21 Viable Populations in Dynamic Forests

I have heard some foresters and biologists say, "We manage habitat, not populations." The Field of Dreams approach to wildlife management: Build it and they will come. But will they? Can they, given the limited mobility of some species and intervening forest conditions now and 50 years from now? If they do come to the new habitat, how long will they last there? How does their presence contribute to ensuring that the greater population is not going extinct? All of these questions relate to understanding population viability.

Population viability analysis (PVA) is a structured approach to examining population performance—to link population performance with the quantity, quality, and distribution patterns of habitat and to predict the probability of population extinction or persistence. The approach is based on a marriage among the concepts of demography, population dynamics, habitat selection, and landscape dynamics. Many of the concepts covered in this book to this point provide the foundation for an assessment of population viability in forested landscapes. PVA models and analyses originally were developed in response to the concern for the persistence of small or isolated populations, a response to law (e.g., the Endangered Species Act and the National Forest Management Act), and to large-scale regional assessments. More recent applications include predicting the potential success of reintroductions of plants and animals and assessing strategic development of habitat improvement projects (Knight 2012, Bonnot et al. 2013). PVA techniques are both elegant and uncertain. PVA is a modeling exercise and, as Box and Draper (1987) have said, "All models are wrong, but some are useful." The results from a PVA can be useful in guiding management alternatives if uncertainty is understood and included in the decision-making process.

EXTINCTION RISKS

It's a hard world out there. As far as we know, all populations will eventually go extinct (including ours!). Large populations will likely last for many generations; small populations are much more vulnerable to extinction. The crux of the population change issue is encapsulated in this formula:

$$N_{(t+1)} = \lambda N(t)$$

This states that the population size at time + 1 (the future) is equal to a change coefficient (λ) multiplied times the current population ($N_{(t)}$). Should λ be a negative number over a long time (long being relative to the generation length for the species), then concerns arise regarding the potential for the species to become extinct. At least four factors are likely to influence the risk of extinction, especially in small populations.

First, vital rates of populations vary from year to year, and place to place, simply by chance alone. Birth rates, death rates, and reproductive rates within an age class typically have a mean value over time in a stable population, but there is also a variability associated with that mean value. In some species, that variability is small (species with low but predictable reproduction, such as bears and people), and for others it is quite large (species with irruptive populations, such as voles and quail). These levels of variability in vital rates apply whether the population is large or small, but in small populations the effect can be quite dramatic. A failure to reproduce for a year (or more, depending on the life span) in a population of 1000 voles may mean a temporary crash, followed by recovery, but a similar event in a population of 10 animals may lead to a population decline from which it cannot recover, due to random shifts in sex ratios and the difficulty in finding mates. This demographic stochasticity is an inherent property of populations, and the variability represented in these vital rates is likely an evolutionary response to unpredictable events of the past. Issues of small populations must be considered relative to the life span of the individuals. Shoemaker et al. (2013) found that long-lived bog turtles have a high probability of persisting even at low population levels.

Second, there are also exogenous events that interact with habitat elements to influence the likelihood that an animal will die, reproduce, or move. Climatic fluctuations from year to year, for instance, can have a significant effect on population change over time (Olson et al. 2004). For instance, an exceptionally rainy year can cause nest failure for some bird species, because nestlings become hypothermic and die. There is some probability that a very wet year will occur, but whether or not it happens is a chance event. The probability of such an event is predictable, but the timing of the actual event is uncertain. These uncertain events, unrelated directly to habitat structure and composition, represent environmental stochasticity. Random events such as storms, droughts, and epizootic diseases that do not affect habitat structure and function, cause vital rates to fluctuate considerably from year to year and place to place. In small populations, these effects can be magnified. An event that increases mortality by 50% in a population of 1000 animals for one year may simply result in population recovery from the remaining 500 individuals over the next few years. But a similar event in a population of 10 individuals can result in an extremely skewed sex ratio by chance alone, causing the population to go extinct.

Third, natural catastrophes, such as hurricanes, fires, and epizootics, which can cause massive changes in vital rates unrelated to habitat structure and composition, are extreme cases of environmental uncertainty. When Hurricane Hugo blasted the Francis Marion National Forest, the majority of nesting cavities for red-cockaded woodpeckers were destroyed (Hooper et al. 1990). These sorts of events cause fluctuations in vital rates that far exceed the expected year-to-year variability seen in most populations and can have devastating consequences for small populations. Dennis et al. (1991) predicted a reasonably high probability of population persistence for Puerto Rican parrots when not accounting for hurricanes, but Hurricane Hugo nearly decimated the population, potentially changing the probability of recovery for this species.

Fourth, in small populations, chance has a huge effect on otherwise subtle changes in genetic variability present in the population. In many instances, the variety of gene expressions, or alleles, represents the potential adaptability of the species to environmental uncertainties. In large populations in dynamic environments, we would expect to see some reasonably high level of heterozygosity (genetic variability) in the population. As populations decline, by chance alone, some alleles may dominate in a population, leading to a preponderance of individuals being homozygous (genetically more uniform) for some traits. This phenomenon is called genetic drift. These changes may make many of the individuals less adaptable to environmental uncertainty associated with those traits. In small populations, this genetic shift can result from increased levels of inbreeding by closely related individuals. In cases where inbreeding leads to reduced fitness in the populations, then inbreeding depression has occurred. In extreme cases, alleles may be entirely eliminated from populations. Regaining that genetic variability would occur either through immigration from surrounding populations (if there are any) or from mutations (most of which are not beneficial). Restrictions in genetic expressions can also be seen as animals disperse to unoccupied patches of habitat and establish a new population. Since a population beginning from just a few individuals is more likely to have a narrow range of alleles in the newly establishing population, the genetic variability in the population can remain low as the population grows, a process termed the *founder effect*. A similar process can occur when a population goes through a genetic bottleneck, or when there is a dramatic decline in the population to low levels, where alleles are lost in the process. During population recovery following the decline, a narrower range of allelic expression may be seen. Founder effects and genetic bottlenecks can lead to populations that are larger (i.e., recovered) but more vulnerable to environmental uncertainties because the alleles needed to cope with those uncertainties had been lost.

Because these four factors (demographic stochasticity, environmental stochasticity, natural catastrophes, and loss of genetic variability) are exacerbated in small populations, conservation biologists and forest planners spend considerable effort managing habitat to ensure recovery of small populations. Population viability analyses are a set of tools available to planners to address these issues when investigating the potential effects of alternative management strategies.

GOALS OF PVAs

There are two major goals usually associated with a PVA: (1) to predict short- or long-term rates of change, and (2) to predict the likelihood of extinction (Beissinger and Westphal 1998). At the very least a manager would like to know what the likely trend in a population might be under various management scenarios or forest plans. Being able to estimate if a population is decreasing or increasing can influence the direction of future management efforts if the species is listed as threatened, or if the species is a potential pest. But if the decline is so severe that questions are raised regarding the potential for a population to go extinct, then a new goal emerges for the analysis.

PVA is an approach often used to predict the probability that a population will go extinct in a given number of years—for instance, to estimate a 95% probability of extinction within 1000 years, 100 years, or 10 years. The assumption behind these analyses is that the shorter the potential time to extinction, the greater the risk of losing the species, simply because the actual time to extinction can never be predicted accurately, given all the uncertainties associated with an extinction event.

Most PVA models are demographic in nature, employing age-specific reproduction and survival rates, but genetic implications have been considered in some models as well, especially when managing endangered species. Genetic PVA models incorporate estimates of effective population size, which is the number of breeding individuals effectively contributing to allele frequencies in a population. The effective population size is usually smaller than the absolute population size, unless breeding is random and the chance of inbreeding is negligible—two assumptions likely to be violated in small populations. From the standpoint of potentially losing alleles in a population, especially in small populations, effective population sizes must be considered.

PVA MODELS

There are five predominant types of demographic models that have been used in analyses of population trends and extinction analyses (Beissinger and Westphal 1998). First, analytical models have been used to examine behavior of a system (or assumptions behind other models), and not usually used to make population predictions (Beissinger and Westphal 1998). Analytical approaches also have been used to simply relate populations to current and likely future conditions using statistical techniques, such as regression, logistic regression, or classification and regression tree analyses. These approaches may be used to examine how a population might react to a change in abundance of habitat, or connectivity, or other factors that do not explicitly take into consideration the demographics of the population, nor its movement capabilities. Analytical approaches such as these may in fact miss changes in populations that could be caused by unrelated changes in birth or death rates. Developing associations does not prove a cause-and-effect relationship, only that several things are related to one another in some way. For instance, using a regression relationship between the number of woodpeckers and the number of snags would be useful for some planning processes, unless some other factor, such as West Nile Virus, caused the population to decline, independent of snag density. Knowledge of birth, death, and survival rates can help to consider both density-dependent and density-independent causes of population change.

A second type of analysis that could be used to assess population trends is a deterministic single-population model. These models are generally based on a Leslie Matrix or a matrix of survival rates and reproduction rates in each of several age classes, to predict change in populations over years (Leslie 1945). In this approach, estimates of birth and death rates by age class are developed from field data, such as banding returns or radio telemetry data. These estimates are used to calculate survival rates, in conjunction with information on reproduction in each age class to calculate population changes from one time step to another. This approach is among the simplest models requiring the least amount of data but it assumes that demographic rates are constant (Caswell 2001). This kind of model has been used to assess changes in marbled murrelet populations, for example (Beissinger 1995, Peery and Henry 2010).

Stochastic single-population models overcome the assumption of constant demographic rates and include variability in estimated demographic rates in the calculations. Interestingly, this approach was adapted from Leslie models and first used in the development of forest management models (Usher 1969). Estimates of variability are incorporated into birth and death rates (and hence survival probabilities), and reproduction rates, to allow multiple projections of population change over time, reflecting the variability in demographic factors. Because these variances represent the stochastic properties of population change, each projection produces a unique trajectory and ending population size. The results of each projection can then be averaged or summarized to develop confidence intervals around population trends and probabilities associated with extinctions. This is a quite commonly used approach, because it attempts to introduce reality into projections, and has been used for species such as brushtail possums in managed forests of Australia (Lindenmayer 1993). Both deterministic and stochastic population models are typically applied to single populations. When a population is segregated spatially into interacting sub-populations, then a different approach is usually taken.

Metapopulation models are used to assess the interacting dynamics among sub-populations representing a metapopulation structure. The metapopulation dynamics are incorporated into the demographic model by using patch-specific demographic rates and dispersal probabilities between the patches (Beissinger and Westphal 1998). Dispersal rules are developed based on patch size and distances between patches. Patch quality, usually indexed to a carrying capacity, can be assumed to vary among sub-populations as well. This approach has been broadly used with many species that are assumed to have a metapopulation structure. For instance, Beier (1996) used a metapopulation model to assess cougar population trends in western United States. When the condition between the patches becomes important to population trends and the configuration and dynamics of the patch conditions is important, then spatially explicit approaches become more useful in assessing risks to species.

Spatially explicit models are designed to consider population dynamics on complex landscapes with varying matrix conditions between patches. These approaches also lend themselves well to assessing the interacting dynamics of populations and underlying vegetation conditions. The approach incorporates a spatial distribution of resources related to habitat quality, as well as movement rules for dispersing animals, to assess responses to land-use changes or management policies (Wilhere and Schumaker 2001). Because of the spatial detail needed and the dynamics associated with underlying resource layers, these sorts of models typically require enormous amounts of data and, until recently, were most often used with species representing a very high risk of loss and associated very high economic importance. These approaches have been used for northern spotted owls (Lamberson et al. 1994) but also, in a broader capacity, for a suite of species in a large ecoregional assessment (Schumaker et al. 2004). With increased computing capabilities and demographic data for more species, spatially explicit PVAs are now commonly conducted in conjunction with dynamic landscape models.

CONDUCTING A PVA FOR A FOREST-ASSOCIATED SPECIES

Because forests are inherently dynamic due to disturbance and regrowth, typically, a dynamic, spatially explicit model is used. HEXSIM (http://www.hexsim.net/) is an example of the type of model typically used for these sorts of analyses (Marcot et al. 2013, Schumaker 2013). There are eight primary steps to conducting such an analysis (other models require similar, but not identical steps).

First, maps of habitat quality for the species must be developed over the extent of the analysis area. This usually entails application of a wildlife habitat-relationships model (WHR, Johnson and O'Neil 2001), but may entail a more detailed habitat-quality estimate (McComb et al. 2002). The maps must be developed both now and for each time-step into the future, over a period of time deemed adequate to assess population trends. These maps should be based on likely changes in habitat structure and composition, due to management and/or natural disturbances expected to occur over the projection period. If you wish to compare population trends among alternative plans or policies, then you will need a different series of maps for each alternative management strategy being assessed.

Second, home ranges or territories are assigned to each map. These are usually represented by cells (squares or hexagons) scaled to the home range size or territory for the species being considered, and overlain on the habitat maps (Figure 21.1). The habitat quality is then aggregated through rules representing the amount of habitat of a certain quality that would be needed by a species in its home range to likely achieve a certain level of reproduction or survival. This is done for each in the series of maps, for each management alternative. Where predator–prey relationships are being considered, then this step must be conducted for both predator and prey species being considered in the simulation.

Third, demographic information for the species must be estimated for each age and sex class (although analyses are often restricted to females, and then a sex ratio is estimated to extrapolate to a total population). Age classes may be aggregated into stages if the parameters do not change appreciably from one year-class to another. These parameters include both the estimated average and associated variance for birth rates, reproduction rates, movement rates, and movement direction (if it is not random). These data are typically extracted from published studies, although, for high-priority species, field data collection may be needed to ensure more accurate estimates of these parameters. At the very least, experts on the species are consulted to provide reasonable estimates.

Fourth, these demographic data are then explicitly related to the habitat-quality estimates assigned to the home range cells, such that lower birth and survival rates occur in lower quality patches, and vice versa (Figure 21.2). This must be done for each cell on each map in the time series, for each management alternative. The actual assignment of a value (e.g., survival) to a cell, is typically conducted in a randomized manner. For instance, the survival values assigned to a cell in a given year will reflect the range of values associated with that parameter in that habitat quality class,

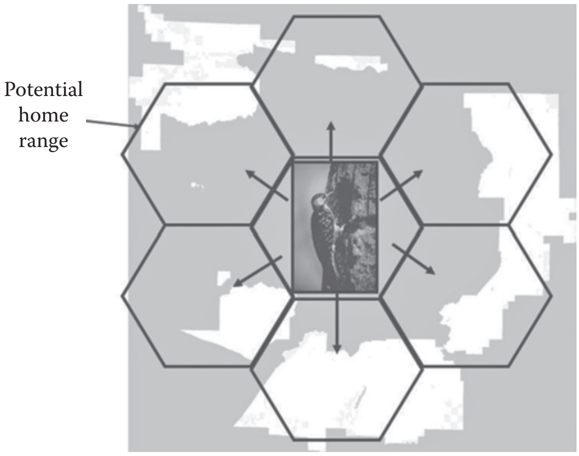

FIGURE 21.1 Simulated home ranges (hexagons) are overlain on maps of habitat availability to estimate the distribution of potentially occupiable home ranges over the extent of the analysis. (Red-cockaded woodpecker photo from Oak Ridge National Laboratory, http://www.esd.ornl.gov/programs/SERDP/EcoModels/rcw.html.)

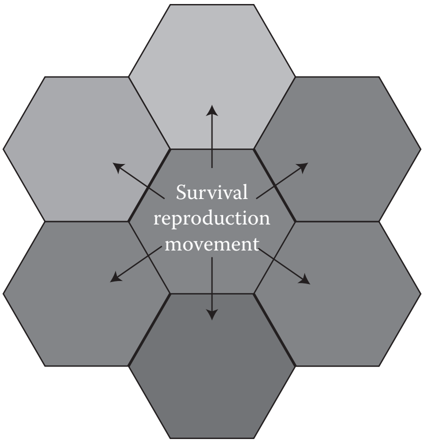

FIGURE 21.2 Demographic parameters are assigned to each home range (hexagon) based on its likely habitat quality. Should an individual arrive at a home range, then a random draw of parameters, from the range of those associated with the home range quality, is assigned to that individual in that time step.

so that demographic stochasticity is represented. But these assignments are made so that the average value among all cells in a habitat quality class is equal to the mean of the published estimates for that habitat-quality class.

Fifth, at this point, individuals or pairs of animals are assigned to each cell on the landscape at time = 0 (current conditions), such that they represent the known or estimated distribution of organisms over the area of assessment. If the distribution is not known, then a random assignment is made. The landscape is now "seeded" with individuals of various age classes and sexes, in home ranges consisting of varying habitat quality. Sixth, the survival, reproduction, and movement rates associated with each cell are then applied to each individual on the landscape and projected forward one time-step, much the way a Leslie matrix projects a population forward in time.

Seventh, and at the same time, the underlying map of habitat quality is changed to reflect forest disturbance and regrowth. This process is repeated for the number of time-steps in the projection period. But, because assignments of demographic parameters represent a stochastic process, many projections must be made to understand probabilities associated with population trends and extinctions.

Finally, once many projections have been made, then averages, probabilities, and confidence intervals can be assigned at each time step (Figure 21.3).

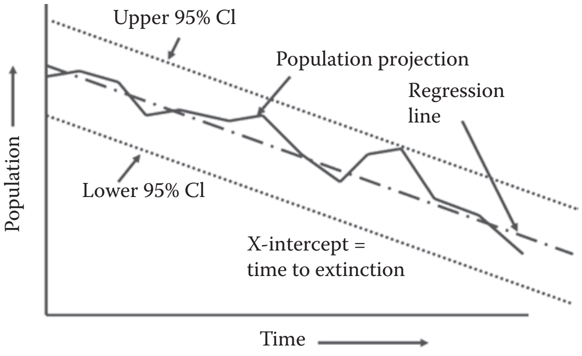

FIGURE 21.3 The results from multiple model runs are used to create an average and confidence intervals (CI) in populations over time. With declining populations, calculating the X-intercept can provide an estimate of the time to extinction.

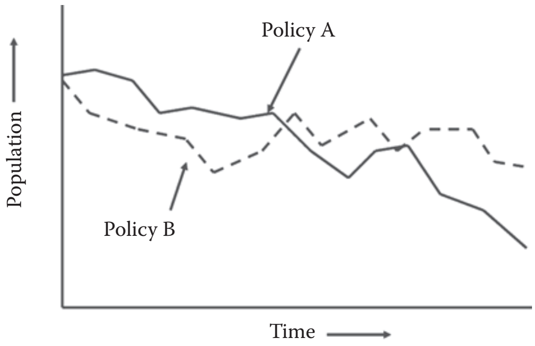

FIGURE 21.4 Trend lines are compared between alternative management strategies or policies. Those policies, likely to provide the most options for the future (longest time to extinction), are assumed to represent less risk to the species.

The resulting estimate might show a declining trend and an estimated time to extinction of 150 years. Should you believe this estimate? Perhaps, in a relative sense, by comparing this estimate to estimates produced for alternative management plans (Figure 21.4). There are so many assumptions and uncertainties represented in each estimate, that the eighth step is to use an adaptive management approach: compare estimates at each time-step between alternative management approaches (e.g., following NEPA, a no action and a preferred alternative). Indeed, the best use of PVAs is in making projections to compare alternatives, selecting a preferred alternative, implementing it, monitoring the responses, and rerunning the PVA with additional data, allowing continual adaptation and improvements to population estimates. Using this process, we also learn about the habitat and demographic characteristics of the species that seem to most influence population change, and can address those factors during planning and management activities.

EXAMPLES OF PVA ANALYSES

Grizzly Bear

One of the earliest attempts at conducting a PVA was for grizzly bears in Yellowstone National Park (Shaffer 1983) in the United States. Subsequent approaches proposed by Dennis et al. (1991) and summarized by Morris et al. (1999) provide an estimate of persistence of this large predatory mammal in the lower 48 states of the United States.

The approach taken by Dennis et al. (1991) is somewhat unique, in that the data on which the analysis is based includes exhaustive counts of individuals in the population, including age and sex cohorts. Despite such exhaustive data, the approach is still based on a number of assumptions using multiple stochastic single-population modeling approaches (Morris et al. 1999):

1. The year-to-year variation in the counts reflects the true magnitude of environmentally-driven variation.
2. Inter-annual environmentally-driven variation is not extreme.
3. The population growth rate is not density-dependent.

Dennis et al. (1991) calculated the extinction time for the population of grizzly bears in the Greater Yellowstone ecosystem. They then extrapolated some of the detailed data from the Yellowstone population to other areas, including the Selkirk range in British Columbia, Northern Divide in Washington and British Columbia, and the Yaak River Valley in Montana, to understand the interacting probabilities of population extinction among these known subpopulations of grizzly bears. The analysis assumes that there is no current movement among the subpopulations, so that

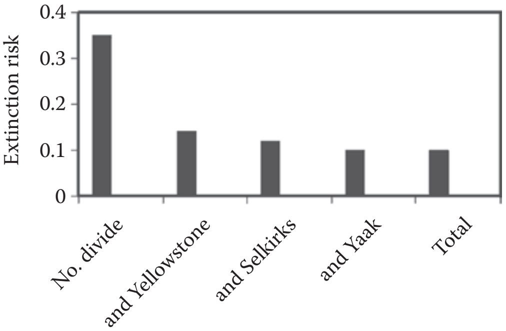

FIGURE 21.5 Extinction risk for cumulative grizzly bear populations among a collection of protected areas. (Redrafted and adapted from Morris, W. et al. 1999. *A Practical Handbook for Population Viability Analysis*. The Nature Conservancy, Arlington, VA, 47 pp.)

is why multiple single-population analyses were conducted, rather than a metapopulation analysis. They found that for the 500-year projection, there was a 9.6% chance of extinction of all populations (Morris et al. 1999). Considering the populations individually, protecting the Yellowstone population provided the greatest opportunity for reducing extinction risk, but adding the Northern Divide population decreased the probability of extinction from 0.342 (for the Northern Divide alone) to 0.134 (Figure 21.5, Morris et al. 1999).

By adding additional subpopulations, the benefits to reductions in extinction decrease only modestly from that point on (Figure 21.5). So if we wished to be sure that grizzly bears were to remain a component of the ecosystems in the lower 48 states of the United States, then maintaining all of these populations would be a reasonable approach, despite concerns over human safety and property damage. But in this example, the estimate of likely extinction (9.6%) is lower than what we might actually expect, because those populations that are closest to one another are likely to be affected by similar factors influencing their populations (e.g., weather, disease, fire, etc.). But even these simple analyses can be used to understand the potential risks of extinctions if certain local populations are lost.

MARBLED MURRELET

McShane et al. (2004) described a stochastic metapopulation model used to assess marbled murrelet persistence within six different zones in the Pacific Northwest. They developed a “Zone Model” in which they estimated population projections for each of six zones within the species geographic range, in California, Oregon, and Washington, for 100 years into the future. They assumed that there would be no change in population vital rates over 40 years, and they did not incorporate habitat changes into the model. Similarly, they did not incorporate possible effects of oceanic regime shifts (which could affect foraging efficiency and, hence, survival and reproduction) into the model. The model is a female-only, multi-aged, discrete-time stochastic Leslie Matrix model (Caswell 1989). They found that all zone populations are in decline (over 40 years) with declines of 2.1%–6.2% per decade (Figure 21.6). Further they predicted extinction within 40 years in two zones, and within 100 years in three zones (only one zone population was predicted to extend beyond 100 years), and that the probability of extinction over 100 years is 16%. By modifying their model parameters, they found a reduced rate of decline in two zones if oil spills and gill nets were eliminated as a source of mortality, pointing out the need to consider not just habitat-mediated effects on population changes. More recently, Peery and Henry (2010) used a PVA to predict that control of corvids (crows and jays) near murrelet nests could also lead to an increase in populations.

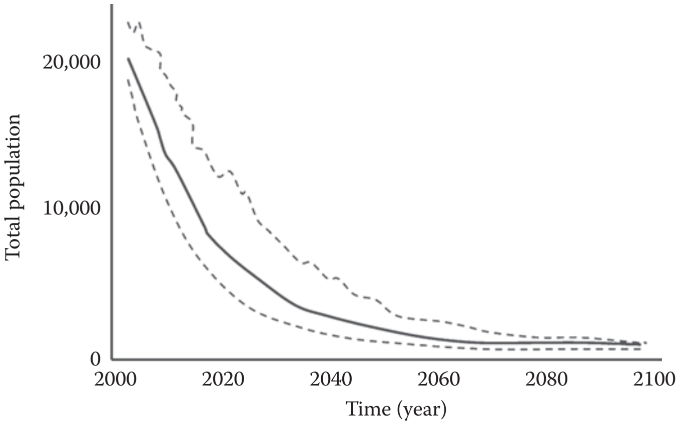

FIGURE 21.6 Predicted populations of marbled murrelets among six zones in Oregon, Washington and California. Solid line is the mean, dashed lines indicate confidence intervals. (Redrafted based on McShane, C. et al. 2004. Evaluation report for the 5-year status review of the marbled murrelet in Washington, Oregon, and California. Unpublished report. EDAW, Inc. Seattle, Washington. Prepared for the U.S. Fish and Wildlife Service, Region 1. Portland, Oregon. With permission.)

NEOTROPICAL MIGRANT BIRDS

Bonnot et al. (2011) developed models for three species of breeding birds in the central Hardwoods region of the United States: wood thrush, prairie warbler, and worm-eating warbler. These three species are sensitive to forest fragmentation, and loss of early successional forest, and interior patches of forest. Habitat suitability was defined for each species to develop a base map consisting of 121 patches for the species, ranging in size from 26 ha to 2.6 million ha, and the landscape was held constant (a static landscape) (Bonnot et al. 2011). A number of assumptions were made regarding demographics and dispersal, but the projection of population growth were verified by comparing results to the Breeding Bird Survey (BBS) data from the region in 1966–2007 (Sauer et al. 2008). The predicted annual decline in wood thrush and prairie warblers differed from BBS estimates by less than 1% and 2%, respectively (Figure 21.7). The authors then explored several restoration options for the species: habitat restoration, with both random and strategic locations of restoration efforts; afforestation, to restore forest cover lost historically; and increased survival, by reducing collisions of migrating birds with communication towers (Bonnot et al. 2013). They found that the abundance of prairie warblers and wood thrushes tripled when forests were replanted, or when collisions with communication towers were reduced, and that for all species, strategic placement of restoration efforts within or near existing protected areas was more successful than random placement (Figure 21.8).

MODEL ERRORS AND UNCERTAINTIES

Models are abstractions of the real world, developed to aid in decision making and to allow managers and scientists to understand complex interacting systems. All model results are incorrect, and we often do not know how incorrect they really are, although the work of Bonnot et al. (2011, 2013), who verified model results based on independent data, indicates that realistic results may be possible for some species. Independent data collected to parameterize the model are not always available, and especially data that shows adverse responses by populations of rare species to management actions that are not only unlikely, but may be illegal. So those using the results from models such as PVAs should verify model projections with independent data when possible, but otherwise

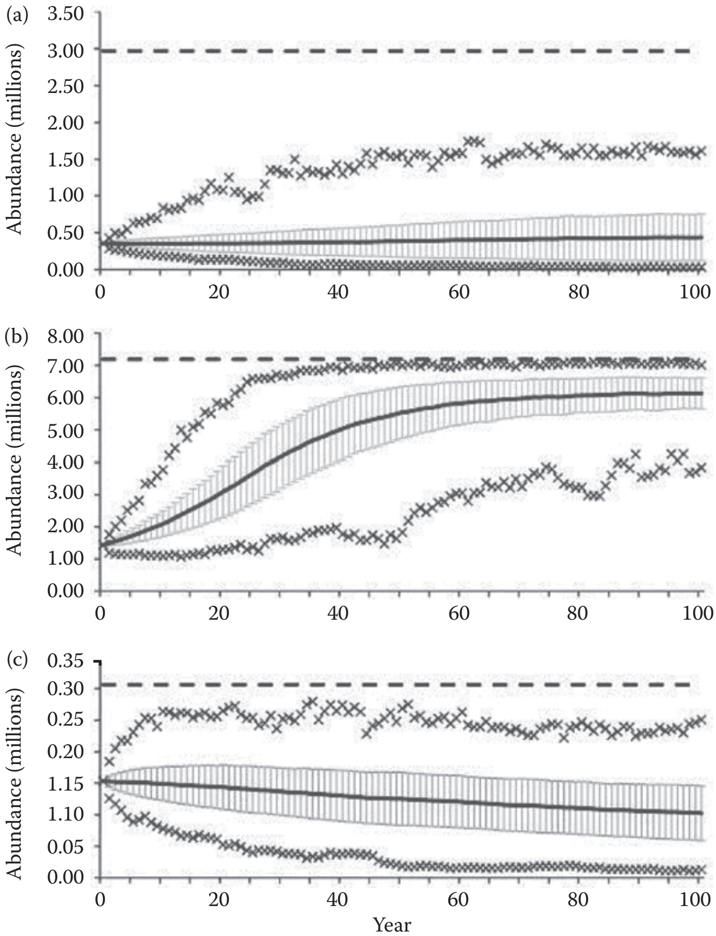

FIGURE 21.7 Estimated carrying capacities (dotted lines) and projected abundances of wood thrush (a), worm-eating warblers (b), and prairie warblers (c), in the Central Hardwoods Bird Conservation Region. Solid lines are mean abundances ±1 SD and are bracketed by minimum and maximum values (x) observed over 1000 simulations. Note: actual growth and trend estimates are based on median abundance rather than mean abundance; therefore, trajectories of graphs may not accurately convey population trends. (Reprinted from *Biological Conservation*, 144, Bonnot, T.W., F.R. Thompson III, and J.J. Millspaugh, Extension of landscape-based population viability models to ecoregional scales for conservation planning, 2041–2053, Copyright 2011, with permission from Elsevier.)

proceed with caution and be fully aware of the potential errors in the models and results. There are four dominant sources of errors—poor data, difficulties in parameter estimation, weak ability to validate or verify models, and effects of alternative model structures—that result in uncertainty in PVA model results (Beissinger and Westphal 1998).

POOR DATA

PVA models are often described as "data hungry." They require a broad suite of demographic information on a variety of habitat types ideally collected over many years to adequately represent inherent demographic and environmental stochasticity. Data should be broadly representative, robust, and unbiased. Such data can be very costly, and the data collection requires strict protocols and large sample sizes. The survey of the northern spotted owl is often used as an example of the cost

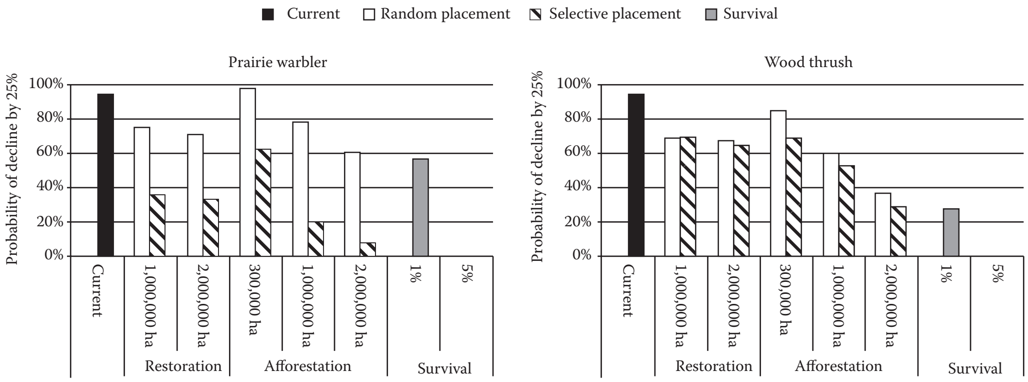

FIGURE 21.8 Projected viability of prairie warbler and wood thrush populations resulting from conservation scenarios. Strategic habitat restoration targeted habitat on protected areas, while strategic afforestation created forests in highly forested, productive landscapes. Bars indicate the probability of the regional population declining by 25%. The current scenario assumes the current landscape with no changes. (Reprinted from *Biological Conservation*, 165, Bonnot, T.W. et al., Landscape-based population viability models demonstrate importance of strategic conservation planning for birds, 104–114, Copyright 2013, with permission from Elsevier.)

associated with gaining adequate information over its geographic range to enable credible PVA projections. Millions of dollars have been spent on data collection for this species and millions of dollars are involved in the product values associated with decisions driven, in part, by PVA analyses. Rarely do we have the amount and quality of data for other species that we have for spotted owls. For many species, the vital rates needed to parameterize a PVA are gleaned from the literature, and usually from studies conducted not specifically designed to provide these parameter estimates. For the vast majority of species, PVA projections are better thought of as hypotheses than as estimates. If the estimates are used in decision making, then a set of assumptions and caveats regarding data quality should accompany the population projections.

DIFFICULTIES IN PARAMETER ESTIMATION

Consider a species' life history, from birth to death. Throughout life, there are events that influence individuals and populations. One critical part of an individual's life that will influence it, if it survives and reproduces, is the period of time immediately after it leaves a nest or den. It is a juvenile, naive to the world, and vulnerable to many factors. Survival during this juvenile stage is a parameter that often emerges as one that greatly influences population dynamics, but it is also one of the most difficult parameters to estimate (Wiens et al. 2006), especially for species that are too small to carry a radio transmitter, or species that are migratory or disperse widely. Dispersal is another parameter that can be difficult to estimate, especially for juvenile individuals in a population (Bonnot et al. 2011), but dispersal estimates are critical to understand the inter-relationships between habitat patch size and proximity (Marcot 2013). In these cases, the technical aspects of PVA modeling may far outweigh our technical capabilities in collecting the data needed to parameterize the models.

WEAK ABILITY TO VALIDATE OR VERIFY MODELS

Although there are independent datasets that can be used to validate various components of a PVA model (e.g., occupancy rates, survival in some age classes, sex ratios), there are little and often no data available to validate these parameters (confirm accuracy), and rarely are monitoring data available to verify projections (assess consistency with trends), but see Bonnot et al. (2011). Indeed, due to lag times associated with population responses to management alternatives, some of which may be novel, it will likely take decades or centuries before monitoring data can provide independent assessments of model performance. Fortunately, when monitoring data are collected, then the resulting data can be used to continually improve model performance and accuracy. Oftentimes funding available to develop recovery plans or management plans may not continue over time, as needed, to acquire the necessary monitoring information.

Effects of Alternative Model Structures

There are several widely used PVA models available now, and there will likely be more in the future, each attempting to include more reality into the model abstractions (Gordon et al. 2004). Each model structure has its own set of strengths and weaknesses with regards to dealing with potential effects of different types of forest management, stochastic events, animal scaling properties and movements, competitors, predators, diseases and parasites, among other factors influencing population dynamics (Beissinger and Westphal 1998). Consequently, projections resulting from one model structure may differ considerably from another. Indeed, projections of future conditions from a range of model structures conducted by different scientists may be one approach to understanding the uncertainties associated with population projections. Consider Bonnot et al.'s (2011) models of bird populations over a region: If they had developed a dynamic landscape model rather than static, would their results have been consistent? If multiple projections using alternative model structures are somewhat consistent in their predicted extinction rates, or population trends, then perhaps more faith can be placed in the results, given the caveats presented in the previous three limitations of all models.

INTERPRETING RESULTS FROM PVA PROJECTIONS

Given the caveats regarding uncertainty and potential errors described in the previous section, it is important to consider how best to use the results of population viability analyses. First and foremost, do not believe the predictions, at least not with the precision that is often implied by the projections. Predicting the future is easy; predicting it reliably is often impossible. Think of weather predictions, for instance. Predicting the weather a week or more into the future (*The Farmer's Almanac* notwithstanding) is much less reliable than predicting it tomorrow, or in the next hour or next minute. The farther into the future the predictions are made, the less reliable the predictions are likely to be. Long-term predictions may be useful to understand factors such as lag effects and stochastic events but should be viewed with considerable caution. PVA projections are best used over relatively short time periods to make decisions, while using the long-term projections as a context for near-term decisions.

The medieval philosopher William of Occam once stated: "One should not increase, beyond what is necessary, the number of entities required to explain anything" (known as Occam's razor). "Keep it simple, stupid" (the KISS principle) is the saying that my high school math teacher espoused. Do not use complex models when simpler, easier-to-comprehend models will provide you with estimates that are of value in decision making. Of course, this is always a tradeoff, because populations and ecosystems are inherently complex. The natural tendency of decision makers is to use the models that best approach reality (most complex) even when they may not be necessary to reach an informed decision.

Model results, if used cautiously, can be used to understand relationships among the various factors influencing population change and to diagnose causes of decline and potential for recovery. These heuristic aspects of modeling (using modeling to teach us something about the system) may represent the most useful approach to PVA modeling, in that it can help generate hypotheses regarding the factors that seem to be most likely to lead a population to extinction (Marcot et al. 2013). These hypotheses can then be tested in the field and controlled settings to allow us to hone in on key factors that can lead to a more efficient population recovery.

Trends are more important than numerical predictions, because numerical predictions will change as parameters are improved. So it is best to use the projection results in a relative—rather than absolute—sense (Beissinger and Westphal 1998). Comparing extinction probabilities, population trends, or times to extinction among management options is more appropriate than saying that the population will go extinct in 40–65 years, for example. These relative comparisons become even more valuable when independent scientists, using a variety of model structures, all produce estimates that support (or contradict) one another. Decisions based on PVAs are usually made based on the credibility of the results, and the credibility is usually much greater in a relative, rather than absolute, sense.

PVA results are often used within a process called risk analysis. Risk analysis is a structured way of analyzing decisions, and the potential effects of those decisions, when the outcomes are uncertain. The process involves identifying options, quantifying or assigning probabilities, and evaluating and selecting management options. This approach is often used when there are multiple interest groups with different and conflicting objectives, the outcomes of management alternatives are uncertain, and any decision may have serious consequences. Risk analysis attempts to structure and quantify management options to help the decision maker to understand the consequences of action or inaction, and choose a decision path. For instance, the Bonnot et al. (2013) PVAs allow managers to understand the potential for management actions to improve habitat and reverse downward trends. The relative effectiveness of different alternatives, in combination with an estimate of costs, can be used to develop an estimate of the return on investment of alternatives, and also assess which alternatives are most socially acceptable.

SUMMARY

Fine-filter analyses often entail an assessment of population trends, and risks of extinction of species, from all or a significant part of its range. These assessments are integral to the development of recovery plans for threatened species, and have been conducted for a wide range of species during ecoregional assessments. There is a range of model structures used to assess future population trends representing a range of ecosystem complexities that are included in the model structures. Those that consider a dynamic landscape, particularly relative to the generation length of the species under consideration, are often selected for use with forest-associated species. Due to the complexities of the model structures however, the results of these projections are best interpreted in a relative—rather than an absolute—sense, to allow comparisons among management alternatives. Further, trends predicted into the near future are usually more reliable than long-term projections. Issues such as data quality, inadequate validation, and environmental uncertainties, all influence the utility of these projections.

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