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Population viability analysis for conservation: the good, the bad and the undescribed

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Abstract

Population viability analysis is used in a variety of ways to solve conservation problems. These uses are defined in part by data availability and theoretical and biological understanding, and in part by social, regulatory and political context. The use of a PVA in one context does not preclude or invalidate its use in another. In this paper we attempt to discuss objectively the role of PVA in population management and conservation planning. We emphasise its role in organising information, engaging stake-holders, and making decisions. To be successful, some traditional views about population models and decision-making need to be suspended and reviewed.

Introduction

The use of population models in conservation biology is at a cross-roads. In the 1980's many believed that population viability analysis (PVA) would provide a comprehensive framework for threatened species management. Early enthusiasm has been tempered by problems with lack of data, lack of validation, and several studies that have demonstrated the sensitivity of results to uncertainty in the data (Taylor 1995, Ruckelshaus et al. 1997). More and more conservation ecologists are expressing disappointment at the inability of PVA to provide verifiable answers, to be impregnable to misinterpretation, or to make the work of an academic conservation ecologist any easier (Doak & Mills 1994, Beissinger & Westphal 1998). Others who view PVA from a more applied perspective and tried to use it to help with environmental legislation, land-use planning and making decisions about the management of populations have also been disappointed (Hamilton & Moller 1995, Harcourt 1995). The role of population modelling in conservation is suffering a backlash from early over-enthusiasm and our unrealistic expectation that PVA would solve all our single species conservation problems. The role of population modelling in conservation biology, and in population management in general, requires reassessment (Shea et al. 1998)

We begin this paper by characterising the different roles PVA can play, roles that apply fairly generally to the application of population modelling tools in conservation. We move to a discussion of what we think a good PVA should be and do. We end with three aspects of population modelling for conservation that require further attention – the role of genetics in PVA, spatial population modelling for management, and the use of decision theory with PVA.

The various roles of PVA

PVAs are constructed at numerous spatial and temporal scales, and with different underlying theoretical bases. Individual-based models can create very detailed forecasts. They have particular utility when details of individual behaviour are important, when genetic processes are to be included in the model, and when the modellers wish to explore the fine detail of the spatial arrangement of individuals and their interactions with environmental variables and management objectives (DeAngelis & Gross 1992, Judson 1994; eg., McCarthy 1996, Letcher et al. 1998). At the other end of the spectrum, incidence functions and related patch-based models ignore the details of population dynamics completely (Hanski et al. 1996). People thinking about applying models to solve a particular problem are confronted with this very broad range of possibilities, and a range of apparently conflicting advice on what can and cannot be done. Below we summarise the different roles of PVA and their associated concerns.

The intellectual curio

PVAs have been considered to be of theoretical interest but little practical value. Caughley (1994) argued that there are two paradigms in conservation biology (see also Caughley & Gunn, 1996). The first is the small population paradigm, driven by theoretical interest in the stochastic processes governing small populations, arising from the mathematics of birth and death processes. Here the concern is with chance extinctions in highly restricted and/or fragmented environments. The second is the declining population paradigm where species have a long-term negative population growth rate throughout their range. In stark contrast to the small population paradigm, this requires immediate pragmatic strategies and population modelling is of little value. Caughley (1994) suggested that the principle contribution of the small-population paradigm was to provide an answer to a trivial question: how long will a population persist if nothing unusual happens? The theory bears ‘tenuous relevance to the problem of aiding a species in trouble’ and any empirical generalisation constructed directly from simple theory is suspect (Harcourt 1995) - it is an ‘intellectual curio’.

The criticisms are certainly valid. However, one can argue that theoretical literature does not search for empirical generalisations. The search is for mathematical generalisations upon which solutions to empirical problems may be formulated. Much of the early PVA literature was motivated by theoretical interest (eg., Goel & Richter-Dyn 1974, Ginzburg et al. 1982, Lande & Orzack 1988, Tuljapurkar 1989). As Caughley (1994) noted, it served to make the scientific foundations upon which pragmatic PVA is built. Robust general principles permeate later applications.

Caughley (1994) and others (eg. Harcourt 1995) have not understood that the distinction between deterministic and stochastic issues is artificial (Boyce 1992). Their narrow view of PVA as a simple, demographic tool that ignores ‘external’ deterministic processes and the ecology of the species is an exaggeration. Any PVA with these characteristics is just badly constructed. The ecology of species and the role of management should be, in the words of Boyce (1992), the nuts and bolts of modelling exercises.

The loaded gun

The loaded gun view contends that PVA is dangerous in the hands of the untrained. This view argues that PVAs built with too little data are suspect and should be handled with care or discarded completely. For example, Harcourt (1995) evaluates PVA models of the Virunga gorilla (*Gorilla gorilla*) and concludes that demography dominates the models at the expense of ecology. This conclusion is echoed by Beissinger & Westphal (1998) who suggest that the advent of easy-to-use computer software makes it ‘too easy’ to construct a model that can be passed off as a sound and useful PVA. Similarly, Reed et al. (1998) argue that when demographic data are absent, effort should be given to more data collection or alternatives to PVA rather than the PVA itself. These arguments rest on the proposition that a lack of data and a poor level of understanding of the ecology of a species may precipitate a degree of uncertainty in models so that the results provide no credible management suggestions (Beissinger & Westphal 1998).

The view that if data are insufficient then there is no point developing a PVA at all reappears from time to time, sometimes motivated by a published result that does not sit well with someone in the scientific or regulatory community. This problem plagues all models, not just PVAs, and it has consequences for model interpretation, sensitivity analysis and the generation of error bounds for stochastic and deterministic expectations (Goodman 1987, Shaffer 1987, Boyce 1992, Burgman et al 1993). However, it does not follow that all PVAs must be based on a full set of credible data. The antidote is not to urge people to desist from building models under some (vaguely specified) circumstances. It is to engage in building a better model that includes the features that the other model has disregarded.

Given we will never have a "complete" data set for any species, we take the view that there are never insufficient data to construct a useful model. Incomplete information does not mean that meaningful results are impossible to obtain because there is very significant value in building a model, for its own sake (Akçakaya et al. 1997). It clarifies assumptions, integrates knowledge from all available sources, and forces biologists to be explicit and rigorous in their reasoning. It allows us to identify, through sensitivity analyses, which model structures and parameters matter (in that they make a difference to the outcome), and which do not. In this sense it is a guide to further data collection (Possingham et al. 1993). It results in a set of logical statements that are internally consistent, and it allows us to explore the consequences of what we believe to be true, even in the absence of all relevant data.

The magnifying glass

Under close scrutiny we will almost certainly find that other models will perform equally well – which one do we choose? This concern about PVA comes from thinking like an ‘ecological detective’ (Hilborn & Mangel, 1997). There will always be more than one plausible model for each natural population, as long as there is more than one ecologist thinking about it. Each of the alternatives represents a different idea of how the world works. It is unwise to discard any plausible hypothesis. Rather, we should treat each one on its merits, reflected in its associated likelihood. For example, Pascual et al. (1997) explores the expectations of a series of structurally different models in determining the best way to manage populations of wildebeest (*Connochaetes taurinus*). In this role, PVAs can be used iteratively to encapsulate the things we know currently, and to provide a benchmark against which we measure the improvement in the status of our knowledge. However, PVAs typically have many parameters, and given the uncertainty around these parameters, there are many ways of getting a good fit from population data to any model.

Models of biological systems are no different from any other scientific tool. If there is not ‘enough’ data to answer the questions at hand, or if the model builder has not taken care to represent ecological ideas and deterministic processes faithfully in the model's equations, PVAs may lead to wrong decisions. There are also many ways to abuse standard statistical tests; the scientific consensus is that the benefits of the availability of powerful computer programs for mathematical and statistical analysis outweigh their disadvantages (Akçakaya & Burgman 1995). The suggestion that analyses may have been made ‘too’ easy (Beissinger & Westphal 1998) emphasises the need for better training and for the specification of standards for a good PVA (see below).

The idea that all plausible models should be explored and their predictions weighted explicitly by the likelihood of the model is reminiscent of a Bayesian view of science (Hilborn & Mangel 1997). Engineering and human health risk analysts distinguish structural uncertainty (different models), natural stochasticity (environmental and demographic stochasticity) and parameter uncertainty (measurement error) (eg. Frey & Rhodes 1996, Cohen et al. 1996). Some elements of structural uncertainty may be examined using Monte Carlo simulation (Frey & Rhodes 1996). If the model structure is incorrect or inappropriate for the species in question, serious errors in prediction are likely. Errors, together with uncertainties, are magnified into the future with each time step, so usually only a few time intervals can be predicted with any certainty. The omission of an important process such as loss of habitat, competition or predation from introduced species, impacts of disease or parasites, or the impacts or rare catastrophic events, may substantially affect what it is best to do to manage a population to avoid extinction (Akçakaya et al. 1997).

The facilitator

Often, a PVA is instrumental in easing the assembly and discussion of a problem. A very large number of PVAs have been conducted with the primary aim of getting people together to discuss a problem and to find a consensus approach to management. For example, Seal (1992) reported conducting 30 Population and Habitat Viability workshops involving 800 people in eight countries. PVAs in this context provide a structured framework that make assumptions plain, and provide a focus for discussions about data, ecological processes and management alternatives. Of course PVA is not essential for this process (Beissinger & Westphal 1998) and one could argue the model plays a subsidiary, and possibly confusing, role to the process of mediation. The confusion can arise when the people concerned become too obsessed with the results of the PVA rather than the process of assembling and integrating information.

The stockbroker

One of the original objectives of developing stochastic models for population dynamics was to weigh expected gains and costs against stochastic catastrophes and uncertain benefits. Risk assessment is often most effective in the role of comparing risks and evaluating the best choice among a range of alternative management options. Managing risks for natural populations results in economic trade-offs within the decision-making framework (Possingham et al. 1993). Decisions made under uncertainty may depend on the attitude of the decision-maker to the prospective risks, the costs of various alternatives (eg. Akçakaya & Raphael 1998), and on how these risks change as circumstances change (Possingham 1997). Such applications make use of formal decision theory to solve problems (Shea et al. 1998). PVA does not include a formal role for decision theory - although there is no reason why the results of a PVA cannot be included in a formal risk-assessment process (Maguire 1987).

Risks must be managed. They are as much a part of the management of threatened species as they are of our personal choices about insurance, investment choices by companies, and strategic defence alliances made by governments. Effective management may be achieved simply by finding a consensus of opinion among scientists, managers and other interest groups, facilitated by workshops.

Often, risk analysis suffers from the fact that it is at a distance from formal decision-making frameworks (Lackey 1997). There is a well-developed literature on cost-benefit analysis and optimal decision making under uncertainty that might be employed to improve decisions about the management of threatened species (Possingham 1996). Our contention is that the most appropriate role for PVA is in comparing risks, rather than measuring risks (Possingham et al. 1993). It is the only available tool for deciding on the allocation of resources to solve problems where the outcomes are inherently unpredictable. It is the only tool available to us that allows assumptions to be stated unambiguously and transparently. That does not mean that these things are always done, only that they should be part of any ‘good’ risk assessment.

The money pit

The cost of carrying out a PVA is not negligible. The naïve manager will often initially view PVA as tool that will deliver answers after an afternoon’s playing on the computer. The appeal of predicting the fate of a species for hundreds of years after guesstimating just a few parameters and then running a fast simulation is appealing. In circumstances where the PVA is used to facilitate discussion, this approach has value. Many species may be ‘workshopped’ in just a week or two with the intent of providing identifying key conservation issues and defining the roles of people interested in conserving the species. We make mistakes in these contexts when we put faith in the absolute values derived from these analyses. Any results derived from a model developed over a few hours cannot be considered reliable, unless the model and the circumstances are so simple and so well understood that the exercise is almost trivial.

We believe that a good management-based PVA will take at least three months using existing software, and several more if one wishes to construct a tailored model. Despite the benefits of model building, there are potential costs. As Beissinger & Westphal (1998) point out, there are real risks of over-interpretation of results and inappropriate belief in model outcomes that are not justified by data. Modelling involves time and money that may be better spent elsewhere. Thus, the scale of the modelling exercise should match the benefits that are likely to result from the exercise.

The roulette wheel

A management decision (such as which patch to purchase first, or which of several populations to target for management) involves a gamble. The dynamics of threatened species, and the management decisions that must be made for them, are acted out on a spatially complex landscape that itself can change randomly through time (Richards & Possingham, in press). In most cases, even if the process could be accurately described mathematically, the optimal management for such a spatially complex stochastic population would be impossible to find mathematically. Our management actions are no different than betting in a game of chance, but one in which we can try to inform ourselves about the different likelihoods of the range of possible events.

While the management of complex non-linear spatial systems may seem daunting – and PVA a crude tool for tackling the problem – surely the tool can, at worst, aid the informed guess of the wildlife manager. In the absence of any other tool even a simple model is better than no model at all.

The correct role for a PVA

Of course, PVA plays all the roles listed above - they are not mutually exclusive. Each of the different roles may be entirely appropriate, depending on context and application. There are good and bad applications of PVAs. Attributes that can seem an advantage – such as model complexity (2.1 ‘the intellectual curio’ and 2.7 ‘the roulette wheel’ above) - can at times be a burden (2.2 ‘the loaded gun’, 2.3 ‘the magnifying glass’ and 2.6 ‘the money pit’ above). These roles are not necessarily criticisms of PVA, but rather are views of a tool that is part of the maturing discipline of conservation biology.

Bearing all these roles in mind we advocate the use of PVA as a decision support tool, rather than as a decision making tool (Possingham et al 1993, Starfield 1997). Disquiet, if not distrust, develops when the model takes over the decision-making process. From our point of view, this unease is well deserved. PVA may play a valuable role in any of the lights in which it is seen. However, we must remember that, by definition ‘All models are wrong but some are useful.’ (Box 1979). The only correct model is an entire reconstruction of the actual system – whereupon it ceases to be a model. The utility of a PVA is determined by several things, including the care taken to include all ecological intuition faithfully, the care taken to represent all views (hypotheses) as structural alternatives, the detail and transparency of statements about assumptions, and the role of the model within the decision-making framework.

One of the most important steps in establishing the credibility of a PVA is to communicate the uncertainties embedded in the model and its assumptions. These will involve natural variation in parameters (spatial, environmental and demographic uncertainty), uncertainty about the true parametric values of the parameters (means, variances, kinds of distributions, dependencies and correlations) and uncertainty about the structure of the model (representing uncertainty about ecological processes). Tools used in communication of these uncertainties include qualitative statements, sensitivity test results, and the use of a variety of graphical representations of the kinds of uncertainty and their consequences for model predictions. Modellers are responsible for communication of these details. Direct communication in workshops provides the least ambiguous form of communication and imparts a degree of ownership of the model to the participants.

The attributes of good PVAs

The attributes that distinguish good risk assessment from poor are debated regularly by the wider community of environmental risk analysts (Power and Adams 1997, Warren-Hicks & Moore 1998). Criticisms of risk assessment models range from a lack of ecological realism (Karr 1995) to objection to their use on the grounds that the analyses are distorted inevitably by the personal values and attitudes to risk of those who build the models (Funke 1995). Furthermore, it may be argued that risk assessment tools (such as PVA) can be used to support almost any predetermined policy position and provide for it a mantle of scientific acceptability (Merrell 1995) when manipulated by a cunning user. These criticisms are, of course, made equally in any scientific arena. There is always a risk that performing of a relatively sophisticated analysis will create the appearance of scientific rigour (Burmaster & Anderson 1994).

Reporting requirements for Monte Carlo simulations should enable reviewers to replicate the analyses. The requirements of a PVA should be such that it is appropriate for the questions at hand, and that it be transparent and internally consistent. The value of any model depends on how clearly and thoroughly its limitations have been communicated. In the spirit of recognising the potential for misapplication of risk assessment, we suggest the following criteria be used to evaluate the quality of a PVA. These attributes are based on the description of protocols for best practice quantitative uncertainty analysis by Burmaster & Anderson (1994), Ferson (1996a,b), Oreskes et al. (1994), Shea et al. (1998), Warren-Hicks & Moore (1998) and Noon et al. (in press).

The most important elements of a successful PVA

- A fundamental understanding of the species' ecology, including what constitutes suitable habitat, and the ability of the species to disperse between patches of habitat
- An understanding of the environmental disturbances that directly threaten (or indirectly threaten through habitat alteration) a species, their probabilities, and impacts on the population (or habitat). This should include the effects of both deterministic threats (eg. timber harvesting, recognising that nothing is completely deterministic), and stochastic threats (eg. hurricanes)
- An understanding of the response of the species to the threats (eg. density dependence)
- An assessment of the current state of the population
- An assessment of the probabilities of future risks

- An evaluation of the habitat as well as the population itself, and
- The extent to which the PVA helps managers make decisions.

In explaining the motivation for, data behind, and implications of, a good PVA the conservation biologists needs to fully describe many things.

Describe the context

- Outline the motivation
- Explain the application of the results
- Identify any sources of contention or any resources that depend on the outcome
- State the position of the modellers in relation to these parameters
- Describe the management objectives, options and indicators of performance, and
- Describe constraints on decision variables and management options.

Describe the model

- Show all formulae,
- Identify components based on
    - scientific or professional consensus
    - professional judgement by an individual
    - policy
- Show alternative components and alternative formulae when no consensus exists
- Demonstrate that units make dimensional sense, and
- Identify critical assumptions.

Describe the data

- Provide an evaluation of the quality of the input data for all the
    - means
    - variances, and
    - dependencies
- Describe procedures used to calibrate parameters
- Discuss the ways in which the model captures structural uncertainty, natural variation, and parameter uncertainty
- Provide sources and values for all parameters (sampling distributions, shape and position parameters, correlation structures), and
- Discuss potential consequences of extrapolations, alternative distributions, kinds of dependencies or correlations.

Describe the analysis

- Describe the ways in which dependencies are handled
- Demonstrate that relationships between variables are feasible and plausible (ie., ensure the correlation structures are self-consistent and that sampled values fall within plausible ranges)
- Describe and evaluate the random number generator used in the analyses
- Describe and rationalise the choice of summary statistics (ie., state variables: interval extinction risk, terminal extinction risk, quasiextinction thresholds, quasiexplosion thresholds, time to extinction, bounds on extinction probabilities, mean population, median population, confidence intervals, interquantile ranges, harvest volumes, translocation numbers, occupancy rates, ranks of management options, costs, benefits)

- Rationalise any sources of ignorance or variability that may contribute to future surprises, and
- Describe approaches for verification and validation of model output.

Describe the output

- Provide complete information on each of the model's state variables
- Provide quantitative, deterministic sensitivity analysis
- Provide quantitative, stochastic sensitivity analysis
- Display central tendencies and tails of the output
- Describe the qualitative fit between model results, *a priori* expectations and empirical observations, and
- Describe the quantitative fit of the model to independent observations.

In judging the adequacy of a model in a given circumstance, there are several things that Monte Carlo simulation cannot do (Ferson 1996a). They include:

- The propagation of non-statistical uncertainty: if uncertainty about parameters or model structures is qualitative, vague or linguistic, then the model cannot account for these uncertainties adequately.
- Provision of reliable quantitative answers when statistical dependencies are unknown, when input distributions are unknown, and when the model structure is unknown. If the knowledge is not available through empirical studies, it must be present in the form of explicit assumptions, evaluation of alternatives, and sensitivity analyses.
- Provision of general bounds on uncertainty. If dependencies are unknown or uncertain, then the model will not provide bounds that are broad as they could be if all possibilities were to be explored (Ferson & Burgman 1995).

The above guidelines are intended to promote PVA quality assurance – something which we have failed to achieve as much as others. In addition, human errors can appear in the form of data transcription errors, incorrect model specification, logical and algorithmic errors, output errors and so on. In complex models, data and computational errors can be exceedingly difficult to detect and correct. Whenever PVAs are submitted for review, the source code or at least the complied computer program used to produce them should be supplied so that models can be tested. This is perhaps the greatest strength of ready-made computer programs; they have the distinct advantage of being relatively free of computational mistakes. Because dealing with uncertainty is a special problem with PVA, both in the context of the input and the output, here we elaborate on some of these issues in more detail.

Dealing with uncertainty and parameter estimation

Models fall into disrepute when the people that build them fail to communicate fully the uncertainties in the model's construction, parameter estimation and output (Burgman et al. 1993). Most, if not all, PVAs constructed to date do not take full account of all sources of uncertainty. They underestimate the full extent of possible outcomes.

Uncertainty about stochasticity has several components. They include measurement error of the moments of the statistical distributions representing natural variation, uncertainty about the form of the statistical distributions from which to draw this variation, uncertainty about the form and strength of dependencies among random variables in the model, and uncertainty about the structure of the equations representing growth, survival, reproduction and dispersal. Most models use a single kind of statistical distribution to represent uncertainty without any clear reasoning for the choice, most use one simple set of linear dependencies without exploring other possible scenarios, and most use a single model structure (McCarthy et al. 1995).

The most important weaknesses of most current PVAs are the failures to propagate correctly the stochasticity and structural uncertainties inherent in the model. These simplifications make the task of generating simulations easy, but they fail to communicate the full extent of our uncertainty in the outcomes. The choices we make about these seemingly arbitrary conditions may make a substantial difference to the model's predictions, particularly in the tails of the distributions (Haas 1997).

There are methods for propagating uncertainty about statistical distributions and dependencies in risk assessment models. Monte Carlo simulation of alternative distributions may be used in what is known as a two-stage analysis (Hoffman & Hammonds 1994, Frey & Rhodes 1996). In these analyses, parameter uncertainty and structural uncertainty are treated in a factorial design in which a range of possible combinations of distributions and parameter settings are trialled, resulting in a cloud of possible trajectories. There have been developments in computations that use the principle of maximum entropy to select distributions to represent uncertainty (e.g., Lee & Wright 1994). Other approaches use probability-bounds calculus (Ferson et al. 1999) to accommodate any level of knowledge about statistical uncertainty, and propagate these uncertainties faithfully through a chain of calculations. Detailed brute-force sensitivity studies should be able to accommodate most (but not all) of these issues, yet most sensitivity studies, when they are included at all, focus on a very limited set of possibilities that underplay important structural and statistical uncertainties.

Having defined how the PVA process should occur, there remain many issues that require further work as we strive for a better product. The resolution of these problems is a future challenge for us all. Three special issues are raised below.

Dealing with spatial complexity

Many recent PVAs include a spatial component which can be explicit (Lindmayer & Possingham 1996) or vague (Hanski et al. 1996). Spatially explicit models are being seen increasingly as an important decision-support tool when we need to make specific spatial decisions – such as where to put a reserve or corridor, and where to protect habitat from disturbance. Unfortunately the introduction of spatial heterogeneity brings with it an avalanche of increased data requirements such as detailed habitat maps, detailed information on movement and associated mortalities, spatial correlations of catastrophes and environmental variability, and dependence of population processes on habitat. Ruckelshaus et al. (1997) evaluated the effect on model predictions of misclassification of habitat suitability, errors in estimation of dispersal distances, and errors in estimation of the mortality rate of dispersers. They found that parameter estimation errors concerning mortality during dispersal can have an important qualitative effect on the predictions of spatially explicit models. They suggest that models of animal movement that depend on GIS maps are sensitive to errors in the data used to construct the representation of habitat. Models may make robust predictions within sets of plausible conditions, and some models make reliable and unbiased predictions when based on sparse data (Groom & Pascual 1997). Increasing model complexity results in realism only if the parameters may be estimated accurately. Estimates based on insufficient data represent additional assumptions.

Increased complexity can sometimes be valuable, even in the absence of requisite data (eg., Letcher 1998), because it allows us to explore ideas, identify important parameters that we may not yet have measured, and makes transparent the assumptions necessary to answer questions put by management. The important point is that the need for data does not vanish when we simplify a model. Rather, the required data are subsumed within the assumptions of the simpler model. The advantage of a complex model is that it forces us to be explicit about these assumptions. Of course, there is a trade-off between the time invested in modelling, and the insight that the model provides. The art of model building is to find this balance.

How important is genetic information?

Since Lande (1987) there has been a minor backlash against the importance of genetic data and processes in making decisions about threatened species management. If were ask some of the questions alluded to above in a genetic context: How expensive is genetic data to get? How will it change our decision-making? What is the relationship between the genetic structure of a population and its demographic processes? Why have so many specie appeared to recover from a seemingly fatal genetic bottleneck? The most apparent role of genetic information comes from molecular ecology, where the data are used to identify the object of any conservation effort (a population, metapopulation or species), and to provide estimates and plausible bounds for demographic attributes that are otherwise impossible to obtain (such as social structure, and dispersal rates) (Frankham 1995a). But the caveats that apply to spatial structure also apply to the population genetic dimension of management. If we do not deal with the genetic implications of population management explicitly, then they become buried in the assumptions of the decision-making process. The advantage of a model that accounts for genetic variation is that it forces us to be explicit about the effects of inbreeding, outbreeding depression, mutational meltdown, and the range of plausible interactions between demographic attributes and genetic composition (Frankham 1995b). Formal sensitivity analysis would allow an evaluation of the potential importance of these features. The fact that we may not know many of the parameters necessary to parameterise such a model does not mean we can subvert the need to know them by ignoring them in a simplified model structure. Experience may allow us to make assumptions and thereby make the process of modelling efficient, but a good model will rationalise these assumptions.

PVA and decision theory

Like much of the theory of conservation biology, PVA outside the context of decision theory is of little practical use (Possingham 1997). For example, what is the value of finding the forest management option that will minimise the extinction probability for an old-growth specialist when that option is unacceptable to the associated timber industry? There may be other solutions that are almost as efficient from the perspective of minimising added risks, but which are much less costly from a social perspective. Costs, constraints and objectives need to be built in to any decision-making process and PVA does not formally allow for these issues to be included.

If we recognise that a population management model for a threatened species is inherently stochastic and decisions are likely to depend on current circumstances (eg., the price of timber) then we must accept that stochastic dynamic programming represents the only way to find the precise optimal strategy (Millner-Gulland 1997, Possingham & Tuck 1998). Given the complexity of the state-space, dynamics and management options the full problem will almost always be insoluble. We believe that the only practical way forward is to develop some robust rules of thumb that work under common scenarios.

Conclusions

In any discipline, there is a time lag between the development of theoretical ideas and their sensible application. The lag is created by the scientific community being duly cautious about developing a consensus on the ways in which a new method is best applied. Improvements in theory will result, ultimately, in better decisions. For the moment, we do the best with what we have. Currently we have tools available to us that we are not using. They include formal propagation of statistical uncertainty, exploration of structural alternatives, and application of decision theory. Hence there remain challenges to theoreticians, empiricists and managers in the development of PVA as a tool. We reassert our final opinion, that when making a decision concerning a threatened species, it is better to make it having tried to build and run a population model, than otherwise. The absence of the requisite data is always going to be problematic, but it is not debilitating, and cannot be avoided by simplifying a model or by deciding to dispense with modelling altogether.

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