

ON THE USE OF DEMOGRAPHIC MODELS OF POPULATION VIABILITY IN ENDANGERED SPECIES MANAGEMENT

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Abstract: We examine why demographic models should be used cautiously in Population Viability Analysis (PVA) with endangered species. We review the structure, data requirements, and outputs of analytical, deterministic single-population, stochastic single-population, metapopulation, and spatially explicit models. We believe predictions from quantitative models for endangered species are unreliable due to poor quality of demographic data used in most applications, difficulties in estimating variance in demographic rates, and lack of information on dispersal (distances, ages, mortality, movement patterns). Unreliable estimates also arise because stochastic models are difficult to validate, environmental trends and periodic fluctuations are rarely considered, the form of density dependence is frequently unknown but greatly affects model outcomes, and alternative model structures can result in very different predicted effects of management regimes. We suggest that PVA (1) evaluate relative rather than absolute rates of extinction, (2) emphasize short-time periods for making projections, (3) start with simple models and choose an approach that data can support, (4) use models cautiously to diagnose causes of decline and examine potential routes to recovery, (5) evaluate cumulative ending functions and alternative reference points rather than extinction rates, (6) examine all feasible scenarios, and (7) mix genetic and demographic currencies sparingly. Links between recovery options and PVA models should be established by conducting field tests of model assumptions and field validation of secondary model predictions.

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Demographic models are commonly used to make decisions for managing wild populations of threatened or endangered (hereafter, “endangered”) species. Often these applications are called Population Viability Analysis or PVA. Population Viability Analysis and the small-population paradigm form cornerstones of modern conservation and wildlife biology (Caughley 1994, Hedrick et al. 1996) and are partly responsible for conservation biology’s emergence as a credible science.

There are many different concepts of what composes a PVA—from simple, deterministic matrix models for estimating population change to complex, spatially explicit individual-based models of landscape and population dynamics. The first applications of PVA were the stochastic models that Shaffer (1981, 1983) developed to investigate grizzly bear (*Ursus arctos*) manage-

ment in Yellowstone National Park. Deterministic demographic analyses had been used for nearly a decade in the management of endangered species (Miller and Botkin 1974). Shaffer’s approach was a new direction in the use of models for conservation because he developed a stochastic population simulation that incorporated chance events (demographic and environmental stochasticity) and produced extinction probabilities. His model also estimated a minimum viable population (MVP) by varying the initial number of individuals to find the smallest population size with a 95% chance of remaining extant after the 100-year simulated time period (Shaffer and Samson 1985). Gilpin and Soulé (1986) broadened the definition of PVA when they used PVA as a heuristic concept to examine the many forces that can affect the viability of a population, including genetic factors. Although they designated the term “Population Vulnerability Analysis” for this ap-

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proach, 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 (Soulé 1987a, Burgman et al. 1993). Although risk analysis seems like an important role for PVA, emphasis in this process is often aimed at model development and outcomes, rather than identification of limiting factors that need to be reversed for a species to recover (Caughley 1994, Caughley and Gunn 1996).

In this paper, we evaluate use of demographic models for managing endangered species. We first review the kinds of models used most often, then examine factors that affect validity and accuracy of model outcomes, and conclude by suggesting how PVA could be used more wisely. The advent of easy-to-use computer software programs (Lindenmayer et al. 1995) has greatly contributed to the proliferation of PVA models, many of which were published since the last thorough review of PVA (Boyce 1992). This paper builds on Boyce's (1992) analysis by emphasizing the structure, function, use, and interpretation of demographic PVA applications. We do not discuss genetic applications of PVA (e.g., estimates of effective population size or pedigree analyses). Although genetic models have at times been important for managing endangered species in the wild (e.g., Hedrick and Miller 1992, Haig et al. 1993), their application has been limited because extinction is usually more affected by demographic than genetic factors (Lande 1988, Boyce 1992), and the currencies of genetics are not easily translated into extinction rates (e.g., loss of heterozygosity and expression of deleterious recessive alleles).

TYPES OF DEMOGRAPHIC MODELS USED IN PVA

In this section, we briefly review 5 types of demographic models that have contributed to development and use of PVA. For each model type, we describe its structure and outputs, review the data required for parameterization, provide examples of applications, and summarize specific assumptions and limitations. Discussion of model accuracy, precision, and validation is presented in the next section.

Analytical Models

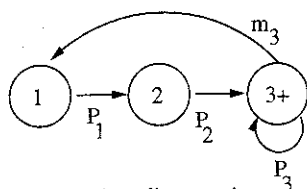
Analytical models can elucidate important principles concerning the process of extinction

and have been used to test model assumptions and determine sensitivity of model parameters. Analytical models are often used to examine system behavior rather than to make quantitative predictions. The simplified, impressionistic nature of some general analytical models, devoid of the complexity of simulation models, can clarify critical aspects of system behavior.

General theoretical models have been used to gain greater understanding of the effects of stochasticity on extinction. Although most extinctions are a function of steady population decline due to deterministic causes rather than chance events (Caughley 1994), a species' final denouement may be caused by stochastic processes. Early models based solely on demographic stochasticity concluded that population persistence increased to the power of the maximum population size (e.g., Richter-Dyn and Goel 1972). However, incorporating variance in population growth rates, due to random environmental fluctuations or environmental stochasticity, showed that times to extinction increased linearly with population size for small populations, but the rate of increase declines as populations grow large (Goodman 1987, Shaffer 1987). Even populations with long-term positive growth rates are susceptible to extinction from environmental variation and catastrophes. Nevertheless, analytical models have shown that a population of modest size can persist for a long time if the long-term growth rate of the population is substantially positive, even in the presence of environmental stochasticity and catastrophes (Lande 1993). Such models also have shown that distribution of times to extinction is often more important to evaluate than mean time to extinction (Ludwig 1996a).

General theoretical treatments also have been important for understanding the effects of spatial subdivision on populations. Levins (1969, 1970) provided the first analytical treatment of metapopulations ("a population of populations") by developing a patch-occupancy model to predict the proportion of occupied patches based on extinction and colonization rates. While his model made many unrealistic assumptions, such as assuming that population size of patches is either zero or at carrying capacity, that all patches are equally likely to be colonized, and that patches have the same size and extinction rate (see Hanski 1991), it provided an important foundation for incorporating spatial structure into population dynamics. For

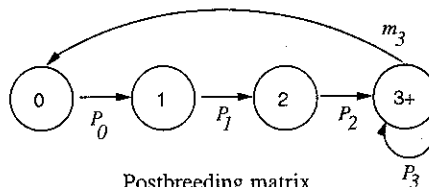
A. Prebreeding Life Cycle



Prebreeding matrix

$$A = \begin{bmatrix} 0 & 0 & m_3 P_2 \\ P_1 & 0 & 0 \\ 0 & P_2 & P_3 \end{bmatrix}$$

B. Postbreeding Life Cycle



Postbreeding matrix

$$A = \begin{bmatrix} 0 & 0 & m_3 P_2 & m_3 P_3 \\ P_0 & 0 & 0 & 0 \\ 0 & P_1 & 0 & 0 \\ 0 & 0 & P_2 & P_3 \end{bmatrix}$$

To calculate the geometric rate of population change:

$$\lambda \text{ is the dominant eigenvalue such that } \lambda [n] = A [n]$$

To calculate the stable age distribution:

$$[w] \text{ is the right eigenvector such that } A [w] = \lambda [w]$$

Fig. 1. Differences in the life-cycle diagram and parameterization of the deterministic single-population matrix model following a prebreeding (A) or postbreeding (B) flow of events for a species with 4 age classes (0 or juveniles, and 1, 2, and ≥ 3 -yr-olds). Individuals of each age class survive with a probability of P , but only adults ≥ 3 years old reproduce with a fecundity of m . No juveniles occur in the prebreeding life cycle or matrix, because censuses are conducted just prior to the breeding period. Thus, surviving young have already become 1-year-olds at a probability of P_0 , which does not appear in the life-cycle diagram but is found in the matrix. The postbreeding life cycle has an extra node and matrix row for juveniles because censuses are conducted immediately after the breeding season. The first row of the postbreeding matrix is different because only a portion of the individuals will survive to the next breeding season, increase in age by 1 year, and reproduce. The basic matrix calculations are illustrated.

example, variations of Levins' metapopulation model have been useful for examining the consequences of habitat destruction, corridors, and disease (Hess 1996a,b).

While analytical models have made important contributions to developing general principles of extinction, they have limited utility for making management decisions. Endangered species are generally characterized by small population sizes, and deterministic analytical models of time to extinction become ineffective due to effects of demographic, environmental, and catastrophic stochasticity (Boyce 1992). Diffusion theory has been used to develop equations to estimate extinction probabilities resulting from stochasticity (Lande and Orzack 1988, Lande 1993, Foley 1994), but results are inaccurate for small populations or populations that fluctuate greatly in size within a single generation (Ludwig 1996a).

Deterministic Single-Population Models

Deterministic demographic models of single populations are among the simplest analyses, formulated as a set of difference equations. Here we treat the frequently employed matrix

formulation (Fig. 1), although our discussion generally applies to other forms. Matrix models have a long history of use in ecology (Caswell 1989) and natural resource management (Getz and Haight 1989) but have only recently become established as a tool for managing endangered species (Crouse et al. 1987, Doak et al. 1994, Silvertown et al. 1996).

Among the different demographic PVA approaches, deterministic single-population models demand the least amount of data (Table 1). They require (1) an understanding of age, stage, or social structure to determine classes for analysis; (2) age or stage of first reproduction; and (3) estimates of reproductive success and survivorship for different ages or stages. The number of columns and rows of the matrix is determined by the number of age or stage classes. Ages are often collapsed into stage classes because field studies are seldom long enough to measure age-specific rates for long-lived organisms, and rates may become nearly constant beyond a certain age. Stages also are more convenient for modeling many fishes, invertebrates, and plants, because growth is indeterminate and demographic rates are better related with

Table 1. Data required for the dominant types of demographic models used in Population Viability Analysis: deterministic single-population (DSP), stochastic single-population (SSP), metapopulation (Meta), and spatially explicit (Space). An "x" indicates data are estimated for the population as a whole, and a "P" indicates data are estimated on a per patch basis.

Data type	Data needs	DSP	SSP	Meta	Space
Demographic	Age or stage structure	x	x	x	x
	Age of first breeding	x	x	x	x
	Mean fecundity for each age or stage	x	x	P	P
	Mean survival for each age or stage	x	x	P	P
	Variance in fecundity		x	x	x
	Variance in survival		x	x	x
	Carrying capacity and density dependence		x	P	P
	Variance in carrying capacity		x	x	x
	Frequency and magnitude of catastrophes		x	x	x
	Covariance in demographic rates			x	x
Landscape	Spatial covariance in rates			P	P
	Patch types			x	x
	Distance between patches			x	x
	Area of patches			x	x
	Location of patches				x
	Transitions among patch types				x
Dispersal	Matrix types				x
	Number dispersing			P	P
	Age class and timing of dispersal			x	x
	Density dependent or independent dispersal			x	x
	Dispersal-related mortality			x	x
	Number immigrating			P	P
	Movement rules				x

size or developmental stage than age. Most matrix models are constructed only for females because male fecundity is often unknown, and rates are usually expressed on a per female basis. The structure and values in the matrix depend on whether it is parameterized as a pre-breeding or postbreeding model (Fig. 1). The 2 approaches differ primarily in the number of matrix rows and the calculation of realized fecundity in the first row of the matrix (Noon and Sauer 1992).

Matrix analyses (Fig. 1) are easily performed with commercially available computer software (e.g., Matlab, Mathematica). Lambda or the geometric rate of increase is the dominant eigenvalue of the matrix, the stable age distribution is calculated from the right eigenvector, and reproductive value is derived from the left eigenvector (Caswell 1989, McDonald and Caswell 1993). Sensitivity can be analyzed in several ways (Caswell 1989), but elasticity is used most frequently and is the proportional change in lambda resulting from a proportional change in a matrix element (de Kroon et al. 1986). Elasticity values have the convenient property of summing to 1 and give a proportional contribution to the total sensitivity of lambda. However, the first row of matrix elements is calculated as a product of both survival and fecun-

dity, so lower-level elasticities must be calculated to partition elasticity among survival and fecundity (Caswell 1989:135; Wisdom and Mills 1997).

Use of deterministic matrix models in population management has grown rapidly since the development of elasticity. Matrix analyses have been used to estimate lambda for sea turtles (Cheloniidae) and to compare effects of changes in matrix elements resulting from management options such as use of turtle excluder devices and egg protection (Crouse et al. 1987, Crowder et al. 1994, Grand and Beissinger 1997). Matrix models have shown that desert tortoises (*Gopherus agassizii*) are most affected by changes in adult mortality (Doak et al. 1994) and have been used to produce rules-of-thumb for plant conservation (Silvertown et al. 1996). Applications with marbled murrelets (*Brachyramphus marmoratus*) compared stable age distributions from matrix models to the ratio of juveniles to after-hatch-year birds to estimate the productivity needed to stabilize populations (Beissinger 1995a, Beissinger and Nur 1997).

Deterministic single-population analyses assume demographic rates are constant or nearly so. This assumption is violated to some extent in all applications. For example, some ecosystems experience severe environmental changes

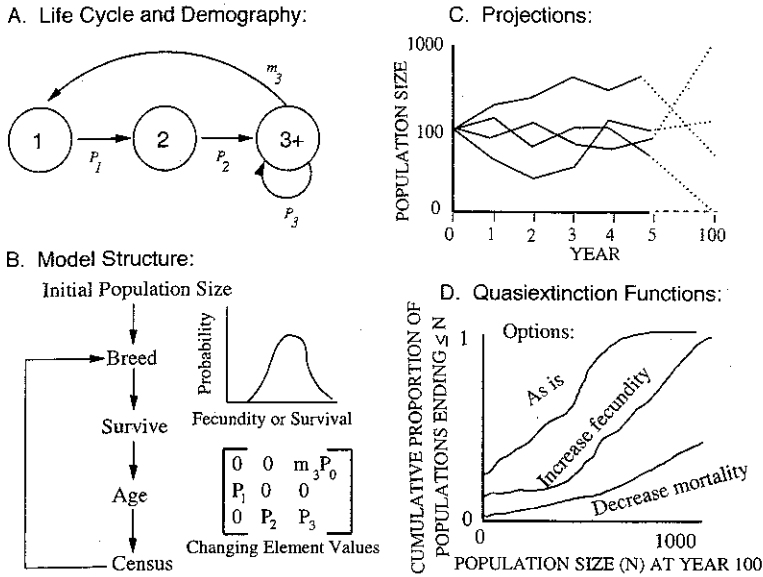


Fig. 2. A simplified example of the structure and outcomes from a stochastic single population Population Viability Analysis model: (A) The life-cycle diagram gives the model age or stage structure; (B) The simplified flow of events that structures the model. Rates for fecundity (breeding) and survival are randomly chosen anew for each time step from underlying distributions and are used in matrix calculations to project the population size at next census; (C) A population is projected over many years, and projections are repeated many times to simulate different possible population trajectories; and (D) Outcomes for various management options are determined, such as the quasiextinction function, extinction rate, or time to extinction. The quasiextinction function incorporates the population size from all projections at a specified time interval and is determined by calculating the cumulative probability for populations ending less than or equal to a particular size at the specified time interval. The extinction rate is where the function intersects the Y-axis.

that can greatly affect demography and occur on relatively short cycles compared to generation time (Beissinger 1986, Grant 1986, Beissinger 1995b). Concerns from violating this assumption depend on how much variation in demographic rates occurs from year-to-year (Wisdom and Mills 1997). Furthermore, positive population growth rates can lead to a false sense of security because environmental variation and catastrophes greatly increase the chance of extinction (Shaffer 1987, Lande 1993, Mangel and Tier 1994), and long-term population growth rates decline as variance in growth rate increases (Tuljapurkar 1989). To cope with this problem, stochastic models are often employed.

Stochastic Single-Population Models

Stochastic demographic models of single populations are probably the most commonly used forms of PVA. Like deterministic single-population models, stochastic single-population models are structured around the life-cycle diagram, and activities follow a prebreeding or postbreeding flow (Fig. 2A). These models use Monte Carlo methods to sample from underlying distributions and project a population for

50, 100, or more years into the future by varying vital rates or lambda for each time step or year (Fig. 2B). Unlike deterministic matrix analyses that produce a single population projection which changes at the rate of lambda, each run of a stochastic model follows a unique trajectory and yields a different ending population size because demographic rates change randomly with each time step (Fig. 2C). Thus, stochastic single-population models yield probabilistic results (Fig. 2D). Models must be run 500–1,000 times to adequately sample combinations of parameter values and explore the full range of model outcomes so that results converge on a set of values for the ending population size (Harris et al. 1987, Burgman et al. 1993).

Ending population sizes produced from stochastic single-population models may be summarized in several ways. The most common model result is the proportion of runs that end at zero ("extinction" rate) or at a small size such as ≤ 25 individuals ("quasiextinction"). No standard time interval or extinction rate defines a viable population, but intervals of 50–200 years and extinction rates of <5% are commonly used to evaluate viability. Another result is to com-

pute the mean or median year of extinction for populations that went extinct ("time to extinction"). The most complete descriptor of model results is to plot the cumulative probability function for ending population size, as it incorporates all ending population sizes (Fig. 2D). This "quasiextinction" function (Ginsburg et al. 1982) is a basic form of risk analysis: as functions shift from left to right on the graph (Fig. 2D), risk to the population declines. The MVP can be found by determining the effects of changing the initial population size on the extinction rate. Although MVPs were among the earliest applications of PVA (Samson et al. 1985, Shaffer and Samson 1985), use declined when the application proved both biologically and politically complex (Soulé 1987b, Gilpin 1996a).

Data requirements for stochastic single-population models are at least twice as great as for deterministic models (Table 1). In addition to average demographic rates, stochastic models require estimates of variance in fecundity and survival for each age or stage class. Variation in demographic rates mimics the effects of environmental stochasticity. Stochastic models should also include carrying capacity and its variance, as well as frequency and effects of catastrophes. Carrying capacity sets an upper limit on how large populations can grow, and models without such limits may overestimate population persistence (Ginsburg et al. 1990). Various functions of density dependence can be used to model the effects of approaching carrying capacity, or a population ceiling size may be designated that acts as a reflective boundary (Burgman et al. 1993). Catastrophes are a form of environmental variation that may be distinguished from environmental stochasticity, by the magnitude of effects on demography. They result in large population declines and greatly increase the chance of extinction (Mangel and Tier 1994), but they are not necessarily rare events (Beissinger 1986, 1995b). Additional factors typically affecting very small populations can be included: (1) demographic stochasticity can be incorporated by tracking individuals and applying demographic rates via binomial distributions, and (2) inbreeding effects can be modeled by randomly assigning lethal recessive alleles to a proportion of the individuals (Lindemayer and Lacy 1995).

To make management recommendations, stochastic single-population models have been used to estimate the likelihood of extinction for

wild populations. For example, models predicted the eastern barred bandicoot (*Perameles gunnii*) had at least an 80% chance of extinction within 15 years (Lacy and Clark 1990), and that piping plovers (*Charadrius melodus*) would go extinct in the Great Plains within 80 years (Ryan et al. 1993). By examining population viability, models also have been used to evaluate the necessity of removing animals from the wild for captive breeding (Lacy et al. 1989, Seal and Lacy 1989).

Effects of different management options can be built into stochastic single-population models, and in this regard they are most useful. For example, the effects of silvicultural practices on a threatened mammal were modeled by examining how changes in carrying capacity affected likelihood of extinction (Lindemayer et al. 1993). A variation of the stochastic modeling approach was developed to examine how ecosystem management options, in the form of the interval between low water conditions, affected viability of snail kites (*Rostrhamus sociabilis*) in the Florida Everglades (Beissinger 1995b). Instead of permitting demographic rates to fluctuate stochastically, they were partitioned among different environmental states (i.e., drought, lag, flood years), and the periodic sequence of environmental states dictated values for vital rates.

Stochastic single-population models do not consider spatial factors that affect extinction rates. Instead of composing a single population, individuals may often be found in subpopulations distributed among different locations in a landscape and connected by dispersal. Such models usually assume a closed population without immigration or emigration. This assumption is often unrealistic because these processes can have important effects on population dynamics (Stacy and Taper 1992). In addition, demography may vary spatially among different habitats or subpopulations (Pulliam 1988); thus, metapopulation and spatially explicit models were developed.

Metapopulation Models

Metapopulations are spatially structured into assemblages of local breeding populations (Fig. 3B). Migration of individuals between patches affects local dynamics, including the possibility of reestablishing populations in a patch after local extinction (Hanski and Simberloff 1997). Spatial variation in colonization and extinction

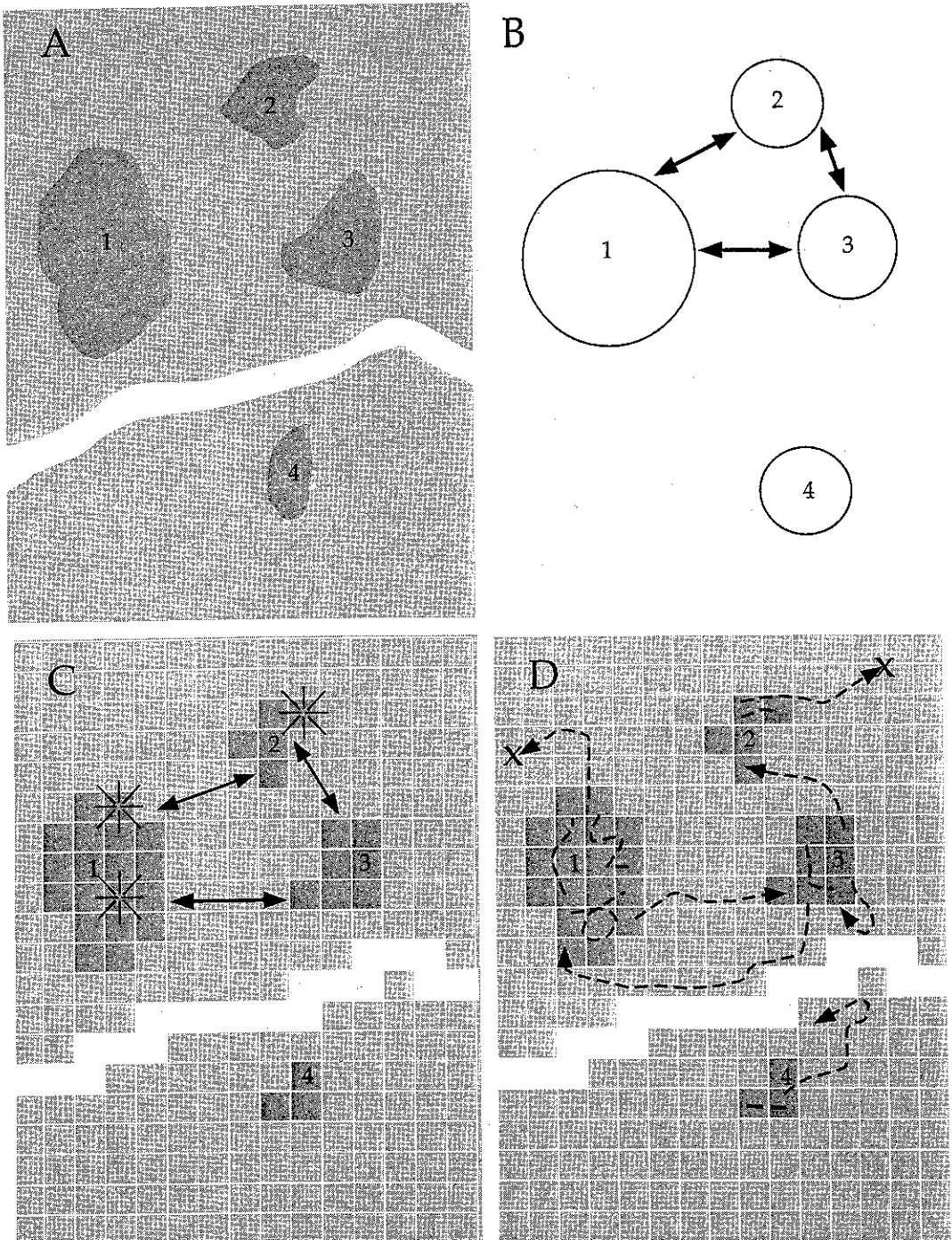


Fig. 3. Demographic Population Viability Analysis models with various degrees of spatial explicitness (modified from Gilpin 1996b). (A) The landscape of interest includes 4 patches of forest (numbered 1-4) that are surrounded by a matrix of agricultural lands (shaded lighter gray) and dissected by a river (shaded white) that acts as a barrier to dispersal; (B) Metapopulation model for the landscape in A, showing linkages between patches by dispersal indicated by arrows. Each patch has its own population dynamics; (C) Cellular automata or grid model for the landscape in A, where the landscape is now represented by grid cells, each with their own population size, immigration and emigration rates, and mortality and survival rates based on the grid characteristics and the characteristics of surrounding grid cells. Short lines indicate influences of neighboring cells, and arrows show dispersal between patches; and (D) Individually based model, where the movement, mortality (indicated by an "X"), and reproduction of each animal is tracked across the landscape. Mortality and demographic rates may differ between the matrix and the patches, and within the patches based on distance from the edge. The river acts as a barrier to movement.

results in 4 types of metapopulation structures (Harrison 1991). We consider only demographic or structured models of metapopulations, the most prevalent application with endangered species, rather than incidence-function approaches based on probability of patch occupancy (Hanski et al. 1995, 1996; Hanski and Simberloff 1997).

Metapopulation structure is incorporated into demographic models via use of dispersing individuals to link habitat patches (Fig. 3B). Such models are multipatch versions of the stochastic single-population models. These models typically incorporate either patch-specific demographic rates (including fecundity and survivorship) or patch-specific estimates for lambda, and dispersal rules that often are based on patch size and interpatch distances. Patch quality can be represented by varying carrying capacity or reproductive output among patches. For example, Lindenmayer and Possingham (1995) used indices of habitat quality to vary maximum number of breeding females in each patch. Metapopulation models usually include demographic and environmental stochasticity and catastrophes, as in stochastic single-population models, with the added dimension that an understanding of covariation of rates between patches may be of salient importance (Harrison and Quinn 1989, Sutcliffe et al. 1997). Model outputs can be expressed as ending metapopulation sizes, the likelihood or the time to extinction for the whole metapopulation, the percentage of patches, or the minimum number of patches or area required for metapopulation persistence (Hanski et al. 1996).

Metapopulation models can be formulated to investigate how metapopulation persistence is affected by number of patches or subpopulations (Goldingway and Possingham 1995, Lindenmayer and Lacy 1995), size of habitat patches (Beier 1996), removal of critical habitat patches (Gibbs 1993), role of succession and disturbances (Menges 1990), and immigration rate (Stacey and Taper 1992, Beier 1996). Moreover, metapopulation models can be used in a sensitivity analysis to determine which parameters are vital and need further quantification.

The advantage of metapopulation models over single-population stochastic models is they partially incorporate spatial realism. Thus, the effects of landscape change can be modeled, including effects of corridors, patch-specific hab-

itat destruction, quality alterations, and changes in interpatch distances. However, dispersal rules and mortality, which are integral to investigating metapopulation persistence, are usually specious because they are based only on distances between patches and do not incorporate matrix characteristics or behavioral rules (Fig. 3B). Moreover, these models do not explicitly consider potentially important effects of the surrounding matrix on demography within patches. When effects of matrix heterogeneity become crucial in predicting viability of a species, modeling may require spatially explicit landscape data.

Spatially Explicit Models

Spatially explicit models have been increasingly used in conservation as awareness of landscape processes has expanded and tools for analyzing landscape-scale phenomena have developed (e.g., Geographic Information Systems; GIS). The spatial distribution of resources can affect species persistence and coexistence (Levin 1992). Spatially explicit models specify location of the desired unit (e.g., individuals or populations) within a heterogeneous landscape and define spatial relations between habitat patches and the matrix (Dunning et al. 1995). Metapopulation models do not include matrix characteristics, and hence are not completely spatially explicit.

The major types of spatially explicit demographic models are the grid-based or cellular automata approach and the individual-based models (Dunning et al. 1995, Gilpin 1996b). In grid-based models, cells are squares of the same size, and their states (i.e., population size or habitat type) are followed through time (Fig. 3C). Cells are influenced by inputs and outputs from neighboring cells (Gilpin 1996b). Grid-based models are most appropriate for abundant organisms, such as plants, insects, or rodents, where monitoring the movement and fate of each individual may be intractable. Patch-specific reproduction and mortality rates are measured by population growth rates, and movement between patches is determined by immigration and emigration rates (Dunning et al. 1995). In individually based models (IBMs), the location of each individual across the landscape is monitored, and fitness characteristics are assigned based on the patches they occupy (Fig. 3D). Thus, each individual inscribes a trajectory over the landscape during the course of

its life. In IBMs with an annual time step, individuals can experience a cycle of breeding, dispersal, and mortality; daily time steps can be used to incorporate predator avoidance, foraging, and growth (Dunning et al. 1995).

Movement rules that explicitly incorporate an animal's perception of the landscape act as important components of spatially explicit models. For example, Turner et al. (1993) developed 3 alternative movement rules for foraging ungulates in winter in Yellowstone National Park. One rule specified a 1 grid-cell maximum movement per time step in the direction that contains the greatest number of resource sites within the search radius, and another rule allowed an ungulate to move among sites until it obtains maximum forage intake or reaches maximum daily distance, while a third rule allowed the animal to move to the nearest unoccupied resource site in the direction that has the greatest number of resource sites. Permeability can be assigned to habitat patches, based on habitat quality (Boone and Hunter 1996).

Spatially explicit models provide a technique for studying ecological processes that operate from local to landscape to global scales. Therefore, they can potentially predict population and community changes in response to land-use changes, climatic alterations, or various management strategies (Turner et al. 1995). Spatially explicit models have been used to design reserves (Price and Gilpin 1996), simulate responses to regional management practices (Boone and Hunter 1996), evaluate translocation options (Akçakaya et al. 1995), and simulate potential effects of forest management policies (McKelvey et al. 1993, Lamberson et al. 1994, Liu et al. 1995).

However, spatially explicit models have immense data requirements (Table 1), which can make development an onerous process (Dunning et al. 1995, Kareiva et al. 1997). The time and resources needed for their construction often restrict their application to species where management decisions have important economic implications. Although understanding dispersal movement is usually problematic, few habitat patches are expected to remain undiscovered if the area being modeled is sufficiently small, regardless of rules chosen. Likewise, dispersal details will be unimportant where high-quality habitat patches tend to be temporally static, because all patches will eventually be colonized. In such cases, the use of spatially ex-

PLICIT models may be superfluous (Dunning et al. 1995).

WHY DEMOGRAPHIC PVA MODELS SHOULD BE USED WITH CAUTION

Demographic PVA models are used to predict short- or long-term rates of population decline or growth and likelihood of extinction decades or centuries in the future. In this section, we examine how inputs, assumptions, and structure of demographic PVA models affect their ability to predict fate of populations with accuracy and precision.

The accuracy and precision of PVA models can be highly affected by a number of factors. Some factors are confined to specific model types, whereas others affect the outcomes of all demographic models. Below we discuss 4 dominant causes of errors that 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 alternate model structures.

Poor Data and Difficulties in Parameter Estimation

Although results from demographic PVA models obviously are affected by estimates of demographic rates used, the poor quality of data used in most applications with endangered species is frequently overlooked. 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 hardly ever known. Survival is often the most difficult vital rate to measure precisely, because it must be distinguished from the probability of resighting (Nichols 1992). Although statistical techniques have been developed to yield accurate estimators of survival and test for differences among ages or stages based on large samples of marked individuals (Lebreton et al. 1992), they require a minimum of 3 years of study to estimate probability of resighting and survivorship for a single year. More years of study may be required to develop precise estimators when the probability of resighting is low. Unfortunately, lack of good survival data can complicate estimation of lambda and extinction rates, because elasticity and sensitivity analyses suggest population change in long-lived vertebrates usually is most affected by changes in adult survivorship (Boyce 1992). Even the parameterization of a deterministic single-popu-

lation model, which requires the least amount of data compared to other PVA approaches (Table 1), is not a trivial matter.

Perhaps no single part of a PVA model needs more justification than the choice of average vital rates. When data on survival and reproduction are unavailable, guesses of mean rates frequently are made using biological intuition or information from a similar species. A more thorough approach is to use life-history theory (e.g., allometry) to justify possible choices (Beissinger and Nur 1997). Nevertheless, exceptions to life-history theory commonly occur. Substituting data from other species or populations is likely to be effective only if uncertainty in rates is fully explored. Sometimes so little is known about demography, and the range of potential vital rates is so large, that model outcomes will vary from complete extinction to no extinction for the same management regimes, depending upon the mean rates chosen. Such was the case when metapopulation and spatially explicit models were recently developed as part of the Pacific Lumber Company Headwaters Forest Habitat Conservation Plan for the marbled murrelet. There are no field measures of survival, age of first breeding, population density and structure, or movements for this species (Beissinger 1995a, Beissinger and Nur 1997). In our opinion, it is a waste of resources to develop stochastic single-population, metapopulation, and spatially explicit PVA models when both demography and dispersal are so poorly known.

To mimic effects of environmental variation, stochastic single-population, metapopulation, and spatially explicit models require estimates for variance in vital rates, which causes the differences among model runs. To obtain good estimates for variance of vital rates, demographic measurements must be 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. Long-term datasets have shown that variance in population size does not begin to asymptote until ≥ 8 –20 years (Pimm and Redfearn 1988, Pimm 1991, Arino and Pimm 1995). Accurate estimates of variance in vital rates probably require at least 1–2 generations of study, which could easily exceed 10–20 years for long-lived vertebrates. Use of data from short-term studies will usually underestimate the variance in vital rates.

The effect of short study periods for estimating variance in vital rates may be offset because estimates of variance derived from field studies implicitly include sampling error, which results in an overestimate of variance. Rarely has the temporal variance in vital rates been decomposed into sampling variation and annual (environmental) variation, which is what interests wildlife managers and conservation biologists. Sampling variance should be discarded because it is caused by errors in parameter estimation rather than a biological process affecting population trajectories (Link and Nichols 1994). Studies of semipalmated sandpipers (*Calidris pusilla*) found sampling error contributed nearly as much to total variance in annual survivorship as did temporal variation (Hitchcock and Gratto-Trevor 1997).

Metapopulation and spatially explicit models are distinguished from other PVA models by incorporating dispersal processes. Unfortunately, our understanding of dispersal is poor for most species. Consequently, dispersal rules are often coarse caricatures of biological reality due to difficulty of empirically determining dispersal distances, age of dispersers, and mortality during dispersal. Biologists often do not know whether individuals disperse only when habitat patches have reached saturation (density dependent), or whether they will always disperse upon reaching a particular age (density independent). Dispersers in models can be characterized as a fixed proportion of the population (Hanski and Thomas 1994), as an age-independent, varying fraction of the population (Lindemayer and Lacy 1995), or as a specific age class whose rate is constant (Lamberson et al. 1994, Beier 1996) or density dependent (Lindemayer and Possingham 1995). Likewise, dispersal mortality and distance can be modeled as a diffusion function with no specific risk attached to mortality (Southgate and Possingham 1995), as a random walk process with mortality as an exponential decay function (Lamberson et al. 1994), or as a constant number that moves to neighboring patches with no additional dispersal mortality (Beier 1996). Rarely is there information on what types of landscape features act as barriers, or whether a species will use corridors (e.g., Haas 1995, Desrochers and Hannon 1997). How many patches will be searched and what level of mortality is associated with dispersal is unlikely to be known (Kareiva et al. 1997). In most models, the flow of individuals

between patches is assumed a stochastic process, but presence of conspecifics can attract dispersers (Smith and Peacock 1990).

Because of the paucity of knowledge, errors in estimating dispersal mortality and distances may be huge. Analysis of error propagation indicates prediction 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). Even under the best circumstances, spatially explicit models may not predict, with certainty, the number of individuals in a landscape (Dunning et al. 1995).

Another source of inaccuracy in spatially explicit models occurs from errors in classifying landscapes. The polished nature of GIS maps provides a misleading impression of infallibility. Openshaw (1989) lists sources of spatial database errors due to (1) inaccurate positioning of objects, (2) incorrect attributes associated with objects and representations (i.e., referencing area objects as points), (3) assuming spatial homogeneity within each map unit for continuous phenomena (i.e., vegetation, soils) and delineating them with sharp boundaries (choropleth maps), (4) GIS operations on spatial data (e.g., transformation and interpolation) and effects of generalization operations (i.e., aggregation), and (5) temporal changes in data. Errors can be expected to propagate in a highly complex and variable fashion, depending on the number of data layers, source and scale of the data, resolution needed, and degree of heterogeneity of the landscape. Nevertheless, for spatially explicit models, errors in classifying and mapping habitat patches may be much less important than errors in our understanding of dispersal processes (Ruckelshaus et al. 1997).

Problems with Model Validation and Structure

While models can be useful for delineating relations among parameters and gaining insight into system behavior, it is unwise to have confidence in quantitative predictions from models that are not validated or confirmed (sensu Orskes et al. 1994) to determine their accuracy (Caswell 1976, Bart 1995, Aber 1997). The primary prediction from most PVA models, the probability of extinction, is very difficult to validate because these models incorporate stochastic processes. Stochastic models predict the outcome of hundreds of populations from 50 to

≥ 100 years into the future. We can not know which of the population traces (Fig. 2C) to compare to our unreplicated, real-world population, even if we had a long population history for comparison. 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 expected population trajectory based on average demographic rates with census data gathered independently provides a way of validating deterministic models or models with deterministic skeletons (Bart 1995, Beissinger 1995b, Higgins et al. 1997, Hitchcock and Gratto-Trevor 1997). For stochastic models, comparing the average population projection to a time series of historic population trends provides a way to examine how well the model captures the dynamics of the system. Although this approach has been used to test PVA predictions (Brook et al. 1997), it does not verify the value of stochasticity used in the model, which is the cause of differences among replicate model runs. Usually the best that can be done is to test model assumptions or secondary predictions such as estimates for means and variances of vital rates, distribution of individuals on landscapes, or movement rules. Confirmation of secondary predictions is rarely done for PVAs, which violates a basic principle for use of models in decision-making (Bart 1995).

Most stochastic single-population, metapopulation, and spatially explicit models project populations for 50, 100, or more years into the future, assuming present conditions reflect future conditions. Rarely have such models incorporated changes in environmental or demographic trajectories, such as habitat loss or restoration (e.g., forest regrowth) or changes in biotic interactions. For example, viability models proposed for the Mariana crow (*Corvus kubaryi*) on Guam, based on current demographic rates, would become obsolete as soon as the main limiting factor responsible for the crow's decline, the brown tree snake (*Boiga irregularis*), is controlled (National Research Council 1997). Similarly, PVA models for tropical fig wasps (Agaonidae and Agaoninae) showed their viability was sensitive to changes in the population biology of their mutualist figs (Anstett et al. 1997).

The form that density dependence and car-

rying capacity have in models can dramatically affect extinction probabilities, yet little is known about effects of density on demography for many endangered species (e.g., Brook et al. 1997). First, stochastic variations in vital rates result in normally distributed population sizes for density-dependent models and lognormally distributed population sizes for exponential growth models (Dennis et al. 1991, Nations and Boyce 1997). Although assuming unbridled growth for endangered species constrained by lack of habitat is unrealistic, this assumption may be a reasonable simplification. Ginzburg et al. (1990) concluded extinction risks decrease when weak density dependence is incorporated, whereas risks increase as density dependence becomes stronger. For functions that do not allow their trajectories to overshoot carrying capacity, such as the Beverton and Holt function, density dependence decreases the likelihood of extinction. Thus, models without density dependence will underestimate the likelihood of extinction. Second, in the Beverton and Holt, Ricker, and Hassell functions, as opposed to the generalized Beverton and Holt or the generalized Ricker, effects of density occur at increasingly higher rates as population size declines toward zero (Getz 1996). If these functions are incorporated into viability models for endangered species, where population sizes are often well below idealized carrying capacity, conservative estimates of population growth will result. Finally, models that do not incorporate Allee effects, which result in decreased fecundity or survival due to underpopulation, will underestimate extinction rates. Because detecting density dependence or Allee effects from field studies is very difficult, it seems prudent to evaluate the likelihood of simulated populations ending at a small size (e.g., 25–50) rather than extinction.

Our understanding of environmental fluctuations and the occurrence of catastrophe is in its infancy. Most stochastic single-population, metapopulation, and spatially explicit models assume environments, and hence populations, fluctuate stochastically. Physical forces that strongly affect demography, (i.e., droughts, floods) can occur on relatively short intervals (e.g., 3–7 yr) and in predictable cycles (Beissinger 1986). Studies of populations over decades (Pimm 1991) or environmental variations over centuries have sometimes uncovered predictability in the form of long chaotic cycles with

periods of generations or decades in length (Laird et al. 1996). Analyses of environmental predictability (Colwell 1974, Stearns 1981, Beissinger and Gibbs 1993) should be undertaken, rather than simply assuming that environmental fluctuations are stochastic. Results could be used to determine if population models should allow demography to vary completely stochastically or be constructed with deterministic kernels based on periodic cycles (Beissinger 1995b, Higgins et al. 1997, Leirs et al. 1997).

Finally, several aspects of model structure can have important effects on predicted rates of extinction. Many vertebrates have complex social systems that may include subadults yet to reach age of first breeding, nonbreeding adults old enough to breed (e.g., helpers or floaters), or senescent adults. An understanding of social structure, in the form of age and stage structure, can have critical effects on model outcomes (McDonald and Caswell 1993, Harcourt 1995). Furthermore, Pascual et al. (1997) showed that stochastic single-population models varying from unstructured to complex age or stage structures can reproduce the same population dynamics but yield different predicted effects of management (harvesting) regimes. Searching for the best model by comparing fit with historic population numbers or demographic parameters proved fruitless. Finally, different computer programs can result in different estimates of population viability from the same dataset (Mills et al. 1996). Variation in outcomes was most affected by differences in how models treated density dependence.

A STRATEGY FOR USING DEMOGRAPHIC PVA MODELS

The previous section raises several important concerns about accuracy and interpretation of results from demographic models of PVA. Demographic data are often inadequate, imprecise, and based on studies too limited in duration to properly estimate variance in vital rates. Most PVA models cannot be validated, projections usually do not incorporate future changes in habitat quality or quantity, and differences in model structure can have strong effects on management recommendations resulting from model output. Even when data are adequate, PVA models can result in large errors in estimating the rate of extinction (Taylor 1995). Taken together, these concerns strongly suggest that one should place very limited confidence

Table 2. Uses of demographic models of population viability. Objectives refer to goals of the model. Decisions are made by interpreting model outputs either in an absolute fashion, based directly on the model outcome, or in a relative fashion, by comparing outcomes among model runs.

Model objective	Interpretation of model output
Estimate likelihood of extinction	Absolute
Assess risks and benefits of management options	Relative
Develop criteria for recovery	Absolute
Classify species' vulnerability (IUCN) ^a	Absolute
Estimate population trends	Absolute
Evaluate research priorities	Relative
Determine size of reserves	Absolute

^a IUCN = International Union for the Conservation of Nature and Natural Resources.

in the extinction estimates generated by these models.

If demographic PVA models are currently incapable of producing accurate estimates of the likelihood of extinction, what should be their role in making management decisions? We believe there are valuable insights that can be gained by use of these models in certain contexts, whereas application in other situations may misdirect efforts. Because standards for the application of PVA models are presently lacking, we present some suggestions below for improving future implementation of PVA.

Evaluate Relative Rather than Absolute Rates of Extinction

An important difference among the major uses of demographic PVA models (Table 2) is how model predictions are interpreted. Model output (e.g., probability of extinction) can be used in an *absolute* fashion by taking the probabilities of extinction at face value to make decisions. For example, when a PVA indicates an inviable population and a species is classified as endangered or captive breeding is recommended, model predictions are used in an absolute fashion. Alternatively, results from PVA models can be used in a *relative* fashion by comparing outcomes among model alternatives. Some have called this dichotomy "quantitative and qualitative predictions" (Ralls and Taylor 1997), but we feel it is more useful to recognize differences in interpretation of model outcomes implied by uses of PVA (Table 2).

In our opinion, the optimal use of PVA is to evaluate relative differences among model outcomes. Models are best used to compare the

outcomes for different scenarios such as changes in vital rates and habitat quantity or quality resulting from management decisions. Such comparisons should concentrate on how well potential management actions perform relative to the baseline of current conditions. Examples include comparison of effects of habitat loss and poaching on elephant (*Loxodonta africana*) viability (Armbruster and Lande 1993), and timber harvesting strategies on the viability of threatened bird and mammal populations (Liu et al. 1995, Lindenmayer and Possingham 1996).

We generally recommend against formulating policies or decisions based on the interpretation of absolute values of extinction from PVA models. For example, recommendations to implement captive breeding have been offered when PVA models predict a moderate likelihood of extinction. Such recommendations base management decisions on the premise that a particular model accurately predicts likelihood of extinction. The advisability of implementing captive breeding needs better justification than projected rates of extinction, because captive breeding is expensive, often unsuccessful, can occur at the near-term expense of wild populations, and is only 1 of many approaches to reverse population declines (Snyder et al. 1996). If PVA models are used to evaluate advisability of implementing captive breeding, they should compare the relative rates of extinction for the wild population from various in situ management options with ex situ options, based on the likelihood that (1) breeding will proceed successfully in captivity; (2) captive-reared animals can be successfully reintroduced into the wild to create a self-sustaining, viable population; and (3) captive-reared individuals will not introduce diseases into the wild population. To the best of our knowledge, a comprehensive PVA comparing these options has not been conducted, although data may exist for doing so in some cases (Bustamante 1996).

Absolute rates from PVA models are incorporated in some of the criteria for classifying threatened species recently developed by the International Union for the Conservation of Nature and Natural Resources (1994). Based on modifications of the scheme proposed by Mace and Lande (1991), criteria included classifying species based on the likelihood of extinction derived from PVA models. Given the lack of accuracy (Taylor 1995) and confidence in predict-

ed rates of extinction, we suggest this criterion should be dropped because the classification scheme includes many other useful criteria.

Use Short-Time Periods for Making Projections

While we have some confidence in today's weather predictions and pay attention to forecasts several days ahead, we have little faith in predictions made months or years in advance. However, models that forecast weather are far more sophisticated and have been well tested and validated compared to demographic models used in PVA.

Many PVA models make long-term predictions of population size for ≥ 100 years into the future, based on current, and sometimes historic, demographic rates and environmental conditions. Such models propagate errors with each time step. An alternative approach would be to use shorter time intervals (i.e., 10, 25, or 50 yr) to minimize error propagation and to evaluate conservative probabilities of extinction (e.g., 1–5%). There is no particular justification for fixing a reference point at a 95% level of population persistence over 100–200 years. Nevertheless, evaluating short-time horizons cannot address questions that require long-term estimates of viability, such as determining the adequacy of current systems of parks and reserves (Table 2). When needed, long-term projections should be viewed as extrapolations of short-term trends for comparing the relative merits of policy options, and not as predictions of viability.

Start with Simple Models and Choose an Approach that Data can Support

The use of stochastic population models increased frequently after biologists realized that populations could go extinct when the long-term rate of population growth (i.e., λ) was positive, due to effects of environmental stochasticity and catastrophes (Shaffer 1981, Goodman 1987). Although these forms of stochasticity are important and stochastic models can yield important insights, the fixation on stochasticity has drawn attention away from the crucial effects deterministic factors have on λ and model outcomes (Caughley 1994). The overall trajectory of an endangered population often has an overwhelming effect on PVA model outcomes (for examples see Lacy and

Clark 1990, Doak et al. 1994, and Beissinger 1995b).

Much can be learned from a deterministic analyses before one develops a stochastic single-population, metapopulation, or spatially explicit model. Analysis of deterministic matrix models can indicate if strong population trends exist, and sensitivity or elasticity analysis can determine what vital rates have the greatest effects on λ . Although influences of factors may change as model complexity increases, deterministic models may give some insight into how we can expect more complex PVAs to perform.

Parsimony should be a goal in model building, but managing real populations often requires answers to particular scenarios that are complex, such as the effect of a proposed Habitat Conservation Plan on viability of an endangered species. In such cases, it is tempting to develop complex, spatially explicit models to estimate likelihood of extinction, if only they did not go so far beyond available data. Unfortunately, such models can require data we may be very unlikely to obtain, such as the probability of mortality during dispersal or details of patch searching behavior, which may have a huge bearing on model outcomes (Kareiva et al. 1997, Ruckelhaus et al. 1997). Policy makers need to understand the limits of our craft to answer such questions. We can develop estimators of population health based on measurable quantities such as amount and distribution of suitable habitat, instead of producing pseudoscientific estimates of extinction. Other, less data-hungry approaches may also be useful to guide management decisions, such as presence-absence models (Kareiva et al. 1997), incidence functions (Hanski et al. 1995), or adoption of principles to guide endangered species recovery (S. R. Beissinger et al. unpublished data). Models of fantasy have an important place in developing theory, but less so in the practice of conservation.

Use Models Cautiously to Diagnose Causes of Decline and Potential for Recovery

Models have been used to diagnose causes of a population decline (Crouse et al. 1987, Doak et al. 1994, Wisdom and Mills 1997) but need to be interpreted very cautiously. Sensitivity analyses, such as elasticity, indicate which vital rates or stages most affect model outcomes and require more study or better parameter esti-

mation. Recommendations based on elasticity analyses assume it is logistically and biologically feasible to increase those vital rates. For several reasons, however, elasticity or sensitivity values do not indicate what factors are causing populations to decline. First, elasticity estimates are not value free, but depend on the vital rates used (Caswell 1996). If a demographic rate is depressed due to effects of a limiting factor, its matrix element(s) will have a smaller elasticity value. Hence, it does not follow that factors or stages associated with this element are less important for management than other elements. For example, elasticities for the Mariana crow on Guam indicate an overwhelming importance of adult survivorship on λ , because successful reproduction has rarely occurred during the past decade due to predation by the brown tree snake (National Research Council 1997; S. R. Beissinger unpublished data). Recovery strategies focused only on adult survivorship would miss the main reason for decline: poor reproduction due to snake predation on eggs and nestlings. Second, elasticity indicates which element to change to obtain the quickest route to population recovery, but not which element is causing the decline. Similarly, recovery will require more time in populations that are declining due to limiting factors operating on elements with low elasticities than with high elasticities. From elasticities, one can identify the potential management strategy that leads to the fastest population recovery, but one cannot conclude which factors limit population growth.

Determining the factors that limit population growth requires comparative and experimental approaches (Caughley 1994, Caughley and Gunn 1996, Peterson and Silvy 1996). Nevertheless, models can indicate levels of recruitment or survival needed to recover populations (Beissinger 1995a, Grand and Beissinger 1997), and model trajectories can be compared to real trajectories to examine hypotheses about limiting factors (Hitchcock and Gratto-Trevor 1997).

Evaluate Cumulative Ending Functions and Alternative Reference Points Rather than Extinction Rates

Stochastic single-population, metapopulation, and spatially explicit models result in several possible currencies, such as time to extinction, probability of extinction, and ending population size. These estimators of viability depend upon the time frame analyzed. Fixing a reference

point of extinction for ending population size is arbitrary because the probability of extinction may rise quickly as the time horizon is lengthened. Furthermore, average time to extinction and ending population size can be misleading indicators because their distributions are highly skewed (Ludwig 1996a). Thus, it is most appropriate to examine the whole distribution of ending population sizes and times to extinction. Cumulative probability functions of ending population size (Fig. 2D) and tails of the distributions are valuable indices. Rather than evaluating extinction rates, it may be more useful to examine the likelihood of a population reaching the point where recovery requires the implementation of expensive options with low success rates such as captive breeding (Snyder et al. 1996). For example, such a limit might be set at 75–100 individuals in the wild for a slowly declining population of a long-lived vertebrate.

Examine all Feasible Models, Options, and Rates

Because of uncertainty in demographic rates and effects of model structure on PVA outcomes (Pascual et al. 1997), it is wise to use multiple models and examine a variety of rates and options when conducting PVAs. Although potential scenarios can be almost endless (Ludwig 1996b), the problem can often be bounded with high and low scenarios. Rather than trying to produce a single best model, it can be important to examine how different model structures affect outcomes and management recommendations by incorporating several models into PVAs (Groom and Pascual 1998).

Springly Mix Genetic and Demographic Currencies

Genetic effects can be incorporated into stochastic single-population, metapopulation, and spatially explicit models by randomly assigning lethal recessive alleles to a portion of the population (e.g., Lindenmayer and Lacy 1995). Little is actually known about the genetic loads in nature, and rarely will data be available for endangered species. Recent results suggest the accumulation of mildly deleterious mutations seems unlikely to pose a significant threat to sexually reproducing vertebrate populations over 45–50 generations (Gilligan et al. 1997). Inbreeding is likely the strongest genetic effect and primarily affects viability of populations with <50–100 breeding individuals (Shaffer

1987, Lande 1993), unless they are highly subdivided (McCarthy et al. 1995). Given the lack of information on the number of lethal equivalents in most populations, it may be useful to simplify model structure to concentrate on measurable demographic parameters and to evaluate quasiextinction rather than extinction rates.

HOW SHOULD PVA MODELS BE INCORPORATED INTO ENDANGERED SPECIES MANAGEMENT?

Use of demographic PVA models has expanded greatly in the past decade (Groom and Pascual 1998), and there is no indication they will go extinct in the near future (Ralls and Taylor 1997). Models are constructions of knowledge and caricatures of reality. By formulating them, a system or problem can be illuminated in a different light. Thus, the heuristic aspects of modeling, rather than the model results, are often the most fruitful (Starfield 1997). When used wisely to formulate and examine recovery approaches by comparing relative outcomes of the models (Table 2), PVAs assume the kind of heuristic role in which models can potentially perform well.

Unfortunately, models can also lead us wildly astray when they do not incorporate important influences, are unwittingly built on erroneous relations, or unintentionally use incorrect parameters (Emlen 1989). For example, use of poor data resulted in recommendations from a model (Nichols et al. 1980) based on erroneous conclusions that the Florida snail kite was a highly "k-selected" species with a low reproductive potential and incapable of rapid population increases or declines, when in fact multiple brooding, an early age of first breeding, and rapid population change characterize the demography of this "r-selected" raptor (Snyder et al. 1989, Beissinger 1995b).

The critical question is when are endangered species recovery programs likely to benefit from the insights of a PVA model, and when are they likely to be lead astray? Even a crude model is often suggested as better than not using a model, but this suggestion is not necessarily true (Emlen 1989). Some researchers suggest models are needed to identify data required for management, but these data are usually well known (Table 1). Models also are not needed to bring researchers together to share and examine data.

In our opinion, whether to develop a model and implement its recommendations depends on the quality of data and our understanding of the system. Doing a credible PVA requires good demography and good ecological modeling. The advent of canned software programs makes it too easy to construct a model that can be passed off as a PVA. Even when little demographic data exist (e.g., the marbled murrelet), someone will construct complex PVA models that are composed of many times more variables parameterized with educated guesses than with data from field measurements. The uncertainty associated with such models is so large that results usually yield no useful or credible guidelines for management. Application of PVA in those situations does little to boost its credibility. When most demographic data are lacking, we agree with Reed et al. (1998) that alternatives to PVA should be considered or priority given to accumulating data, before serious resources are committed to developing a complex PVA model.

As of January 1997, there were nearly 1,700 species on the U.S. endangered species list. Given the data requirements (Table 2), it is an unusual endangered species for which enough information is known to allow the legitimate use of stochastic single-population, metapopulation, and spatially explicit models. The problem is exacerbated for newly listed species, which usually have not received in-depth studies. For them, PVA cannot represent anything more than an exploratory exercise on a theoretical organism. Suggestions to streamline the Recovery Plans by mandating PVAs for each endangered species would only institutionalize wasteful practices.

While models are among the few tools that we have to predict the future, demographic PVAs are not currently capable of forecasting when species will go extinct, and perhaps they may never be able to fully achieve this goal. What demographic PVAs can highlight is the uncertainty behind decision-making in terms of how little we often know about population processes of paramount conservation importance, or how ignorant we are about which management strategies will work best. Uncertainty is inherent in decision-making but is not an excuse for not making decisions. Population Viability Analysis models can be helpful in this regard because they can be used to screen hypotheses for causes of decline, evaluate relative differences among potential management options,

and make explicit the relations among various factors. New PVA approaches (Boyce et al. 1994) are being developed that more directly relate occupancy and demography to habitat modeling using resource-selection functions based on landscape-scale variables (Manly et al. 1993). But PVA models cannot be substituted for field studies and experiments to determine limiting factors that need to be reversed, or to test management options.

Needed are direct links between field recovery options and demographic PVA models. Links may be partly accomplished by conducting field tests of model assumptions and by validating secondary model predictions. These activities are rarely undertaken after a PVA model has been developed, but they should be required before model results are taken seriously. Population Viability Analysis models were successful in determining resource management decisions for spotted owls (*Strix occidentalis*) and grizzly bears because models were followed by comprehensive field studies and were reviewed and revisited time after time in a process similar to adaptive management (Boyce 1993). These models were a step rather than an end-point in the recovery process. Ideally, funds to implement strategic field studies and validate secondary model predictions should be committed by the time a PVA workshop is held or a model is developed. If such an approach were implemented, it would result in the kinds of knowledge that would promote species recovery, improve our understanding of critical population processes, and increase the predictive capabilities of future PVA models.

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