

CHAPTER
Application of Population
Viability Analysis to
Landscape Conservation
Planning

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The concept of population viability is a central tenet of landscape planning and management. Maintaining biological diversity and therefore the viability of all species presents a significant constraint in designing working landscapes that can produce the goods and services society desires. Large-scale landscape planning to maintain biodiversity usually integrates coarse-scale assessments of land use change with systematic evaluations of its effects on the likelihood of species becoming extinct years in the future, or their population viability (Andelman et al. 2001; Noon et al. 2003; Noon et al., this volume).

Population viability is challenging, however, to define and to evaluate. There is no standard definition of a viable population in terms of the time horizon or level of acceptable risk of extinction, and there is no standard definition of what comprises a population viability analysis (PVA). The first PVAs were quantitative modeling exercises that estimated the risk of extinction within a specified time period (Shaffer 1981, Gilpin and Soulé 1986). The output of a probabilistic estimate of extinction from a stochastic model differentiated PVA from earlier deterministic models used to guide the recovery of endangered species (Beissinger 2002), but PVA has been used to describe analysis outcomes ranging from workshops to the results of expert panels. There are recent suggestions, however, that the term *PVA* should be restricted to analytical or simulation models that use data to estimate the risk of extinction or a closely related measure of population health, such as the proportion of simulated populations that end below some size after a specified period of time or quasiextinction (Ralls et al. 2002, Reed et al. 2002). A viable population is one that does not exceed this measure of risk. An acceptable risk of extinction, and the time horizons over which they should be assessed, should be set at levels that scientists, decision makers, and society are willing to accept.

Extinction risk is difficult to assess in part because it is a stochastic process affected by many factors. Estimates of long-term means and variances for birth and death rates, population growth rate, immigration and emigration rates,

and density-dependent relationships are needed (Beissinger and Westphal 1998). Genetic and catastrophic processes should be incorporated because they can play critically important roles in population viability when a long time period is considered—but unfortunately they are often ignored (Mangel and Tier 1994, Allendorf and Ryman 2002). Assessing extinction risk must project these processes into the future in relation to potential scenarios of environmental change. Models have become a useful tool for integrating the effects of these multiple forces on the risk of extinction.

In this chapter, we briefly review available methods for assessing population viability and discuss which models are useful under different circumstances. We then discuss how they may be used in making decisions about landscape design and conclude with a discussion of the uncertainties inherent in population viability analysis.

METHODS OF MODELING POPULATION VIABILITY

There are many methods for modeling population viability (Table 2-1). They include demographic models that assess the impact of management on the rate of population growth or risk of extinction, analyses of occupancy using presence-

Table 2-1 Types of Models and Analyses that have been Used to Assess Viability and the Kinds of Data they Require (Modified From Andelman et al. 2001)

Type	Analysis	General Data Needs				
		Habitat Maps	Occurrence	Demography	Dispersal	Pop. Estimate
Demographic	Matrix	No	No	Population	No	No
	Stochastic PVA	No	No	Population	No	Population
	Metapopulation	Current, Future	Population, Patches	Patch	Population	Patch
	Spatially Explicit	Current, Future	Individuals, Patches	Individual	Individual	Patch
Occupancy	Incidence Function	Current	Population, Patches	No	No	No
	Patch Turnover	Current	Population, Patches	No	No	No
Population	Trend Analysis	No	No	No	No	Population, Index
Genetic	Effective Size	No	No	Population	No	Population

absence data, population trend analysis, and genetic models that assess the loss of genetic diversity. We briefly review these methods below, but see [Beissinger and Westphal \(1998\)](#), [Andelman et al. \(2001\)](#), [Possingham et al. \(2001\)](#), [Morris and Doak \(2002\)](#), and [Beissinger et al. \(2006\)](#) for more in-depth discussions.

Demographic models explicitly incorporate birth and death rates, and to varying degrees the processes that affect them, and are often used to evaluate population viability ([Beissinger and McCullough 2002](#)). Demographic models vary in complexity from deterministic matrix models of a single population to stochastic, spatially explicit individual-based models (IBMs) that keep track of each individual on specific landscapes ([Table 2-1](#)).

Deterministic single-population matrix models (hereafter “*matrix models*”) use a set of equations (one for each age or stage class), which are often formulated into a matrix, to predict population size at time $t+1$ from information on the survival, growth, and reproduction of individuals at time t . Matrix models can be used to make estimates of the geometric rate of population growth (λ), to indicate population characteristics such as the distribution of individuals among age classes (stable age distribution) or the reproductive value of age classes, and to evaluate the relative influence of demographic rates on population change (sensitivity or elasticity analysis; [Caswell 2001](#)). Matrix population models have limited use in assessing viability because they only indicate whether and how fast a population is increasing or decreasing, and do not give an estimate of the risk of extinction. Nevertheless, a sensitivity analysis of a matrix provides useful insights into population viability because it can indicate how changes in specific demographic rates impact rates of population change (e.g., reproductive success versus adult survival). Recently, this sort of analysis has been adapted to include the costs of conservation actions to assist decision makers choosing among management options ([Baxter et al. 2006](#)).

Stochastic single population PVA models (hereafter *stochastic PVA models*) project populations for 50, 100, or more years into the future by allowing demographic rates to change using the Monte Carlo method, which samples rates randomly from predetermined distributions. Each run of a stochastic model follows a unique trajectory and yields a different ending population size, so models must be run 500 to 1000 times to explore the full range of parameter values and portray the distribution of possible ending population sizes ([Harris et al. 1987](#), [Burgman et al. 1993](#)). In addition to estimates of mean age- or stage-specific survival and fecundity, stochastic models require estimates of variance in fecundity and survival for each age or stage class to model the effects of demographic and environmental stochasticity. Stochastic PVA models should also include carrying capacity and its variance ([Ginzburg et al. 1990](#)), and the frequency and effects of catastrophes. They can also incorporate processes that may occur when populations become small, such as Allee effects or inbreeding depression. Stochastic PVA models yield the proportion of runs that end at population size zero (“extinction” rate) or at a small size such as <25 individuals (“quasiextinction” rate), or the mean or median year of extinction for populations that went extinct (“time to extinction”). Perhaps the most complete descriptor of model

results is the cumulative probability function for ending population size, or the “quasiextinction function” (Ginzburg et al. 1982, Burgman et al. 1993). All these outputs can be expressed in relation to changes in landscape management or planning scenarios.

Demographic models of metapopulations can examine relationships between landscape structure and population dynamics by incorporating site-specific effects on demography. Compared to stochastic PVA models, they incorporate additional details of patch-specific demography, dispersal, and landscape dynamics to project population dynamics into the future (Hanski 2002; Harrison and Ray 2002; Akçakaya and Brook, this volume). These so-called *patch models* track individuals in populations as they reside only within these habitat patches and their movement among them. Population dynamics within each patch are modeled as in stochastic single-population PVA models, with the additional steps of determining the number of individuals that will disperse from and migrate to each patch. Patch metapopulation models provide output on population trajectories, risk of population extinction or decline, and related measures of population size.

Spatially explicit population models (SEPMs) are complex simulation models that may be built for single populations or a metapopulation to model movements of individuals across a diverse landscape, or the response of populations to changing landscape structure. They incorporate exact spatial locations of individuals, habitats, barriers to dispersal, and other landscape characteristics. SEPMs are often individual-based models (IBMs), where individuals are placed in known locations and assigned demographic traits based on the habitat where they are located. Two common forms of spatially explicit population models are as follows:

1. *Grid or cell-based models* track population sizes in equal-sized cells, which are typically the building blocks of larger habitat patches and are influenced by the inputs and outputs of neighboring cells. They are often used for abundant organisms, where modeling the movement or fate of each individual may be intractable, such as plants, insects, or rodents (Bradstock et al. 1996, Price and Gilpin 1996); and
2. *Individual-based models* track the location and behavior of every individual. They have been applied to determine the distribution of suitable habitat at multiple scales (Hatten and Paradzick 2003), simulate responses to regional management practices (Boone and Hunter 1996), predict regions of future human-wildlife conflicts (Treves et al. 2004), and simulate the effects of forest management policies (McKelvey et al. 1993, Lamberson et al. 1994, Liu et al. 1995, Walters et al. 2002).

Output from SEPMs is composed of averages over individuals to yield population statistics, such as population size at a specific time, population trajectories, or time to extinction.

Stochastic patch occupancy models (SPOMs) rely on simple presence-absence data obtained from single or multiple surveys to estimate the probability that a patch is occupied and to project metapopulation dynamics into the future (Day and Possingham 1995, Hanski 1998, Thomas and Hanski 2004). Etienne et al. (2004) reviewed the two types of SPOMs: (1) The incidence function approach combines the pattern of patch occupancy with relationships derived from biogeography to estimate colonization and extinction rates (Hanski 1999); and (2) the patch-turnover approach uses observed patch colonizations and extinctions (Sjogren-Gulve and Ray 1996, Kindvall 2000, Sjogren-Gulve and Hanski 2000). An important recent advance for parameterizing occupancy models accounts for imperfect detection to estimate patch occupancy (MacKenzie et al. 2006). Occupancy models can be applied to simulate metapopulation dynamics by substituting new patch-area, patch-isolation, or other landscape characteristics into a simulation model (Hanski 1999, Hanski and Gaggiotti 2004).

Population trend analysis creates models of population fluctuations from count data, such as the number of individuals in a population surveyed over multiple years, to project populations into the future and estimate extinction risk (Morris and Doak 2002). Count data may be relatively easy and cheap to collect compared to detailed demographic data. The simplest conceptual model of population growth is $N_{t+1} = \lambda N_t$ where N_t is the number of individuals in the population in year t , and λ is the population growth rate. λ and variation in λ may be dependent or independent of density, and are functions of many of the same factors that influence demographic rates discussed previously, as well as immigration and emigration (Peery et al. 2006). Dennis et al. (1991) developed an approach that extracts a maximum likelihood estimator of growth rate and its confidence interval, which has become widely used in analyses of extinction risk. It assumes that population changes can be approximated by a simple diffusion process with drift, which may work as long as density dependence is not strong, data gaps in the time series are few, and sampling error is not extensive (Dennis et al. 1991, Holmes and Fagan 2002, Morris and Doak 2002, Holmes 2004, Staples et al. 2004). Applications have been diverse and growing (Buena and Gerber 2004, Gonzalez-Suarez et al. 2006, Thomson and Schwartz 2006). Accurate prediction of extinction risk, however, often requires decades-long time series of data (Fieberg and Ellner 2000, Lotts et al. 2004).

The concept of *effective population size* or N_e has been used to evaluate genetic considerations into PVA (Haig and Ballou 2002). N_e , defined as the number of individuals in a population that contribute genes to the next generation, measures the effect of genetic drift on a natural population. It is a useful way to evaluate the magnitude of genetic loss over time in a small population by comparing how it deviates from an “ideal” population, or by examining the relationship between N_e and the actual or census population size (N) (Waples 2002). Characteristics of an ideal population are both genetic and demographic, and include large and stable size, equal genetic contribution by both sexes, no

inbreeding, equal family size, and nonoverlapping generations. Most organisms violate some or all of these characteristics. N_e is often substantially less than N , usually only 10–25% of total population size (Frankham 1995, Waples 2002). N_e was one of the first measures of population viability. Frankel and Soulé (1981) suggested that small populations should try to attain an N_e of 50 individuals over the short term and N_e of 500 individuals over the long term (the “50/500 rule”). More recently, Franklin and Frankham (1998) argued that an N_e of 500–1000 would be appropriate, and Lande (1995) suggested a minimum effective size of 5000 was more appropriate. Debate continues and no clear consensus has yet emerged on what level of N_e is needed to maintain viability (Waples 2002, Beissinger et al. 2006). In viability assessments, it seems most satisfactory to consider how various landscape scenarios affect the factors that contribute to N_e , but to avoid comparing N_e estimates to specific numeric goals (Beissinger et al. 2006).

WHEN SHOULD PVA MODELS BE USED AND WHICH ONE(S)?

All methods of assessing viability have some utility, and they all explicitly or implicitly use a model—even expert opinion PVAs (Burgman 2005). Methods that use formal mathematical models for analyzing viability are usually preferable to less quantitative methods, such as indices of rarity and expert opinion, when there is some knowledge of demography, dispersal, habitat use, and threats. The advantages of a formal model often lie mostly in its transparency and repeatability (Burgman and Possingham 2000). Creating a formal model often involves a necessary trade-off between generality, precision, and realism (Levins 1968, Beissinger et al. 2006). The range of possible methods in Table 2-1 offers a trade-off between complexity of analysis and generality of results. None might provide perfect analysis alone, but all can provide important insights when used together as one of several analyses that compose a viability assessment. Statistical models (e.g., incidence function models) may yield precise model outputs for some situations, but their generality may extend only to a specific set of data and they may have limited applicability due to assumption of a stationary landscape configuration required by the model (Hanski 2002). The most realistic models for landscape planning are often stochastic PVA, patch occupancy, metapopulation, or spatially explicit models that can be developed for specific species, management scenarios, or landscapes. These models, however, often yield less precise or more uncertain results because they are stochastic and because all model parameters can rarely be estimated from data specific to the system of interest.

The choice of a PVA model will often be determined by the objectives of the analysis, the data that are available, and the assumptions that are realistic to

make (Ralls et al. 2002). The typical objective of a viability assessment in large-scale landscape planning is to determine which land management actions would be most beneficial or least injurious to a set of species. This concerns comparing risk to a species posed by different management options relative to one another (i.e., *relative risk*), rather than estimating an accurate risk or impact from a particular management action (i.e., *absolute risk*). A model that attempts to estimate absolute risk should strive to develop an accurate, comprehensive representation of reality and would include all factors influencing the probability of extinction (Ralls et al. 2002). Building models that can accurately estimate absolute extinction risk and the data required for these models are, for most species, still beyond our capabilities (Ludwig 1996, 1999; Fieberg and Ellner 2000). Models designed to compare differences among management options (i.e., estimate relative risks of extinction), however, may be less comprehensive than a model intended to estimate absolute risk of extinction and can be useful for assisting in decision making. The general consensus in the literature is that because of uncertainties in estimates of extinction risk, PVA is probably most useful in ranking alternative management policies' or scenarios' uncertainty (Possingham et al. 1993, Lindenmayer and Possingham 1996, Beissinger and Westphal 1998, Reed et al. 2002, Drechsler et al. 2003, Wintle et al. 2003).

Analyzing viability for large landscapes requires many species to be considered and increases the demand for data, affecting which analyses are appropriate. More complex models require greater technical skills and more time to create. Viability assessments for most species should be conducted from the scale of one or more National Forests to the scale of bioregions by comparing relative differences of the impacts of different planning scenarios. Thus, the potential for building PVA models is likely to be limited to a few or at most a dozen of the 50–300 species that are likely to need assessment when managing large-scale landscapes. Expert opinion in some form, elicited in a structured fashion and clearly documented, may be used to assess viability for the majority of affected species (Andelman et al. 2001, Burgman 2005).

USING PVA TO INFORM LARGE-SCALE LANDSCAPE PLANNING, MANAGEMENT, AND POLICY DECISIONS

We now consider how PVAs can be used to aid landscape planning and policy decisions, and issues surrounding the use of PVA in this context. What sort of large-scale landscape management decisions might a PVA help inform? Examples include (1) deciding which areas are priorities for protection or land acquisition, such as Strategic Habitat Conservation Areas identified by the Florida Fisheries and Wildlife Commission (Kautz and Cox 2001); (2) assessing and designing alternative management regimes, such as logging, to minimize the impact on biodiversity (Montgomery et al. 1994, Fox et al. 2004, Nalle et al. 2004);

(3) setting take levels for harvested species, such as fisheries or game (Milner-Gulland et al. 2001, Sethi et al. 2005); and (4) testing theory for biodiversity conservation and landscape design to be applied through rules of thumb or other ways to real-world decisions (McCarthy et al. 2001, Carroll et al. 2003, Lindenmayer et al. 2003, Nicholson et al. 2006).

PVAs have also been used to provide information that can, in turn, be used in either systematic conservation planning or to design landscapes. Examples of such use include (1) setting minimum population or patch sizes for single species or multispecies systematic conservation planning (e.g., Strategic Habitat Conservation Area in Florida [Burgman et al. 2001, Kautz and Cox 2001, Cowling et al. 2003]); (2) ascribing the value of a given area to viability, such as using the intrinsic growth rate λ of an area or the contribution of an area to the overall growth rate (Calkin et al. 2002, Noss et al. 2002, Carroll et al. 2003); and (3) parameterizing statistical approximation models (Calkin et al. 2002, Haight et al. 2002, Nalle et al. 2004). They may also be used to rank alternative management decisions in a decision analysis context, as we discuss next.

Decision Theory and PVA

To get the most out of a PVA when making management decisions, one should invoke a decision analysis framework (Maguire 1986), where the goals and constraints of the problem are explicitly defined (Shea et al. 1998, Possingham et al. 2002, Drechsler and Burgman 2004). In a single species example, the problem formulation may be as simple as comparing the viability of the species under a business-as-usual scenario versus an active management plan (e.g., captive breeding or preservation of critical habitat). It may be framed as a cost-benefit analysis: how much benefit (e.g., reduction in extinction risk) is gained as the amount of area protected increases or timber harvest is forgone (Montgomery et al. 1994)?

When we have the luxury of constructing PVA models for more than one species, we have the capacity to consider a much wider range of biodiversity needs, but it also entails a more complex decision model (Nicholson and Possingham 2006). How do we balance the competing needs of several species when each has different management preferences (Noon et al., this volume)? For example, a species with large area requirements may have higher viability when one or two large areas of habitat are protected, whereas a dispersal-limited species would benefit more from good corridors connecting areas of suitable habitat, while another species needs more frequent burns or predator removal. When one makes decisions that take into account the needs of different species, explicit goals and a structure for making decisions (i.e., decision theory or decision analysis) become even more important (Drechsler and Burgman 2004, Nicholson and Possingham 2006).

There are many ways in which assessment of viability for many species can inform management decisions. Multicriteria decision analysis can be used to

make a decision based on the ranking of the management alternatives for each of the species (e.g., [Drechsler and Burgman 2004](#), [Nicholson and Possingham 2007](#)). Similar to a voting system, an overall ranking can be derived by finding the management alternative that ranks highest for the most species. Species may be weighted to emphasize keystone species or species with higher risks of extinction. Alternatively, the probabilities of extinction can be combined to form a benefit or utility function. The simplest of these functions might be to add the extinction risks together to yield a cost, the expected number of extinctions, which we attempt to minimize. However, there are several ways to derive an overall benefit function, including minimizing the chance of any species becoming extinct or of all becoming extinct ([Hof and Raphael 1993](#), [Nicholson and Possingham 2006](#)). An index can also be developed to combine assessments of viability for multiple species across a landscape ([Akçakaya 2000](#), [Carroll et al. 2003](#), [Root et al. 2003](#)). For example, [Root et al. \(2003\)](#) generated a multiple-species index of conservation value, combining species-specific habitat suitability, extinction risk, and contribution to population viability estimated using a stochastic metapopulation model.

Using PVA in an Optimization Framework

Population models may also be used in an optimization framework, where an algorithm is used to find the landscape configuration that maximizes the viability of one or more species. There are few examples of population models being used directly in designing optimal landscapes, primarily because the simulations needed to assess the likelihood of extinction in a stochastic model constrain the size and complexity of the problems that can be included in an optimization framework. Some methods exist for finding the optimal landscape design for a single species (e.g., [Hof and Raphael 1997](#), [Hof et al. 1999](#), [Moilanen and Cabeza 2002](#)), but they tend to be based on simpler types of population models. Stochastic individual-based models or stage-based matrix models could not be used in such an optimization framework because computing power limits the number of simulations required (at least for the time being). Because there are so many spatial options to explore in optimal landscape design, finding the best option can only be achieved if the performance of each option can be evaluated extremely quickly, i.e., in fractions of a second. Simulation-based PVA does not run this quickly.

The computational constraints of single species problems become even more exacerbated when trying to consider multiple species within a landscape optimization framework ([Noon et al.](#), this volume; [Haight and Gobster](#), this volume). The few examples of multiple-species optimization based on population models have been simple deterministic or approximation models. [Nicholson et al. \(2006\)](#) used a spatially realistic metapopulation model, which approximated the results of a stochastic approximation model ([Frank and Wissel 2002](#)), to maximize the expected number of persistent species in a reserve system for a case study of 10 species. In a case study of 92 species, [Hof and Bevers](#)

(Hof and Raphael 1993, Hof et al. 1994, Bevers et al. 1995) used simple area-based viability functions to maximize the persistence across multiple species using a variety of utility functions, including maximizing the expected number of viable species and maximizing the chance that all species persist. Rothley (2002) used a deterministic Lotka-Volterra model for two-species predator-prey conservation. Araújo and Williams (Araújo and Williams 2000, Williams and Araújo 2000) used the probability of occurrence to approximate probability of persistence when maximizing expected number of persistent species for 174 tree species. McCarthy et al. (2006) developed theory, rather than found optimal solutions, for a general case where dispersal between populations was ignored.

Each of the models used in the preceding examples relied on simplifications and assumptions, but they provide frameworks that can be built upon as computational power increases to permit more complex models. Their consideration of landscape processes, such as local extinction dynamics and dispersal among populations, provide an improvement on more static methods for landscape design that only consider the presence of species or landscape indices, rather than species persistence (Williams et al. 2005, Nicholson et al. 2006). There is no doubt that we will need to further develop these ideas as we strive to include the idea of conservation adequacy into landscape planning.

The Certainty of Needing to Deal with Uncertainty in PVAs

The only certainty in PVA is that there is uncertainty, and a lot of it. Uncertainties can exist in the estimates for the model parameters, the structure of the model, GIS habitat layers, and other model components. Dealing with uncertainty forms an important component of a decision theory approach to management (Shea et al. 1998). Therefore, any discussion of population modeling cannot be complete without at least a brief consideration of the impact of uncertainty on management decisions, and an overview of some of the tools that are available for considering and including uncertainty when making management decisions using PVAs.

Regan et al. (2002) reviewed types of uncertainty in ecology and conservation biology, and what they mean for decision making. Epistemic uncertainty is uncertainty associated with knowledge of the state of a system. The parameters the model misestimated may be due to measurement error, systematic error (bias), natural variation, and inherent randomness (stochasticity). Also, results of the model may be uncertain due to the way in which the model structure is represented and due to subjective judgment in the interpretation of the results. Linguistic uncertainty arises because language can be ambiguous and vague (Regan et al. 2002).

Uncertainty also results from the inherent trade-off in the duration of the time span analyzed in a PVA and the accuracy of its predictions (Beissinger and Westphal 1998). Viability assessments should ensure that activities to be conducted over the planning period do not compromise the long-term persistence

of a species. Assessments over long time spans are especially important for long-lived organisms with long generation times (Lande 2002). Yet, errors (i.e., uncertainties) are propagated with each time step (often one year) that the model or assessment evaluates into the future.

Since uncertainty in model outcomes will occur regardless of the measures, time span, and model used in the analysis, good PVAs will analyze and present this uncertainty. Analysis of uncertainty in model performance should include a sensitivity analysis to understand the influence of individual parameters on model outcome (Mills and Lindberg 2002, Burgman et al. 2005, Wintle et al. 2005). An increasingly large array of methods is available for making decisions under uncertainty (Burgman 2005). Cross and Beissinger (2001) and Cariboni et al. (2007) reviewed sensitivity methods for PVA models and ecological models, respectively. Perhaps the most comprehensive way to deal with uncertainty is to include it directly in the model using a Bayesian PVA (Goodman 2002, Wade 2002). Another method for explicitly considering uncertainty in the decision process is information gap decision theory (Ben-Haim 2006), which provides a framework for making decisions where severe parameter uncertainty exists. Several examples exist of the application of information gap theory to conservation problems that use population models (Burgman 2005, Regan et al. 2005, Halpern et al. 2006, Nicholson and Possingham 2007). Attention should also be paid to interactions between parameters and the influence of functions or relationships built into the model, as well as basic model structures (e.g., density dependence).

SUMMARY

Population viability analysis has an important role to play in ecosystem management and conservation planning for large landscapes. The concept of population viability is central to landscape planning because the modern theory of conservation planning demands that we consider the notion of adequacy (Possingham et al. 2006). Population viability analysis represents a “fine filter” approach to conservation planning compared to the coarse filter approach, which posits that the majority of species can be protected by conserving examples of natural vegetation communities (Noon et al. 2003). Coarse filter approaches to landscape planning use distribution maps of land cover to inform the conservation of entire species assemblages (Groves et al. 2002), but have had equivocal success (Scott et al. 2002). A credible assessment approach to maintain a diversity of plant and animal communities in large landscapes is one that combines both coarse and fine filters using PVA for rare and at-risk species, for indicator species that provide information on the state of a given ecosystem, and for focal species that play significant functional roles in ecosystems (Noon et al. 2003).

LITERATURE CITED

- Akçakaya, H. R. 2000. Conservation and management for multiple species: Integrating field research and modeling into management decisions. *Environmental Management* 26:S75-S83.
- Allendorf, F. W., and N. Ryman. 2002. The role of genetics in population viability analysis. Pages 50-85 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Andelman, S. J., S. Beissinger, J. F. Cochrane, L. Gerber, P. Gomez-Priego, C. Groves, J. Haufler, R. Holthausen, D. Lee, L. Maguire, B. Noon, K. Ralls, and H. Regan. 2001. Scientific standards for conducting viability assessments under the National Forest Management Act: Report and recommendations of the NCEAS Working Group. National Center for Ecological Analysis and Synthesis, University of California, USA. <<http://www.fs.fed.us/psw/rsl/projects/wild/lee/lee3.pdf>>.
- Araújo, M. B., and P. H. Williams. 2000. Selecting areas for species persistence using occurrence data. *Biological Conservation* 96:331-345.
- Baxter, P. W. J., M. A. McCarthy, H. P. Possingham, P. Menkhorst, and N. McLean. 2006. Accounting for management costs in sensitivity analyses of matrix population models. *Conservation Biology* 20:893-905.
- Beissinger, S. R. 2002. Population viability analysis: Past, present, future. Pages 5-17 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Beissinger, S. R., and D. R. McCullough editors. 2002. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Beissinger, S. R., J. R. Walters, D. G. Catanzaro, K. G. Smith, J. B. Dunning, Jr., S. M. Haig, B. R. Noon, and B. Stith. 2006. Modeling approaches in avian conservation and the role of field biologists. *Ornithological Monographs* 59.
- 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.
- Ben-Haim, Y. 2006. *Information-gap decision theory: Decisions under severe uncertainty*. Second edition. Academic Press, London, United Kingdom.
- Beyers, M., J. Hof, B. Kent, and M. G. Raphael. 1995. Sustainable forest management for optimizing multispecies wildlife habitat: A coastal Douglas-fir example. *Natural Resource Modeling* 9:1-23.
- Boone, R. B., and M. L. Hunter. 1996. Using diffusion models to simulate the effects of land use on grizzly bear dispersal in the Rocky Mountains. *Landscape Ecology* 11:51-64.
- Bradstock, R. A., M. Bedward, J. Scott, and D. A. Keith. 1996. Simulation of the effect of spatial and temporal variation in fire regimes on the population viability of *Banksia* species. *Conservation Biology* 10:776-784.
- Buenau, K. E., and L. R. Gerber. 2004. Developing recovery and monitoring strategies for the endemic Mount Graham red squirrels (*Tamiasciurus hudsonicus grahamensis*) in Arizona. *Animal Conservation* 7:17-22.
- Burgman, M. A. 2005. *Risks and decisions for conservation and environmental management*. Cambridge University Press, Cambridge, United Kingdom.
- Burgman, M. A., S. Ferson, and H. R. Akçakaya. 1993. *Risk assessment in conservation biology*. Chapman and Hall, London, United Kingdom.
- Burgman, M. A., D. B. Lindenmayer, and J. Elith. 2005. Managing landscapes for conservation under uncertainty. *Ecology* 86:2007-2017.
- Burgman, M., and H. P. Possingham. 2000. Population viability analysis for conservation: The good, the bad and the undescribed. Pages 97-112 in A. G. Young and G. M. Clarke, editors. *Genetics, demography and viability of fragmented populations*. Cambridge University Press, London, United Kingdom.
- Burgman, M. A., H. P. Possingham, A. J. J. Lynch, D. A. Keith, M. A. McCarthy, S. D. Hopper, W. L. Drury, J. A. Passioura, and R. J. Devries. 2001. A method for setting the size of plant conservation target areas. *Conservation Biology* 15:603-616.

- Calkin, D. E., C. A. Montgomery, N. H. Schumaker, S. Polasky, J. L. Arthur, and D. J. Nalle. 2002. Developing a production possibility set of wildlife species persistence and timber harvest value. *Canadian Journal of Forest Research* 32:1329–1342.
- Cariboni, J., D. Gatelli, R. Liska, and A. Saltelli. 2007. The role of sensitivity analysis in ecological modelling. *Ecological Modelling* 203:167–182.
- Carroll, C., R. F. Noss, P. C. Paquet, and N. H. Schumaker. 2003. Use of population viability analysis and reserve selection algorithms in regional conservation plans. *Ecological Applications* 13:1773–1789.
- Caswell, H. 2001. *Matrix population models: Construction, analysis, and interpretation*. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Cowling, R. M., R. L. Pressey, M. Rouget, and A. T. Lombard. 2003. A conservation plan for a global biodiversity hotspot—the Cape Floristic Region, South Africa. *Biological Conservation* 112:191–216.
- Cross, P. C., and S. R. Beissinger. 2001. Using logistic regression to analyze the sensitivity of PVA models: A comparison of methods based on African wild dog models. *Conservation Biology* 15:1335–1346.
- Day, J. R., and H. P. Possingham. 1995. A stochastic metapopulation model with variability in patch size and position. *Theoretical Population Biology* 48:333–360.
- Dennis, B., P. L. Munholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. *Ecological Monographs* 61:115–143.
- Drechsler, M., and M. A. Burgman. 2004. Combining population viability analysis with decision analysis. *Biodiversity and Conservation* 13:115–139.
- Drechsler, M., K. Frank, I. Hanski, R. B. O'Hara, and C. Wissel. 2003. Ranking metapopulation extinction risk: From patterns in data to conservation management decisions. *Ecological Applications* 13:990–998.
- Etienne, R. S., C. J. F. ter Braak, and C. C. Vos. 2004. Application of stochastic patch occupancy models to real metapopulations. Pages 105–132 in I. Hanski and O. Gaggiotti, editors. *Ecology, genetics, and evolution of metapopulations*. Elsevier Academic Press, New York, New York, USA.
- Fieberg, J., and S. P. Ellner. 2000. When is it meaningful to estimate an extinction probability? *Ecology* 81:2040–2047.
- Fox, J. C., T. J. Regan, S. A. Bekessy, B. A. Wintle, M. J. Brown, J. M. Meggs, K. Bonham, R. Mesibov, M. A. McCarthy, S. A. Munks, P. Wells, R. Brereton, K. Graham, J. Hickey, P. Turner, M. Jones, W. E. Brown, N. Mooney, S. Grove, K. Yamada, and M. A. Burgman. 2004. Linking landscape ecology and management to population viability analysis: Report 2: Population viability analysis for eleven forest dependent species. University of Melbourne report prepared for Forestry Tasmania.
- Frank, K., and C. Wissel. 2002. A formula for the mean lifetime of metapopulations in heterogeneous landscapes. *American Naturalist* 159:530–552.
- Frankel, O. H., and M. E. Soulé. 1981. *Conservation and evolution*. First edition. Cambridge University Press, London, United Kingdom.
- Frankham, R. 1995. Effective population size-adult population size ratios in wildlife: A review. *Genetical Research* 66:95–107.
- Franklin, I. R., and R. Frankham. 1998. How large must populations be to retain evolutionary potential? *Animal Conservation* 1:69–73.
- Gilpin, M. E., and M. E. Soulé. 1986. Minimum viable populations: Processes of species extinction. Pages 19–34 in M. E. Soulé, editor. *Conservation biology: The science of scarcity and diversity*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Ginzburg, L. R., S. Ferson, and H. R. Akçakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conservation Biology* 4:63–70.
- Ginzburg, L. R., L. B. Slobodkin, K. Johnson, and A. G. Bindman. 1982. Quasiextinction probabilities as a measure of impact on population growth. *Risk Analysis* 2:171–181.
- Gonzalez-Suarez, M., K. E. McCluney, D. Aurioles, and L. R. Gerber. 2006. Incorporating uncertainty in spatial structure for viability predictions: A case study of California sea lions (*Zalophus californianus californianus*). *Animal Conservation* 9:219–227.

- Goodman, D. 2002. Predictive Bayesian population analysis: A logic for listing criteria, delisting criteria and recovery plans. Pages 447–469 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Groves, C. R., D. B. Jensen, L. L. Valutis, K. H. Redford, M. L. Shaffer, J. M. Scott, J. V. Baumgartner, J. V. Higgins, M. W. Beck, and M. G. Anderson. 2002. Planning for biodiversity conservation: Putting conservation science into practice. *BioScience* 52:499–512.
- Haig, S. M., and J. D. Ballou. 2002. Pedigree models for managing small populations in the wild. Pages 388–405 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Haight, R. G., B. Cypher, P. A. Kelly, S. Phillips, H. P. Possingham, K. Ralls, A. M. Starfield, P. J. White, and D. Williams. 2002. Optimizing habitat protection using demographic models of population viability. *Conservation Biology* 16:1386–1397.
- Halpern, B. S., H. M. Regan, H. P. Possingham, and M. A. McCarthy. 2006. Accounting for uncertainty in marine reserve design. *Ecology Letters* 9:2–11.
- Hanski, I. 1998. Metapopulation dynamics. *Nature* 396:41–49.
- Hanski, I. 1999. *Metapopulation ecology*. Oxford University Press, New York, New York, USA.
- Hanski, I. 2002. Animal metapopulations in highly fragmented landscapes and PVA. Pages 86–108 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Hanski, I., and O. Gaggiotti. 2004. Metapopulation biology: Past, present, and future. Pages 3–22 in I. Hanski and O. Gaggiotti, editors. *Ecology, genetics, and evolution of metapopulations*. Elsevier Academic Press, New York, New York, USA.
- Harris, R. B., L. A. Maguire, and M. L. Shaffer. 1987. Sample sizes for minimum viable population estimation. *Conservation Biology* 1:72–76.
- Harrison, S., and C. Ray. 2002. Plant population viability and metapopulation-level processes. Pages 109–122 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Hatten, J. R., and C. E. Paradzick. 2003. A multiscaled model of southwestern willow flycatcher breeding habitat. *Journal of Wildlife Management* 67:774–788.
- Hof, J., M. Bevers, L. Joyce, and B. Kent. 1994. An integer programming approach for spatially and temporally optimizing wildlife populations. *Forest Science* 40:177–191.
- Hof, J., and M. G. Raphael. 1997. Optimization of habitat placement: A case study of the northern spotted owl in the Olympic Peninsula. *Ecological Applications* 7:1160–1169.
- Hof, J., C. H. Sieg, and M. Bevers. 1999. Spatial and temporal optimization in habitat placement for a threatened plant: The case of the western prairie fringed orchid. *Ecological Modelling* 115:61–75.
- Hof, J. G., and M. G. Raphael. 1993. Some mathematical-programming approaches for optimizing timber age-class distributions to meet multispecies wildlife population objectives. *Canadian Journal of Forest Research* 23:828–834.
- Holmes, E. E. 2004. Beyond theory to application and evaluation: Diffusion approximations for population viability analysis. *Ecological Applications* 14:1272–1293.
- Holmes, E. E., and W. F. Fagan. 2002. Validating population viability analysis for corrupted data sets. *Ecology* 83:2379–2386.
- Kautz, R. S., and J. A. Cox. 2001. Strategic habitats for biodiversity conservation in Florida. *Conservation Biology* 15:55–77.
- Kindvall, O. 2000. Comparative precision of three spatially realistic simulation models of metapopulation dynamics. *Ecological Bulletin* 48:101–110.
- Lamberson, R. H., B. R. Noon, C. Voss, and K. S. McKelvey. 1994. Reserve design for territorial species: The effects of patch size and spacing on the viability of the northern spotted owl. *Conservation Biology* 8:185–195.
- Lande, R. 1995. Mutation and conservation. *Conservation Biology* 9:782–791.

- Lande, R. 2002. Incorporating stochasticity in population viability analysis. Pages 18–40 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Levins, R. 1968. *Strategies of adaptation*. Pages 10–38 in *Evolution in changing environments*. Princeton University Press, Princeton, New Jersey, USA.
- Lindenmayer, D. B., and H. P. Possingham. 1996. Ranking conservation and timber management options for leadbeater's possum in southeastern Australia using population viability analysis. *Conservation Biology* 10:235–251.
- Lindenmayer, D. B., H. P. Possingham, R. C. Lacy, M. A. McCarthy, and M. L. Pope. 2003. How accurate are population models? Lessons from landscape-scale tests in a fragmented system. *Ecology Letters* 6:41–47.
- Liu, J., J. B. Dunning, Jr., and H. R. Pulliam. 1995. Potential effects of a forest management plan on Bachman's sparrows (*Aimophila aestivalis*): Linking a spatially explicit model with GIS. *Conservation Biology* 9:62–75.
- Lotts, K. C., T. A. Waite, and J. A. Vucetich. 2004. Reliability of absolute and relative predictions of population persistence based on time series. *Conservation Biology* 18:1224–1232.
- Ludwig, D. 1996. Uncertainty and the assessment of extinction probabilities. *Ecological Applications* 6:1067–1076.
- Ludwig, D. 1999. Is it meaningful to estimate a probability of extinction? *Ecology* 80:298–310.
- MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey, and J. E. Hines. 2006. *Occupancy estimation and modeling*. Academic Press, San Diego, California, USA.
- Maguire, L. A. 1986. Using decision-analysis to manage endangered species populations. *Journal of Environmental Management* 22:345–360.
- Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. *Ecology* 75:607–614.
- McCarthy, M. A., H. P. Possingham, J. R. Day, and A. J. Tyre. 2001. Testing the accuracy of population viability analysis. *Conservation Biology* 15:1030–1038.
- McCarthy, M. A., C. J. Thompson, and N. S. G. Williams. 2006. Logic for designing nature reserves for multiple species. *American Naturalist* 167:717–727.
- McKelvey, D., B. R. Noon, and R. H. Lamberson. 1993. Conservation planning for species occupying fragmented landscapes: The case of the northern spotted owl. Pages 424–452 in P. M. Kareiva, J. G. Kingslover, and R. B. Huey, editors. *Biotic interactions and global change*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Mills, L. S., and M. S. Lindberg. 2002. Sensitivity analysis to evaluate the consequences of conservation actions. Pages 338–366 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Milner-Gulland, E. J., K. Shea, H. Possingham, T. Coulson, and C. Wilcox. 2001. Competing harvesting strategies in a simulated population under uncertainty. *Animal Conservation* 4:157–167.
- Moilanen, A., and M. Cabeza. 2002. Single-species dynamic site selection. *Ecological Applications* 12:913–926.
- Montgomery, C. A., G. M. Brown, Jr., and D. M. Adams. 1994. The marginal cost of species preservation: The northern spotted owl. *Journal of Environmental Economics and Management* 26:111–128.
- Morris, W. F., and D. F. Doak. 2002. *Quantitative conservation biology: Theory and practice of population viability analysis*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Nalle, D. J., C. A. Montgomery, J. L. Arthur, S. Polasky, and N. H. Schumaker. 2004. Modeling joint production of wildlife and timber. *Journal of Environmental Economics and Management* 48:997–1017.
- Nicholson, E., and H. P. Possingham. 2006. Objectives for multiple-species conservation planning. *Conservation Biology* 20:871–881.

- Nicholson, E., and H. P. Possingham. 2007. Making conservation decisions under uncertainty for the persistence of multiple species. *Ecological Applications* 17:251–265.
- Nicholson, E., M. I. Westphal, K. Frank, W. A. Rochester, R. L. Pressey, D. B. Lindenmayer, and H. P. Possingham. 2006. A new method for conservation planning for the persistence of multiple species. *Ecology Letters* 9:1049–1060.
- Noon, B. R., D. D. Murphy, S. R. Beissinger, M. L. Shaffer, and D. Dellasala. 2003. Conservation planning for U.S. National Forests: Conducting comprehensive biodiversity assessments. *BioScience* 53:1217–1220.
- Noss, R. F., C. Carroll, K. Vance-Borland, and G. Wuerthner. 2002. A multicriteria assessment of the irreplaceability and vulnerability of sites in the Greater Yellowstone Ecosystem. *Conservation Biology* 16:895–908.
- Peery, M. Z., B. H. Becker, and S. R. Beissinger. 2006. Combining demographic and count-based approaches to identify source-sink dynamics of a threatened seabird. *Ecological Applications* 16:1516–1528.
- Possingham, H. P., D. B. Lindenmayer, and M. A. McCarthy. 2001. Population viability analysis. Pages 831–844 in S. Levin, editor. *The encyclopedia of biodiversity*. Volume 4, Academic Press, San Diego, California, USA.
- Possingham, H. P., D. B. Lindenmayer, and T. W. Norton. 1993. A framework for the improved management of threatened species based on PVA. *Pacific Conservation Biology* 1:39–45.
- Possingham, H. P., D. B. Lindenmayer, and G. N. Tuck. 2002. Decision theory for population viability analysis. Pages 470–489 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Possingham, H. P., K. A. Wilson, S. Andelman, and C. H. Vynne. 2006. Protected areas: Goals, limitations, and design. Pages 509–533 in M. J. Groom, G. K. Meffe, and C. R. Carroll, editors. *Principles of conservation biology*. Third edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Price, M. V., and M. Gilpin. 1996. Modelers, mammalogists, and metapopulations: Designing Stephens' kangaroo rat reserves. Pages 217–240 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C., USA.
- Ralls, K., S. R. Beissinger, and J. F. Cochrane. 2002. Guidelines for using PVA in endangered species management. Pages 521–550 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Reed, J. M., L. S. Mills, J. B. Dunning, Jr., E. S. Menges, K. S. McKelvey, R. Frye, S. R. Beissinger, M.-C. Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. *Conservation Biology* 16:7–19.
- Regan, H. M., Y. Ben-Haim, B. Langford, W. G. Wilson, P. Lundberg, S. J. Andelman, and M. A. Burgman. 2005. Robust decision making under severe uncertainty for conservation management. *Ecological Applications* 15:1471–1477.
- Regan, H. M., M. Colyvan, and M. A. Burgman. 2002. A taxonomy and treatment of uncertainty for ecology and conservation biology. *Ecological Applications* 12:618–628.
- Root, K. V., H. R. Akçakaya, and L. Ginzburg. 2003. A multispecies approach to ecological valuation and conservation. *Conservation Biology* 17:196–206.
- Rothley, K. D. 2002. Dynamically-based criteria for the identification of optimal bioreserve networks. *Environmental Modeling and Assessment* 7:123–128.
- Scott, J. M., P. J. Heglund, M. L. Morrison, J. B. Haufler, M. G. Raphael, W. A. Wall, and F. B. Samson. 2002. *Predicting species occurrences: Issues of accuracy and scale*. Island Press, Washington, D.C., USA.
- Sethi, G., C. Costello, A. Fisher, M. Hanemann, and L. Karp. 2005. Fishery management under multiple uncertainty. *Journal of Environmental Economics and Management* 50:300–318.
- Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131–134.
- Shea, K., P. Amarasekare, P. Karelva, M. Mangel, J. Moore, W. W. Murdoch, E. Noonburg, A. M. Parma, M. A. Pascual, H. P. Possingham, C. Wilcox, and D. Yu. 1998. Management of populations in conservation, harvesting and control. *Trends in Ecology and Evolution* 13:371–374.

- Sjogren-Gulve, P., and I. Hanski. 2000. Metapopulation viability analysis using occupancy models. *Ecological Bulletin* 48:53-71.
- Sjogren-Gulve, P., and C. Ray. 1996. Using logistic regression to model metapopulation dynamics: Large-scale forestry extirpates the pool frog. Pages 111-137 in D. R. McCullough, editor. *Metapopulations and wildlife conservation*. Island Press, Washington, D.C., USA.
- Staples, D. F., M. L. Taper, and B. Dennis. 2004. Estimating population trend and process variation for PVA in the presence of sampling error. *Ecology* 85:923-929.
- Thomas, C. D., and I. Hanski. 2004. Metapopulation dynamics in changing environments: Butterfly responses to habitat and climate change. Pages 489-514 in I. Hanski and O. Gaggiotti, editors. *Ecology, genetics, and evolution of metapopulations*. Elsevier Academic Press, New York, New York, USA.
- Thomson, D. M., and M. W. Schwartz. 2006. Using population count data to assess the effects of changing river flow on an endangered riparian plant. *Conservation Biology* 20:1132-1142.
- Treves, A., L. Naughton-Treves, E. K. Harper, D. J. Mladenoff, R. A. Rose, T. A. Sickley, and A. P. Wydeven. 2004. Predicting human-carnivore conflict: A spatial model derived from 25 years of data on wolf predation on livestock. *Conservation Biology* 18:114-125.
- Wade, P. R. 2002. Bayesian population viability analysis. Pages 213-238 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Walters, J. R., L. B. Crowder, and J. A. Priddy. 2002. Population viability analysis for red-cockaded woodpeckers using an individual-based model. *Ecological Applications* 12:249-260.
- Waples, R. S. 2002. Definition and estimation of effective population size in the conservation of endangered species. Pages 147-168 in S. R. Beissinger and D. R. McCullough, editors. *Population viability analysis*. University of Chicago Press, Chicago, Illinois, USA.
- Williams, J. C., C. S. ReVelle, and S. A. Levin. 2005. Spatial attributes and reserve design models: A review. *Environmental Modeling and Assessment* 10:163-181.
- Williams, P. H., and M. B. Araújo. 2000. Using probability of persistence to identify important areas for biodiversity conservation. *Proceedings of the Royal Society of London Series B* 267:1959-1966.
- Wintle, B. A., R. P. Kavanagh, M. A. McCarthy, and M. A. Burgman. 2005. Estimating and dealing with detectability in occupancy surveys for forest owls and arboreal marsupials. *Journal of Wildlife Management* 69:905-917.
- Wintle, B. A., M. A. McCarthy, C. T. Volinsky, and R. P. Kavanagh. 2003. The use of Bayesian model averaging to better represent uncertainty in ecological models. *Conservation Biology* 17:1579-1590.