

Lecture 15. Minimum Viable Population Models, Estimating Population Persistence Probabilities, Review.

Reading:

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821-841.

Optional:

Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481-506.

A standard definition of a population is “a group of individuals of the same species occupying a defined area at the same time” (Hunter 1996). Two procedures are commonly used for evaluating the viability of a population, or the probability that the population will survive for some specified time. Population viability analysis (PVA) is the methodology of estimating the probability that a population of a specified size will persist for a specified length of time. The minimum viable population (MVP) is the smallest population size that will persist some specified length of time with a specified probability. In the first case, the probability of extinction is estimated, whereas in the second, the number of animals is estimated that is needed in the population to meet a specified probability of persistence. For a population that is expected to go extinct, the time to extinction is the expected time the population will persist. Both PVA and MVP require a time horizon, i.e., a specified, but arbitrary, time to which the probability of extinction pertains.

The topic of PVA has become very popular, with 2 recent books (Beissinger and McCullough 2002, Morris and Doak 2002) providing extensive coverage of the topic.

Definitions and criteria for viability, persistence, and extinction are arbitrary, e.g., a 95% probability of a population persisting for at least 100 years (Boyce 1992). Mace and Lande (1991) discuss criteria for extinction. Ginzburg et al. (1982) suggest the phrase “quasiextinction risk” as the probability of a population dropping below some critical threshold, a concept also promoted by Morris and Doak (2002), Ludwig (1996a) and Dennis et al. (1991). Schneider and Yodzis (1994) use the term quasiextinction to mean the population dropped to only 20 females remaining.

The usual approach for estimating persistence is to develop a probability distribution for the number of years before the model “goes extinct”, or below a specified threshold. The percentage of the area under this distribution where the population persists beyond a specified time period is taken as an estimate of persistence. To obtain MVP, probabilities of extinction are needed for various initial population sizes. The expected time to extinction is a misleading indicator of population viability (Ludwig 1996b) because for small populations, the probability of extinction in the immediate future is high, even though the expected time until extinction may be quite

large. The skewness of the distribution of time until extinction thus makes the probability of extinction for a specified time interval a more realistic measure of population viability.

Simple stochastic models have yielded qualitative insights into population viability questions (Dennis et al. 1991). But because population growth is generally considered to be nonlinear, with nonlinear dynamics making most stochastic models intractable for analysis (Ludwig 1996b), and because catastrophes and their distribution pose even more difficult statistical problems (Ludwig 1996b), analytical methods are generally inadequate to compute these probabilities. Hence, computer simulation is commonly used to produce numerical estimates for persistence or MVP. Analytical models lead to greater incites given the simplifying assumptions used to develop the model. However, the simplicity of analytical models precludes their use in real analyses because of the omission of important processes governing population change such as age structure and periodic breeding. Lack of data suggests the use of simple models, but lack of data really means lack of information. Lack of information suggests that no valid estimates of population persistence are possible, since there is no reason to believe that unstudied populations are inherently simpler (and thus justify simple analytical models) than well-studied populations where the inadequacy of simple analytical models is obvious. The focus of this paper is on computer simulation models to estimate population viability via numerical techniques, where the population model includes the essential features of population change relevant to the species of interest.

The most thorough, recent reviews of the PVA literature are provided by Beissinger and Westphal (1998) and Boyce (1992). Shaffer (1981, 1987), Soulé (1987), Nunney and Campbell (1993) and Remmert (1994) provide an historical perspective of how the field developed.

Qualitatively, population biologists know a considerable amount about what allows populations to persist. Some generalities about population persistence (Ruggiero et al. 1994) are:

1. connected habitats are better than disjointed habitats;
2. suitable habitats in close proximity to one another are better than widely separated habitats;
3. late stages of forest development are often better than younger stages;
4. larger habitat areas are better than smaller areas;
5. populations with higher reproductive rates are more secure than those with lower reproductive rates; and
6. environmental conditions that reduce carrying capacity or increase variance in the growth rates of populations decrease persistence probabilities.

This list should be taken as a general set of principles, but you should recognize that exceptions will occur often. In the following section, I will discuss these generalities in more detail, and in particular, suggest contradictions that occur.

Typically, recovery plans for an endangered species try to 1) create multiple populations of the species, so that a single catastrophe will not wipe out the entire species, and 2) increase the size of each population so that genetic, demographic, and normal environmental uncertainties are less threatening (Meffe and Carroll 1994:191-192). However, Hess (1993) argues that connected populations can have lower viability over a narrow range in the presence of a fatal disease transmitted by contact. He demonstrates the possibilities with a model, but doesn't have data to support his case. However, the point he makes seems biologically sound, and the issue can only be resolved by optimizing persistence between these two opposing forces.

Spatial variation, i.e., variation in habitat quality across the landscape, affects population persistence. Typically, extinction and metapopulation theories emphasize that stochastic fluctuations in local populations cause extinction and that local extinctions generate empty habitat patches that are then available for re-colonization. Metapopulation persistence depends on the balance of extinction and colonization in a static environment (Hanski 1996, Hanski et al. 1996). For many rare and declining species, Thomas (1994) argues (1) that extinction is usually the deterministic consequence of the local environment becoming unsuitable (through habitat loss or modification, introduction of a predator, etc.); (2) that the local environment usually remains unsuitable following local extinction, so extinctions only rarely generate empty patches of suitable habitat; and (3) that colonization usually follows improvement of the local environment for a particular species (or long-distance transfer by humans). Thus, persistence depends predominantly on whether organisms are able to track the shifting spatial mosaic of suitable environmental conditions or on maintenance of good conditions locally.

Foley (1994) uses a model to agree with 5 above, that populations with higher reproductive rates are more persistent. However, mammals with larger body size can persist at lower densities (Silva and Downing 1994), and typically have lower annual and per capita reproductive rates. The predicted minimal density decreases as the -0.68 power of body mass, likely because of less variance in reproduction relative to life span.

The last item on the list above suggests that increased variation in time leads to lower persistence (Shaffer 1987, Lande 1988, 1993). One reason that increased temporal variation causes lowered persistence is that catastrophes, such as hurricanes, fires, or floods are more likely to occur in systems with high temporal variation. Populations in the wet tropics can apparently sustain themselves at densities much lower than those in temperate climates, likely because of less environmental variation. Basically the distinction between a catastrophe and a large temporal variance component is arbitrary, and on a continuum (Caughley 1994). Further, even predictable effects can have an impact. Beissinger (1995) models the effects of periodic environmental fluctuations on population viability of the snail kite (*Rostrhamus sociabilis*).

Few empirical data are available to support the generalities above, but exceptions exist. Berger (1990) addressed the issue of MVP by asking how long different-sized populations persist. He presents demographic and weather data spanning up to 70 years for 122 bighorn sheep (*Ovis canadensis*) populations in south-western North America. His analyses reveal that: (1) 100

percent of the populations with fewer than 50 individuals went extinct within 50 years; (2) populations with greater than 100 individuals persisted for up to 70 years; and (3) the rapid loss of populations was not likely to be caused by food shortages, severe weather, predation, or interspecific competition. Thus, 50 individuals, even in the short term of 50 years, are not a minimum viable population size for bighorn sheep. However, Krausman et al. (1993) questioned this result, because they know of populations of 50 or less in Arizona that have persisted.

Pimm et al. (1988) and Diamond and Pimm (1993) examined the risks of extinction of breeding land birds on 16 British islands in terms of population size and species attributes. Tracy and George (1992) extended the analysis to include attributes of the environment, as well as species characteristics, as potential determinants of the risk of extinction. Tracy and George (1992) conclude that the ability of current models to predict the risk of extinction of particular species on particular island is very limited. They suggest models should include more specific information about the species and environment to develop useful predictions of extinction probabilities. Haila and Hanski (1993) criticized the data of Pimm et al. (1988) as not directly relating to extinctions because the small groups of birds breeding in any given year on single islands were not populations in a meaningful sense. Although this criticism may be valid, most of the “populations” that conservation biologists will study will be questionable “populations”. Thus, results of the analysis by Tracy and George (1992) do contribute useful information. Specifically, small populations of small-bodied birds on oceanic islands (more isolated) are more likely to go extinct than are large populations of large-bodied birds on less isolated (channel) islands. However, interaction of body size with type of island (channel vs. oceanic) indicated that body size influences time to extinction differently depending on the type of island. The results of Tracy and George (1992, 1993) support the general statements presented above. As with all ecological generalities, exceptions quickly appear.

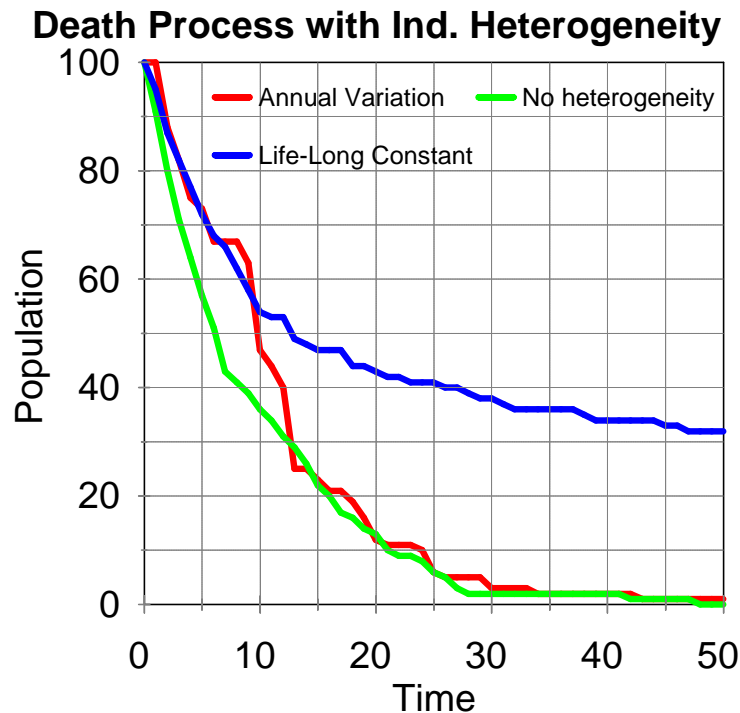
Typically, extinction and metapopulation theories emphasize that stochastic fluctuations in local populations cause extinction and that local extinctions generate empty habitat patches that are then available for re-colonization. Metapopulation persistence depends on the balance of extinction and colonization in a static environment. For many rare and declining species, Thomas (1994) argues (1) that extinction is usually the deterministic consequence of the local environment becoming unsuitable (through habitat loss or modification, introduction of a predator, etc.); (2) that the local environment usually remains unsuitable following local extinction, so extinctions only rarely generate empty patches of suitable habitat; and (3) that colonization usually follows improvement of the local environment for a particular species (or long-distance transfer by humans). Thus, persistence depends predominantly on whether organisms are able to track the shifting spatial mosaic of suitable environmental conditions or on maintenance of good conditions locally.

Many factors affect the persistence of a population. What components are needed to provide estimates of the probability that a population will go extinct, and what are the trade-offs if not all these components are available?

1. A basic population model is needed. A recognized mechanism of population regulation, density dependence, should be incorporated, because no population can grow indefinitely. "Of course, exponential growth models are strictly unrealistic on time scales necessary to explore extinction probabilities." (Boyce 1992:489). The population cannot be allowed to grow indefinitely, or persistence will be over estimated. Further, as discussed below, the shape of the relationship between density and survival and reproduction can affect persistence, and density dependence cannot be neglected for moderate or large populations (Ludwig 1996b). Density dependence can provide a stabilizing influence that increases persistence in small populations.
2. Demographic variation must be incorporated in this basic model. Otherwise, estimates of persistence will be too high because the effect of demographic variation for small populations is not included in the model.
3. Temporal variation must be included for the parameters of the model, including some probability of a natural catastrophe. Examples of catastrophes are fires (e.g., Yellowstone National Park, USA, during 1988), hurricanes, typhoons, earthquakes, extreme drought or rainfall resulting in flooding, etc. Catastrophes must be rare, or else the variation would be considered as part of the normal temporal variation. However, the covariance of the parameters is also important. Good years for survival are likely also good years for reproduction. Vice versa, bad years for reproduction may also lead to increased mortality. The impact of this correlation of reproduction and survival can drastically affect results. For example, the model of Stacey and Taper (1992) of acorn woodpecker population dynamics performs very differently depending on whether adult survival, juvenile survival, and reproduction are bootstrapped as a triplet, or as individual rates across the 10 year period. By allowing the correlation of the survival rates and reproduction, persistence is improved, mainly because the effects of one year in the data with both low juvenile survival and low reproduction is somewhat ameliorated by always combining these 2 rates.
4. Spatial variation in the parameters of the model must be incorporated if the population is spatially segregated. If spatial attributes are to be modeled, then immigration and emigration parameters must be estimated, as well as dispersal distances. The difficulty of estimating spatial variation is that the covariance of the parameters must be estimated as a function of distance, i.e., what is the covariance of adult survival of 2 subpopulations as a function of distance?
5. Individual heterogeneity must be included in the model. Individual heterogeneity requires that the basic model be extended to an individual-based model (DeAngelis and Gross 1992). As the variance of individual parameters increases in the basic model, the persistence time increases (Conner and White 1999, White

2000). Thus, instead of just knowing estimates of the parameters of our basic model, we also need to know the statistical distributions of these parameters across individuals. This source of variation is not mentioned in discussions of population viability analysis, e.g., Boyce (1992), Remmert (1994), Hunter (1996), Meffe and Carroll (1994), or Shaffer (1981, 1987). However, recent articles (Kendall and Fox 2002, Fox and Kendall 2002) recognize individual heterogeneity, and in particular, discuss how individual heterogeneity reduce the impacts of demographic stochasticity in PVAs. An important consequence is that almost all PVA overestimate the importance of demographic stochasticity and, therefore, the risk of extinction (Fox and Kendall 2002).

Many studies have demonstrated individual heterogeneity of individual survival and reproductions, e.g., Clutton-Brock (1982) demonstrated lifetime reproductive success of female red deer (*Cervus elaphus*) varied from 0 to 13 calves reared per female. Differences in the frequency of calf mortality between mothers accounted for a larger proportion of variance in success than differences in fecundity. Suppose the population has a large variance of adult survival, i.e., some adults have very high survival whereas other have much lower survival. Assume that adult survival rates are an individual characteristic, i.e., an individual's survival rate might fluctuate with temporal variation, but individuals with high survival will always have higher survival than individuals with low survival rates. Compare this situation to the typical model where all animals have the same survival rate. We find that persistence is greatest in populations with high variation of basic population parameters because some individuals have much greater survival potential than average, and thus are not removed from the population at the average rate. A third possibility is that individual heterogeneity exists in the population, but the relative survival rates do not endure across time. That is, an individual with high survival in year 1 may have the lowest survival in year 2. Because of this random fluctuation across years, each individual's expected survival probability across several years would be the same, but with more variation than if each had the same survival rate. The effect of each of these 3 assumptions is shown in the following graph of a simple death process.



As the variance of individual parameters increases in the life-long model, the persistence time increases. The above graph was generated assuming average annual mortality was 0.1. For the “no heterogeneity” model, each animal had probability 0.9 of surviving 1 additional year. In the annual variation model, an animal’s annual mortality rate was selected from a beta distribution with $\alpha = 1$ and $\beta = 9$, giving a mean of $\frac{\alpha}{\alpha + \beta} = 0.1$ and variance $\frac{\alpha\beta}{(\alpha + \beta)^2(\alpha + \beta + 1)} = 0.00818$, with the mode $\frac{\alpha - 1}{\alpha + \beta - 2} = 0$ (mode only for $\alpha \geq 1$). For the life-long model, an animal’s life-long mortality rate was selected from a beta distribution with $\alpha = 1$ and $\beta = 9$, giving the same mean and variance as for the annual rate model. If the beta distribution parameters are changed to increase the variance in the life-long model, e.g., $\alpha = 0.5$ and $\beta = 4.5$, then even greater persistence is achieved. In contrast, changing the beta distribution parameters of the annual rate model to these same values only increases the variance of the estimated persistence time, not the expected value.

6. For short-term projects, the above sources of variation may be adequate. However, if time periods of more than a few generations are projected, then genetic variation should be considered. I would expect the population to change as selection takes place. Even if no selection is operating, then genetic drift is

expected for small population sizes. However, the importance of genetic effects is still an issue in question, e.g., Joopouborg and Van Groenendael (1996). Lande (1988, 1995) has suggested either demographic variation and/or genetic effects can be lethal to a small population.

7. For long-term persistence, we must be willing to make the assumption that the system will not change, i.e., the levels of stochasticity will not change through time, the species will not evolve through selection, and the supporting capacity of the environment (the species habitat) remains static. That is, natural processes such as long-term succession and climatic change do not affect persistence, and that humans cease and desist, given that humans have been responsible for most recent extinctions! To believe the results, we have to assume that the model and all its parameters stays the same across inordinately long time periods.

After examining this list, I am sure you agree with Boyce (1992:482): "Collecting sufficient data to derive reliable estimates for all the parameters necessary to determine MVP is simply not practical in most cases." Of course, limitations of the data seldom slow down modelers of population dynamics. Further, managers are forced to make decisions, so modelers attempt to make reasonable "guesses".

ESTIMATION OF VARIANCE COMPONENTS

The implication of the list of requirements in the previous section is that population parameters or their distributions are known without error, i.e., exact parameter values are observed, not estimated. In reality, we may be fortunate and have a series of survival or reproduction estimates across time that provides information about the temporal variation of the process. However, the variance of this series is not the proper estimate of the temporal variation of the process. This is because each of our estimates includes sampling variation, i.e., we only have an estimate of the true parameter, not its exact value. To properly estimate the temporal variation of the series, the sampling variance of the estimates must be removed. The previous lecture demonstrated a technique to remove sampling variance from a series of estimates, i.e., a method to estimate the process variance.

A second approach is to incorporate additional information from covariates. Individual heterogeneity occurs in both reproduction and survival. Estimation of individual variation in reproduction is an easier problem than estimation of individual variation in survival because some animals reproduce more than once, whereas they only die once. Bartmann et al. (1992) demonstrated that over-winter survival of mule deer fawns is related to their weight at the start of the winter. Thus, one approach to modeling individual heterogeneity is to find a correlate of survival that can be measured, and develop statistical models of the distribution of this correlate. Then, the distribution of the correlate can be sampled to obtain an estimate of survival for the individual. Łomnicki (1988) also suggests weight as an easily measured variable that relates to an animal's fitness.

To demonstrate this methodology, I will use a simplification of the logistic regression model of Bartmann et al. (1992):

$$\log\left(\frac{S}{1-S}\right) = \beta_0 + \beta_1 \text{Weight} \quad ,$$

where survival (S) is predicted as a function of weight. Weight of fawns at the start of winter was approximately normally distributed with mean 32 kg and standard deviation 4.2. To simulate individual heterogeneity in over-winter fawn survival, values can be drawn from this normal distribution to generate survival estimates.

This model can be expanded to incorporate temporal variation (year effects), sex effects, and area effects, as described for mule deer fawns by Bartmann et al. (1992). An example of modeling temporal variation in greater flamingos (*Phoenicopterus ruber roseus*) as a function of winter severity is provided by Cézilly et al. (1996). The approach suggested here of modeling winter severity as a random variable and estimating survival as a function of this random variable is an alternative to the variance estimation procedures of the previous section. Both provide a mechanism for injecting variation into a population viability model. The main advantage of using weather data to drive the temporal variation of the model is that considerably more weather data is available than is biological data on survival or reproductive rates.

The major drawback of the indirect estimation approach proposed here is that sampling variation of the functional relationship is ignored in the simulation procedure. That is, the logistic regression model includes sampling variation because its parameters are estimated from observed data. The parameter estimates of the logistic regression model include some unknown estimation error. Their direct use results in potentially biased estimates of persistence, depending on how much sampling error is present. Thus, a “good” model relating the covariate to the biological process is needed.

A third method is demonstrated by Stacy and Taper (1992) when they used a bootstrap procedure to incorporate temporal variation into a model of acorn woodpecker (*Melanerpes formicivorus*) population viability. They used estimates of adult and juvenile survival and reproductive rates resulting from a 10-year field study to estimate population persistence. To incorporate the temporal variation from the 10 years of estimates, they randomly selected with replacement 1 estimate from the observed values to provide an estimate in the model for a year.

This procedure is known in the statistical literature as a bootstrap sampling procedure. The technique is appealing because of its simplicity. However, for estimating population viability, a considerable problem is inherent in the procedure. That is, the estimates used for bootstrapping contain sampling variation and demographic variation, as well as the environmental variation which the modeler is attempting to incorporate. To illustrate how demographic variation is included in the estimates, consider an example population of 10

animals with a constant survival rate of 0.55. Thus, the actual temporal variation is zero, yet a sequence of estimates of survival from this population would suggest considerable variation. That is, the estimates of survival would have a variance of $0.55(1 - 0.55)/10 = 0.02475$ if all 10 animals had a survival probability of 0.55. Further, the only observed values of survival would be 0, 0.1, ..., 1.0. However, if the size of the population is increased to 100, you find that the variance of the sequence of estimates is now 0.002475, a considerable decrease from above. Thus, randomly sampling the estimates from a population of size 10 results in considerably more variation than from a population of 100. As a result, the demographic variation from the sampled population will be incorporated into the persistence model if the bootstrap approach is used.

A similar example can be used to demonstrate that sampling variation is also inherent in bootstrapping from a sample of observed estimates. Suppose a sample of 10 radiocollared animals is used to estimate survival for a population of 100,000 animals, i.e., the finite sample correction term can be ignored. The sampling variation of the estimates would be $S(1 - S)/10$, where S is the true survival rate for the population assuming all animals had the same survival rate. Now if a sample of 100 radiocollared animals is taken, the sampling variation reduces to $S(1 - S)/100$. Thus, randomly sampling estimates with a bootstrap procedure incorporates the sampling variation of the estimates into the persistence model. As a result of the increased variation, persistence values will be underestimated.

Therefore, I suggest using sparingly the bootstrap approach demonstrated by Stacey and Taper (1992). Persistence estimates developed with this procedure will generally be too low, i.e., you will conclude the population is more likely to go extinct than it really will. However, methodologies such as shrinkage estimation of variances (K. P. Burnham, Pers. Commun.) may prove useful in removing sampling variance from the estimates, and make the bootstrap procedure more applicable to estimating population persistence.

INCORPORATION OF PARAMETER UNCERTAINTY INTO PERSISTENCE ESTIMATES

Unbiased estimates of process variances such as temporal and spatial variation can be achieved. In this section, I will examine how to incorporate uncertainty of the parameter estimates into the estimates of persistence, and in the process, provide an unbiased estimate of persistence given the population model.

Any model developed to estimate population persistence will have several to many parameters that must be estimated from available data. Each of these estimates will have an associated estimate of its precision in the form of a variance, assuming that statistically rigorous methods were used to estimate the parameter from data. In addition, because some of the parameters may have been estimated from the same set(s) of data, some parameters in the model may have a non-zero covariance. Thus, the vector of parameter estimates ($\hat{\theta}$) used in the model to estimate persistence has the variance-covariance matrix $[V\hat{\theta}]$ to measure uncertainty.

Typically, statisticians use the delta method (e.g. Seber 1982:7-9) to estimate the variance of a function of parameters from a set of parameter estimates and their variance-covariance matrix. In the context of persistence, the variance of the estimate of persistence (\hat{p}) would be estimated as

$$\text{Var}(\hat{p}) = \frac{\partial f(\underline{\theta})^T}{\partial \underline{\theta}} \text{Var}(\hat{\underline{\theta}}) \frac{\partial f(\underline{\theta})}{\partial \underline{\theta}}$$

where $\hat{p} = f(\hat{\underline{\theta}})$. That is, the function f represents the model used to estimate persistence. However, for realistically complex persistence models, the analytical calculation of partial derivatives needed in this formula is likely not feasible.

The lack of explicit analytical partial derivatives suggests that numerical methods be used. The most feasible, albeit numerically intensive, appears to be the parametric bootstrap approach (Effron and Tibshirani 1993, Urban Hjorth 1994). With a parametric bootstrap, a realization of the parameter estimates is generated based on their point estimates and sampling variance-covariance matrix using Monte Carlo methods. Likely a multivariate normal distribution will be used as the parametric distribution describing the set of parameter estimates, although other distributions or combinations of distributions may be more realistic biologically. Using this set of simulated values in the persistence model, persistence is estimated. This step will require a large number of simulations to properly estimate persistence with little uncertainty, typically 10000 simulations are conducted. Then, a new set of parameter values are generated and persistence again estimated. This process is repeated for many sets of parameter estimates (at least 100, but more likely 1000) to obtain a set of estimates of persistence. The variation of the resulting estimates of persistence is then a measure of uncertainty attributable to the variation of the parameter estimates as measured by their variance-covariance matrix. The process is diagrammed as:

PARAMETRIC BOOTSTRAP LOOP (1000 iterations):

 Select realization of parameter estimates

 MONTE CARLO LOOP (10000 iterations):

 Tabulate percentage of model runs resulting in persistence

 END MONTE CARLO LOOP

 END PARAMETRIC BOOTSTRAP LOOP

However, even more critical to our viability analysis is the fact that the mean of this set of 1000 estimates of persistence is likely less than the estimate we obtained using our original point estimates of model parameters. More formally, the expected value of estimated persistence $[E(\hat{p})]$ is less than the value of persistence predicted by our model using the point estimates of its parameters, i.e., $E(\hat{p}) < f[E(\hat{\theta})]$, an example of Jensen's inequality. This difference is due to large probabilities of early extinction for certain parameter sets that are likely given their sampling variation (Ludwig 1996a). Thus, to estimate persistence, the mean of the bootstrap estimates of persistence should be used, and not the estimate of persistence obtained by plugging our parameter estimates directly into our population model.

Confidence intervals on persistence could be constructed using the usual $\pm 2SE$ procedure based on the set of 1000 estimates. This confidence interval represents the variation attributable to the uncertainty of the parameter estimates used in the model. Uncertainty about the model is not included in this confidence interval, because the model is assumed to be known. However, a better confidence interval will probably be achieved by sorting the 1000 values into ascending order and using the 25th and 975th values as a 95% confidence interval. This procedure accounts for the likely asymmetric distribution of the estimates of persistence.

DISCUSSION

The real problem with PVA is not the model, but obtaining the data to drive the models (Ruggiero et al. 1994, Ludwig 1999). Much of the published work on PVA ignores this essential (Thomas 1990). For example, Mangel and Tier (1994) simplify the process to the point that they miss major issues concerning data reliability and quality of the product (estimates of persistence). Their 4 "facts" are:

1. "A population can grow, on average, exponentially and without bound and still not persist." This is because of catastrophes that will bring even a thriving population to zero.
2. "There is a simple and direct method for the computation of persistence times that virtually all biologists can use." They suggest a simple model with one age class and a population ceiling that the population cannot exceed, but the ceiling does not cause density dependence effects of growth parameters. As a result, their approach to estimating persistence is likely to underestimate persistence if the ceiling is set too low because the population can never grow away from the absorbing state of extinction.
3. "The shoulder of the MacArthur-Wilson model occurs with other models as well, but disappears when catastrophes are included." They suggest a slow, steady rise in persistence times as the population ceiling is increased.

4. "Extinction times are approximately exponentially distributed and this means that extinctions are likely." Thus, they conclude the most likely value of a population is zero, i.e., the mode of an exponential distribution. I believe this result is because of the simplistic assumptions they have used to obtain it. Realistic models that incorporate the sources of variation described above will not result in such simplistic results.

Another misguided example is Tomiuk and Loeschke (1994). Their mathematics cover up the real problem of obtaining realistic estimates of the parameter values to use in the models. Their model emphasizes demographic variation, and ignores the bigger issues of temporal variation and individual heterogeneity.

A common problem with PVA is that the sampling variation of the parameter estimates is ignored. Examples are Stacey and Taper (1993) and Dennis et al. (1991). In both cases, estimates of persistence are too pessimistic because the sampling variation of the population parameters is included in the population model as if it were temporal variation.

"Most PVAs have ignored fundamentals of ecology such as habitat, focusing instead on genetics or stochastic demography." (Boyce 1992:491). For small populations (<50) of endangered species, such a strategy may be justified, particularly for short term predictions. But incorporating only demographic variation results in over estimates of persistence, because temporal variation has been ignored. On the other hand, the remaining survivors of an endangered species may be the individuals with strong survival and reproductive rates, and so the lack of individual heterogeneity may under estimate persistence.

The above studies should not lead the reader to believe that useful attempts to estimate persistence do not exist. Schneider and Yodzis (1994) developed a model of marten (*Martes americana*) population dynamics that incorporated the behavior and physiology of individual martens, spatial dynamics, and demographic and environmental stochasticity. Undoubtedly some readers would quibble with some of the assumptions and data used to build the model, but I would contend that a realistic model with some of the inputs "guessed" is a much more reasonable approach than a simplistic model that ignores important processes affecting persistence. Further, such realistic models identify data needs that can be addressed with time, even though the actual estimate of persistence is of questionable value. The alternative of using simplistic and naive models assures invalid estimates and little progress in improving the situation, with a rapid loss of credibility by the field of conservation biology.

Murphy et al. (1990) have proposed two different types of PVA. For organisms with low population densities that are restricted to small geographic ranges (typical vertebrate endangered species), genetic and demographic factors should be stressed. For smaller organisms such as most endangered invertebrates, environmental uncertainty and catastrophic factors should be stressed because these organisms are generally restricted to a few small habitat patches, but are capable of reaching large population sizes within these patches. Nunney and Campbell (1993)

note that demographic models and genetic models both have resulted in similar estimates of minimum viable population size, but that the ideal spatial arrangement of reserves remains an issue.

Lande (1995) suggests that genetic mutations may affect fitness, and thus ignoring genetic effects results in underestimates of viability. Mutation can affect the persistence of small populations by causing inbreeding depression, by maintaining potentially adaptive genetic variation in quantitative characters, and through the erosion of fitness by accumulation of mildly detrimental mutations. Populations of 5000 or more are required to maintain evolutionary viability. Theoretical results suggest that the risk of extinction due to the fixation of mildly detrimental mutations may be comparable in importance to environmental stochasticity and could substantially decrease the long-term viability of populations with effective sizes as large as a few thousand (Lande 1995). If these results are correct, determining minimum viable population numbers for most endangered species is an exercise in futility, because almost all of these populations are already below 5000.

Conservation biologists would like to have “rules of thumb” to evaluate persistence (Boyce 1992), for example the magical Franklin-Soulé number of 500 (Franklin 1980, Soulé 1980) that is the effective population size (N_e) to maintain genetic variability in quantitative characters. Unfortunately, these rules lack the realism to be useful. The Franklin-Soulé number was derived from simple genetic models, and hence lacks the essential features of a PVA model discussed here. Attempts with simplistic models such as Mangel and Tier (1994) and Tomiuk and Loeschcke (1994) also do not provide defensible results because of the lack of attention to the biology of the species and the stochastic environment in which the population exists. Until conservation biologists do good experimental studies to evaluate population persistence empirically, I question the usefulness of “rules of thumb” and simplistic models suggested various places in the literature.

In the meantime, until rigorous experimental work can be conducted, conservation biologists should borrow information from game species, where long-term studies have been done that will provide estimates of temporal and spatial variation and individual heterogeneity. Rules of thumb that predict temporal variation in survival as a function of weather, or individual variation in survival as a function of body characteristics, provide alternative sources of data. For at least some game species, data exist to develop such rules. Further, these kinds of data will probably never be available for many endangered species: the opportunity to collect such data was lost with the decline of the population to current (threatened) levels. Thus, I suggest the use of surrogate species to help meet the data needs of realistic models of persistence. Taxonomically related species may provide information, although species in the same ecological guild may also provide information on temporal and spatial variation.

CONCLUSION

In summary, most estimates of population viability are nearly useless because one or more of the following mistakes or omissions are made in developing a model to estimate persistence.

1. The model ignores spatial variation which will increase population viability. As suggested by Stacey and Taper (1992) immigration can occasionally rescue a population from extinction.
2. The model uses estimates of temporal variation that are at best, poor guesses. This statement assumes that the modeler understood the difference between process variation and sampling variation. Often, sampling variation is assumed to substitute for process variation, and, as a result, the estimates of persistence are too pessimistic. Sampling variation has nothing to do with population persistence. Estimates of population parameters must not be treated as if they are the true parameter value.
3. The model uses demographic variation as a substitute for temporal variation in the process, and ignores true temporal variation.
4. The model ignores life-long individual heterogeneity that increases population viability, and assumes that all individuals endure the same identical survival and reproduction parameters. Such a naive assumption results in population viability being underestimated.
5. The model assumes that current conditions are not changing, i.e., the stochastic processes included in the model are assumed constant for the indefinite future. Loss of habitat and other environmental changes that affect these stochastic processes are ignored. Thus, as discussed by Caswell (1989), the model is likely not useful in forecasting (i.e., predicting what will happen), but is useful in projecting (i.e., predicting what would happen if conditions do not change).

Before you use the estimates of persistence from any population viability analysis, compare your approach to obtain the estimate against the necessary components discussed here. If you discover omissions and errors in the approach used to obtain the estimate, recognize the worth or lack thereof of the estimate of persistence. Although the estimates of persistence obtained from a PVA may have little value, the process of formulating a model and identifying missing information, i.e., parameters that are poorly estimated, may still have value in developing measures to conserve the species in question (Beissinger and Westphal 1998).

Literature Cited

Bartmann, R. M., G. C. White, and L. H. Carpenter. 1992. Compensatory mortality in a Colorado mule deer population. *Wildlife Monograph* 121:1-39.

- Beissinger, S. R. 1995. Modeling extinction in periodic environments: Everglades water levels and Snail Kite population viability. *Ecological Applications* 5:618-631.
- Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. *Journal of Wildlife Management* 62:821-841.
- Beissinger, S. R., and D. R. McCullough, editors. 2002. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA. 577 pp.
- Berger, J. 1990. Persistence of different-sized populations: an empirical assessment of rapid extinctions in bighorn sheep. *Conservation Biology* 4:91-98.
- Boyce, M. S. 1992. Population viability analysis. *Annual Review of Ecology and Systematics* 23:481-506.
- Caswell, H. 1989. *Matrix population models*. Sinauer Associates, Sunderland, Massachusetts, USA. 328 pp.
- Caughley, G. 1994. Directions in conservation biology. *Journal of Animal Ecology* 63:215-244.
- Cézilly, F., A. Viallefont, V. Boy and A. R. Johnson. 1996. Annual variation in survival and breeding probability in greater flamingos. *Ecology* 77:1143-1150.
- Clark, T. W., P. C. Paquet, and A. P. Curlee. 1966. Special section: large carnivore conservation in the Rocky Mountains of the United States and Canada. *Conservation Biology* 936-936.
- Clutton-Brock, T. H., F. E. Guinness, and S. D. Albon. 1982. *Red deer behavior and ecology of two sexes*. University Chicago Press, Chicago, Illinois. 378 pp.
- Conner, M. M., and G. C. White. 1999. Effects of individual heterogeneity in estimating the persistence of small populations. *Natural Resource Modeling* 12:109-127.
- DeAngelis, D. L. and L. J. Gross, eds. 1992. *Individual-based models and approaches in ecology: populations, communities, and ecosystems*. Chapman & Hall, New York, New York, USA. 525 pp.
- Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* 6:115-143.
- Diamond, J., and S. Pimm. 1993. Survival times of bird populations: a reply. *American Naturalist* 142:1030-1035.

- Efron, B. and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman & Hall, New York, New York, USA. 436 pp.
- Foley, P. 1994. Predicting extinction times from environmental stochasticity and carrying capacity. *Conservation Biology* 8:124-136.
- Fox, G. A., and B. E. Kendall. 2002. Demographic stochasticity and the variance reduction effect. *Ecology* 83:1928-1934.
- Franklin, I. R. 1980. Evolutionary changes in small populations. Pages 135-149 *In* M. E. Soulé and B. A. Wilcox, eds. *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Ginzburg, L. R., L. B. Slobodkin, K. Johnson, A. G. Bindman. 1982. Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis* 2:171-181.
- Haila, Y., and I. K. Hanski. 1993. Birds breeding on small British islands and extinction risks. *American Naturalist* 142:1025-1029.
- Hanski, I. 1996. Metapopulation ecology. Pages 13-43 *in* *Population Dynamics in Ecological Space and Time*, O. E. Rhodes, Jr., R. K. Chesser, and M. H. Smith, eds. University Chicago Press, Chicago, Illinois, USA.
- Hanski, I., A. Moilanen, and M. Gyllenberg. 1996. Minimum viable metapopulation size. *American Naturalist* 147:527-541.
- Hess, G. R. 1993. Conservation corridors and contagious disease: a cautionary note. *Conservation Biology* 8:256-262.
- Hunter, M. L., Jr. 1996. *Fundamentals of conservation biology*. Blackwell Science, Cambridge, Massachusetts, USA. 482 pp.
- Joopouborg, N., and J. M. Van Groenendael. 1996. Demography, genetics, or statistics: comments on a paper by Heschel and Paige. *Conservation Biology* 10:1290-1291.
- Kendall, B. E., and G. A. Fox. 2002. Variation among individuals and reduced demographic stochasticity. *Conservation Biology* 16:109-116.
- Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.
- Lande, R. 1993. Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *American Naturalist* 142:911-927.

- Lande, R. 1995. Mutation and conservation. *Conservation Biology* 9:782-791.
- Lomnicki, A. 1988. Population ecology of individuals. Princeton University Press, Princeton, New Jersey, USA. 223 pp.
- Ludwig, D. 1996a. Uncertainty and the assessment of extinction probabilities. *Ecological Applications* 6:1067-1076.
- Ludwig, D. 1996b. The distribution of population survival times. *American Naturalist* 147:506-526.
- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80:298-310.
- Mace, G. M., and R. Lande. 1991. Assessing extinction threats: toward a reevaluation of IUCN threatened species categories. *Conservation Biology* 5:148-157.
- Mangel, M. and C. Tier. 1994. Four facts every conservation biologist should know about persistence. *Ecology* 75:607-614.
- Meffe, G. K., and C. R. Carroll. 1994. Principles of conservation biology. Sinauer Associates, Inc., Sunderland, Massachusetts, USA. 600 pp.
- Morris, W. F., and D. F. Doak. Quantitative conservation biology: theory and practice of population viability analysis. Sinauer Associates, Sunderland, Massachusetts, USA. 480pp.
- Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. *Conservation Biology* 4:41-51.
- Nunney, L. and K. A. Campbell. 1993. Assessing minimum viable population size: demography meets population genetics. *Trends in Ecology and Evolution* 8:234-239.
- Pimm, S. L., H. L. Jones, and J. M. Diamond. 1988. On the risk of extinction. *American Naturalist* 132:757-785.
- Remmert, H. (ed.). 1994. Minimum animal populations. Springer-Verlag, New York, New York, USA. 156 pp.
- Ruggiero, L. F., G. D. Hayward, and J. R. Squires. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. *Conservation Biology* 8:364-372.

- Schneider, R. R., and P. Yodzis. 1994. Extinction dynamics in the American marten (*Martes americana*). *Conservation Biology* 4:1058-1068.
- Seber, G. A. F. 1982. Estimation of animal abundance and related parameters. 2nd ed. Macmillan, New York. 654 pp.
- Shaffer, M. L. 1981. Minimum population size for species conservation. *BioScience* 31:131-134.
- Shaffer, M. L. 1987. Minimum viable populations: coping with uncertainty. Pages 69-86 in M. E. Soulé, editor. *Viable populations for conservation*. Cambridge University Press, Cambridge, England.
- Silva, M. and J. A. Downing. 1994. Allometric scaling of minimal mammal densities. *Conservation Biology* 8:732-743.
- Soulé, M. E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. Pages 151-170 In M. E. Soulé and B. A. Wilcox, eds. *Conservation biology: an evolutionary-ecological perspective*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Soulé, M. E. 1987. *Viable Populations for Conservation*. Cambridge University Press, New York, New York, USA. 189 pp.
- Stacey, P. B. and M. Taper. 1992. Environmental variation and the persistence of small populations. *Ecol. Applications* 2:18-29.
- Thomas, C. D. 1994. Extinction, colonization, and metapopulations: environmental tracking by rare species. *Conservation Biology* 8:373-378.
- Tomiuk, J. and V. Loeschke. 1994. On the application of birth-death models in conservation biology. *Conservation Biology* 8:574-576.
- Tracy, C. R., and T. L. George. 1992. On the determinants of extinction. *American Naturalist* 139:102-122.
- Tracy, C. R., and T. L. George. 1993. Extinction probabilities for British island birds: a reply. *American Naturalist* 142:1036-1037.
- Urban Hjorth, J. S. 1993. *Computer intensive statistical methods*. Chapman & Hall, London, United Kingdom. 263 pp.

White, G. C. 2000. Population viability analysis: data requirements and essential analyses. Pages 288-331 *in* L. Boitani and T. K. Fuller, eds. *Research Techniques in Animal Ecology*. Columbia University Press, New York, New York, USA.