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Population Viability Analysis: Past, Present, Future

Steven R. Beissinger

Population viability analysis (PVA) has become a cornerstone of conservation science. It is both a process and a tool that has been used to create theory, to analyze data and project population trends, and to make policy decisions. Viability is a pervasive concept that has contributed almost as much to theory as it has to application. PVA has provided a framework for understanding how stochastic events and processes affect the chances of extinction (Lande, chap. 2 in this volume). The role of stochasticity in extinction has been called the *small-population paradigm* (Caughley 1994). Few scientists challenge the notion that genetic, demographic, and environmental stochasticity and catastrophes can result in extinction, although the relative role of each process is often debated (Lande 1988, 1993; Allendorf and Ryman, chap. 4 in this volume). Yet it is the way in which we apply viability concepts to evaluating risks and recovery strategies for populations, species, and ecosystems in trouble that has sometimes engendered controversy over both scientific theories and public policy (Mann and Plummer 1999; Shaffer et al., chap. 7 in this volume).

Perhaps these disagreements stem partly from differences in the way that viability processes interact with the processes of recovering endangered species, which Graeme Caughley (1994) so elegantly defined as the *declining-population paradigm*. The declining-population paradigm consists of determining if there is a population trend, identifying what element of the organism's demography is depressed, determining the environmental or intrinsic factors that cause the depressed rate, and then examining what can be done to correct these limiting factors. In this paradigm, stochasticity is rarely identified as a specific cause of poor reproduction or survival, perhaps with the exception of some genetic factors like inbreeding. The declining-population paradigm and the small-population paradigm offer complementary ways of analyzing the same problem, and they may lead to similar or contradictory conclusions (Boyce, chap. 3 in this volume).

This chapter reviews the past, present, and future of PVA from the perspective of a conservation biologist who works at the interface of academia and management and advocates good science rather than a

particular conservation philosophy. In doing so, I try to bridge the worlds of model builders and legacy builders. I begin by examining the history and growth of PVA over the past 20 years and review how it has evolved to date. I next consider the criticisms of PVA and how it has been applied in conservation. I conclude by speculating about how PVA might look in the future.

HISTORY AND GROWTH OF PVA

While the history of PVA is short (Soulé 1987a), the nature of PVA has changed greatly over time. At the beginning of the 1960s, prior to the passage of the first U.S. Endangered Species Act in 1966, the most threatened and publicly visible endangered species in the United States were the California condor (*Gymnogyps californianus*), whooping crane (*Grus americana*), tule elk (*Cervus elaphus nannodes*), and black-footed ferret (*Mustela nigripes*). It is notable that PVA did not contribute to the recovery of any of these species, except after the fact for the condor and ferret, although deterministic demographic models that estimated the rate of annual population growth had been used to make management recommendations for the whooping crane (Miller and Botkin 1974) and for the California condor (Mertz 1971).

PVA was spawned by a controversy in the late 1970s over the Yellowstone National Park population of grizzly bears (*Ursus arctos*). The controversy centered on the recommendations made by wildlife researchers John and Frank Craighead and their colleagues regarding the consequences of closing the park dumps to the bear population. Craighead et al. (1973) used a computer model to show that mortality from the park's approach to problem bears was driving the population to extinction, which led to a review by a National Academy of Sciences committee (Cowan et al. 1974). As a member of the committee, Dale McCullough developed an alternative model that led to differing predictions about the grizzly bear's fate and which was subsequently published (McCullough 1978, 1986). Both models were deterministic models, although McCullough (1986) and Avrin (1976) investigated stochastic recruitment. A model for the grizzly bear that included both demographic and environmental stochasticity was later developed by Mark Shaffer in 1978 as part of his Ph.D. dissertation at Duke University, and to him goes the credit for the first true PVA.

Shaffer's approach (1981) was a new direction in the use of models for conservation, because he developed a stochastic population simulation that incorporated chance events—specifically demographic and environmental stochasticity—and produced extinction probabilities. His model also estimated a minimum viable population size (MVP) by

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Shaffer's MVP paper was followed by the publication of Frankel and Soulé's *Conservation and Evolution* in 1981. Here for the first time genetic approaches to evaluate the viability of populations were detailed in one place, building on the work of Denniston (1978). The short-term and long-term effects of inbreeding and genetic drift were placed in a framework that clarified their erosive impacts on genetic diversity. Here is where the 50/500 rule for effective population sizes, which had recently been proposed by Franklin (1980) and Soulé (1980), was stated in a manner that became etched into the conservation consciousness, for better or worse, as one of the few rules of thumb that conservation biologists have produced to judge viability.

Soon papers that estimated MVP size began to appear (Schonewald-Cox et al. 1983; Lacava and Hughes 1984; Lehmkuhl 1984; Shaffer and Samson 1985; Menges 1986; Reed et al. 1988). Most of these works employed genetic approaches to determine MVPs by adapting and parameterizing demographic equations for estimating effective population size that had been part of classical population genetics theory. I suspect that demographic applications of PVA lagged behind genetic applications because of the difficulty and time involved in developing Monte Carlo computer applications that were needed to produce MVPs based on stochastic population simulations. Let's not forget that in the mid-1980s the personal computer was just making its appearance on the commercial market, and programming in FORTRAN for mainframe computers using decks of cards could hardly be called user-friendly.

In 1986 the work of Michael Gilpin and Michael Soulé put PVA on

firmer footing. Gilpin and Soulé (1986) broadened the definition of PVA when they used it as a heuristic concept to examine the many forces that interact in vortices that can affect the viability of a population, including genetic factors. Although they designated the term "Population Vulnerability Analysis" for this approach, the term never became widely used. However, the idea of PVA as a process of risk analysis emerged, where hazards are identified, risks are considered, and a model is developed in the final step.

The Gilpin and Soulé paper made its debut in 1985 at the Ann Arbor, Michigan, meeting where the Society for Conservation Biology was established. Prior to that meeting, there was a workshop that gathered a few scientists together to work on the MVP concept. The result was a series of papers published in *Viable Populations for Conservation* (edited by Soulé [1987b]) that established PVA as both a process and a technique. Concurrently, Gilpin and Soulé were working on the first metapopulation PVA model for a threatened water snake (Soulé 1989).

PVA applications grew rapidly in the late 1980s and early 1990s, largely due to two factors. First, zoological parks quickly employed the power of genetic viability concepts to help them manage small populations in captivity to minimize the loss of genetic diversity. Robert Lacy, Jon Ballou, Kathy Ralls, Ulysses Seal, and others developed workshops and computer software programs to assist zoos in managing captive populations. The application of the small-population paradigm has been extremely successful in this regard. Second, demographic PVAs proliferated rapidly with the development of a variety of computer software packages, such as VORTEX, the RAMAS series, and ALEX, that made Monte Carlo population simulations relatively easy to perform (Lindenmayer et al. 1995). These software packages put PVA on the desktop computer of every interested conservation biologist and empowered users who were computer literate but who were not computer programmers. The advent of these computer programs, as much as any other single factor, promoted the rapid proliferation of PVA as a tool for evaluating conservation problems.

As the power of personal computers has grown over the past decade, approaches for modeling populations have changed. Ease of computation led to exploring a greater number of scenarios in simulation models and to more sophisticated sensitivity analyses (Mills and Lindberg, chap. 16 in this volume). Also, in the past 20 years PVA models have become more complex as we began to incorporate spatial processes. Models grew from single populations to metapopulation models that treated demography at the level of a homogeneous patch, then matured to grid models that created spatially explicit addresses for groups of

individuals that allowed them to take on demographic characteristics based on the surrounding grid squares, and finally ripened to the current trend of individual-based models that track each individual as it lives, dies, and moves among landscape elements (Beissinger and Westphal 1998).

The increase in model complexity was driven by the need to consider a variety of processes and scales that affect both organisms and management decisions, and by the growth of GIS and remote sensing technologies. The "rediscovery" of Levins's metapopulation concept (1969, 1970) and its application to conservation biology spawned a new spate of theory, more field studies, and sophisticated modeling efforts. Furthermore, Pulliam's work (1988) on sources and sinks reminded us that demography could vary across a landscape. Hanski (chap. 5 in this volume) and Harrison and Ray (chap. 6 in this volume) summarize advances in this field and the applicability of metapopulation models to animal and plant populations, respectively.

With new technologies, conservation biologists now had the tools to make relatively detailed habitat maps. All that was required to build models that were spatially explicit was the ability to construct complex computer programs. The increased complexity of spatially explicit and individual-based models was seductive because they could be applied to specific conservation situations, such as the loss of particular patches to habitat destruction or the role of dispersal corridors (Dunning et al. 1995). However, increasing the complexity of models also greatly inflated the number of model parameters that had to be estimated (Beissinger and Westphal 1998; Ralls et al., chap. 25 in this volume). It is an unusual endangered species for which we have enough data to estimate most parameters in these models. Such species are either inherently easy to study or their welfare is threatened by the extraction of very valuable resources, which results in large financial investments in field research. Even in these cases, data that are critical to model outcomes—such as mortality rates in relation to movement—may not exist.

CURRENT ISSUES IN THE USE OF PVA

Despite the prevalent position of PVA in conservation science, there has been growing concern over how PVA models are used for making conservation decisions (Boyce 1992; Ralls and Taylor 1997; Beissinger and Westphal 1998; Groom and Pascual 1998; Reed et al. 1998). Criticisms have been raised over the manner that inputs, assumptions, and structure of demographic PVA models affect their ability to predict the fate of populations with accuracy and precision. Four dominant causes of errors result in uncertainty in the outcomes predicted by PVA models:

(1) poor data, (2) difficulties in parameter estimation, (3) weak ability to validate models, and (4) effects of alternative model structures.

Rarely have detailed field studies with adequate sample sizes been used for developing mean estimates of vital rates, and causes and timing of mortality are seldom known. In animals, survival is often the most difficult vital rate to measure precisely because it must be distinguished from the probability of resighting (Nichols 1992). Although sophisticated mark-recapture statistical techniques have been developed to yield accurate estimators of survival and test for differences among individuals of different ages or stages (Lebreton et al. 1992; White et al., chap. 9 in this volume), they require a minimum of three years of study to estimate probability of resighting and survivorship for a single year, and more years to develop precise estimators when the probability of resighting is low. Unfortunately, lack of good survival data can complicate estimation of population change and extinction rates, because elasticity and sensitivity analyses suggest that population change in long-lived organisms is usually most affected by changes in adult survivorship (Boyce 1992; Silvertown et al. 1993; Pfister 1998; Sæther and Bakke 2000). Estimating survival of adults is much less of a problem in plant studies, since they are nonvagile, but survival of seeds and mating success are correspondingly difficult to measure (Doak et al., chap. 15 in this volume). In addition, survival is difficult to estimate for perennials that experience dormancy. As a way to circumvent this problem, mark-recapture models were recently adapted to estimate dormancy and survival rates for rare perennials (Shefferson et al. 2001).

It is equally challenging to develop robust variance estimators for stochastic models (White et al., chap. 9 in this volume). We still require formal definitions of demographic and environmental stochasticity for age- and stage-structured models, which are well tested and confirmed, to incorporate into PVA software (Sæther and Engen, chap. 10 in this volume). Furthermore, accurate estimates for variance of vital rates may require demographic measurements made over many years to sample the range of environmental variation. Rare events, such as 1-in-50- or 100-year droughts, floods, fires, or storms, likely have large effects on variance estimates and population viability (Ludwig 1996, 1999). Long-term studies have shown that estimated variance in population size does not begin to asymptote until after 8 to 20 years, if at all (Pimm 1991). Use of data from short-term studies will usually underestimate the variance in vital rates. However, the effect of short study periods may be offset because estimates of variance derived from field studies include sampling error, which results in an overestimate of variance (Beissinger and Westphal 1998; White et al., chap. 9 in this volume).

Dispersal rates are an important component of metapopulation and spatially explicit models, but our understanding of dispersal is very poor for most species (Hanski, chap. 5 in this volume; Harrison and Ray, chap. 6 in this volume). Consequently, dispersal rules are often coarse caricatures of biological reality due to the difficulty of empirically determining dispersal distances, age of dispersers, and mortality during dispersal. Errors are most exacerbated for species with low success in finding suitable habitat, precisely the situation for many endangered species in fragmented landscapes (Kareiva et al. 1997).

Once a PVA model is constructed and parameterized, it is unwise to place great confidence in its outputs until the model has been tested to determine its accuracy and ability to make predictions (Oreskes et al. 1994; Bart 1995). PVA models are rarely tested against independently gathered field data, so validating their primary prediction, the probability of extinction, is very difficult (Belovsky et al. 1999, chap. 13 in this volume). True validation would require tracking scores of replicate populations that experienced similar conditions and comparing predicted to observed frequencies of extinction, something that is far better suited to the laboratory than to the field. Comparing the average population projection to a time series of population size (e.g., Brook et al. 2000) does not verify value of environmental stochasticity or the magnitude and frequency of catastrophes used in the model, which are a primary cause of differences among replicate model runs and the likelihood of extinction. Usually the best that can be done is to test model assumptions or secondary predictions other than time to extinction, such as estimates for means and variances of vital rates, the distribution of individuals on landscapes, or movement rules. Attempting to confirm secondary predictions could lead to real improvements in the predictive ability of PVA models.

Uncertainty is just about the only certainty in PVA. How we deal with uncertainty in making decisions with PVA models is the subject of much ongoing work. Incorporating Bayesian statistical approaches into PVA is an alternative to frequentist statistics that offers a new way to incorporate uncertainty into model building (Wade, chap. 11 in this volume). Taylor et al. (chap. 12 in this volume) examine the performance of this approach for listing species under ESA and determining what level of threat they should be assigned. Alternatively, one can construct a prediction interval for comparison with model results (Sæther and Engen, chap. 10 in this volume). Still another approach to uncertainty is to take a decision-analysis perspective to examine costs and benefits and then rank management options (Possingham et al., chap. 22 in this volume).

In the absence of data, sensitivity analyses are often recommended to determine which parameters most affect model outcomes and require more study or better parameter estimation. Sensitivity analyses, such as elasticity, have also been used to rank options for conservation actions (Mills and Lindberg, chap. 16 in this volume). However, such analyses do not indicate what factors are causing populations to decline, and elasticity estimates are not value free, but depend on the vital rates used (Caswell 1996, 2001). If a demographic rate is depressed due to the effects of a limiting factor, its matrix element(s) will have a smaller elasticity value and would wrongly suggest that stages associated with this element are less important for management than other elements (Beissinger and Westphal 1998). A little-appreciated insight from sensitivity analyses is that recovery will require more time in populations that are declining due to limiting factors operating on elements or variables with low sensitivity than on those with high sensitivity. From elasticity or other kinds of sensitivity analyses, one can identify the potential management strategy that leads to the fastest population recovery, but one cannot conclude which factors limit population growth.

An important conceptual issue is the need to incorporate genetics in our understanding of population viability and the application of PVA. While genetics was central in many early applications of PVA, the pendulum swung during the last decade to demographic applications, and presently genetics is not well integrated into PVA. Most would agree that this was a good trend, but the momentum in thinking is shifting again, and it is time to reexamine the proper blend of genetics and demography (Allendorf and Ryman, chap. 4 in this volume). Examining the interaction of genetics and demography is problematic, in part because of the difficulty of translating genetic currencies of heterozygosity and diversity into a probability of extinction. We still have few direct studies that link genetic diversity to individual survival and fitness. Even rarer are demonstrations of the role of genetics on the viability of populations. Just considering the negative effects of inbreeding, it can be difficult to say how genetics should be incorporated into demographic models; for example, should it affect juvenile mortality, adult mortality, or litter or clutch size? It can be hard to know the magnitude of the impacts of inbreeding, or what demographic characteristic it will affect.

There are, however, a number of ways that genetics can be better incorporated into PVA. Hedrick (chap. 17 in this volume) describes how molecular genetics has been able to answer a variety of questions that are notoriously difficult for demographic studies to tackle. Estimates of effective population size (N_e) have been one of the main genetic approaches used to assess viability. Yet there are still improvements that

Analyses are often recommended to predict model outcomes and require sensitivity analyses, such as elasticity analyses (see options for conservation actions in this volume). However, such analyses are often difficult for populations to decline, and elasticity analyses depend on the vital rates used. If the growth rate is depressed due to the loss of a dominant element(s) will have a smaller elasticity than other elements (Beissinger 2002). The insight from sensitivity analyses is that time in populations that are dependent on elements or variables with low elasticity. From elasticity analyses, one can identify the potential management actions for population recovery, but one cannot predict population growth.

There is a need to incorporate genetics into conservation and the application of PVA. The primary applications of PVA, the use of demographic applications, and the use of genetics into PVA. Most would agree that the momentum in thinking is shifting toward a proper blend of genetics and demography (see 4 in this volume). Examining the role of genetics is problematic, in part because of the different currencies of heterozygosity and genetic diversity. We still have few direct measures of individual survival and fitness. Even the use of genetics on the viability of populations, the effects of inbreeding, it can be incorporated into demographic models, juvenile mortality, adult mortality, and the ability to know the magnitude of the genetic characteristic it will affect. The use of genetics can be better integrated into PVA (see 7 in this volume) describes how to answer a variety of questions that require genetic studies to tackle. Estimates of the impact of one of the main genetic approaches are still improvements that

can be made to estimating N_e , and this concept can be better integrated into PVA (Waples, chap. 8 in this volume). Another useful genetic approach, pedigree analysis, has often been used with captive animals but has rarely been employed with wild populations, where it could make important contributions (Haig and Ballou, chap. 18 in this volume). Do we need to develop a genetic PVA that would estimate genetic goals to complement management directives from demographic PVAs?

THE FUTURE OF PVA

Given the issues facing PVA, what will be its future? Single-species conservation approaches like PVA are sometimes pitted against multispecies conservation approaches currently in vogue such as identification and preservation of biodiversity hot spots, landscape conservation planning, and ecosystem conservation. Do we really need PVA in the age of GAP analysis to identify where reserves should be placed, campaigns to establish border-to-border wilderness, implementation of ecosystem management approaches such as President Clinton's Northwest Forest Plan, and complex reserve selection algorithms?

Yes! PVA appears unlikely to go extinct in the near future because of the kinds of challenges that conservation biologists and decision makers need to address. The problems of managing small or declining populations of threatened species inside and outside of reserves that motivate us to construct formal models and conduct PVAs will not only continue into the foreseeable future, but are likely to grow in prominence as the human population continues to expand and its enterprises threaten more species.

There are, however, disparate views of the directions that PVA might evolve. It seems natural to incorporate some PVA approaches as part of a risk-management framework, and decision makers need and want the kind of information that PVA can provide (Goodman, chap. 21 in this volume). Optimists suggest expanding PVA from static to dynamic models that incorporate human factors like land use, economics, and politics that affect the future of the earth's biological diversity (Lacy and Miller, chap. 23 in this volume). With increased computing and remote sensing capabilities, it is easy to envision models that will become more complex and be limited primarily by ability of field biologists to provide critical data (Beissinger et al. 2002). Pessimists, however, argue that PVA will decline in importance because PVA models cannot and will never be able to accurately predict extinction rates, and past attempts to implement truly adaptive management have a mixed record at best (Ludwig and Walters, chap. 24 in this volume).

If PVA models are not ready to make forecasts of the future trajectory

of a population 25 years down the road, let alone the 50, 100, or 1,000 years that models have been used to project, what should their role be in making management decisions? Some uses of PVA interpret model output in an absolute fashion by assuming that the models are predicting the fate of a population (Beissinger and Westphal 1998). Other uses of PVA compare relative differences among scenarios to rank model alternatives. It makes sense to treat applications of PVA that interpret model output in an absolute and relative fashion differently (Ralls et al., chap. 25 in this volume).

Currently, PVA lacks standards or guidelines for use. What is a PVA? What is a viable population? There is no established definition of what passes for a respectable PVA, or a consensus of what constitutes a viable population in terms of time horizons or levels of acceptable risk of extinction. What type of PVA model is appropriate, given the many types of models that can be used? What makes a good PVA? When should we use PVA instead of alternative approaches for gaining understanding, estimating risk, and making decisions? Ralls et al. (chap. 25 in this volume) discuss these issues and offer initial suggestions for establishing criteria to judge the merits of a PVA and guidelines for its use.

However PVA is used in the future, the added scrutiny that PVA has recently received from scientists has already raised the bar for what constitutes a good PVA. It will become harder to use guesses or poorly documented inputs in PVA models instead of rigorously developed estimates for vital rates and other model parameters. Models that have not thoroughly explored the sensitivity of model outputs to changes of each parameter and explored how changes in model structure affect model outcomes are unlikely to be well received. Likewise, models that do not incorporate or analyze the role of uncertainty on model predictions are certain to fail.

In conclusion, the future of PVA depends very much upon the way that conservation biologists develop and apply PVA models, and how they sell model results to policymakers and managers. PVA has had few successes in the policy process, but the need remains as great as ever (Shaffer et al., chap. 7 in this volume). Laws mandate that decisions must be made on the fate of species. How PVA reinvents itself and evolves in the future is up to us.

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guidelines for use. What is a PVA? no established definition of what a viable or levels of acceptable risk of extinction, given the many types of models makes a good PVA? When should we reach for gaining understanding, Ralls et al. (chap. 25 in this volume) offers suggestions for establishing guidelines for its use.

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depends very much upon the way we use and apply PVA models, and how we use them and managers. PVA has had few needs and the need remains as great as ever (see also Ralls et al. 1998). Laws mandate that decisions be made. How PVA reinvents itself and

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