouse, D. T., Heppell, S. S. and Martin, T. H. 1994. Predicting the impact of turtle excluder devices on loggerhead sea turtle populations. – Ecol. Appl. 4: 437-445.

DeAngelis, D. L. and Gross, L. J. (eds) 1992. Individual-based Models and Approaches in Ecology: Populations, Communities and Ecosystems. – Chapman and Hall, New York.

Ebenhard, T. 2000. Population viability analyses of Swedish wolves, otters and peregrine falcons. – Ecol. Bull. 48: 000-000.

Elith, J. 2000. Quantitative methods for modeling species habitat: comparative performance and an application to Australian plants. – In: Ferson, S. and Burgman, M. (eds), Quantitative Methods for Conservation Biology. Springer-Verlag, New York, pp.39-58 (in press).

Ferson, S., Root, W. T. and Kuhn, R. 1998. RAMAS Risk Calc: Risk Assessment with Uncertain Numbers. – Applied Biomathematics, Setauket, New York.

Fleishman, E., Jonsson, B. G. and Sjögren-Gulve, P. 2000. Focal species modeling for biodiversity conservation. – Ecol. Bull. 48: 000-000.

Gilpin, M. E. 1988. A comment on Quinn and Hastings: extinction in subdivided habitats. – Conserv. Biol. 2: 290-292.

Goldstein, P. Z. 1999. Functional ecosystems and biodiversity buzzwords. – Conserv. Biol. 13: 247-255.

Gärdenfors, U. 2000. Population viability analysis in the classification of threatened species: problems and potentials. – Ecol. Bull. 48: 000-000.

Hanski, I. 1994. A practical model of metapopulation dynamics. – J. Anim. Ecol. 63: 151-162.

Hanski, I. 1999. Metapopulation ecology. – Oxford University Press, Oxford.

Hedrick, P. W., Lacy, R. C., Allendorf, F. W. and Soulé, M. E. 1996. Directions in conservation biology: comments on Caughley. – Conserv. Biol. 10: 1312-1320.

IUCN. 1994. International Union for the Conservation of Nature Red List Categories. – IUCN Species Survival Commission, Gland, Switzerland.

Kiester, A. R., et al. 1996. Conservation prioritization using GAP Data. – Conserv. Biol. 10: 1332-1342.

Kindvall, O. 2000. Comparative precision of three spatially realistic simulation models of metapopulation dynamics. – Ecol. Bull. 48: 000-000.

Lacy, R. C. 1993. VORTEX: A computer simulation model for population viability analysis. – Wildl. Res. 20: 45-65

Lacy, R. C. 2000a. Considering threats to the viability of small populations with individual-based models. – Ecol. Bull. 48: 000-000.

Lacy, R. C. 2000b. Structure of the VORTEX simulation model for population viability analysis. – Ecol. Bull. 48: 000-000.

LaHaye, W. S., Gutierrez, R. J. and Akçakaya, H. R. 1994. Spotted owl metapopulation dynamics in southern California. – J. Anim. Ecol. 63: 775-785.

Lawton, J. H. 1999. Are there general laws in ecology? – Oikos 84: 177-192.

Lennartsson, T. 2000. Management and population viability of the pasture plant *Gentianella campestris*: the role of interactions between habitat factors. – Ecol. Bull. 48: 000-000.

Levins, R. 1969. Some demographic and genetic consequences of environmental heterogeneity for biological control. – Bull. Entom. Soc. Amer. 15: 237-240.

Mace, G. M. and Lande, R. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. – Conserv. Biol. 5: 148-1157.

McCarthy, M. A. and Broome, L. S. 2000. A method for validating stochastic models of population viability: a case study of the mountain pygmy-possum (*Burramys parvus*). – J. Anim. Ecol. (in press).

McCarthy, M. A., Lindenmayer, D. B. and Possingham, H. P. 2000. Testing spatial PVA models of Australian treecreepers (Aves: Climacteridae) in fragmented forest. – Ecol. Appl. (in press).

Margules, C. R., Nicholls, A. O. and Pressey, R. L. 1988. Selecting networks of reserves to maximise biological diversity. – Biol. Conserv. 43: 63-76.

Master, L. L. 1991. Assessing threats and setting priorities for conservation. – Conserv. Biol. 5: 559-563.

McGarigal, K. and Marks, B. J. 1995**.** FRAGSTATS: spatial pattern analysis program for quantifying landscape structure. – Gen. Tech. Rep. PNW-GTR-351. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, Oregon. 122 pp.

Menges, E. S. 2000. Applications of population viability analyses in plant conservation. – Ecol. Bull. 48: 000-000.

Mills, L. S., Fredrickson, R. J. and Moorhead, B. B. 1993. Characteristics of old-growth forests associated with northern spotted owls in Olympic national park. – J. Wildl. Managem. 57: 315-321.

Millsap, B. A. et al. 1990. Setting the priorities for the conservation of fish and wildlife species in Florida. – J. Wildl. Manage. (Suppl) 54 :5-57.

Pearce, J.L., Burgman, M. A. and Franklin, D. C. 1994. Habitat selection by helmeted honeyeaters. – Wildl. Res. 21: 53-63.

Pimm, S. L. and Lawton, J. H. 1998. Planning for biodiversity. Science 279: 2068-2069.

Possingham, H., Ball, I. and Andelman, S. 2000. Mathematical methods for identifying representative reserve networks. – In: Ferson, S. and Burgman, M. (eds), Quantitative Methods for Conservation Biology. Springer-Verlag, New York, pp.291-306 (in press).

Pressey, R. L., Humphries, C. J., Margules, C. R., Vane-Wright, R. I. and Williams, P. H. 1993. Beyong opportunism: key principles for systematic reserve selection. – TREE 8:124-128.

Pressey, R. L., Possingham, H. P., Margules, C. R. 1996. Optimality in reserve selection algorithms: when does it matter and how much? – Biol. Conserv. 76:259-267.

Scott, J. M., Davis, F., Csuti, B., Noss, R. F., Butterfield, B., Groves, C., Anderson, H., Caicco, S., D'Erchia, F., Edwards Jr., T. C., Ulliman, J. and Wright, R. G. 1993. Gap Analysis: A geographic approach to protection of biological diversity. – Wildl. Monogr. 123.

Simberloff, D. 1998. Flagships, umbrellas, and keystones: is single-species management passé in the landscape era? – Biol. Conserv. 83: 247-257.

Sjögren-Gulve, P. 1994. Distribution and extinction patterns within a northern metapopulation of the pool frog, *Rana lessonae*. – Ecology 75: 1357-1367.

Sjögren-Gulve, P. and Ray, C. 1996. Using logistic regression to model metapopulation dynamics: large-scale forestry extirpates the pool frog. In: McCullough, D. R. (ed.), Metapopulations and wildlife conservation. – Island Press, Washington, D.C., pp. 111-137.

Sjögren-Gulve, P. and Hanski, I. 2000. Metapopulation viability analysis using occupancy models. – Ecol. Bull. 48: 000-000.

Solow, A. R. 1993. Inferring extinction from sighting data. – Ecology 74: 962-964.

Stacey, P. B., Johnson, V. A. and Taper, M. L. 1997. Migration within metapopulations: the impact upon local population dynamics. – In: Hanski, I. and Gilpin, M. E. (eds), Metapopulation biology: ecology, genetics, and evolution. Academic Press, San Diego, pp. 267-291.

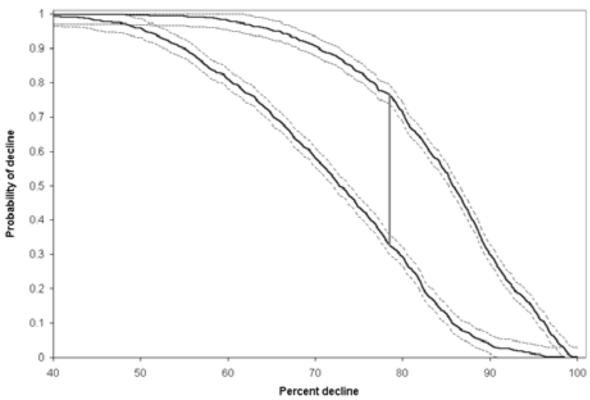
Straw, J. A., Wakely, J. S. and Hudgins, J. E. 1986. A model for management of diurnal habitat for American Woodcock in Pennsylvania. – J. Wildl. Managem. 50: 378-83.

UNCED. 1992. The United Nations Convention on Biological Diversity. – Rio de Janeiro.

Verboom, J., et al. 1991. European nuthatch metapopulations in a fragmented agricultural landscape. – Oikos 61: 149-156.

Verner, J., Morrison, M. L. and Ralph, C. J. (eds) 1986. Wildlife 2000: Modeling Habitat Relationships of Terrestrial Vertebrates. – University of Wisconsin Press, Madison.

Vos, C. C., ter Braak, C. F. J. and Nieuwenhuzen, W. 2000. Incidence function modelling and conservation of the tree frog in the Netherlands. – Ecol. Bull. 48: 000-000.



[Picture from (from Sjögren-Gulve and Ray 1996, © Island Press]

Fig. 1. Examples of outputs from population viability analyses (PVAs) with a structured model and an occupancy model, respectively. (a) Risk of decline of a Northern Spotted Owl metapopulation, simulated with a structured PVA model (based on Akçakaya and Raphael 1998). The top curve gives the risk under an assumed timber harvest, and the bottom curve assumes no habitat loss. Each point on the curve shows the probability that the metapopulation abundance will fall by the given percentage from the initial abundance anytime during the next 100 years. The vertical bar shows the maximum difference between the two curves. In this example, the maximum difference is at a 78% decline. The risk of a 78% decline from the initial abundance is about 0.33 without habitat loss, and about 0.77 with habitat loss due to the assumed timber harvest. (b) Predicted temporal change in the proportion of 102 ponds occupied by pool frogs (*Rana lessonae*) when large-scale forestry is omnipresent at the Baltic coast of east-central Sweden. The risk of regional extinction is 0.999 within 15 census intervals (i.e., 53 years) and medium time to regional extinction is 18 years (from Sjögren-Gulve and Ray 1996, © Island Press).

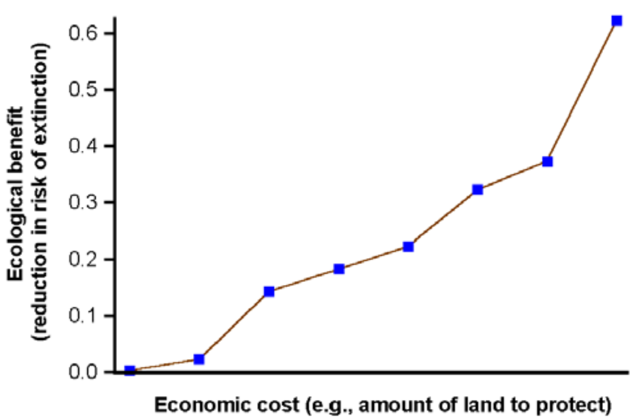


Fig. 2. An example of cost-benefit analysis with the results of a series of PVAs. Each point on the curve gives the result of one PVA, which assumes a certain amount of effort for conservation. This effort is quantified in the x-axis as the cost (e.g., the cost of setting aside a certain amount of land for protection of the species). The result of the PVA is expressed as the reduction in extinction risk from the no-action (i.e., no conservation scenario) and plotted in the y-axis.