

Emerging Issues in Population Viability Analysis

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Abstract: *Population viability analysis (PVA) has become a commonly used tool in endangered species management. There is no single process that constitutes PVA, but all approaches have in common an assessment of a population's risk of extinction (or quasi extinction) or its projected population growth either under current conditions or expected from proposed management. As model sophistication increases, and software programs that facilitate PVA without the need for modeling expertise become more available, there is greater potential for the misuse of models and increased confusion over interpreting their results. Consequently, we discuss the practical use and limitations of PVA in conservation planning, and we discuss some emerging issues of PVA. We review extant issues that have become prominent in PVA, including spatially explicit modeling, sensitivity analysis, incorporating genetics into PVA, PVA in plants, and PVA software packages, but our coverage of emerging issues is not comprehensive. We conclude that PVA is a powerful tool in conservation biology for comparing alternative research plans and relative extinction risks among species, but we suggest caution in its use: (1) because PVA is a model, its validity depends on the appropriateness of the model's structure and data quality; (2) results should be presented with appropriate assessment of confidence; (3) model construction and results should be subject to external review, and (4) model structure, input, and results should be treated as hypotheses to be tested. We also suggest (5) restricting the definition of PVA to development of a formal quantitative model, (6) focusing more research on determining how pervasive density-dependence feedback is across species, and (7) not using PVA to determine minimum population size or (8) the specific probability of reaching extinction. The most appropriate use of PVA may be for comparing the relative effects of potential management actions on population growth or persistence.*

Uso y Temas Emergentes del Análisis de Viabilidad Poblacional

Resumen: *El análisis de viabilidad poblacional (AVP) es una herramienta de uso común en el manejo de especies en peligro. No hay un proceso único que constituya al AVP, pero todos los enfoques tienen en común la estimación del riesgo de extinción (o cuasi extinción) o la proyección del crecimiento poblacional, ya sea bajo las condiciones actuales o las esperadas del manejo propuesto. A medida que aumenta la sofisticación del modelo, y que se dispone de programas de cómputo que facilitan el AVP sin necesidad de experiencia en modelaje, hay una mayor posibilidad de desaprovechar el modelo y una mayor confusión en la interpretación de los resultados. En consecuencia, discutimos el uso práctico y las limitaciones del AVP en la planificación de conservación y discutimos algunos temas emergentes del AVP. Revisamos temas vigentes que son prominentes en el AVP, incluyendo el modelaje espacialmente explícito, el análisis de sensibilidad, la inclusión de la genética en el AVP, AVP en plantas y paquetes de cómputo de AVP, sin embargo nuestra revisión*

de los temas emergentes no es amplia. Concluimos que el AVP es una herramienta poderosa para la biología de la conservación para comparar planes de investigación alternos y los riesgos de extinción entre especies, pero sugerimos precaución en su uso: (1) porque el AVP es un modelo cuya validez depende en la eficacia de la estructura del modelo y la calidad de los datos, (2) los resultados deberían presentarse con la evaluación de su confiabilidad, (3) la construcción del modelo y sus resultados deberían ser sometidos a revisión externa y (4) la estructura del modelo, los datos y los resultados deberían ser tratadas como hipótesis a probar. También sugerimos (5) restringir la definición del AVP para desarrollar un modelo cuantitativo formal, (6) realizar más investigación para determinar que tan extensa es la reacción de las especies a la denso-dependencia y (7) no utilizar el AVP para determinar el tamaño poblacional mínimo u (8) la probabilidad específica de extinción. El uso más adecuado del AVP puede ser para comparar los efectos relativos de las acciones de manejo sobre el crecimiento de la población o su persistencia.

Introduction

One of the most powerful and pervasive tools in conservation biology is population viability analysis (PVA). There is no consensus on the definition of a PVA, and use of the term has ranged from qualitative, verbal processes without models to mathematically sophisticated, spatially explicit, stochastic simulation models. What all uses of PVA have in common, however, is an assessment of the risk of reaching some threshold, such as extinction, or of the projected growth for a population, either under current conditions or those predicted for proposed management. We would like to see the definition of PVA narrowed to quantitative modeling, as does Ralls et al. (2002), and here we focus on model-based PVAs. Because PVA is used increasingly in policy development and management planning, it should be based on the best available science.

The use of PVA has increased greatly in the last decade as scientists and natural resource managers have sought ways to assess the extinction risks of species (Beissinger 2002). The types of PVA vary widely, and there are a variety of packaged modeling programs available for the assessment of population viability. These have made PVA relatively painless to use for the mathematically unsophisticated or the hurried researcher seeking quick answers to important questions. As we discuss later, however, PVA should not be used superficially. Early viability assessment focused on estimating minimum viable population size, a concept that has long been recognized (Allee 1931; Leopold 1933). Despite recognition that population viability is determined by a combination of factors (Shaffer 1981), the first viability analyses focused on subsets of factors (demographic stochasticity [Shaffer 1983]; genetic stochasticity [LaCava & Hughes 1984; Lehmkuhl 1984]). Although Gilpin and Soulé (1986) reinforced and expanded on Shaffer's (1981) argument that viability is multifaceted, current viability analyses typically incorporate only demographic and environmental stochasticity, often ignoring potential risks due to genetic factors and catastrophes. In addition, increasingly sophisticated models are required if one wishes to account for strong interspecific interactions,

such as mutualism (e.g., Anstett et al. 1995, 1997). Given the extensive and often central use of PVA in managing species and the potential for misuse of models and their output (e.g., Taylor 1995; Beissinger & Westphal 1998; Ludwig 1999), it is important to review and assess PVA as a tool in conservation biology. It is not our purpose to review PVA or stochastic demographic modeling, both of which have been reviewed (Boyce 1992; Beissinger & Westphal 1998; Groom & Pascual 1998); recent treatments of metapopulations (e.g., Hanski 1999) also make it unnecessary to review this topic. Rather, our goals are to (1) discuss the practical use and limitations of PVA in conservation planning, (2) present some emerging issues of PVA, and (3) offer suggestions on the appropriate uses of PVA in conservation planning and management.

PVA in Practice

One reason for the popularity of PVA is the ability of models to provide apparently precise results. We discuss a variety of issues that relate to how PVAs should be conducted, including skepticism about the numeric output. We discuss spatially explicit modeling, sensitivity analysis, incorporating genetics into PVA, and the use of packaged viability computer programs. This paper is not intended to be a how-to manual for PVA. Instead, our goal is to address in detail some of the emerging issues about the use of PVA in the hopes of clarifying and directing research on these topics.

Spatially Explicit Models

It is well established that the primary factor affecting the viability of many rare species is loss of habitat (Wilcove et al. 1998). Populations can be affected by the actual loss of habitat from a region, by changes in the suitability of remaining habitat patches, or by landscape factors such as the isolation or connectedness of the habitat fragments remaining after habitat loss. If the spatial distribution of habitat potentially affects the viability of a

study population, then a PVA developed for this population must explicitly deal with changes in habitat quality and quantity across space (Pulliam et al. 1992).

Population viability models can incorporate space in several different ways. When a species is limited by the amount of suitable habitat present within a region, but is unaffected by the distribution of habitat patches, then a researcher can conduct a PVA by tracking the total amount of habitat present in a landscape. An analytical or statistical model that includes this kind of tracking has a spatial component and may be completely adequate in the majority of cases. In other situations, however, the exact spatial locations of habitat patches, individuals, barriers to dispersal, and other landscape features might be important in determining population viability. In these cases, models must integrate space to a greater degree than by simply tracking total amounts of habitat.

A good example of a metapopulation for which spatial issues are of great importance is the population of California Spotted Owls (*Strix occidentalis occidentalis*) inhabiting the transverse ranges of southern California (Noon & McKelvey 1992; LaHaye et al. 1994). This population exists in conifer forests on isolated mountain ranges separated by extensive areas of chaparral. Most known subpopulations are small, 2–65 pairs. If there were no immigration between these subpopulations, local extinctions in the near future would be likely. If, however, there is free interchange among subpopulations and habitat is stable, population size could be relatively large (376–578 pairs) and therefore less prone to extinction. Forest management plans that could change the spatial distribution of suitable habitat could therefore have dramatic effects on the owl if these plans increase or decrease successful dispersal. To evaluate specific management proposals in this case, a PVA that explicitly incorporates space is preferable.

Models that incorporate the exact spatial and temporal location of objects into their structure are said to be spatially explicit. Objects might include patches of habitat, individual organisms, barriers to dispersal, foraging or breeding locations, or items associated with mortality factors such as human-dominated features. Published PVAs for the California Spotted Owl and California Gnatcatcher (*Poliophtila californica*) were designed to be spatially explicit to test the effects of human land-use changes in specific regions (Lamberson et al. 1994; Akçakaya & Atwood 1997). Nevertheless, even when spatially explicit models are preferred to solve a particular management problem, there are pitfalls in their use. Their structure and design have been reviewed elsewhere (e.g., Dunning et al. 1995), so we briefly comment on their design and concentrate more on their use for PVA.

At least theoretically, spatially explicit models can be designed to track the set of species found in different

patches of habitat (community-based models), the dynamics of populations in different patches (population-based models), or the movements and fates of individual organisms across a complex landscape (individual-based models). Individual-based simulation models assign to individuals habitat-specific demographic traits based on where individuals are, and they move individuals based on specific dispersal rules. Individual-based models then average across individuals to gain population statistics, such as time to extinction or population size at specific moments in a simulation period.

Spatially explicit models have been used to address at least two kinds of conservation questions. First, simulations of populations on hypothetical landscapes have been used to ask general questions on how viability might be affected by changes in habitat quality or quantity across large regions. For instance, Bachman's Sparrows (*Aimophila aestivalis*) are endemic to pine woodlands of the southeastern United States, where they occupy two habitat types, older mature forest (>80 years old) and clearcuts (<10 years old). In most areas, mature forest is extremely rare, and sparrows are usually found in clearcuts. Pulliam et al. (1992) used a general spatial model to determine whether sparrow population size was sensitive to the amount of mature forest in a given landscape. Population trends were simulated in a series of hypothetical landscapes that differed in amount of mature habitat. The simulated population trajectories varied dramatically across the different landscapes, suggesting that the mature habitat was more important than its relative rarity suggested (Pulliam et al. 1992). Hypothetical landscapes did not resemble any particular real-world landscape. Instead, this set of simulations was designed to determine if the rare habitat type had the potential to influence sparrow population dynamics.

A different use of spatially explicit models is to examine the potential effects of a specific landscape change proposed for a specific, real-world landscape. For example, for the California Spotted Owl metapopulation described above, a forest manager might ask whether a specific change in management strategy is likely to change the future distribution of suitable habitat in a way that could negatively effect the local owl subpopulations. To answer this type of question, one must incorporate a facsimile of the actual landscape into the modeling exercise, because general simulations on hypothetical landscapes are not specific enough to answer the question. Later modeling exercises with the Bachman's Sparrow model examined a series of proposed management actions in a U.S. Forest Service District by simulating related habitat changes on a 5000-ha portion of the study region (Liu et al. 1995). Results suggested that several proposed actions designed to benefit the endangered Red-cockaded Woodpecker (*Picoides borealis*) would change the study landscape in ways that could also benefit the sparrow.

In research modeling the consequences of spatial changes, the goal should not be to predict the actual changes in population viability due to changes across the landscape. The combination of large data requirements and potential for error in estimating model parameters make the acceptance of any single model prediction problematic. The most valuable uses of spatial PVA models may be in the identification of extreme population responses to landscape change and possibly to rank landscape-change scenarios and their potential to affect target populations. For example, if all simulated populations go extinct quickly in response to a specific change scenario, then that scenario is one to avoid.

Spatially explicit, individual-based models are extremely data-hungry. This is true to some extent of all PVAs (Beissinger & Westphal 1998; Reed et al. 1998), but spatially explicit models add the requirements of several unique kinds of data: the distribution and quality of habitat in the real world, local habitat-specific demography, and an idea of dispersal patterns and movement rules. Such detail is rarely available for most species. Sensitivity analyses can be used to identify the model parameters on which model performance is most dependent. Once these critical parameters are identified, researchers can concentrate field efforts for gathering habitat-specific data on them.

Spatially explicit models must specify the habitat needs of the population so that the model can determine how individuals are distributed across the landscape at each time step. The uncertainties associated with projecting the habitat relationships of organisms can be significant. Holthausen et al. (1994), for example, found that changing habitat relationships across a range reasonably supported by data had a far greater effect on modeled population dynamics than did changing proposed land management plans. A PVA should express these uncertainties as a formal part of their results. An approach followed by Holthausen et al. (1994) was to provide several scenarios to cover the range of potential habitat assumptions. Another method is to use Monte-Carlo methods to explore the entire range of potential input parameters (Lamberson et al. 1994).

Results should also be presented to express the range of possible results and the uncertainty associated with this range, rather than as just a single value such as mean time to extinction. In the Bachman Sparrow model described above, the "typical" population trajectory of the Forest Service landscape was highly nonlinear (simulated populations usually dropped sharply and then slowly increased over a 50-year period, Liu et al. 1995). Single metrics such as mean population size at the end of the simulation were relatively uninformative about the population curve, whereas the proportion of runs that were increasing, decreasing, or stable at different points in the simulations captured the population dynamics better. Similarly, Taylor et al. (2000) argue that

trends analysis is a more appropriate approach to analyzing management models when uncertainty is a significant factor among the model variables. Another approach to addressing uncertainty is to conduct power analyses to explore the degree to which the models can express reliable results (Thompson et al. 2000). Wade (2000) argues that Bayesian approaches to decision-making, which define probabilities of potential results, may be more appropriate than traditional statistical approaches to the hypothesis testing about population viability when uncertainty about population trends is great.

Spatially explicit models require information on how organisms disperse across complex landscapes. Dispersal data are notoriously difficult to gather. The primary problem is logistical: detecting dispersers that leave a study site in random directions becomes increasingly difficult as the potential area to be searched increases. Detection of long-distance dispersers can be especially challenging (Baker et al. 1995). For organisms with specific habitat needs (e.g., wetlands or specific age classes of habitat), the search for successful dispersers can be simplified if the required habitat patches are discrete and limited in the landscape (e.g., Breininger 1999). Recent developments in radiotelemetry, especially miniaturized transmitters, have allowed researchers to follow individual organisms during dispersal (Cohn 1999). As these field studies accumulate, modeling studies can assess the effects of estimation errors for various dispersal parameters on the performance of spatial PVAs.

Ruckelshaus et al. (1997) used modeling of a hypothetical population to evaluate the dispersal data requirements of spatially explicit models. They found that errors in estimating disperser mortality can cause large prediction errors, greater than those introduced by errors in estimating mobility errors or errors in landscape classification. Their study suggests that complex, spatially explicit models may be greatly susceptible to error propagation and should be used with caution. In comparing a set of viability models with actual field distributions of three species in fragmented landscapes, however, Lindenmayer et al. (2000) found that it was only the most complex versions of their models that accurately approximated the field distributions. The modeling approach of Ruckelshaus et al. (1997) has been strongly criticized as an inaccurate portrayal of the potential errors (Mooij & DeAngelis 1999; South 1999; but see Ruckelshaus et al. 1999). But the basic points of Ruckelshaus et al. (1997) remain important: gathering field data on dispersal and mortality during dispersal for most species is both critical and difficult, and models dependent on these data must be interpreted with caution and care.

Fortunately, not all landscape models need to be spatially explicit. For instance, some landscape studies have shown that the most important landscape variable af-

fecting populations is the amount of suitable habitat within a reasonable distance of a study site, but the arrangement of habitat explained little of the population dynamics (McGarigal & McComb 1995). In these cases, PVA can include relevant landscape variation with an analytical function, thus avoiding the greater complexity of fully spatially explicit models. Although the disadvantages of spatially explicit models might be daunting, the benefits can make their use worthwhile. Even with the limitations described above, spatially explicit models allow population dynamics to be studied at the spatial and temporal scales at which real-world landscape changes actually operate. If researchers want to study the population viability of an organism in a complex landscape and viability is likely to be affected by habitat connectivity, patch isolation, or other landscape patterns, then the researchers should invest the effort to build accurate PVA models that are spatially explicit.

Sensitivity Analysis and Confidence in Predictions

Sensitivity analysis can complement the predictions that arise from PVA by providing constructive insights into factors that most affect population growth or quasi-extinction probability. There are several approaches for conducting sensitivity analysis, ranging from analytical sensitivity and elasticity analysis to PVA-based modeling to approaches that might be considered hybrids of the first two (Caswell 1989; Akçakaya & Raphael 1998; Cross & Beissinger 2001; Mills & Lindberg 2002). In addition to providing insights into efficient ways to increase the growth of declining populations or slowing the growth of pest species, sensitivity analysis can benefit researchers by identifying factors whose estimation is most critical for population-level studies (Reed et al. 1993). Sensitivity analysis can include spatial dynamics, thereby evaluating the relative impact of within- versus among-population processes on metapopulation persistence or growth (Akçakaya & Bauer 1996; Mills & Lindberg 2002).

Although sensitivity analysis helps to identify actions that can be taken after traditional PVA has identified a problem, it is critical to account for not only the extent to which equal changes in different vital rates affect population growth or extinction, but also the amount that different rates could change. Vital rates that have a large absolute or proportional effect on population growth rate, but that naturally vary little, will not alter population trajectories under management (Gaillard et al. 1998; Mills et al. 1999; Wisdom et al. 2000). Also, the outcome of sensitivity analysis depends on whether sampling variation, which does not affect the organism, is included with the estimates of process (temporal and spatial) variation (Ludwig 1999; Mills & Lindberg 2002). The issue of separating process from sampling variation was raised recently as an essential distinction for popula-

tion dynamics and trend monitoring (Link & Nichols 1994; Caswell et al. 1998; Thompson et al. 1998) as well as for PVA (Beissinger & Westphal 1998; Ludwig 1999; White et al. 2002).

Because the insights provided by sensitivity analysis can change with changes in a population's carrying capacity (Beissinger & Westphal 1998), successional status (Silvertown et al. 1996), and population growth (cf. Watkinson & Sutherland 1995), a small measured sensitivity does not necessarily mean that a parameter always has such an effect on population growth. Other caveats include the fact that the mathematics of sensitivity analysis does not address the political, logistical, or financial factors that will affect our ability to manipulate different rates (Nichols et al. 1980; Silvertown et al. 1996; Citta & Mills 1999). The applicability of various types of sensitivity analysis to conservation decision-making have been discussed extensively in recent papers (Benton & Grant 1999; Mills et al. 1999, 2002; Cross & Beissinger 2001; Ehrlén et al. 2001).

An emerging approach to dealing with uncertainty in model structure and parameter estimates is to use Bayesian statistics, an alternative to frequentist approaches that most of us learned in statistics classes. Bayesian PVAs directly incorporate uncertainty into the model (Goodman 2002; Wade 2002) and have been used to classify risks to species for listing under the U.S. Endangered Species Act (Taylor et al. 2002). Bayesian PVA approaches also can be useful for recovery planning, and their application is likely to increase when easy-to-use computer software becomes available.

Making Genetic Concerns Relevant to PVA

Genetic concerns are relevant in PVA if they affect demographic rates such that population persistence is compromised. Lande (1988) cautioned against approaches that focus entirely on genetic stochasticity, and although he ended with a plea for synthetic thinking, some subsequent papers interpreted his arguments as concluding that genetic factors were unimportant to analysis of deterministic and stochastic events (e.g., Caro & Laurenson 1994; Caughley 1994). The dichotomy between genetic and nongenetic factors is false: inbreeding depression interacts with demographic factors to affect persistence (e.g., Leberg 1990; Soulé & Mills 1992, 1998; Mills & Smouse 1994; Newman & Pilon 1997). For example, Westemeier et al. (1998) tracked demographic and genetic changes in Greater Prairie Chickens (*Tympanuchus cupido*) in Illinois for 35 years, providing evidence for genetic factors interacting with deterministic habitat loss and stochastic variation to spiral population size downward.

When and how should genetic effects be incorporated into PVA models? The short answer to this complex

question is that inbreeding depression will be most relevant in populations that are small, isolated, and historically large (outbred) and have low intrinsic population growth rate (Allendorf & Ryman 2002). A "small" population may be defined as an effective population size (N_e) of less than about 100 (translating to census population sizes of about 500-1000; Frankham 1995a; Waples 2002), the level at which inbreeding depression may have population-level effects (Mills & Smouse 1994; Lindenmayer & Lacy 1995; Lynch et al. 1995). "Isolated" populations are more susceptible to inbreeding depression because even small amounts of gene flow (1-10 individuals per generation) can ameliorate the effects of inbreeding while allowing for local adaptation (Spielman & Frankham 1992; Hedrick 1995; Mills & Allendorf 1996). The criterion of "historically large" is a possible flag for including genetic factors in a PVA because it is possible that populations will become less affected by inbreeding as natural selection removes deleterious alleles during slow inbreeding. If this is the case, then large populations that suddenly become small will have greater inbreeding depression than will populations that have been small for a long time. But, such purging of deleterious alleles can have demographic costs and may not substantially reduce inbreeding depression (Hedrick 1995; Ballou 1997; Lacy 1997; Allendorf & Ryman 2002; Byers & Waller 1999), suggesting that population history may not reliably predict the relevance of inbreeding depression.

Once the decision has been made to include genetic effects in a PVA, one must decrement vital rates (birth and death rates) according to the calculated inbreeding coefficient (loss of heterozygosity) and the cost of inbreeding. For a range of animal species, the cost of inbreeding has been quantified for juvenile survival (Ralls et al. 1988; Laikre & Ryman 1991; Lacy 1993), adult survival (Jiménez et al. 1994), and reproduction (e.g., Ballou 1997; Lacy & Horner 1997). Other demographic effects from inbreeding are possible, including shifts in sex ratio (Soulé 1980; Wilmer et al. 1993) and ability to tolerate environmental perturbations (Frankham 1995b). Many of these estimates of the cost of inbreeding were measured in captivity, so they may underestimate inbreeding effects on fitness under natural conditions (Leberg 1990; Lacy 1997; Frankham 1998; Crnokrak & Roff 1999). In these empirical studies and in PVA models that incorporate inbreeding depression, the cost of inbreeding is typically expressed as the average number of lethal equivalents per gamete or per diploid individual. Lethal equivalents are the number of single alleles (or a combination of partially deleterious alleles) per gamete which cause death when homozygous. For example, one lethal equivalent may be a single allele that is lethal when homozygous or 10 alleles each with a 0.10 probability of causing death when homozygous. For plants, specific data on inbreeding costs are more

sparse, but both inbreeding depression and outbreeding depression are relevant (Ellstrand & Elam 1993).

In the most comprehensive quantification of the cost of inbreeding to date, Ralls et al. (1988) found that lethal equivalents per diploid individual for juvenile survival in 30 mammal species in zoos ranged from -1.4 to 30.3, with a median of 3.1. For two additional species of ungulate and one species of monkey, Lacy (1993) estimated lethal equivalents of 2.3, 1.0, and 7.9, respectively.

Although there is little doubt that genetic factors should often be included in PVA, the multitude of factors that will affect the cost of inbreeding and our lack of comprehensive data on vital rates across taxa mandates that a range of values be considered. For example, a range of plausible lethal equivalents could be used for a range of different vital rates. Similarly, because genetic effects can take some time to manifest themselves as changes in population vital rates and growth rate, and can act in a threshold manner (Allendorf & Ryman 2002), the length of time for PVA projections (e.g., 100 vs. 200 years) should also be varied. Finally, although inbreeding depression is usually the primary genetic concern in PVA, a decrease in genetic variation can also reduce the ability of a population to adapt to changing environments. This becomes especially important in longer-range PVA models (Lande 1995; Lacy 1997).

PVA of Plants

Each taxonomic group has its own nuances in terms of the model structure and parameter inclusion required for PVA, which presents challenges to conservation biologists. We discuss these problems in some detail for plants to provide an example for would-be modelers; some of the problems apply to other taxa as well. Population viability analyses for plants are limited by good data for certain parts of the plants' life cycles, episodic recruitment, environmental variation, and a research emphasis on issues unrelated to conservation (Schemske et al. 1994; Doak et al. 2002). Gathering these data is difficult in short-term studies; the median length of study for plant PVAs is only 4 years (Menges 2000).

Individual reproductive success in plants often cannot be calculated because the origins of individual seedlings are obscure. In addition, many plant populations have seed dormancy, so separate long-term field experiments are needed to quantify seed-bank dynamics (Kalisz & McPeck 1992), which can contribute greatly to population growth and extinction avoidance (Quintana-Ascencio 1997; Doak et al. 2002). Another type of dormancy that is easier to incorporate into PVAs is that of established plants (Lesica & Steele 1994). Plant dormancy makes short-term estimates of mortality rates suspect, and population dynamics might need to be simulated

under multiple scenarios (Guerrant 1995). For perennial plants, the incorporation of dormancy is conceptually simple and requires detailed monitoring of individual plants in the field in conjunction with the use of mark-recapture statistics to separate mortality from dormancy (Shefferson et al. 2001).

Even large amounts of data, particularly monitoring data, can be insufficient for the development of confident PVAs. For example, despite 11 years of monitoring data on 14 permanent plots spread throughout the range of a rare cactus, the question of its persistence was not solvable (Warren et al. 1993; Frye 1996a, 1996b). This species is a long-lived perennial and its recruitment is probably episodic. Episodic recruitment can be modeled stochastically using matrices representing recruitment and nonrecruitment years if one can reliably estimate the frequency of recruitment years (Menges & Dolan 1998) and simultaneously estimate the strength of recruitment for each episode. Gross et al. (1998) used a size-based matrix population model to evaluate the relative importance of added controlled burns, reduced human use, and a combination of the two to the protection of mountain golden heather (*Hudsonia montana*). They found that particular combinations of burning and reduced human use could result in recovery.

Environmental variability is a problem in modeling plant populations. In general, commercially available software cannot model the population dynamics of plants in disturbance and recovery cycles, a common situation for endangered plants. Approaches include using projection matrices representing different times since disturbance and varying disturbance frequencies (Oostermeijer et al. 1996; Quintana-Ascencio 1997; Enright et al. 1998). More explicit treatment of different types of variation—successional, disturbance, spatial, temporal—will undoubtedly increase the accuracy and precision of persistence scenarios. Despite patchy distributions, many plant species are not appropriate for metapopulation modeling (Harrison & Ray 2002) because either nothing is known of their immigration and emigration rates or because their dispersal distances are so short that metapopulation models are questionable. In some cases, incidence-based metapopulation models might be appropriate (e.g., Quintana-Ascencio & Menges 1996; Harrison & Ray 2002).

Population viability analyses in plants have not related demographic viability to genetic variation. One study found that more genetically variable populations have higher viability once management effects are accounted for (Menges & Dolan 1998). In another species, demographic and genetic factors are considered in evaluating the effects of fire-management tactics on extinction risk (Burgman & Lamont 1992). Heterozygosity has been related to individual fitness in at least one wild plant species (Oostermeijer et al. 1995), but this relationship is not universal (Savolainen & Hedrick 1995).

Can a reasonable and prudent researcher develop a reliable PVA of a rare or endangered plant? Yes, given resources and time. The main concern for plant PVA is not the adequacy of mathematics, even when complex life histories are involved, but the availability of data. Such data acquisition is not glamorous, and more resources are often invested in modeling than in the acquisition of field data. Nevertheless, only understanding the biology of the species will ensure reliable PVAs.

“Canned” Viability Programs

The development of computer software that is easy to access and that does not require mathematical or programming knowledge, might be partly responsible for the extensive use of PVA (Beissinger 2002). This raises the problem of the appropriateness of the software to a given species. Model parameters must be chosen because of their biological significance and not because of their presence in the software menu. Mills et al. (1996) found that, using the same data, different input and output formats of various PVA computer packages could lead to different predictions of persistence. Incorporating density dependence caused the largest discrepancies among programs. These results led Mills et al. (1996) to recommend that multiple PVA programs be used (also see Lindenmayer et al. 1993), that at least one scenario with density dependence be considered, and that qualitative results be emphasized over quantitative predictions. Brooks et al. (1997) compared predictions from five packaged programs to observations from field data and found persistence projections similarly overoptimistic for all packages. Predictions of carrying capacity based on habitat area were also overly optimistic, which should concern resource managers trying to model viability based on habitat characteristics (e.g., Roloff & Hauler 1997). Similarly, Lindenmayer et al. (2000) found that a commonly used viability program overestimated the number of occupied patches and the total abundance of three Australian marsupials for which the authors had considerable field data. On the other hand, Brook et al. (2000) found good predictive accuracy for 21 species for which long-term data sets were available to check predictions. These species tended to have low annual variation in population-size and vital-rate estimates. Only the most complex versions of simulations produced results congruent with field distributions in this study. Unfortunately, in these projects it was only the availability of accurate field data, combined with hindsight, that allowed a correct model to be constructed (Mills et al. 1996; Lindenmayer et al. 2000). The value of using “canned” programs is that the computer codes have been checked carefully for errors. They should be used with caution, however, and we suggest that combinations of people do the modeling, including those who know the species and those who have expe-

rience modeling viability. This increases the likelihood that the model will be used appropriately and that problems will be recognized.

Alternatives to Stochastic Demographic Simulation

There are few model-based alternatives to stochastic demographic simulation modeling for estimating the likelihood of extinction. Growth rates and extinction probabilities can be predicted based on time-series data of population sizes (Dennis et al. 1991). Dennis et al.'s (1991) model uses census data across years to calculate a distribution of observed λ s, and populations are projected from this distribution rather than by fitting parameters to a population model. Because this is a stochastic model, extinction probabilities can be determined from a large number of runs. In their model, Dennis et al. (1991) assume that population counts are accurate, variance in λ is due to environmental variability rather than sampling error, any systematic population increase or decline occurs at a constant rate, and population growth is density-independent, among other assumptions. This approach appears robust to large sample errors (on the order of 25%) (e.g., Fagan et al. 1999; Brook et al. 2000; Meir & Fagan 2000). Sampling errors easily can exceed 25%, however, as observed by Dunham et al. (2002; surveys of salmonid nests showed sampling errors alone as high as 250%). Dennis et al.'s (1991) model has been used widely, and model corrections are being created that account for some violations of the model assumptions (e.g., Foley 1994). But work by Fieberg and Ellner (2000) and Ludwig (1999) suggests that, even with perfect knowledge, estimates of extinction probability based on this approach are accurate to only 20% of the length of the time series (e.g., a 20-year time series of populations sizes would allow estimates of extinction probabilities 4 years into the future).

Another extensively used alternative to stochastic demographic simulation modeling is the incidence function model, which applies to metapopulation persistence (Hanski 1994a, 1994b, 1999; Hanski et al. 1996). Data required for this model are presence-absence information for patches of suitable habitat, habitat size, and the spatial distribution of habitats (Hanski 1999, 2002). Incidence patterns are used as estimates of colonization and extinction parameters in the landscape. If some estimate exists of the minimum area that will support the target species, persistence of the collective populations can be predicted. As with all models, this procedure is based on assumptions, including the following: slice-in-time surveys are representative of distributions over time; within-patch dynamics can be ignored; empty, suitable habitat can be identified; and habitat quality does not vary among patches. Use of incidence functions is still in the early stages of development, but it holds promise for

species that do not lend themselves to traditional demographic modeling. The advantage of these models over traditional PVA is that detailed demographic data are not required.

Using PVA in Conservation Biology

Population viability analysis has been, and will continue to be, a useful tool in conservation biology; however, it has limitations, and a number of publications have discussed appropriate and inappropriate uses of PVA in conservation planning (e.g., Caughley 1994; Ruggiero et al. 1994; Taylor 1995; Ralls & Taylor 1997; Beissinger & Westphal 1998; Reed et al. 1998; Ralls et al. 2002). We reiterate some of their concerns and recommendations, and add some of our own.

Restrict the definition of PVA to the development of a formal model to estimate extinction risk and closely related parameters, such as N_e , which played an early role in population viability estimation but recently has been ignored. This definition would also include λ (the finite rate of increase); however, there is a growing discontent in the scientific community about the value of this composite parameter. This definition excludes panel or committee opinions and other verbal models that evaluate viability (Menges 2000; Ralls et al. 2002).

Population viability analysis should be treated as a model. Models are simplifications of the real world, so no model is entirely correct. Nevertheless, models often provide approximations or insights from heuristic analysis of alternative management plans (Burgman et al. 1993). Before using model results, it is essential to test them or at least part of them with independent field data. The validity of a calculated probability of extinction or quasi-extinction for a given population depends on the appropriateness of the model structure, parameters, and parameter values (e.g., Beissinger & Westphal 1998; Groom & Pascual 1998). Equation selection and parameterization determine the behavior of the model. Some equations are used because they are realistic for some species. Before constructing or using a model, however, one must ensure that the equations used are valid for the biological system of interest. It is also important to distinguish patterns that are due to model structure. For example, in a logistic model of population growth, carrying capacity limits population size. Parameter values must be reasonably accurate for the model to provide reasonable predictions.

There are variables or relationships that have strong effects on population persistence, such as the presence of density dependence (e.g., Stacey & Taper 1992), or Allee effects (e.g., Groom 1998). More research should be focused on determining how pervasive these effects are across species.

Population viability analysis should not be used to determine minimum population sizes, because it is the wrong conservation focus (M. E. Gilpin & M. E. Soulé, unpublished data). Minimum critical sizes are sensitive to small errors in demographic data, and models are not accurate enough to make such precise predictions.

Results should be presented in terms of uncertainty. The outcomes of many PVAs are presented as mean time to extinction and the percentage of simulated populations still persisting at the target conservation time. These measures can be misleading and do not provide a manager with the information required to assess various management options. The distribution of mean time to extinction from simulations is usually positively skewed. Thus, the mean is typically larger than the median, so the median time to extinction might be more appropriate for reporting population persistence (Dennis et al. 1991; Boyce 1992; Mills et al. 1996). It would be even more valuable to present the distribution of persistence times, as is done for ending population size (i.e., the quasi-extinction function) (Ginzburg et al. 1982; Burgman et al. 1993; Beissinger & Westphal 1998). Reporting results in generations as well as years can be valuable. Because projections include uncertainty, comparing relative differences among different model scenarios is more defensible, as is providing ranges of prediction values. Whether or not PVA models can validly predict extinction probabilities, particularly without sufficient data to parameterize them, has been debated but not resolved (Akçakaya & Burgman 1995; Harcourt 1995*a*, 1995*b*; Walsh 1995; Ludwig 1999). Johnson and Braun (1999) provide a recent example of sensible handling of many of the statistical issues raised by Ludwig (1999). When data for demographic modeling are available but scant and/or poor, the modeling process should be used to focus research on gathering needed data, rather than on doing a PVA per se.

The most common criterion of viability, for a population to have an $x\%$ probability of persisting y years, is arbitrary (Shaffer 1981). An alternative criterion of viability could be not exhibiting a statistically significant decline over the target time period (Reed et al. 1998). Population viability analysis should not focus only on the probability of reaching extinction; it also should evaluate the probability of reaching management or quasi-extinction thresholds (Ginzburg et al. 1990; Scott et al. 1995).

Independent scientific review of PVA models, results, and management recommendations is critical, because it allows independent assessment of all aspects of the model and its proposed application. This review should not be restricted to publishing papers in scientific journals; external scientific review can be done as needs arise.

Model design, parameter values, and predictions should be treated as hypotheses to be tested with real

populations. Consequently, PVA should be an adaptive process that can be incorporated into research (e.g., Lacy 1994; Seal 1994; Lindenmayer et al. 2000). If PVA is used to compare alternative management regimes, habitats, or populations, small differences among them should be interpreted with caution.

Despite these caveats and limitations, population viability analysis remains an important tool for conservation biologists in effecting positive management action. Endangered-species conservation is an enormously complex task, however, requiring the assembly of diverse expertise, exchange of knowledge, consensus building, and mobilization of disparate resources. Unless these tasks are addressed explicitly, the results from population viability analysis might have little relevance.

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