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# POPULATION VIABILITY ANALYSIS*

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## INTRODUCTION

Population viability analysis (PVA) is a process. It entails evaluation of data and models for a population to anticipate the likelihood that a population will persist for some arbitrarily chosen time into the future (125, 128). A closely related concept is minimum viable population (MVP) analysis. An MVP is an estimate of the minimum number of organisms of a particular species that constitutes a viable population. Reference is also made to population vulnerability analysis which is a negative appellation for PVA. PVA embraces MVP, but without seeking to estimate the absolute minimum population necessary to keep a species viable (136).

In the United States, the US Forest Service has a mandate to preserve viable populations on its lands under the National Forest Management Act (158). Likewise, the US Fish and Wildlife Service and the National Marine Fisheries Service have been evaluating PVAs for many species or populations proposed for listing under the Endangered Species Act (152). Establishing criteria for what constitutes a viable population is no longer strictly an academic pursuit.

PVAs have been attempted for at least 35 species; perhaps the most celebrated are those for the grizzly bear *(Ursus arctos horribilis)* (126, 129, 144), and the northern spotted owl *(Strix occidentalis caurina)* (18, 79, 95, 98a). Most PVAs are simulation studies that remain unpublished, or when published, they may only include outlines of model structure (95, 126, 131). Others invoke analytical methods or "rules of thumb," always burdened with severe assumptions (31, 152). PVAs vary according to the ecology of the species, the expertise of the modelers, and the extent of available data.

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There are no guidelines on what constitutes a valid PVA, and because each case is unique, I am loathe to devise any. Any attempt is qualified that involves a population simulation or analysis with the intent of projecting future populations or estimating some extinction or persistence parameter, e.g. time to extinction, probability of extinction, probability of persisting for 100 years, etc. Definitions and criteria for viability, persistence, and extinction are arbitrary, e.g. ensuring a 95% probability of surviving for at least 100 years. Discussion of such criteria can be found in Mace & Lande (92) and Thompson (152).

Collecting sufficient data to derive reliable estimates for all the parameters necessary to determine MVP is simply not practical in most cases. It is further questionable how well ecologists can predict the future (34), particularly over time horizons necessary to project extinctions. On the other hand, Soulé(136) suggests that managers have the right to expect population biologists to project the number of animals necessary to ensure the long-term viability of a population. But to do so has proven to be dangerous ground (83) which risks damaging the credibility of conservation biologists.

My purpose in this review is an attempt to place PVA and MVP on more comfortable ground by identifying a realistic domain. I maintain that PVA ought to be an integral part of any species management plan, but rather than being so presumptuous as to claim that we can actually use modeling to define a MVP, or to estimate the probability of extinction, I use it as a forum to champion the adaptive management approach of Holling (67) and Walters (162). For those all-too-frequent cases that cannot wait for a full-blown PVA, I review empirical evidence suggesting that use of rules-of-thumb for MVPs may not be unrealistic.

## MODELING EXTINCTION

Fundamental to MVP is the fact that small populations are more likely to go extinct than larger ones due to inbreeding depression and genetic drift, or simply the threat of chance birth or death events (demographic stochasticity). Under high environmental variance or catastrophes, however, maintaining MVP may not be as effective a conservation target as would be managing for spatial configuration and location of habitats (38, 85, 106, 128). Irrespective of the target, the objective of PVA is to provide insight into how resource management can change parameters influencing the probability of extinction. This change may entail lengthening the expected time to extinction, $E(T)$, or reducing the probability of extinction within some time frame.

The most appropriate model structure for a PVA depends on the availability of data and the essential features of the ecology of the organism. In this section

I review structural features of PVA and extinction modeling. I begin with a discussion of stochastic variation, a necessary element in any consideration of extinction processes, and then review approaches focusing on genetics, demography, and ecology. I conclude with the argument that all of these elements ought to occur together in the same model. Because of the complexity of such a model, most PVAs will enter the realm of computer simulation modeling.

## *Stochasticity*

Random events can be extremely important in extinction, especially for small populations, the target of most PVA (121). In a sense, the distinction between deterministic and stochastic processes in ecology is artificial because all ecological processes are stochastic. Maynard Smith (97) points out that "the use of deterministic rather than stochastic models can only be justified by mathematical convenience." For heuristic purposes, use of deterministic models is appropriate. For example, our understanding of a simple model of competition or predation would only be obfuscated by the complex mathematics of a stochastic version. Because they are more tractable, deterministic models may yield robust results; stochastic models are often too complex to be solved analytically and thus require use of simulation methods.

Usually, conclusions from stochastic models in ecology are strikingly different from deterministic ones (26). This is generally true because of (i) large variances, (ii) nonlinear functions, and (iii) highly skewed or otherwise non-normally distributed variables. The significance of high variance is easy to understand in the context of extinction (85). Less transparent is the fact that virtually all ecological processes are nonlinear (17, 122). When the system contains nonlinearities, its behavior may differ markedly due to Jensen's inequality which states that for any concave function, $\phi$, of a random variable $X$, $E[\phi(X)] \leq \phi[E(X)]$; the reverse inequality applies for a convex function (72). The greater the magnitude of nonlinearity, say as measured by the second derivative, the greater will be the effect of randomness.

Sampling from a skewed distribution can yield peculiar behaviors in stochastic models. This is illustrated by exponential population growth in a random environment, i.e. random growth rate (88). Under such a model, population sizes at some future time are lognormally distributed (31, 154). This distribution arises because a series of good years will lead to extraordinarily large population sizes due simply to the geometric nature of population growth. Sequential sampling from such skewed distributions of $N(t)$ results in the most likely population sizes (mode) being less than the mean. As a consequence we obtain the seemingly paradoxical observation that the growth rate for a typical sample path "will in general be less than the growth rate of

average population" (154). Because population dynamics generally involve intrinsically multiplicative processes (83), we may expect complications due to distributional properties to be common.

Environmental stochasticity or "noise" is handled poorly in most PVA models. Environmental stochasticity in nature is not the unstructured "white" noise of a random number generator or "epsilon" term. Rather environmental stochasticity carries structure, such as autocorrelation and distributional properties, stemming from the manner in which errors are propagated through the system (101, 102, 108, 140). It really makes a big difference which variables in the system are fluctuating due to the environment, because this can affect the structure and dynamics of the system. Error propagation (including sampling error) can be examined by simulation methods (104), yet there has been little study of this problem in ecology.

This all calls for detailed understanding of the variance structure of populations (55). To understand the role of stochasticity in population extinction, we must understand how environmental variability affects the organism. Thus it will be a fundamental challenge in any PVA to decide how to model environmental stochasticity. Because data are limited, sampling variance may often overwhelm attempts to decompose variance into individual and environmental components. If sampling variance is included in a simulation model, projected variability will be much larger than in the true population.

### *Genetics*

The ultimate objective behind PVA is to develop prescriptions for species survival for the purpose of preserving genetic diversity (136); thus it seems appropriate that models of genetic variation ought to contribute to the formulation of a PVA. We know that small population size can result in inbreeding depression in some populations, which may increase the risk of extinction for the population (81, 111, 112). We also know that small population size can reduce genetic variation through drift, thereby reducing the raw material for evolutionary change, and genetic variation can be essential to ensure preadaptation to disease, competition, or predation (45). But what we do not know is how much and what type of genetic variation is most important to preserve.

Templeton (149) makes a convincing argument for placing priority in conservation on unique evolutionary lineages such as species or subspecies. But even within a taxonomic group there are many forms of genetic variation, which may respond differentially to particular conservation strategies. Genetic variation is revealed by restriction site analysis of mitochondrial DNA, karyotypy, electrophoresis of allozymes, heritability of quantitative traits (40),

and morphological variation (but see 69). And it is possible for many of these measures to vary almost independently of one another (80, 165). Genetic variation within populations often is measured by mean heterozygosity or the proportion of alleles that are heterozygous. Yet, if preadaptation to future insults from other species (disease, parasites, competitors, predators) is the reason to preserve genetic variation, it may be important to focus on preserving rare alleles (45). Perhaps the number of alleles per locus is a more important measure of genetic variation (2a).

Because quantitative traits are most frequently the target of natural selection, Lande & Barrowclough (81) argue that heritability should be monitored as a measure of genetic variation for conservation. Yet, from a pragmatic perspective, we know that estimates of heritability are often difficult to interpret because the response to selection can be greatly complicated by maternal effects (3). Relatively low levels of genetic variation may confer substantial heritability to some quantitative traits (90). There is also the difficulty of deciding which quantitative traits should be measured. Following Lande & Barrowclough's (81) rationale, the most important traits ought to be those that are most frequently the target of natural selection. Yet, these are exactly the traits expected to bear the lowest heritability as a consequence of selection (16, 40).

How genetic variation is structured within populations can also bear on conservation strategies (12). Many population geneticists believe that spatial heterogeneity is one of the most important mechanisms maintaining genetic variation in natural populations (63). Whether or not this pertains to the importance of inbreeding in natural populations has become the source of a fascinating debate (112, 130), but irrespective of this, there is no question that spatial variation in genetic composition of populations can be substantial. We are just beginning to understand the role of population subdivision on genetic structure and heritability (161). How significant is local adaptation? How important is coadaptation of gene complexes (149)? Although spatial structuring of genetic variation is complex and interesting, it is not clear that our understanding is sufficient to use it as a basis for manipulating populations for conservation. Attempts to manage the species by transplanting individuals between subpopulations is an effective tool to maintain or increase genetic variation within populations (57) but may destroy variance among populations.

The solution to this dilemma may ultimately entail foreseeing the sorts of threats a species is likely to encounter. If local subpopulations are likely to be threatened by habitat destruction or political unrest, it may be extremely important to maintain geographic variants to ensure that the species can continue to survive in other localities (see 142, 149). However, if future

threats due to diseases and parasites are expected, there may be a premium on ensuring the maximum allelic diversity throughout the population (not necessarily all in one place—96).

Is there an optimum amount of mixing among subpopulations that maximizes total genetic variance in the population? Because different genes or gene complexes are found in within-vs-among subpopulation components of genetic variation, a general answer to this question probably does not exist. Furthermore, the genetic variance within populations is a convex function of dispersal (migration) with maximum variance at the highest possible dispersal. Likewise, variance among populations is a convex function of dispersal but with maximum variance at zero dispersal (25). The sum of these two functions is similarly convex, and no intermediate maxima exist. Thus, we need to minimize dispersal among sites to preserve geographic variation while ensuring large enough numbers in subpopulations to avoid inbreeding loss of genetic variance.

An approach commonly used in trying to determine a genetic basis for MVP is to examine effective population size, $N_e$ (113). $N_e$ gives insight into the potential consequences of genetic drift to loss of genetic diversity, but as is the case for measures of genetic variation, we have numerous measures of effective population size, depending upon the mechanisms affecting drift. For example, Ewens (37) reviews the calculation of $N_{ei}$ relative to inbreeding, $N_{ev}$ for the variance in gene frequencies among subpopulations, $N_{ee}$ targeting the rate of loss of genetic variation, and $N_{em}$ for mutation effective population size. Still more measures may be derived. For example, $N_e^{(meta)}$ defines the effective population size in a metapopulation experiencing repeated extinction-recolonization events (49). Each of these basic measures of $N_e$ is then subject to adjustment for unequal sex ratio, age structure (65, 66), and variable population size (59). There is no sound basis for selecting one of these basic measures of $N_e$ over another, yet as Ewens (37) shows, they can lead to much different conclusions about MVP.

I conclude by agreeing with Shaffer (128) and Lande (80) that modeling genetics is not likely to be as important as modeling demographic and ecological processes in the formulation of a PVA. This does not imply that genetic considerations are not important; rather, in many cases we do not yet understand the genetics well enough to use it as the basis for management. There is an urgent need for research on the link between genetics and demography (80, 94; cf 111). This conclusion also does not imply that models of genetic variability should not form the basis for PVAs. Indeed, I think this would be a novel approach for species in which erosion of genetic variability is likely to be an important consideration in the future management of a species, such as the African wild dog (*Lycaon pictus*) which has a highly subdivided population (51). But as Lande has emphasized (80), demography

and associated ecology are likely to be of more practical significance than genetics in most PVAs.

## *Birth-Death and Demography*

BIRTH AND DEATH PROCESSES Possibly the simplest approach to modeling extinction is a stochastic birth-death process (53, 91, 116), assuming independent, Poisson-distributed births and deaths. Demographic "accidents" are most likely in small populations due to sampling effects, i.e. simply because individuals do not survive for the same length of time, and individuals vary in the number of offspring they bear. This approach has been used to solve for $E(T)$ as a function of population size, $N$, given density-dependent per capita birth, $b_N$, and death rates, $d_N$:

$$E(T) = \sum_{i=1}^{N} \sum_{j=i}^{N_m} (1/jd_j) \prod_{n=i}^{j-1} (b_n/d_n) \qquad 1.$$

up to a maximum possible population size, $N_m$.

As one might expect, such sampling effects are extremely sensitive to population size (53, 91), and these effects usually can be ignored if the population is larger than about 30 individuals (depending on age structure). The exception is where a population is divided into a large number of subpopulations, each so small that it faces a risk of chance demographic extinction. If recolonization is slow, there can be a significant risk to loss of the entire population by demographic stochasticity alone (103).

Environmental stochasticity is much more significant than sampling or demographic stochasticity, except for very small populations (54, 55, 74, 85, 129). Recalling the assumption of Poisson distribution for births ($b_N$) and deaths ($d_N$), the variance in per capita growth rate at population size $N$ ($r_N = b_N - d_N$) is simply

$$Var(r_N) = (b_N + d_N)/N \qquad 2.$$

Recognizing this, Leigh (85) and Goodman (54, 55) rewrote the birth-death process model (Eq. 1) to make $E(T)$ a function of the variance in $r_N$, $Var(r_N)$:

$$E(T) = \sum_{i=1}^{N} \sum_{j=i}^{N_m} \{[2/j(jVar[r_j]-E[r_j]) \prod_{n=i}^{j-1} [nVar(r_n)+E(r_n)]/[nVar(r_n)-E(r_n)]\} \qquad 3.$$

Here, $Var(r_N)$ somehow becomes environmental variance (152), albeit still a function of the magnitude of $b_N$ and $d_N$. The important outcome of the modified birth-death process model is that $E(T)$ increases with population size more slowly when environmental variance is high (55). Goodman (55) validated predictions of the modified birth-death process model by simulating a more complex population that included density dependence and age structure, and he generally found good concordance between simulation results and

analytical predictions from the birth-death model. However, ecological applications of birth-death process models have been criticized for several reasons.

Early interpretations that populations of more than 20–30 individuals were unlikely to risk extinction (91, 116, 132) were a concern given their basis solely in stochastic demography (129, 164). The use of a reflecting boundary, $N_m$, for maximum population size is unrealistic (30, 94), although this is resolved by Goel & Richter-Dyn (53). Additionally, the fact that the models are in continuous time renders it "highly questionable" (83) because of the importance of seasonal structure in the population. The assumption at Eq. 2 which is the basis for Eq. 3 (152) also merits consideration. For constant $E(r_N)$, increasing variance in $r_N$ is accomplished by increasing birth and death rates. This is reasonable enough given explicit assumptions in the birth-death model but bears rather heavily on Belovsky's (6) attempt at empirical verification for Eq. 3 which draws on comparative analyses of the maximum demographic potential for $r$ and $b$ in mammals.

Another matter of concern in all models that predict the time to extinction, in general, is that $E(T)$ can be a misleading characterization of the likelihood of extinction (31, 41, 55). The distribution of time to extinction is positively skewed in each of these models, as well as in the age-structured model (82). The $E(T)$ is substantially greater than the median or mode of the distribution, because a few populations take extraordinarily long times to become extinct. The time to extinction most likely to occur (mode) or the middle of the distribution (median) may be more meaningful measures than the mean.

Despite these difficulties and restrictive assumptions, Leigh (85) and Goodman (54, 55) made an important point by clarifying that "demographic uncertainty" is most likely to be a concern only at low population sizes, whereas environmental uncertainty can pose significant risks for considerably larger populations (cf 101, 102 for similar results based on branching processes). Understanding the variation in population parameters attributable to environmental fluctuations is clearly fundamental to any PVA (55).

DEMOGRAPHIC PROJECTIONS Although "demographic uncertainty" is usually approached using birth-death process models, these models, in fact, do not contain age structure. This may be a serious shortcoming because age structure per se can have a significant effect on population trajectories and thereby on the probability of extinction (82, 154, 156).

Many PVAs employ projection matrices, such as the Leslie matrix, as age-structured models of population growth (95, 126). The Leslie matrix and similar stage-structured models have mathematical properties that give great insight into processes of population growth (24).

For example, sensitivity of population growth rate, $r$, to perturbations in

vital rates ($P_x$, $F_x$) for a Leslie/Lefkovitch matrix can be solved analytically (i.e. $dr/dP_x$ or $dr/dF_x$)(24, 79, 99). Understanding the response of growth rate to perturbations at various points in the life table may yield insight into how one should target management (79). For long-lived species, such as the spotted owl, adult survival is a very sensitive demographic parameter, whereas in species with shorter generation times, fecundity can be much more important (83, 99).

In nature, the elements of a projection matrix are random variables (14, 153) or functions of the environment (134, 160). Forecasted trajectories of population size depend not only on the schedule of vital rates, but also on the variance in these rates (156). It is important to note that variation in vital rates creates disequilibrium in age structure that further complicates the dynamics. The variance in population growth rate is thus attributable to both the variation in vital rates and the variance in population structure. For demography of humans in the United States in 1960, approximately two thirds of the variance in growth rate can be attributed to variance in vital rates, whereas about one third is due to fluctuations in age structure (154).

Projection matrices in their simplest form are models of exponential population growth. As such, there are essentially two possible outcomes of these models: they increase exponentially to infinity, or decrease to extinction. If the dominant eigenvalue for the average projection matrix is less than one, extinction is assured. But even when the average projection matrix might predict an increasing population, extinction may also occur when vital rates vary (14, 74, 156). Of course, exponential growth models are strictly unrealistic on time scales necessary to explore extinction probabilities.

FORECASTING METHODS Development of theory and applications of forecasting mostly have occurred in economics, but the opportunity exists to apply many of these procedures to population projections. Projecting a stochastic process into the future poses problems. First, one must assume that the mechanisms generating the historical data remain intact and unchanged in the future. Second, one must select the correct structural model that drives the population process or risk serious errors in prediction. Third, errors in predictions are magnified progressively into the future such that usually only a few time intervals can be predicted with any confidence or reliability (31a).

A time series model commonly used for forecasting is the ARIMA (auto-regressive integrated moving average) model (10, 15, 19, 31a, 154). Least-squares regression is used to calculate the dependence of $N(t)$ on lags of the entire time series, $N(t\text{-}1)$, $N(t\text{-}2)$ . . . $N(t\text{-}p)$. Differencing is employed to remove trends, and moving averages can be calculated to smooth out high-frequency noise. The resulting equation is then extrapolated into the future beginning from the last observed data point. The population's trajectory

determines the forecast. Thus, if the trajectory does not show a population decrease, the forecast may continue to increase without bound. Confidence intervals around the forecasted value will, nevertheless, include 0 at some future time, but this will include sampling error and will be much shorter than $E(T)$. Many statistical software packages include programs that perform ARIMA forecasting.

A simplistic approach to forecasting can be derived from a diffusion model without age structure (31, 64). Itô calculus is used to solve a stochastic differential equation model of exponential population growth. The probability distribution function of extinction is the inverse Gaussian distribution (similar to the lognormal), and $E(T) = (x_0-x_E)/a$, where $x_0$ is the $\log_e$ of the initial population size, $x_E$ is the positive population size defined to constitute extinction (e.g. 1 in sexually reproducing species), and $a$ is the average growth rate for the population. A maximum likelihood estimator (MLE) for $\hat{a} = ln(n_q/n_0)/(t_q - t_0)$, which only requires knowledge of the initial, $n_0$, and final censuses, $n_q$, at times $t_0$ and $t_q$ respectively. Or alternatively one may use a linear regression approach (31). MLEs for $\sigma^2$ are also easily calculated (31, 64).

Although easy to use, one must imagine that the population trajectory observed thus far will also apply into the future. Also, any structural features of the population process, e.g. density dependence, which are reflected in the time series are overlooked in the estimator of $\hat{a}$ (154).

Building on the results of Tuljapurkar & Orzack (156) and Heyde & Cohen (64), Lande & Orzack (82) also modelled stochasticity as a diffusion process for exponential age-structured populations. Simulation trials were used to validate their estimators for $\hat{a}$ and $\hat{\sigma}^2$. Although Lande & Orzack (82) emphasize that only three parameters are needed to use their model, one of these parameters is initial total reproductive value which requires complete life history and age-structure data!

A third approach to forecasting is to characterize the time series of vital rates with ARIMA, and then to insert these models into a projection matrix (84, 154). Such a "time-series matrix" retains more of the dynamic consequences of age structure, and therefore population fluctuations ought to be more realistic. I am unaware of any applications of this method in conservation biology.

For each of these forecasting models we assume a density-independent population. If density dependence acts in an age-specific manner (which it usually does: 43, 44), the complications to the age structure make it difficult to derive analytical results for the distribution of extinction times. Given that density dependence exists in natural populations (133), even in "density vague" populations (143), I am skeptical about using density-independent formulations except in two cases: (i) very small populations where density

dependence may be inconsequential relative to demographic stochasticity (55), or (ii) for short-term forecasting. Further research is needed to develop forecasting models with ecologically realistic structures, e.g. with density dependence. But in the meantime, Monte Carlo simulation procedures (60, 118) can be used to generate estimates and distributions for extinction parameters for models with density dependence.

Sensitivity to initial conditions ensures that long-term forecasting will be unsuccessful for chaotic populations (122), but nonlinear forecasting methods may improve short-term forecasts for populations embedded in complex ecosystems (145). Populations experiencing fluctuations due to time-lagged processes may be particularly suited to one of several nonlinear methods reviewed by Casdagli (23). Software for generating forecasts and calculating confidence intervals is described by Schaffer & Tidd (123). Unfortunately, these methods work best for time series longer than are available for most endangered species.

## *Ecology*

Although much of the literature on PVA has focussed on issues of genetics and stochastic demography, it is clear that ultimate causes and threats of extinction are primarily ecological. Loss or degradation of habitat is the most significant factor threatening species extinctions in the future (107, 164). For avian taxa currently endangered by extinction, 82% are associated with habitat loss, 44% with excessive take, 35% by introductions, and another 12% are threatened by chemical pollution or the consequences of natural events (148).

Most PVAs have ignored fundamentals of ecology such as habitat, focusing instead on genetics or stochastic demography. Although ecological factors influence demographic variables, seldom is our understanding sufficienct to isolate these effects. A more appropriate approach for many species may be to model the habitat for the species and various strategies for managing this habitat. For example, Foin & Brenchley-Jackson (42) modelled the salinity, transpiration, and soil moisture of *Spartina* salt marshes in southern California, which is essential habitat for the endangered light-footed clapper rail. Reliable demographic details for the Rail were unavailable, and the only connection between the bird and the habitat was a linear relationship between the biomass of Pacific cordgrass, *Spartina foliosa*, and the number of rails.

Most demographic PVAs performed thus far do not model ecological consequences of other species, e.g. predators, competitors, parasites, disease. In particular, exotic species can be a major threat in some systems (159). For example, invasions of exotics may be less likely in communities that possess a diversity of native taxa (114). In some species, dynamics of disease may be the most significant consideration in a PVA (35, 96). Understanding such relationships is necessary to predict population viability.

Regrettably PVAs often do not explicitly include management (136). Consider, for example, application of a forecasting method to a population trajectory for a species whose decline can be attributed to habitat loss. It makes no sense to extend such a trajectory if all remaining habitat for the species is now protected. Yet, this is precisely the inference that one would draw in applying a forecasting model (cf 31, 82). Leaving management out of a PVA is unfortunate because one of the greatest values of PVA modeling is the opportunity to evaluate the efficacy of various management options (67).

Indeed, it is the absence of ecology and management from most attempts at PVAs that is their biggest weakness. These processes ought to be the nuts and bolts of such modeling exercises! The power of ecological modeling rests in our ability essentially to play with nature to anticipate the consequences of various management scenarios (56, 139, 147). Some aspects of ecology such as density dependence, spatial heterogeneity, and the Allee effect are of particular significance to PVA because they have major consequences to the probability of extinction.

DENSITY DEPENDENCE The simplest possible model of population growth is an exponential population growth model. It has no ecology. The simplest possible ecological model is a density-dependent model such as the logistic. The existence of negative feedbacks in compensatory density dependence dampens population fluctuations and can greatly reduce the probability of extinction (52). In model selection, the principle of Occam's Razor is commonly invoked, whereby one requires statistical evidence for the existence of density dependence before adopting the more complex density-dependent model. I submit that, instead of requiring statistical demonstration of density dependence, one should test for deviations from a null model of logistic density dependence.

This is not to say that estimating parameters for a density dependent model is not without its difficulties (98, 141), in particular, lack of independence in a time series of census data (20, 110). One can avoid some of these problems by examining density dependence in survival or fecundity, while controlling for key environmental parameters (83). Elements of a projection matrix can be made functions of density, yielding dynamics qualitatively similar to the logistic (134, 160). Because sufficient data are seldom available to do justice to characterizing a density dependent function, one may need to resort to using a form consistent with that observed for similar taxa (43, 44). Because of the difficulties with parameterization of density dependence, it has been argued that it may be most conservative to use density-independent models because they were thought to bear higher probabilities of extinction (41, 52). But this is not necessarily true; for example, extinction under density

dependence is imminent if all habitat for a species has disappeared. Furthermore, I do not accept this rationale on the grounds that reasonable behavior of the model should be a high priority in model validation (56).

THRESHOLDS At low densities, an Allee effect creates a positive relationship between per capita population growth rate and population size. This can be caused by difficulties in finding mates (30), difficulty in fending off predators or competitors (11, 28), social or physiological facilitation (80), or reduced predation efficiency (8). Similarly, low density consequent to habitat fragmentation may result in high juvenile mortality during dispersal (78, 79).

The consequences of Allee effects for PVA are exceedingly important because these mechanisms create threshold or critical population sizes below which extinction is much more probable or inevitable. As an example, Lande (78) presents a model where limitations to juvenile dispersal can create an extinction threshold in territorial species, which has been used in PVAs for the spotted owl (79, 151).

However, the mechanisms creating an Allee effect are not well understood except in a few species (11, 75). As a result we do not know the generality of the phenomenon. It has, however, been postulated to occur in a broad diversity of taxa (30, 78—80). Paucity of empirical evidence is in part due to the difficulty of studying populations at low densities. Experimental work such as that by Crowell (29) should help to identify the characteristics of species most likely to experience Allee effects and afford a more objective basis for incorporating relevant statistical functions into PVAs (cf 30).

Inbreeding depression can be modeled demographically as an Allee effect because its effect becomes more severe as population density becomes less. However, inbreeding is more complex because inbreeding depression is expected to erode with time as deleterious alleles are eliminated by a combination of drift and selection (80, 81). Dennis (30) reviews models that can be used to describe the Allee effect, and their statistical properties.

SPATIAL STRUCTURE "Habitat fragmentation is the most serious threat to biological diversity and is the primary cause of the present extinction crisis," Wilcox & Murphy observe (164). It would seem, therefore, that spatial structure should be incorporated into most PVAs. Yet, because partitioning a population into spatial subunits can be complex to model and parameterize, it is often ignored.

Spatial heterogeneity and dispersal can stabilize population fluctuations (46, 68) but can also have complex consequences depending on nonlinearities in the system (27). Asynchrony can average out fluctuations caused by demographic or environmental stochasticity, and if spatially removed, asynchrony may ensure species survival in the face of catastrophes (47). Of course,

correlated fluctuations among subpopulations can drastically reduce $E(T)$ (48).

Incorporation of spatial structure into ecological models has involved a diversity of approaches including reaction-diffusion equations (86), discrete interacting subpopulations envisioned on a grid (157), and Markov transition matrices (1). Diffusion usually has a stabilizing effect on the dynamics of single-species models, tending to average population fluctuations in space. But when spatial structure is combined with ecological interactions, e.g. competition or predation, then instability and spatial patterns can emerge. Spatial models in discrete time also show the potential for very complex dynamics, using integrodifference equations (76), or predator-prey difference equations with dispersal simulated on a grid (61).

Spatial structure adds so much complexity to ecological models that generalities can be difficult to obtain (27, 39). For example, depending upon the species in question, corridors among habitat units may be either beneficial or detrimental. Corridors can reduce consequences of inbreeding or demographic stochasticity by facilitating dispersal among sites; but they can also serve as transmission routes for disease, exotic species, or predators (127, 132a).

Recently, considerable work has focussed on metapopulation models, where the occupancy of discrete habitat patches or islands is a consequence of a balance between dispersal and extinction processes (1, 49, 87). Fahrig & Paloheimo (39) show how inter-patch dynamics is fundamental in determining population size in spatially structured models. As the distance between habitat patches increases, say as a consequence of habitat fragmentation, inter-patch dispersal is expected to decrease. The ability of dispersers to detect new habitat patches can be an exceedingly important factor determining population size, patch occupancy, and probability of extinction (39, 78). This has been the guiding principle behind PVAs for the spotted owl by Lande (79) and Thomas et al (151).

The geometry of habitat can be critical (157) and virtually impossible to model with analytical techniques. In a simulation model for the spotted owl, the landscape of suitable habitat has been mapped on a geographic information system (GIS) and imported into a dispersal simulation model (98a). This technology has great potential for coping with the complex problem of identifying an appropriate spatial structure for population modeling.

MULTI-SPECIES SYSTEMS To construct a PVA, it is fundamental to develop an understanding of the mechanisms regulating population size (133). Single species models of populations are probably unrealistic characterizations of most populations, because population regulation actually entails dynamic interactions among species, e.g. plant-herbivore, predator-prey, parasite-host

interactions. Herein lies a serious dilemma for PVA. We do not understand multispecies processes well enough for most species to incorporate such complexity into a PVA.

Modeling ecological processes ideally should include the interface with demography. For example, the dynamics of disease in a population can ultimately be determined by demographic processes. Demographic disequilibria sustained by stochastic perturbations in vital rates can result in sustained epidemiological fluctuations (155). Indeed, such interactions between time delays created by age structure and by ecological interactions may be a key to understanding dynamic behavior in general (62). But, of course, to model such processes requires detailed information on the age specificity of the ecological process.

Ecological processes are inherently nonlinear. This fact, along with the destabilizing effects of environmental seasonality and trophic-level interactions, means that complex dynamics, including chaos, are to be expected in many biological populations. It has been argued that chaos seldom occurs in ecological systems because species would be expected to go extinct when chaotic fluctuations reduce populations to low levels (9, 119). This is not necessarily true because a variety of mechanisms can ensure persistence. In particular, refugia and spatial heterogeneity (2, 71) can buffer local populations against extinction. And even if chaotic fluctuations were to cause local extinction, areas may be repopulated in the sense of a metapopulation (61, 119).

If anything, however, recent advances in nonlinear dynamics have made it clear that even simple ecological systems can possess remarkably complex dynamics. The implication is that such complex dynamics may frustrate our ability to predict long-term trajectories necessary to estimate extinction times. If we are to consider PVAs for chaotically fluctuating populations, the only hope may be to focus attention on the mechanisms that bound a systems dynamics, e.g. refugia, spatial heterogeneity, switching to alternative prey.

These remarks only give a glimpse into the true complexity of ecological systems. In performing PVAs we do not yet know how much complexity is necessary to capture the essence of the system. Deciding how much complexity is necessary should be based on advice from field biologists and managers, who have the best sense, and invariably on the availability of data.

### *Interactions Among Mechanisms*

Because several mechanisms can contribute to extinction, and because each is complex in its own right, the usual approach has been to consider the mechanisms only piecewise, one or two at a time. In this approach, one might learn which mechanism appears to be most sensitive and which requires the largest MVP.

Unfortunately this approach is flawed because the interaction among components may yield critical insight into the probability of extinction. Indeed, if Gilpin & Soule's (50) idea of extinction vortices has any validity, the synergism among processes—such as habitat reduction, inbreeding depression, demographic stochasticity, and loss of genetic variability—is exactly what will be overlooked by viewing only the pieces.

It is feasible and straightforward to build a simulation model containing both demographic and environmental stochasticity, postulated consequences of inbreeding depression, Allee effects, habitat trajectories, and consequent ramifications to carrying capacity, etc, all in the same model. Then one can conduct a sensitivity analysis to learn which parameters have the most significant consequences, and one can simulate management alternatives to view their expected consequences. Furthermore, simulation offers the power to explore propagation of variances and the effects of various types of randomness for complex systems which cannot be understood except in the full-blown model (104, 118). All these things are possible, but in practice our ability to predict the behavior of complex ecological systems has been less than exemplary (34).

## WHAT MAKES A GOOD PVA AND WHO DECIDES?

PVA may be a more ominous proposition than population biologists are accustomed to, given that PVAs have been challenged in court (5, 151). Some of the lessons learned from previous court challenges of population models may be instructive. For example, the statistical reliability of population projections is likely to be scrutinized, and it is therefore important that parameter estimation, robustness of models, and confidence limits for projections be carefully considered. How defensible is time to extinction, for example, if it carries confidence intervals spanning two orders of magnitude?

Presentation of results can be a delicate matter. Even though the model may be complex, it is essential that explanation be clear and understandable to nonscientists. Substantial testimony in one of the spotted owl hearings was ignored by the judge in her ruling because she did not understand the modeling. Yet, to oversimplify may risk misrepresentation.

There exists a delicate trade-off between building a model that realistically captures the essential ecology of the organisms and keeping the model simple enough that the number of parameters for estimation is reasonable (33). One of the beauties of some of the forecasting methods is that straightforward methods exist for extrapolating the confidence intervals and distributional properties of forecasts (31, 31a, 64). But use of such simple models requires bold assumptions about exponential population growth and perpetuation of population trajectories. For models that are more ecologically realistic,

however, such variance estimators do not exist, requiring use of simulation methods, e.g. bootstrapping and jackknifing (100). There are no rules, but a strategic modeler will use the simplest possible model that still retains the essential features of the system's ecology.

To anticipate extinction probabilities, it is essential to understand the structure of variance, particularly environmental variance (cf 55, 99, 101, 102). Yet, obtaining good estimates of variances for environmental and demographic parameters requires vast amounts of data. Most PVAs conducted thus far have been unable to do justice to variance estimation. Shaffer (126) was unable to distinguish between sampling and environmental variance for demographic parameters of grizzly bears. Lande (79) estimated only the binomial component of sampling variance surrounding demographic parameters for the spotted owl.

For time series of population size, variances often increase as the sample size increases (108). At the very least, it would appear from data presented by Pimm & Redfearn (108) that 8 years of data are needed to stabilize the variance in insect census data, and 30–40 years for birds and mammals (150). To characterize the autocorrelation structure in a time series will require even more data, yet autocorrelation is known to be important in predicting extinction probabilities (101, 102).

A large literature exists on the philosophy and methods for simulation modeling in ecology (56, 58, 104, 118, 139, 147). Likewise, there are several book-length treatises on estimation of population and ecological parameters (77, 115, 117, 124, 138, 163). Some parameters such as survival or coefficients for multispecies interactions can present serious estimation problems. And in many cases there is little hope because data are unavailable or insufficient. In these instances, one may use data from similar species or areas, use a simpler model encumbered by unrealistic assumptions on the structure of the system, or explore the behavior of the system over a range of reasonable parameter values.

Deriving statistically reliable estimates for MVP is clearly a difficult if not impossible task. But it can be an even tougher task to extrapolate from the MVP into estimating the area of habitat necessary to support such a population, which requires a detailed understanding of a species' habitat requirements (13). Patches of habitat must not only be larger than some critical size (80), they must also be in a suitable geometric configuration to ensure dispersal among habitat units. Management for spotted owls (151) provides a complex case study.

Grant (56) suggests four important components for validating any PVA model. First, does the model address the problem? Because the "problem" is usually a management issue, it may be useful to interface the PVA with risk analysis (93). Second, does the model possess reasonable structure and

behavior? The third step is to attempt a quantitative assessment of the accuracy and precision of the model's outputs and behavior. And fourth is to conduct a sensitivity analysis of the model by changing selected parameters in the model by an arbitrary amount and then studying system response and behavior.

Given careful consideration of the audience (i.e. who decides?), these validation approaches offer useful baseline criteria for evaluating a PVA model. But still, finding the appropriate balance between complexity and statistical reliability will be arbitrary and difficult to evaluate. Following these validation criteria, some approaches are fundamentally insufficient as PVAs, for example, simple calculations of $N_e > 50/500$, or projections of Leslie matrices until extinction. Examples of PVAs that have been particularly successful at stimulating enlightened management include those for grizzly bears (126,144) and spotted owls (98a, 151).

## GETTING EMPIRICAL

We cannot expect that simulation PVAs will be conducted for most endangered species. Data are often insufficient, time is critical, PVAs can be costly, and there are simply too many species needing attention (136). For these reasons, there continues to be great interest in the formulation of "rules of thumb" for MVP, and the $N_e > 50/500$ guidelines for short-term versus long-term MVPs are commonly cited (136, 152).

The original formulation of these rules of thumb was genetically based, but not based upon defensible criteria (37, 81). Nevertheless, there is empirical evidence that such rules of thumb may be of appropriate magnitude. Studies of extinction of bighorn sheep (*Ovis canadensis*)(7), and birds on oceanic or habitat islands (70, 109, 137) consistently show that $N < 50$ is clearly insufficient and the probability of extinction was higher or even certain for such small populations. Populations of $50 < N < 200$ were marginally secure, and when $N > 200$, populations were apparently secure over the limited time frames of these studies (see 150). Clearly applications of such limited observations are restricted to particular taxa, and we would expect much larger population sizes to be necessary for insect populations, for example. And there are obvious advantages to maintaining three or more replicate populations (136).

There is opportunity to expand the empirical basis for PVA and rules of thumb (150). This should include extinction studies based upon empirical observations from islands, and experimental work with replicated small populations (29). We need to understand which factors contribute to extinction probabilities for various taxa. For example, social behavior has been shown to be an important contributor in primates (32). And it is of great interest to know whether herbivores undergo greater population fluctuations

than do predators (6). Will simple single-species models suffice for herbivores whereas models incorporating trophic-level dynamics are essential for predators (94)?

Which demographic components are most critical in determining extinction probabilities? Karr (73) found that forest undergrowth bird species that have gone extinct on Barro Colorado Island (BCI) have, on average, lower survival rates, and that species with lower survival rates disappeared earlier. There was little evidence that $N$ contributed significantly to these extinctions on BCI. Other life history traits may also be important, e.g. do smaller species undergo more violent population fluctuations, thereby predisposing them to a higher probability of extinction (108, 150)?

If conservation biology is truly going to be a scientific discipline (105), it must become more actively involved in experimental research. Experimental manipulation of habitats to determine the consequences to species richness, extinction, population turnover, and dispersal are on target (e.g. 89, 120). Likewise, much could be gained by performing PVAs for species in no danger of extinction, where populations could be manipulated experimentally to rigorously test the predictions of the model.

## CONCLUSIONS: VIABILITY OF PVA?

Constructing models to include many of the complexities of the ecology of organisms presents no particular difficulties, but we simply do not have sufficient data to validate such models for most endangered species. It is seldom, if ever, that replications exist (34); thus conclusions cannot be robust (83). A great danger exists that resource managers may lend too much credence to a model, when they may not fully understand its limitations.

Nevertheless, there is too much to be gained by developing a stronger understanding of the system by modeling, to shirk modeling for fear of its being misinterpreted. PVA as a process is an indispensable tool in conservation, and it involves much more than feeble attempts to estimate MVP or probabilities of extinction. PVA entails the process of synthesizing information about a species or population, and developing the best possible model for the species given the information available. When done properly this involves working closely with natural resource managers to develop a long-term iterative process of modeling and research that can reveal a great deal about how best to manage a species. Done properly PVA can be a variation on Holling (67) and Walter's (162) notion of adaptive management, which has proven to be a powerful tool in many areas of resource management.

Adaptive management proposes application of different management tactics in time and space to develop a better understanding of the behavior of the system (162). For application to endangered species problems, when possible,

implementation of various management strategies should be attempted in spatially separated subpopulations. By so doing, one can evaluate the efficacy of various conservation strategies. Active manipulation must be part of such a program, i.e. habitat manipulation, predator or disease control, manipulation of potential competitors, provisioning, transplanting individuals from other subpopulations to sustain genetic variation, supplementation of population with releases of captive stock, etc. Monitoring of the genetic and population consequences of such manipulations then provides data to validate and/or refine the PVA model.

PVA raises a large number of exciting research questions in population ecology and genetics. One promising theoretical area appears to be expanding theory and applications of extinction processes in age-structured populations, e.g. developing applications from the general theory outlined by Aytheya & Karlin (4)(cf 83, 101, 102, 154). Existence of true threshold populations, i.e. a definitive MVP, depends upon the existence of a density-dependent mechanism such as the Allee effect or inbreeding depression (111). We have distressingly little empirical data on these processes in natural populations to peovide a basis for parameterization of models (30, 78). This must be one of the most urgent research needs for PVA.

Practical guidelines or "rules of thumb" for MVP may not be as impractical as I believed before commencing with this review. It is intriguing that five different studies synthesizing data on extinction for different vertebrate taxa have revealed that populations below 50 consistently show a high probability of extinction, whereas populations above 200 are often reasonably secure given protected habitats (7, 70, 109, 137, 150). Clearly applications of such limited observations are restricted to particular taxa, and we would expect much larger population sizes necessary for insect populations, for example (150). But these studies exemplify the further field studies that are desperately needed.

Most important, I am confident that PVA will prove to be a valuable tool as we face the extinction crisis (114). Time is not available to perform PVAs for all of the species for which it is warranted (128, 136). Indeed, single-species approaches to conservation are too limited in scope for most applications in tropical conservation (22; contra 21, 132). We must choose species for PVAs wisely, because protecting diverse communities and keystone species may afford disproportionate benefits (137a).

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