1. **POPULATION VIABILITY ANALYSIS**

**6.1. Introduction**

Conservation biologists managing threatened populations are frequently confronted with questions such as: “How many tortoises should be maintained in a particular reserve to ensure that a population will be thriving 100 years from now?” “How many caribou should be released on this mountaintop to successfully reestablish a population?” “What recovery objective should be set for this endangered orchid?” Answers to these fundamental questions are rarely intuitive; many variables interact to determine the size of a population and how long it might persist. Often, the only way to gain insight is to develop a mathematical model of the population and to use it to perform a *population viability analysis* or *PVA*.

Conservation biologists often ask, “What is a *minimum viable population*?” Or, more fully, “For this particular population, what is the smallest that it can be and still have a reasonable probability of surviving for some time into the future?” The story of Noah in the Bible indicates just two: one male and one female. However, population biologists have shown that Noah would have to have been extremely lucky or to have enjoyed long-term divine intervention, because most populations this small are doomed to extinction. A technique used to estimate minimum viable populations (MVP) is called population viability analysis, often abbreviated as PVA. In a general sense, any systematic attempt to understand the processes that make a population vulnerable to extinction could be called a PVA. In practice, the term usually refers to using models to predict the likely fate of a population. At their simplest, these models are deterministic predictions of what will happen to a population that has certain rates and degrees of variability of natality and mortality. Here we will focus on the most common form of PVA models, those that focus on a single population and incorporate an element of stochasticity, or randomness.

To understand the stochastic approach to PVA you have to appreciate the role of probability in the extinction of populations; in many respects PVA evolved out of risk assessment, which is based on probabilities. Evidences show that sooner or later all populations become extinct; only *when* and *why* are left to chance. Let us start with “when” by considering two generic predictions. First, the smaller a population is, the greater the probability that it will become extinct in a given span of time. Conversely, the longer the time period being considered is, the greater the probability that a population of a given size will become extinct.

Conservation biologists translate these ideas into real-world predictions that usually take one of two forms: (1) a dodo population needs to have at least *x* individuals if it is to have a 95% probability of surviving for 500 years; or (2) a population of 25 dodos has an *x*% probability of surviving 500 years if current conditions persist. (The figures 95% and 500 years are arbitrary; 90% and 99%, 100 and 1000 years are also used commonly. In reality these models cannot distinguish, with confidence, between a 90% and 99% probability of extinction over such long periods.) One key objective of PVA is to replace these *x* values with good predictions. Another objective is to understand “why” the population will become extinct – what factors will be responsible – because this will give conservationists some guidance on how to direct their management.

**An example**. Consider the following model of a population in which the total number of individuals (*N*) can change over a discrete interval of time (from *t* to *t* + 1) only because of births and deaths in the population:

***Nt* + 1 = (*Nt* × *S*) + (*Nt* × *B* × *S*)**

Where *S* is the probability of an individual surviving from *t* to *t* + 1 and *B* is the number of offspring produced on average per individual at each time interval. The (*Nt* × *S*) component of the equation represents the survival of adults from one time step to the next, and (*Nt* × *B* × *S*) represents the production of offspring and their subsequent survival.

If *N*t = 10, *S* = 0.5, and *B* = 1, then the population will remain stable at ten individuals no matter how far we project it into the future (10 = [10 × 0.5] + [10 × 1 × 0.5]). Also, its probability of extinction is zero (Fig. 7.7). Because this model’s parameters do not vary, it is termed a *deterministic model* and it always provides a single, discrete prediction.

We know that population parameters are not fixed, however, so this prediction is not very useful. We need to add some elements of variation to the model to make it a *stochastic model* and thus a more realistic assessment of the population’s future. To construct a stochastic model we should incorporate stochastic factors that play roles in population extinction. The factors are discussed in the next paragraphs.

* 1. **The stochasticities that contribute to extinction**

There are four interacting factors or processes that might contribute to a population’s extinction. These are referred to as stochasticities – uncertainties – to emphasize that they were based on probabilities.

1. **Demographic stochasticity**

Demographic stochasticityis uncertainty resulting from random variation in reproductive success and survivorship at the individual level. The importance of demographic issues is best illustrated with a simple hypothetical example. If 95% of a population of 10,000 frogs were killed by a disease, the 500 remaining could probably rebuild the population over several years. In contrast, if 95% of a population of 100 frogs died, there is a fair chance that the remaining five frogs might be all males, perhaps because females were more susceptible to the disease. Alternatively, they might be two large females and three males too small to mate with them effectively. You can imagine many scenarios; the point is that with very small populations there is a fair chance that extinction will occur simply because of vagaries in the age and sex structure of the population. This is a very real issue for small populations (e.g. island-bound foxes off the California coast).

In some species it is not sufficient to have a balanced age and sex structure; apparently, there must be a fairly large number of individuals to provide enough social stimulation for reproduction. This is called the *Allee effect* after Warder Allee (1931), who, having noted that species such as red deer and starlings thrive only in social groups, suggested that they require the stimulation of a group to breed. It has been suggested that the extinction of the passenger pigeon, which often nested in huge colonies, may have been hastened because natality dropped after populations became too low to provide enough social stimulation. For some species, issues such as group defense against predators or efficiency in finding food may also explain a need for group living. An extreme case of the need for sociality could occur if a species became so rare and widely dispersed that individuals had difficulty finding one another; this may be an issue for whales that travel over immense spans of ocean. It is easy to envision a rare plant (of a species incapable of self-fertilization or vegetative reproduction) failing to reproduce because no pollen ever arrived from another plant.

To predict the effects of demographic factors we need estimates of demographic parameters such as the population’s size, sex, and age structure, and its natality and mortality rates. Ideally, we would have specific natality and mortality rates for each age group and gender; for example, what is the probability of a three-year-old female surviving until she is four years old? How many young will she probably produce? It is often necessary to use rough estimates of these parameters because it is too difficult and expensive to gather the required data.

1. **Environmental stochasticity**

Environmental stochasticityrefers to random variation in components of habitat quality, such as climate, nutrients, water, cover, pollutants, and relationships with other species that might be prey, predators, competitors, parasites, or pathogens. At a conceptual level it is easy to understand how these factors are related to a population’s probability of surviving. However, translating these relationships into quantitative predictions becomes very complex, and thus most

PVAs either do not include any environmental stochasticities or include only a few factors that are thought to be limiting. When environmental stochasticities are incorporated into a PVA, this is usually done by making a link between certain key environmental factors and one or more demographic parameters. For example, because weather is so important for the survival of mammals, a PVA for the endangered San Joaquin kit fox includes a predicted relationship between annual variation in precipitation and the number of individuals surviving.

1. **Catastrophes**

Catastrophesare dramatic events such as droughts or hurricanes that occur at random intervals. In a sense they are a form of environmental stochasticity, but they differ in that they are discrete, specific events rather than continuous variation in a parameter such as temperature that is routinely affecting population dynamics, and they usually exert much greater effects. In the context of PVAs, their predicted effect on a population is usually modeled differently. They are predicted to kill a portion of the population outright at some irregular interval rather than having a continuous effect on a parameter such as natality. Their effects can be greater than all other factors combined.

1. **Genetic stochasticity**

Genetic stochasticityis random variation in the gene frequencies of a population resulting from genetic drift, bottlenecks, inbreeding, and similar factors. These processes are understood well enough in some experimental situations, notably with *Drosophila* fruit flies, to allow population biologists to make quantitative estimates of their effect. Unfortunately, it is probably a significant extrapolation to use numbers based on fruit fly research in PVAs for all the species in which these processes have not been studied. For example, our understanding of genetics would suggest that northern elephant seals should be suffering severely from inbreeding problems because in the 1890s they had apparently been reduced by overhunting to fewer than 20 individuals. However, they do not seem to have any genetic problems. Perhaps they are very lucky; perhaps the potential for inbreeding depression is intrinsically low in elephant seals. Among the four factors listed here, genetic stochasticities probably have the least effect on MVP estimates, especially for short-term predictions, although long-term population persistence is ultimately dependent on maintaining genetic diversity.

These four factors cannot be incorporated into a model in a simple, additive fashion. They all interact with one another in a complex manner that is likely to involve positive- feedback loops that collectively constitute what has been described as an extinction “vortex”. For example, one form of environmental stochasticity, habitat fragmentation, can easily curtail dispersal among subpopulations and thus profoundly reduce exchange of genetic material and increase inbreeding. Consider the extinction of the heath hen, a subspecies of prairie chicken that used to range along the United States’ Atlantic coast from Maine to Virginia (Fig. 5.1). After environmental factors (overhunting and habitat degradation) reduced the heath hen to one population on a small island, it succumbed to a catastrophic fire, more environmental problems (predation and disease), a demographic imbalance (too few females), and perhaps a genetic problem manifested as sterility.



**Fig. 5.1.** A combination of factors drove the heath hen, once

 widespread in the eastern United States, into extinction,

 including environmental stochasticity (unusual weather

 events), demographic stochasticity (skewed sex ratios),

 genetic stochasticity (loss of genetic variation due to small

 population size), and catastrophes(fires).

Combining all the various parameters that might affect population viability for a given species into a truly comprehensive model would be nearly impossible, although some very complex and sophisticated models have been created. Furthermore, if a realistic, comprehensive model could be created, another huge hurdle would remain: obtaining reasonable numbers to plug into the model. Even basic parameters such as age-specific natality and mortality have not been measured for most species and are not easily obtained. Despite these reservations, PVAs do not have to be comprehensive to be useful. In fact, even relatively simplistic PVAs based on different computer software have been demonstrated to be surprisingly accurate and concordant in their predictions.

PVA models are best thought of as a method for organizing and enhancing our understanding of the factors that shape a population’s likelihood of persistence, as well as for comparing the effects of different management alternatives on relative probabilities of extinction.

PVA should be regarded primarily as a tool for guiding research, management, and policy and for synthesizing knowledge about a species. PVA is an extraordinary tool for understanding how a population works and what influences its ups and downs. There are, however, generally too many uncertainties about the details of the models to permit using them to make definitive statements about the precise fate of particular populations.

Finally, the focus on populations in this chapter is a good reminder that conservation biologists may at times become too fixated on the global extinction of entire species and thus overlook the slow, incremental loss of populations that is likely to lead to species extinctions. The hidden scale of population extinction is quite alarming. With an estimated 220 populations per species, there are some 1.1–6.6 billion genetically distinct populations globally, which translates into a population extinction rate 432 times greater than that of species loss.