A PRACTICAL HANDBOOK FOR POPULATION VIABILITY ANALYSIS

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CHAPTER ONE: WHAT IS POPULATION VIABILITY ANALYSIS, AND WHY THIS HANDBOOK?

The 1997 document Conservation by Design: A Framework for Mission Success states that the conservation goal of The Nature Conservancy is "the long-term survival of all viable native species and community types through the design and conservation of portfolios of sites within ecoregions." In an ideal world, conservation organizations like TNC would seek to preserve every location that harbors a rare, threatened, or endangered species. But in the real world, financial considerations make this strategy impossible, especially given the number of species whose status is already cause for concern. Thus it is an inescapable fact that for all but the rarest of species, TNC will need to focus on preserving only a subset of the known populations, and upon this choice will rest the success of the entire mission. To make this choice, Conservancy staff require the means to find answers, at the very least qualitative and conditional ones, to two critical questions. First, what is the likelihood that a known population of a species of conservation concern will persist for a given amount of time? Second, how many populations must be preserved to achieve a reasonable chance that at least one of them will avoid extinction for a specified period of time? The goal of this handbook is to introduce practical methods for seeking *quantitative* answers to these two questions, methods that can provide some guidance in the absence of highly detailed information that is unlikely to be available for most rare species. The use of such methods has come to be known as population viability analysis (PVA).

Broadly defined, the term "population viability analysis" refers to the use of quantitative methods to predict the likely future status of a population or collection of populations of

conservation concern. Although the acronym PVA is now commonly used as though it signified a single method or analytical tool, in fact PVAs range widely both in methods and applications. Among the most influential PVAs to date is one of the original analyses of Northern Spotted Owl data (Lande 1988). This work relied upon quite simple demographic data, and its main points were that logging could result in owl population collapse and that the data available at that time were insufficient to determine how much forest was needed for the owl population to persist. This second point is important, as it emphasizes that PVAs can be highly useful even when data are sparse. Another influential PVA (Crouse et al. 1987) used a more complex size-structured model to assess the status of loggerhead sea turtles and to ask whether protecting nestlings on beaches or preventing the death of older turtles in fishing trawls would have a greater effect on enhancing population recovery. This single PVA played a critical role in supporting legislation to reduce fishing mortality of turtles (Crowder et al. 1994). More recent PVAs have involved yet more complex spatial models, for example of individual Leadbeater's Possums (Lindemeyer and Possingham 1994). Furthermore, while most PVAs are ultimately concerned with assessing extinction risks, they are often motivated by the need to address specific problems, for example sustainable traditional use levels of forest palms (Ratsirarson et al. 1996), the risks posed by different poaching techniques to wild ginseng populations (Nantel et al. 1996), or loss of movement corridors (Beier 1993). The uniting theme of PVAs is simply that they all are *quantitative* efforts to assess population health and the factors influencing it.

This handbook grew out of a workshop held at the National Center for Ecological Analysis and Synthesis in Santa Barbara, CA, in February, 1998, in which ecologists from four universities (the authors of this handbook) and TNC practitioners came together to explore how quantitative methods from the field of population biology might be used to inform TNC decision

making. Prior to the workshop, TNC participants were asked to supply data sets that exemplify the types of information that TNC or Heritage employees and volunteers would collect about species of conservation concern. In Chapter 2, we classify the data sets into 3 categories, which we then use as a starting point to identify a few quantitative methods that we describe in detail in the subsequent chapters. In Chapters 3 and 4, we review methods for assessing viability of single populations when the data represent census counts or demographic information about individuals, respectively. In Chapter 5, we address the question of how to assess regional viability when a species is distributed across multiple populations of varying size and "quality".

We begin with two important caveats. First, this handbook does not attempt to review the field of population viability analysis as a whole, but instead focuses on the subset of all available PVA methods that we deemed, through our interactions with TNC biologists, to be the most practical given the types of data typically available. Second, population viability analyses, because they are typically based upon limited data, MUST be viewed as tentative assessments of current population risk based upon what we now know rather than as iron-clad predictions of population fate. Thus, as we will argue repeatedly below, we should not put much faith in the exact predictions of a single viability analysis (e.g. that a certain population will have a 50% chance of persisting for 100 years). Rather, a better use of PVA in a world of uncertainty is to gain insight into the *range* of likely fates of a single population based upon 2 or more different analyses (if possible), or the *relative* viability of 2 or more populations to which the same type of analysis has been applied. When data on a particular species are truly scarce, performing a PVA may do more harm than good. In such cases, basing conservation decisions on other methods (e.g. the known presence/absence of a species at a suite of sites, or its known habitat requirements) makes far better sense. We discuss the question of when NOT to perform a PVA

in greater detail in the final chapter of this handbook. Thus, while we view PVA as a potentially useful tool, we do not see it as a panacea.

While data scarcity is a chronic problem facing all decision making in conservation, we should also recognize that it is often feasible to collect additional data to better inform viability assessments. Indeed, TNC and Heritage personnel are constantly collecting new information in the course of monitoring sites for rare and threatened species. Simple counts of the number of individuals of a certain species at a site over a number of years are often made with other purposes in mind, but they can also serve as grist for a population viability analysis. We hope that awareness of the possible use of monitoring data in PVA will lead TNC/Heritage biologists to consider ways that their monitoring schemes can maximize the usefulness of monitoring data for future viability assessments, without entailing costly changes in existing monitoring protocols. In Chapter 6 of this handbook, we make easy-to-follow recommendations for how the design of monitoring strategies can best meet the data requirements of PVA.

Before proceeding to the consideration of typical TNC data sets, we say a brief word about the structure of this handbook. To illustrate the application of each method, we provide step-by-step examples, usually using one of the TNC/Heritage data sets. These worked examples are featured in Key Boxes that are set aside from the background text of the handbook. We also use Key Boxes to highlight key assumptions or caveats about each of the methods we review. While the Key Boxes emphasize the methods we have found to be the most practical, it is also important to point out that more complex population viability analyses may be possible in cases in which more data are available. Because we do not have the space to thoroughly review these more complex (and therefore less frequently useful) analyses in a handbook of this length,

we have also included Optional Boxes that give a brief overview of other methods and provide

references that will allow the interested reader to learn more about them.

Finally, we make one further point of clarification. In this handbook, we aim to quantify

the likelihood of persistence of a population (that is the collection of individuals of a single

species living in a prescribed area) or a set of populations over a specified time period. We use

the terms "population" and "element occurrence" (or "EO") interchangeably. Thus we use

"EO" to refer to a population of a single species, which we realize is a more restricted usage of

the term than the one used by TNC/Heritage biologists, which defines elements as "viable native

species AND communities" (see Conservation by Design). We emphasize that the methods we

review are NOT intended to be used to determine the long-term viability of communities.

However, we note that PVAs targeted at populations of dominant or characteristic species in a

particular community type may serve as useful tools for evaluating the viability of community

occurrences.

CHAPTER TWO: LETTING THE DATA DETERMINE AN APPROPRIATE METHOD

FOR POPULATION VIABILITY ANALYSIS

The first rule of population viability analysis is: "let the data tell you which analysis to perform". While population biologists have developed a vast array of complex and mathematically sophisticated population models, it is our view that when data are limited (as they almost always will be when we are dealing with the rare, seldom-studied species that are the typical concern of conservation planners) the benefits of using complex models to perform population viability analyses will often be illusory. That is, while more complex models may promise to yield more accurate estimates of population viability because they include more biological detail (such as migration among semi-isolated populations, the effects of spatial arrangement of habitat patches, and the nuances of genetic processes such as gene flow and genetic drift), this gain in accuracy will be undermined if the use of a more complex model requires us to "guess" at critical components about which we have no data. Instead, our philosophy is that the choice of models and methods in PVA should be determined primarily by the type of data that are available, and not the other way around.

With this philosophy in mind, and to get an idea of the kinds of data that TNC biologists will typically have at their disposal to perform population viability analyses, we asked workshop participants to provide us with data sets that had been collected in conjunction with TNC field offices. We received 26 data sets, which included information about 25 species of conservation concern. We classified these data sets according to the type of data, the number of locations, and the number of years in which data were collected. By "type of data", we mean whether the persons who collected the data recorded the PRESENCE OR ABSENCE of the species at a

location, COUNTS of individuals in one or more life stages, or DEMOGRAPHIC information about individual organisms (that is, whether each individual survived from one census to the next and if so, its size at each census and the number of offspring it produced in the time interval between the censuses).

This survey of data sets highlights four patterns (Table 2.1, Fig. 2.1). First, count data is the most common type of information in this sample of TNC data sets. Second, relatively long duration studies tended to focus on only a single site, while multi-site studies typically involved only one or a few censuses, which is not surprising given the limited resources available to monitor populations of conservation concern. Only one of the 26 data sets included information from more than 8 sites in more than 3 years. Third, demographic data sets, because they are more difficult to collect, tend to include fewer years on average than do count data. Fourth, the data set that included the most sites comprised presence/absence data. The single example of presence/absence data here surely underestimates the true frequency of such data sets in Heritage data bases. While information about presence/absence of a species is critically important in identifying high-priority sites for acquisition or preservation (Church et al. 1996, Pressey et al. 1997), such data sets lack the population-level details required for a PVA, and we do not address them further in this handbook.

To the extent that this informal sample gives a rough idea of the types of data accessible to TNC biologists, it suggests three themes about how PVA might best serve TNC decision making processes. First, our informal survey of data sets shows that counts of the number of individuals in one or more populations over multiple years will be the most common information upon which population viability analyses will need to be based, but that in some cases (most likely for umbrella or indicator species, and those for which particular reserves have been

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especially established) more detailed analyses based upon demographic information will be feasible. Second, while information will sometimes be available to perform PVAs on multiple local populations, most decisions about the number of occurrences needed to safeguard a species will require extrapolation from information collected at only one or a few populations at best. Third, the kinds of information that are *missing* from these data sets is also noteworthy. None of them include any information about genetic processes or, in the case of data sets that include multiple occurrences, about rates of dispersal of individuals among populations. Thus we conclude that more complex models that require this information will not be justified in most cases. We reiterate these themes in the following chapters.

Thus Fig. 2.1 suggests three general classes of data sets that provide information that can be used to perform a PVA:

- Counts of individuals in a single population obtained from censuses performed over multiple years;

- Detailed demographic information on individuals collected over 3 or more years (typically at only 1 or 2 sites); and

- Counts from multiple populations, including a multi-year census from at least one of those populations.

Each of these classes require somewhat different methods for population viability analysis. Fortunately, population biologists have developed methods to deal with each of these situations. Table 2.2 summarizes the data requirements for PVA based upon each of these three classes of data, and points to where each type of PVA is presented in this handbook.

Table 2.1: Data sets contributed to the TNC PVA workshop.

Species	Type of Data	No. of sites	No. of years
Shale barren rockcress, *Arabis serotina*	Counts	1	6
Shale barren rockcress, *Arabis serotina*	Counts	17	3
Dwarf trillium, *Trillium pusillum*	Counts	1	4
Eriocaulon kornickianum	Counts	1	3
Mesa Verde cactus, *Sclerocactus mesae-verdae*	Counts	1	10
Mancos Milkvetch, *Astragalus humillimus*	Counts	1	8
Knowlton's cactus, *Pediocactus knowltonii*	Counts	1	11
Lesser prairie chicken, *Tympanuchus pallidicinctus*	Counts	1	13
Seabeach pinweed, *Amaranthus pumilus*	Counts	18	8
Golden Alexanders, *Zizia aptera*	Counts	1	7
Oenothera organensis	Counts	8	2
Arizona stream fish (7 species)	Counts	1	1
Red-cockaded woodpecker, *Picoides borealis*	Counts	2	12
Bog turtle, *Chlemmys muhlenbergii*	Counts	7	3
Kuenzler hedgehog cactus, *Echinocereus fendleri* var. *kuenzleri*	Demographic	1	2
Ornate box turtle, *Terrapene ornata*	Demographic	1	8
Larimer aletes, *Aletes humilis*	Demographic	2	7
Mead's milkweed, *Asclepias meadii*	Demographic	1	4
Trollius laxus	Demographic	1	3
Cave salamander, *Gyrinophilus palleucus*	Presence/Absence	20	1

Table 2.2: A classification of PVA methods reviewed in this handbook.

Number of populations or EOs included in the analysis:	Type of data collected:	Minimum number of years of data per population or EO:	PVA method:	Where to look in this handbook:
One	Counts	10 (preferably more)	Count-based extinction analysis	Chapter 3
One	Demographic information	2 or more	Projection matrix models	Chapter 4
More Than One	Counts	10 (preferably more) for at least one of the populations	Multi-site extinction analysis	Chapter 5

FIG. 2.1: Characteristics of 20 data sets on rare species considered in the PVA Workshop (see

Table 2.1 for information on the species included).
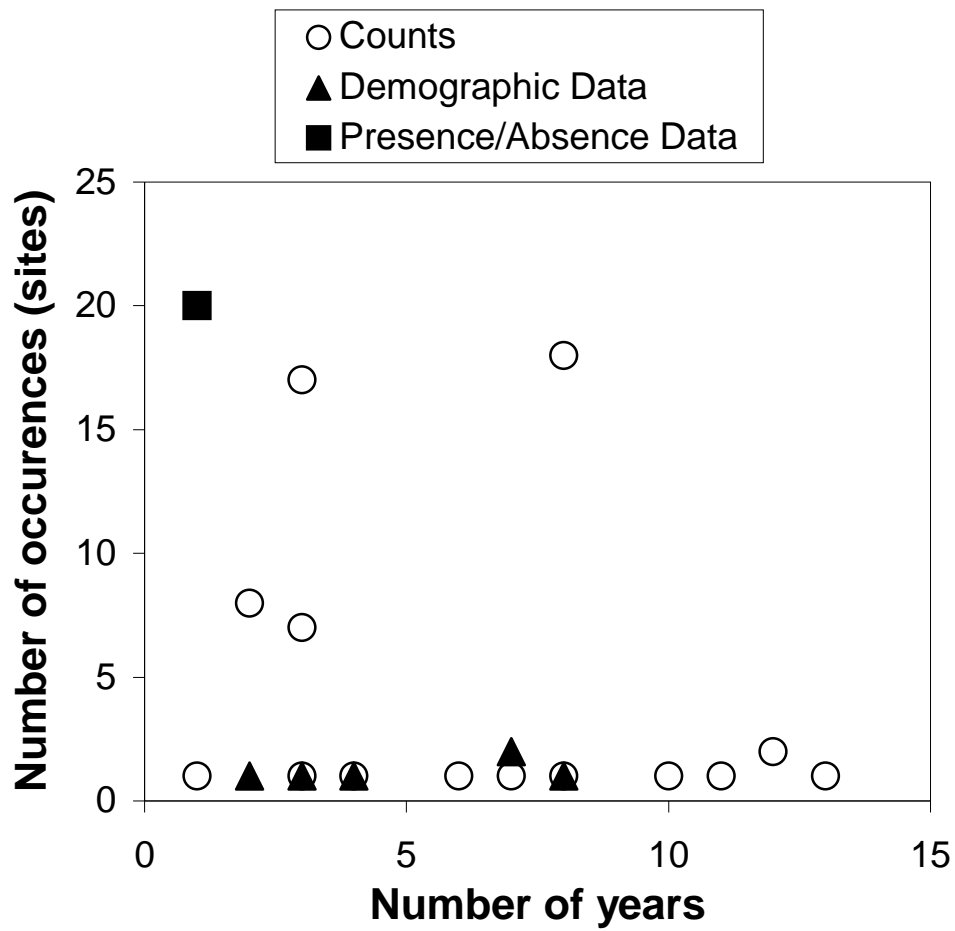
CHAPTER THREE: USING CENSUS COUNTS OVER SEVERAL YEARS TO ASSESS POPULATION VIABILITY

As we saw in Chapter 2 (FIG. 2.1), the type of population-level data that is most likely to be available to conservation planners and managers is count data, in which the number of individuals in either an entire population or a subset of the population is censused over multiple (not necessarily consecutive) years. Such data are relatively easy to collect, particularly in comparison with more detailed demographic information on individual organisms (see Chapter 4). In this chapter, we review an easy-to-use method for performing PVA using count data. The method's simplicity makes it applicable to a wide variety of data sets. However, several important assumptions underlie the method, and we discuss how violations of these assumptions would introduce error into our estimates of population viability. We also point to other, similar methods that can be employed in the face of biological complexities that make the simpler method less appropriate.

In a typical sequence of counts from a population, the numbers do not increase or decrease smoothly over time, but instead show considerable variation around long-term trends (see examples in FIG. 3.1). One factor that is likely to be an important contributor to these fluctuations in abundance is variation in the environment, which causes the rates of birth and death in the population to vary from year to year. The potential sources of environmentally-driven variation are too numerous to list fully here, but they include inter-annual variation in factors such as rainfall, temperature, and duration of the growing season. Most populations will be affected by such variation, either directly or indirectly through its effects on interacting species (e.g. prey, predators, competitors, diseases, etc.). When we use a sequence of censuses

to estimate measures of population viability, we must account for the pervasive effect of environmental variation that can be seen in most count data. To see how this is done, we first give a brief overview of population dynamics in a random environment, and then return to the question of how count data can be used to assess population viability.

Population dynamics in a random environment:

Perhaps the simplest conceptual model of population growth is the equation

$$N(t+1) = \lambda\, N(t), \qquad\qquad\qquad (3.1)$$

where $N(t)$ is the number of individuals in the population in year t, and λ is the population growth rate, or the amount by which the population multiplies each year (the Greek symbol "lambda" is used here by tradition). If there is no variation in the environment from year to year, then the population growth rate λ is a constant, and only three qualitative types of population growth are possible (FIG. 3.2a): if λ is greater than

one, the population grows geometrically; if λ is less than one, the population declines geometrically to extinction; and if λ exactly equals one, the population neither increases nor declines, but remains at its initial size in all subsequent years. But when variation in the environment causes survival and reproduction to vary from year to year, the population growth rate λ must also be viewed as varying over some range of values. Moreover, if the environmental fluctuations driving changes in population growth include an element of unpredictability (as factors such as rainfall and temperature are likely to do), then we must face the fact that we cannot predict with certainty what the exact sequence of future population growth rates will be. As a consequence, even if we know the current population size and both

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the average value and the degree of variation in the population growth rate λ, the best we can do is to make probabilistic statements about the number of individuals the population will include at some time in the future. To illustrate, FIG. 3.2b shows a hypothetical population governed by the same equation we saw above, but in which the value of the population growth rate λ in each year was generated on a computer so as to vary randomly around an average value. Each line in the figure can be viewed as a separate "realization" of population growth, or a possible trajectory the population might follow given a certain average value and degree of variability in λ.

Fig. 3.1b illustrates three important points about population growth in a random or "stochastic" environment. First, the possible realizations of population growth diverge over time, so that the farther into the future predictions about likely population size are made, the less precise they become. Second, the realizations do not follow very well the predicted trajectory based upon the average population growth rate. In particular, even though the average λ in this case would predict that the population should increase at a slow rate, a few realizations explode over the 20 years illustrated, while others decline (thus extinction is possible even though the average of the possible population trajectories increases). Third, the endpoints of the 20 realizations shown are highly skewed, with a few trajectories (such as the one illustrated in red) winding up much higher than the average λ would suggest, but most ending below the average. This skew is due in part to the multiplicative nature of population growth. Because the size of the population after 20 years depends on the product of the population growth rate in each of those years, a long string of chance "good" years (i.e. those with high rates of population growth) would carry the population to a very high level of abundance, while "bad" years tend to confine the population to the restricted zone between the average and zero abundance.

Skewness in the distribution of the likely future size of a population is a general feature of a wide variety of models of population growth in a stochastic environment. In fact, we can make the even more precise statement that for many such models, the endpoints of multiple independent realizations of population growth will lie approximately along a particular skewed probability distribution known as the log-normal, or equivalently that the natural log of population size will be normally distributed (see Box 3.1). This important result means that we can use the normal distribution (whose properties are well understood, as it underlies much of modern statistical theory) to calculate measures of viability, such as the probability that the population will be above some threshold size a given number of years into the future, or the likely number of years before the population first hits the threshold. But before we can calculate these measures, we must first estimate two parameters that describe how the normal distribution of the log of population size will change over time: μ, which governs change in the mean of the normal distribution, and σ^2, which governs how quickly the normal distribution's variance will increase over time (Box 3.1). Both of these parameters will have important effects on measures of population viability, so we require a method to estimate their values using count data.

Using count data to estimate population parameters:

Brian Dennis and colleagues (Dennis et al. 1991) have proposed a simple method for estimating μ and σ^2 from a series of population censuses. The method involves two easy steps: 1) calculating simple transformations of the counts and of the years in which counts were taken, and 2) performing a linear regression (Box 3.2). The results of the regression yield estimates of μ and σ^2.

Measures of viability based upon μ and σ^2:

Once we have estimated the parameters μ and σ^2 from count data, we can calculate several measures of the viability of the population from which the counts were obtained (Box 3.3). One is the average value of the population growth rate, $\overline{\lambda}$. This value indicates whether the *average* of the possible population trajectories will tend to increase ($\overline{\lambda} > 1$), decrease ($\overline{\lambda} < 1$), or remain the same ($\overline{\lambda} = 1$) over one census interval (thus $\overline{\lambda}$ describes the blue line in Fig. 3.2B). Keep in mind that some, or even most, realizations of population growth may decline even if their average increases (see Fig. 3.2B). The confidence interval for $\overline{\lambda}$ is also informative, because only if the entire confidence interval lies above or below the value 1 can we say (for example with 95% confidence) that the average of population trajectories will increase or decrease, respectively.

Because the average value of the population growth rate doesn't do a good job of predicting what most population realizations will do, two other viability measures, the mean time to extinction and the probability that extinction has occurred by a certain future time, may be calculated. These require us to specify an initial population size (typically the most recent count) and an "extinction" threshold. The "extinction" threshold need not be set at zero abundance. For a non-hermaphroditic species, we may wish to set the threshold at 1, at which point the population would be *effectively* extinct. It may be reasonable to set the threshold at even higher levels, such as the abundance at which genetic drift or demographic stochasticity reach a pre-determined level of importance, or the lowest level of abundance at which it remains feasible to attempt intervention to prevent further decline. Once we arrive at an appropriate threshold, based upon biological, political, and economic considerations, we can define a population above the threshold to be viable, and can calculate both the mean time to attain the threshold given that

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it is reached and the probability that the population has fallen below the threshold by a specified time in the future (Box 3.3).

Because it is relatively easy to calculate, much theoretical work has focused on the mean time until an extinction threshold is reached. But we must be careful here, because the mean time to extinction will almost always *overestimate* the time it takes for most doomed realizations to reach a threshold. This fact traces back to the skewness in population abundance that develops in a stochastic environment (FIG. 3.2b). The large fraction of realizations that hover at low abundance are likely to dip below the threshold at relatively short times, while the few realizations that grow rapidly at first will likely take a very long time before they experience the long string of bad years necessary to carry them below the threshold. These later trajectories have a disproportionate effect on the mean time to extinction. For this reason, the mean time to extinction is a potentially misleading metric for PVA.

A better measure of the time required for most populations to attain the threshold is the median time to extinction, which is one of several useful measures that can easily be obtained from the so-called "cumulative distribution function," or CDF, of the conditional time to extinction (Box 3.3). In effect, the conditional extinction time CDF asks the question: "if the extinction threshold is going to be reached eventually, what is the probability that a population starting at a specified initial size will have already hit the threshold at a certain time in the future?" Thus the conditional extinction time CDF considers only those population realizations that will eventually fall below the threshold; this will include all possible realizations if μ is less than or equal to zero, but only a subset of realizations if μ is greater than zero (see Box 3.3). *When the estimated value of μ is negative (so that eventual extinction is certain), the conditional extinction time CDF is the single most useful viability measure one can compute.*

From the CDF, one can read the median time to extinction as the time at which the probability of

extinction first reaches a value of 0.5 (FIG. 3.6); for the reason given above, the median time to

extinction is typically shorter than the mean time to extinction. The time to any other "event",

such as the probability of extinction first exceeding 5% (or to put it in a more positive light, the

probability of population persistence first falling below 95%), can also be easily read off the

CDF. The CDF also clearly shows the probability of population persistence until any given

future time horizon, which itself may be dictated by management considerations. ***Even if the

estimated value of μ is positive (so that only a subset of the possible realizations will ever hit

the extinction threshold), calculating the conditional extinction time CDF is still valuable,

because it can be used in combination with the probability of ultimate extinction to compute

the likelihood that extinction will have occurred by a given future time horizon*** (see Box 3.3).

*Uses of the Extinction Time Cumulative Distribution Function in Site-based and Ecoregional

Planning:*

      Because the conditional extinction time CDF encapsulates so much useful information

about population viability, we now give three examples that show how the CDF can be used to

inform decisions about the viability of individual element occurrences (EOs), or about which of

several EOs should receive the highest priority for acquisition or management.

      Perhaps the most valuable use of the CDF is to make comparisons between the relative

viabilities of 2 or more EOs. Ideally, we would have a series of counts from each EO. For

example, FIG. 3.1B&C show the number of adult birds during the breeding season in

populations of the federally-listed red-cockaded woodpecker in central Florida and in North

Carolina. Applying the methods outlined in Boxes 3.2 and 3.3 yields the CDFs in FIG. 3.7A.

Both because it has a more negative estimate for μ (-0.083 vs -0.011) and a smaller initial size, the Florida population has a much greater probability of extinction at any future time than does the North Carolina population.

Often we will not have independent census data from each EO about which we must make conservation decisions. However, if we have a single count of the number of individuals of a particular species in one EO, we can use count data from multiple censuses of the same species at a second location to make a ***provisional*** viability assessment for the first EO when no other data are available. For example, Dennis et al. (1991) calculated the extinction time CDF for the population of grizzly bears (*Ursus arctos*) in the Greater Yellowstone ecosystem, using values of μ and σ^2 estimated from aerial counts of the number of adult females over 27 years, a starting population of 47 females (the number estimated in 1988, the last census available to them), and an "extinction" threshold of 1 female (Fig 3.7B). A second isolated population of grizzly bears occupying the Selkirk Mountains of southern British Columbia consists of about 20 adults, or roughly 10 adult females. If we have no information about the Selkirk Mountains population other than its current size, we may as well use the CDF for the Yellowstone population to give us a *relative* sense of the viability of the Selkirks population. In so doing, we are assuming that the environments (including the magnitude of inter-annual variation) and the human impacts at the two locations are similar, an assumption which could be evaluated using additional information on habitat quality, climatic variation, and land-use patterns. Accepting these assumptions, and using the CDF from the Yellowstone population, the Selkirks population of 10 females would have an 31-fold greater probability of extinction at 100 years (Fig 3.7B; for an extension of this analysis to multiple sites, see Box 5.2). For species of particular concern, it may be possible to improve upon this approach by compiling count data from multiple locations.

We could then estimate *average* values for the parameters μ and σ² to provide ballpark

assessments of viability for EOs with only a single census, or choose the location with the most

similar environment for comparison.

As a final use of the CDF, we point out that even in the absence of any count data for a

species of critical concern, knowledge of how the CDF is affected by its underlying parameters

can help us to make *qualitative* assessments of relative viability, especially if we can use natural

history information to make inferences about the local environment of an EO or about the life

history of the species in question. For example, we will frequently be able to make an educated

guess that one EO's environment is likely to be more variable than another's in ways that will

affect population growth. Similarly, some species will have life history features (e.g. long-lived

adults) that buffer their populations against year-to-year environmental variation. If the effects

of environmental variation on the population growth rate are less for one species or EO than

another, then its σ² value will be smaller. Such differences in σ² influence the CDF even when

its other determinants (μ and the starting and threshold population sizes) are fixed (FIG. 3.7C).

Thus we can state that, all else being equal, the greater the environmentally-driven fluctuations in

population growth rate the greater will be the risk of extinction at early time horizons, a

qualitative statement that nonetheless provides some useful guidance.

Assumptions in Using the Method of Dennis et al.:

As with any quantitative model of a complex biological process, PVA using count data

relies upon simplifying assumptions. In Box 3.4, we list the most important assumptions we are

making when we apply the method of Dennis et al. to a series of counts and then estimate

measures of population viability. The fact that these assumptions are explicit is an advantage of

a quantitative approach to evaluating viability, relative to an approach based upon general natural history knowledge or intuition. By evaluating whether the assumptions are met, we can determine whether our analysis is likely to give unreliable estimates of population viability, but more importantly, we can often determine whether violations of the assumptions are likely to render our estimates (e.g. of time to extinction) optimistic or pessimistic. By "optimistic" and "pessimistic", we mean, for example, that the true time to extinction is likely to be shorter or longer than the estimated value, respectively. If we know that the estimated time to extinction for an EO is short but pessimistic, we should be more cautious in assigning a low viability ranking, while a long but optimistic estimate should not inspire complacency.

We now give a few brief examples illustrating how, by evaluating the assumptions in Box 3.4, we can make more informed viability assessments. One life history feature that may cause Assumption 1 (Box 3.4) to be violated is dormant or diapausing stages in the life cycle, such as seeds in a seed bank or diapausing eggs or larval stages of insects and freshwater crustaceans. Because they are difficult to census accurately, these stages are typically ignored in population counts, but as a result the counts may not represent a constant fraction of the total population. For example, when the number of above-ground individuals in a plant population is zero, total population size is not necessarily zero, as some individuals may remain in the seed bank. If the subpopulation in the seed bank is more buffered from environmentally-driven fluctuations than is the above-ground population (as is likely to be the case in environments that favor the evolution of dormant life stages in the first place), then extinction times estimated from the above-ground population alone may underestimate the true value for the entire population, and thus provide a (potentially highly) pessimistic measure of population viability. For organisms such as desert annual plants in which a large and persistent fraction of the population

is likely to go uncensused, the method of Dennis et al. is probably not an appropriate way to estimate extinction risk.

In Assumption 2 (Box 3.4), observation error is the failure to count accurately the true number of individuals in a population at any one time. Observation error can be caused by a host of factors, such as complex background vegetation that makes some individuals difficult to detect, multiple counts of the same individual for mobile organisms (or by different members of the census team), incorrect species identification, or sampling variation introduced when a partial census (e.g. quadrat or transect sampling) is use to infer total population size or when indirect measures of abundance (e.g. scat, tracks or hair snags) are used. Such errors will lead to a pessimistic measure of viability over the short term, because they will cause the estimated value of σ^2 to be an overestimate of the true environmentally-driven component of variation in the counts, and a higher σ^2 predicts a greater likelihood of extinction over short times (see FIG. 3.7C). Repeated sampling of the same area (see Chapter 6 of this handbook) and "ground-truthing" indirect measures of abundance are two ways to estimate the magnitude of observation errors. We must also be aware of the fact that short sequences of counts will tend to misrepresent the true environmental component of variability, because they will tend not to include extreme values.

One violation of the assumptions that will cause viability estimates to be optimistic is the existence of intermittent catastrophes (Assumption 3), such as rare ice storms, droughts, severe fires, etc., which introduce the possibility of sudden declines in abundance not accounted for in our estimate of σ^2. More detailed methods have been developed to include catastrophes in estimates of time to extinction (see the methods of Mangel and Tier 1993 and Ludwig 1996, which also allow density dependence; see below). However, with most short-term count data, we

will lack sufficient information to estimate the frequency and severity of rare catastrophes, information that more detailed methods require if they are to provide more accurate assessments of extinction time. Thus in practice, we may need to be content with the statement that if catastrophes do indeed occur, our assessments of extinction risk based upon short-term census data will likely underestimate the true risk. If catastrophes do occur but with similar intensity and frequency across multiple EOs, we can still use the method of Dennis et al. to assess *relative* viability. Of course the converse, failure to account for rare good years, will have a pessimistic effect on the estimated extinction risk.

The ways in which density dependence (i.e., the tendency for population growth rate to change as density changes; see Assumption 4) may alter our estimates of extinction risk are more complex. A decline in the population growth rate as density increases will tend to keep the population at or below a carrying capacity. Unlike the predictions of the geometric growth model upon which the viability measures of Dennis et al. are based, such regulated populations cannot grow indefinitely, and the probability of ultimate extinction is always 1 (although the time to extinction may be extremely long). On the other hand, declining populations may receive a boost as density decreases and resources become more abundant; because estimates of μ based upon counts taken during the decline do not account for this effect, they may result in pessimistic estimates of extinction risk. Finally, the opposite effect may occur if a decline in density leads to difficulties in mate finding or predator defense and a consequent *reduction* in population growth rate. The downward spiral created by these so-called "Allee effects" results in extinction risks that become greater and greater as the population declines, and causes estimates of extinction risk made by ignoring these effects to be overly optimistic.

As with catastrophes, including density dependence in viability assessments will generally require more data, but there are ways to do so. Statistical methods developed by Pollard et al. (1987) and by Dennis and Taper (1994) allow one to test whether the counts show any evidence of density dependence (but see Shenk et al. 1998). If the population growth rate does depend upon density, density-dependent versions of the geometric growth equation 3.1 can be fit to the count data, using nonlinear rather than linear regression techniques (Middleton and Nisbet 1997). However, it is an inescapable fact that, because density-dependent models require us to estimate at least three parameters (for example, the carrying capacity in addition to μ and σ^2), they will require more censuses to achieve a similar degree of estimation accuracy. In addition, for most density-dependent population growth models, there are no simple mathematical formulae for extinction probability or time to extinction, and we must rely upon computer simulations to calculate them (for example, see Ludwig 1996 and Middleton and Nisbet 1997). One exception that has received a great deal of attention from theoretical population biologists is a model in which the population grows exponentially up to a ceiling, above which it cannot go. In this case, mathematical formulae for the mean time to extinction have been derived by several authors (Box 3.5). Examining the relationship between time to extinction and the "height" of the population ceiling provides a way to ask how the maximum population size a particular EO will support should influence its rank (Box 3.5).

Summary and Conclusions: Prospects for Using Count Data to Perform Population Viability Analyses:

In summary, the procedure we have described above provides a straightforward method to obtain quantitative measures of population viability using data from a series of population

censuses. The principal advantage of the method is its simplicity, in terms of both its data requirements and the ease of calculating viability measures. Other than simply recording the presence or absence of a species, population censuses are likely to be the simplest way that field biologists can collect data. However, to apply the methods described above, censuses must be conducted over a reasonable number of years. *We recommend that ten censuses should be viewed as an absolute minimum when applying this method, and more would be preferable* (see Chapter 7). But when an adequate number of censuses are available, both the linear regression and the calculation of viability measures such as the extinction time CDF can be performed in short order using software available on almost any desktop computer.

Users of count-based PVA need to be aware of its limitations when the underlying assumptions (Box 3.4) are violated. Because of these limitations, the method we have presented here is not a panacea for making conservation decisions in a world of sparse data, but neither are these limitations a fatal flaw that renders the method unusable. We reiterate that because the assumptions are explicit, the exercise of calculating the extinction time CDF (for example) is still useful, because we will often be able to gauge in which direction our estimate is in error (something which cannot always be said about viability measures obtained in other ways, such as through expert opinion). Moreover, if we know that a particular factor (such as density dependence in the population growth rate) has been omitted in a consistent way across multiple PVAs, they may still provide us with useful guidance about how risks are likely to differ among species or EOs. In essence, we argue that count-based PVA is best viewed as a tool that provides us with *relative* measures of the "health" of two or more populations, measures that decision-making agendas such as ecoregional planning require us to make. That is, while we would not put much credence in a particular numerical value of a viability measure (for example, the

estimated median time to extinction for the lesser prairie chicken population of 22 years (Fig. 3.6)), we can be more comfortable accepting that median extinction time estimates of, for example, 100 and 500 years for two EOs warn us of potentially real differences in the viability of those populations. Assessing the reliability of viability measures when the underlying assumptions of the method are violated is currently an area of active research in population biology. But at the present time, we believe it would be a shame not to make use both of the available data (e.g. FIG 2.1) and of the simple tools at hand to bring some quantitative rigor to the process of determining the relative ranks of multiple occurrences of rare and unique species.

- -

BOX 3.1 (Optional): Probability Distributions Describing Population Size in a Randomly Varying Environment

We saw in FIG. 3.2b that possible realizations of population growth in a stochastic environment become skewed, with a few high-abundance realizations outweighed by a large number of low-abundance realizations. If we were to simulate a large number of such realizations and then divide them into abundance "bins" at several different times, we would get the following sequence of histograms (FIG. 3.3), which clearly shows the skewness in population abundance. Note that with the passage of time, both the average value and the degree of spread in these histograms increases. If we make the size of the "bins" smaller and smaller, the histograms in Fig. 3.3 will come to resemble the skewed probability distribution known as the log-normal. If abundance has a log-normal distribution, then the natural log of abundance will have a normal distribution, whose mean and variance will also change over time (FIG. 3.4). Measures of population viability are derived directly from this shifting normal distribution. For example, the probability that the population lies below the threshold at a certain time is simply the area under the normal distribution below the threshold (shown in red in FIG. 3.4). The time until the threshold is first attained is also determined by the normal distribution (see Box 3.3). The shifting normal distribution is completely described by two parameters. The parameter μ determines how quickly the mean increases (if μ is greater than zero, FIG. 3.4a) or decreases (if μ is less than zero, FIG. 3.4b). The second parameter, σ^2, determines how quickly the variance in the normal distribution increases. Clearly if μ is less than zero, extinction is certain, but even if μ is positive (i.e. the population is expected to grow on average), there will be some chance

that the population falls below the threshold, particularly if the variance increases rapidly (i.e. if σ^2 is large). Thus to measure a population's risk of extinction, we must know the values of both μ and σ^2.

BOX 3.2 (Key): Estimating Useful Parameters from a Series of Population Censuses

Dennis et al. (1991) outlined the following simple method to estimate the parameters μ and σ^2 from a series of counts from a population:

- First, choose pairs of counts N(i) and N(j) from adjacent censuses i and j performed in years t(i) and t(j).

- Second, calculate the transformed variables $x = \sqrt{t(j) - t(i)}$ and

  $y = \ln\left(N(j)/N(i)\right)\Big/\sqrt{t(j) - t(i)} = \ln\left(N(j)/N(i)\right)/x$ for each pair.

- Third, use all the resulting pairs of x and y to perform a linear regression of y on x, *forcing the regression line to have a y-intercept of zero* (FIG. 3.5).

The slope of the resulting regression line is an estimate of the parameter μ. The mean squared error, which can be read from the Analysis of Variance table associated with the regression, is an estimate of the parameter σ^2.

As an illustration of the method, the following data were collected in a monitoring study of the federally-listed Knowlton's cactus (*Pediocactus knowltonii*) made over 11 years by R.L. Sivinski at its only known location in San Juan County, New Mexico (see Fig. 3.1A). The data are summed counts of the number of individual plants in ten permanent 10 square meter plots (an eleventh plot was omitted because all the individuals were removed in 1996 by cactus poachers!). The transformed variables x and y are also shown. Note that an advantage of the Dennis et al. method is that it does not require that censuses be performed year after year without fail. For example, monitoring of Knowlton's cactus was incomplete in 1989, and omitting that

census results in adjacent counts in 1988 and 1990 that are 2 years apart. We simply use an x

value of $\sqrt{2} = 1.414$ and a y value of $\ln(340/248)/\sqrt{2}$ for that pair of counts in the regression.

Year	$x = \sqrt{t(j) - t(i)}$	Count	$y = \ln(N(j)/N(i))/x$
1986		231	
1987	Sqrt(1987-1986) = 1	244	ln(244/231)/1 = 0.054751
1988	1	248	0.016261
1990	1.414	340	0.223104
1991	1	331	-0.02683
1992	1	350	0.055815
1993	1	370	0.05557
1994	1	411	0.10509
1995	1	382	-0.07317
1996	1	278	-0.3178
1997	1	323	0.150031

Once x and y have been calculated, the linear regression can be performed by any

statistical package or even by basic spreadsheet programs. The following output was produced

using Microsoft Excel (with the Analysis Toolpak installed) to perform a linear regression on the

transformed Knowlton's cactus data above (and forcing the y-intercept to be zero by checking

the "**Constant is Zero**" option in the Regression window):

ANOVA

	df	SS	MS	F	Significance F
Regression	1	0.00432	0.00432032	0.20502671	0.662721138
Residual	9	0.189648	0.021072		
Total	10	0.193968			

Red

	Coefficients	Standard Error	t Stat	P-value	Lower 95%	Upper 95%
Intercept	0.00000	#N/A	#N/A	#N/A	#N/A	#N/A
X Variable 1	0.03048	0.04377	0.69631	0.50382	-0.06853	0.12949

```
┌─────────┐ ┌────────┐
│  Green  │ │  Blue  │
└─────────┘ └────────┘
```

First check to see that the number highlighted in green is zero; if not, you failed to check the

"**Constant is Zero**" box, and must redo the regression. The number highlighted in blue is the

slope of the linear regression, which provides an estimate of the parameter μ. The number in red

in the ANOVA table is the mean squared error, which is an estimate of σ^2. For Knowlton's

cactus, these estimates indicate that μ is positive and σ^2 is less than μ, as is expected given that

the counts show an increasing trend without a great deal of inter-annual variability (Fig. 3.1A).

In contrast, the estimated μ and σ^2 for the lesser prairie chicken (Fig. 3.1E) are –0.106 and 0.097,

respectively; the negative value of μ reflects the sharp decline of this population.

Note that the last column of the ANOVA table above indicates that this is a non-

significant regression ($p>0.05$). This should not deter us from using our estimated μ and σ^2 to

calculate viability measures; we are using linear regression here to find the best-fit values of the

parameters given the data, not to statistically test any particular hypotheses.

Regression methods also allow one to detect outliers (years of unusually high population

growth or unusually steep decline) in the count data. If these outliers coincide with events such

as a change in the census protocol or one-time human impacts (e.g. oilspills) that are unlikely to

recur, we may wish to omit them when estimating μ and σ^2. One can also test statistically

whether μ and σ^2 differed before and after a management strategy was instituted or a permanent

change in the environment took place. Interested reader should consult Dennis et al. (1991).

BOX 3.3 (Key): Measures of Viability Based on the Parameters μ and σ^2

Once the procedure outlined in Box 3.2 has been performed to estimate the parameters μ and σ^2,

a suite of measures describing the population's growth and risk of extinction can be calculated

(Dennis et al. 1991). In this box, we show how to calculate four of these measures that are either

the most commonly used or the most informative. To make these calculations easier, we give

protocols to perform them using Microsoft Excel (readers interested in the original mathematical

formulae should consult Dennis et al. 1991). An Excel spreadsheet that calculates these

measures and others given by Dennis et al. (1991) can be obtained by contacting W.F. Morris.

1) The Average Population Growth Rate, $\overline{\lambda}$:

The average population growth rate $\overline{\lambda}$ is simply the base of natural logarithms, e, raised to the

power $\mu + \frac{1}{2} \sigma^2$. To calculate $\overline{\lambda}$, its continuous-time analog $\overline{r}$, and their approximate 95%

confidence intervals using Excel, follow these steps:

1) In cells **E3** and **E4** of an Excel worksheet, enter the duration of the counts in years (i.e. the

year of the last count minus the year of the first count) and the total number of inter-census

intervals (the number of counts minus one), respectively. Note that these numbers will not be

equal if censuses were not performed in some years; for example, for Knowlton's cactus (Box

3.2), these numbers are 11 and 10.

2) In cells **E5** and **E8**, enter the estimated values of μ and σ^2, respectively.

3) Enter the following formulae in the appropriate cells, which will yield the measures indicated:

Measure:	Cell:	Excel Formula:
Continuous rate of increase, $\bar{r}$:	**E12**	**=E5 + E8/2**
Lower 95% confidence limit for $\bar{r}$:	**E13**	**=E12 + NORMSINV(0.025) * SQRT(E8*((1/E3)+(E8/(2*(E4-1)))))**
Upper 95% confidence limit for $\bar{r}$:	**E14**	**=E12 - NORMSINV(0.025) * SQRT(E8*((1/E3)+(E8/(2*(E4-1)))))**
Average finite rate of increase, $\bar{\lambda}$:	**E15**	**=EXP(E12)**
Approximate lower 95% confidence limit for $\bar{\lambda}$	**E16**	**=EXP(E13)**
Approximate upper 95% confidence limit for $\bar{\lambda}$	**E17**	**=EXP(E14)**

For Knowlton's cactus (Box 3.6, Fig. 3.1A), the estimated average population growth rate $\bar{\lambda}$ is 1.04 with a 95% confidence of 0.96 to 1.14. Thus while the best estimate indicates the average of the possible population realizations will grow, the data do not allow us to rule out the possibility of a decline.

2) The Probability of the Population Reaching a Lower Extinction Threshold:

If μ is negative, then all population realizations will decline eventually, and the probability is 1 that any threshold lower than the current population size will eventually be reached (i.e. extinction is certain to occur). However, even if μ is positive, an extinction threshold may nevertheless be reached owing to the chance occurrence of a sequence of bad years (see Box 3.1). To calculate the probability of ultimate extinction, make the following additions to worksheet you began above:

1) In cell **E11**, enter the formula **=(E4-1)*E8/E4**, which will calculate a slightly different estimate of σ^2 to be used in subsequent calculations.

2) In cells **E19** and **E20**, enter the current population size and the extinction threshold, respectively.

3) Calculate the probability that the extinction threshold is eventually reached by entering the formula **=IF(E5<0,1,(E20/E19)^(2*E5/E11))** in cell **E22**.

For Knowlton's cactus, the estimate of μ is positive (Box 3.2), and using a current population size of 323 (the size of the last count taken) and an extinction threshold of 10 plants, the estimated probability of ultimate extinction is only 0.000014. Thus the available data suggest that the risk of extinction faced by the only known population of this cactus is not very great (provided that poaching can be prevented). In contrast, the lesser prairie chicken population in Fig. 3.1E (for which the estimated μ is negative; see Box 3.2) has an ultimate extinction probability of 1.

3) The Mean Time to Extinction:

The mean time to extinction given that the extinction threshold is reached (which is *not* certain to occur if μ is greater than zero; see Section 2 in this Box) is simply the difference between the natural logs of the initial population size and the extinction threshold, divided by the absolute value of μ. It is easily calculated by adding the following elements to the Excel worksheet begun above:

1) Enter the formula **=LN(E19/E20)** in cell **E21**. Cell **E21** will now contain the difference between the natural logarithms of the initial and threshold population sizes.

2) Enter the formula **=E21/ABS(E5)** in cell **E23**, which will then contain the mean time to extinction. Incidentally, entering the formulae **=IF(E23+NORMSINV(0.025)**

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*SQRT((E21^2)*E$11/((E5^4)*E3))<0,0,(E23+NORMSINV(0.025)*SQRT((E21^2)*E11/((

E5^4)*E3)))) and =E23-NORMSINV(0.025)*SQRT((E21^2)

*E11/((E5^4)*E3)) in cells **E24** and **E25** will yield the lower and upper 95% confidence limits

for the mean time to extinction, respectively.

For Knowlton's cactus, the mean time required for the census counts to decline from 323

to 10 plants is 114 years. But remember, this calculation only applies to those realizations of

population growth that eventually reach the extinction threshold; our calculation of the

probability of ultimate extinction in Section 2 of this Box indicates that the estimated mean time

to extinction will apply to only a small fraction of all possible realizations (about one in

100,000). For this reason, we suggest that *the mean time to extinction should only be used as a*

measure of extinction risk when the estimate of μ is negative (because only then does it apply to

every population realization). One such example is the lesser prairie chicken (Fig. 3.1E). The

mean time to an extinction threshold of 10 individuals for this sharply declining population is

only 32.1 years, indicating not only that ultimate extinction is a certainty (see Section 2 above),

but that the extinction threshold is likely to be reached quite soon.

Due to skewness in population size (Fig. 3.3), the confidence interval for the mean time

to extinction is usually large; for the lesser prairie chicken, it ranges from 0 to 77 years.

4) The Cumulative Distribution Function (CDF) for the Conditional Time to Extinction:

Next, we can extend our Excel worksheet to calculate the conditional extinction time CDF given

that the extinction threshold will be attained. The extinction time CDF gives the probability,

considering only those realizations of population change that ultimately fall below the extinction

threshold, that the threshold has already been reached at a given time. Hence as with the mean

time to extinction, the extinction time CDF applies to all realizations if μ<0, but to only a subset

of realizations if μ>0. To calculate it, we use the standard normal cumulative distribution

function NORMSDIST provided by Excel:

1) Fill column **B** downward from cell **B31** with a series of times at which you wish to compute

the CDF. For most purposes, every 5 years from 5 to 1000 years is adequate (the sequence

"Edit-Fill-Series" from the pull-down menu will allow you to accomplish this easily).

2) In cell **D31**, enter the following formula:

=NORMSDIST((-E21+ABS(E5)*$B31)/SQRT($E$11*$B31))

+EXP(2*E21*ABS(E5)/E11)*NORMSDIST((-E21-

ABS(E5)*$B31)/SQRT($E$11*$B31)). Now select cell **D31**, drag downward to the row

corresponding with the last entry in Column B that you created in step 2, and then type Ctrl-D;

column **D** will now be filled with the values of the CDF that correspond to the times in Column

B. You can treat these 2 columns as a table in which you can look up values of the CDF at

different times, or you can use Excel to create a graph of the CDF versus time (for example, Fig.

3.6 shows a graph of the CDF for the lesser prairie chicken, and indicates how several measures

of population viability (including the median time to extinction) can be read from the graph).

5) *Using the Extinction Time CDF When μ is Positive:*

When μ is positive, the extinction time CDF must be interpreted with caution, *because it does*

not apply to all population realizations (only to those that will eventually reach the extinction

threshold). For example, the median time to extinction from the CDF (not shown) for the

Knowlton's cactus population in Fig. 3.1A is 105 years (using a current population size of 323

and an extinction threshold of 10 plants). This does NOT mean that half of all realizations will

have reached the extinction threshold by 105 years, but instead that *half of the realizations that*

will eventually hit the threshold (which represent only about 1 in 100,000 possible realizations)

will have done so by 105 years. Given the positive value of μ, the underlying population model

predicts that the remaining 99,999 of 100,000 realizations will NEVER hit the extinction

threshold. Nevertheless, the conditional extinction time CDF is still valuable even when μ is

positive, for the following reason. We can calculate the *total probability* that the population has

gone extinct by a given future time horizon, *accounting for ALL possible realizations*, if we

calculate both the probability that the extinction threshold is reached eventually (see Section 2 of

this Box) and the conditional extinction time CDF. The total probability that extinction occurs

by, say, 100 years is the probability that extinction will occur eventually multiplied by the

conditional probability that extinction will have occurred by 100 years *given that it will occur*

eventually, which is precisely what the conditional extinction time CDF tells us. For Knowlton's

cactus, the value of the CDF at 100 years is 0.455, so the total probability of reaching an

extinction threshold of 10 plants by 100 years is 0.000014 (see Section 2 above) multiplied by

0.455, or 0.0000064, a rather small number. By performing a calculation such as this, we could

compare the relative viabilities of two populations, one with postive and one with negative μ,

whereas it would be inappropriate to compare directly the CDFs of the two populations.

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BOX 3.4 (Key): Assumptions of PVA Using the Method of Dennis et al.

1) The data represent exhaustive counts of individuals in the population, estimates of total

population size, or counts of a subset of the individuals (e.g. adult females, individuals in

quadrats that sample a constant proportion of the area occupied by the population, etc.)

comprising a fraction of the entire population that does not change over time.

2) The year-to-year variation in the counts reflects the true magnitude of environmentally-driven

variation. We must have performed censuses in a sufficient number of years to accurately assess

the year-to-year variation in the population growth rate. Furthermore, the variation in the counts

must not be due primarily to observation error in estimating population size each year.

3) Inter-annual environmentally-driven variation is not extreme. In particular, we assume there

are no large-magnitude fluctuations caused by extreme catastrophes or unusually good years.

4) The population growth rate is not affected by density, and thus does not change as the

population increases or decreases.

_____

**BOX 3.5 (Optional): Density-Dependent Models**

When a population's growth rate declines with increasing density, the population will not

continue to grow exponentially, but will typically approach a carrying capacity, usually denoted

K. A mathematically simple way to approximate this effect is to allow the population to grow

exponentially until it reaches K, when further population growth ceases. This model of

"exponential growth up to a ceiling" allows us to ask how the mean time to extinction of a

population currently at the ceiling increases as the ceiling itself increases. Because the "height"

of the ceiling will be determined by the amount of habitat available to the population, this is

another way of asking how the spatial extent of an EO will influence population viability.

Approximate formulae for relationship between the mean time to extinction and the height of the

population ceiling have been derived by several authors, including Lande (1993), Foley (1994),

and Middleton et al. (1995).

Here we give a brief overview of the results of Lande (1993). When the parameter μ is

positive, the mean of the normal distribution of the log of population size will increase over time

(FIG. 3.4); that is, most population realizations will grow. Nevertheless, some realizations will

fall below the extinction threshold, and this outcome will be more likely if σ^2 is large. In fact,

the magnitude of the environmentally-driven variation in the population growth rate, as

embodied by the parameter σ^2, will have a pervasive effect on how the extinction time depends

on the height of the population ceiling, K. Lande showed that if μ is positive and the ceiling is

sufficiently high, the mean time to extinction will be approximately proportional to $K^{2\mu/\sigma^2}$. The

ratio of μ to σ^2 thus determines the shape of the relationship between the mean time to extinction

and the population ceiling (FIG. 3.8). If σ^2 is small relative to μ (i.e. less than 2μ), the extinction

time increases faster than linearly as the ceiling is increased; increasing σ^2 until it equals and then surpasses 2μ will cause the scaling of extinction time vs height of the ceiling to become linear and then less-than-linear. Thus if environmental variability is high, we may face a law of diminishing returns; by increasing the ceiling (for example by increasing the amount of habitat available to the population), we may gain a disproportionately small increase in the mean time to extinction. *The important conservation message is that highly variable populations will continue to be prone to rapid extinction caused by a chance sequence of bad years even when the maximum population size becomes large.* Thus even if we are unable to estimate K accurately, obtaining estimates of μ and σ^2 using the method of Dennis et al. (Box 3.2) may still give us generally useful information about how increasing the available habitat will buffer a population from extinction. Finally, if μ is negative (that is, the population declines over the long run), then the mean extinction time scales as the natural log of the population ceiling, which also increases in a less-than-linear fashion as the ceiling increases (FIG. 3.8). Useful approximations for the distribution of extinction times (not just the mean extinction time) as a function of the height of the ceiling were derived by Middleton et al. (1995).

FIG. 3.1: Examples of count data: A) Knowlton's cactus in New Mexico (data provided by R. Sivinski); B&C) Red-cockaded woodpecker in North Carolina and central Florida (data provided by J. Hardesty); D) Grizzly bears in the Greater Yellowstone Ecosystem (reproduced from Dennis et al. 1991); E) Lesser prairie chicken in Caprock Wildlife Management Area, NM (data provided by K. Johnson).
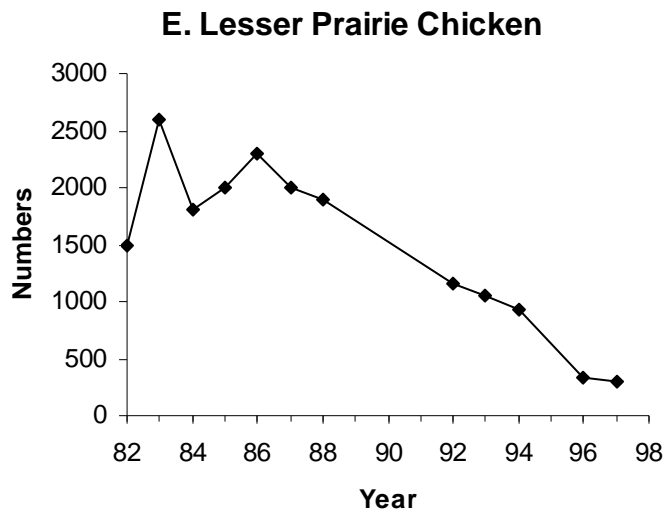

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E. Lesser Prairie Chicken
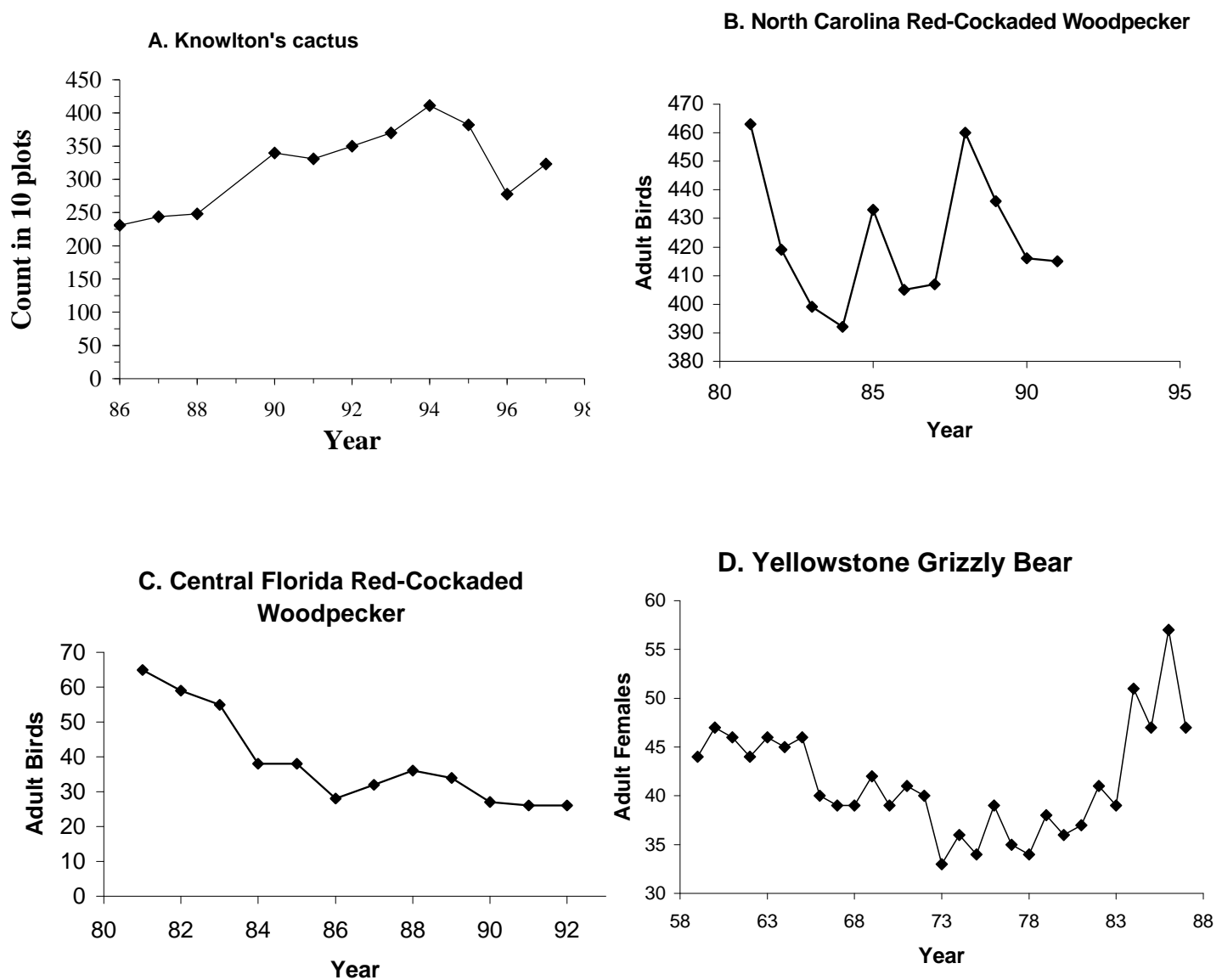
FIG. 3.2: Population growth described by a geometric growth model $N(t+1) = \lambda\, N(t)$ in (A) a constant or (B) a stochastically-varying environment.
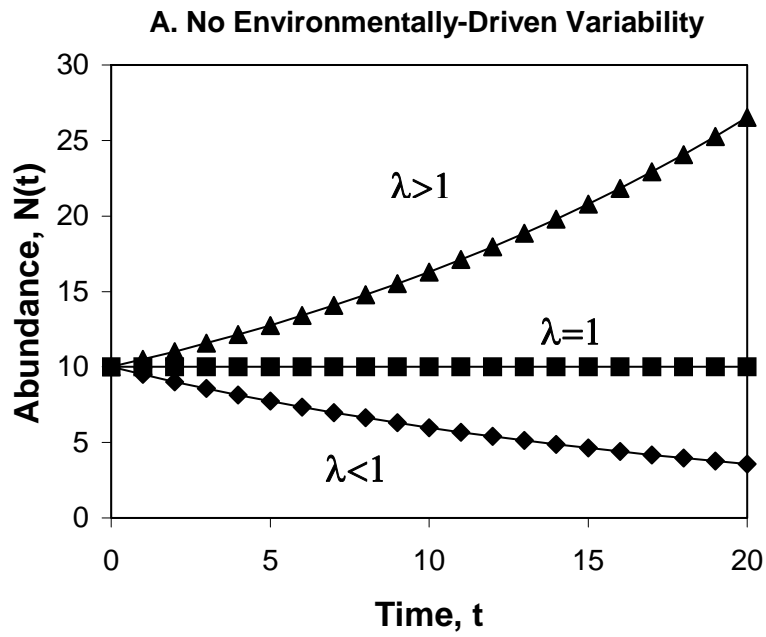
A. No Environmentally-Driven Variability

Fig. 3.2 (cont.)

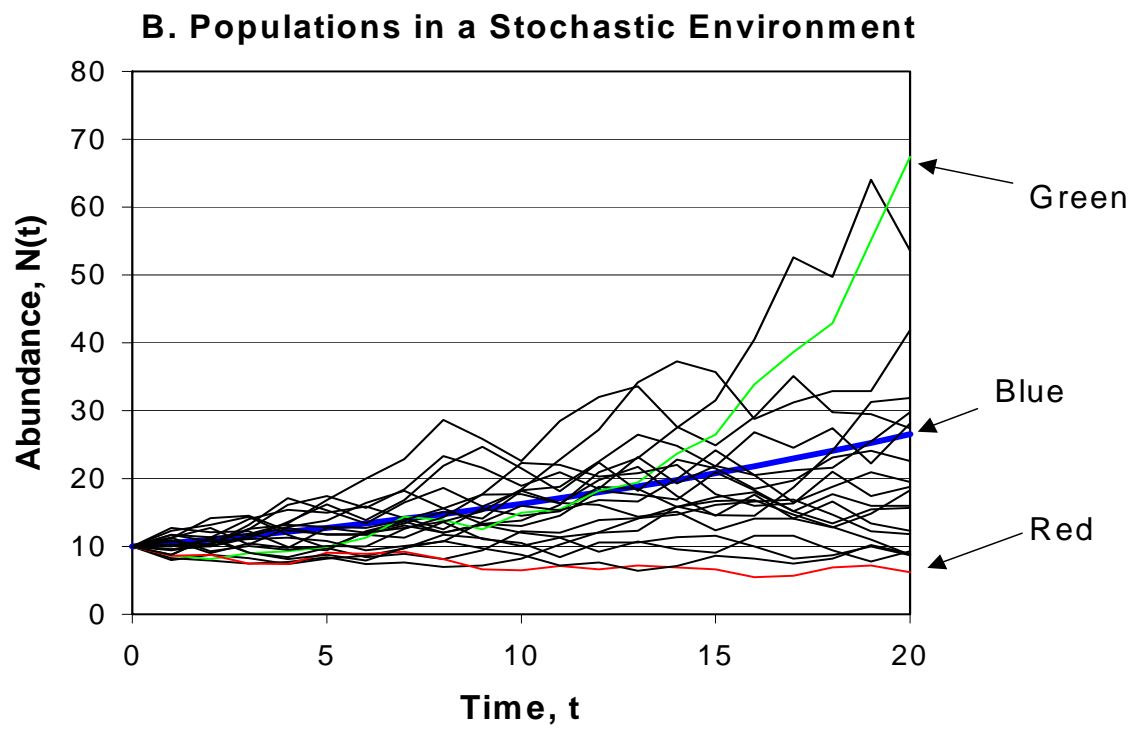**B. Populations in a Stochastic Environment**

FIG. 3.3: Log-normal distributions of abundance in a population growing exponentially in a stochastic environment.
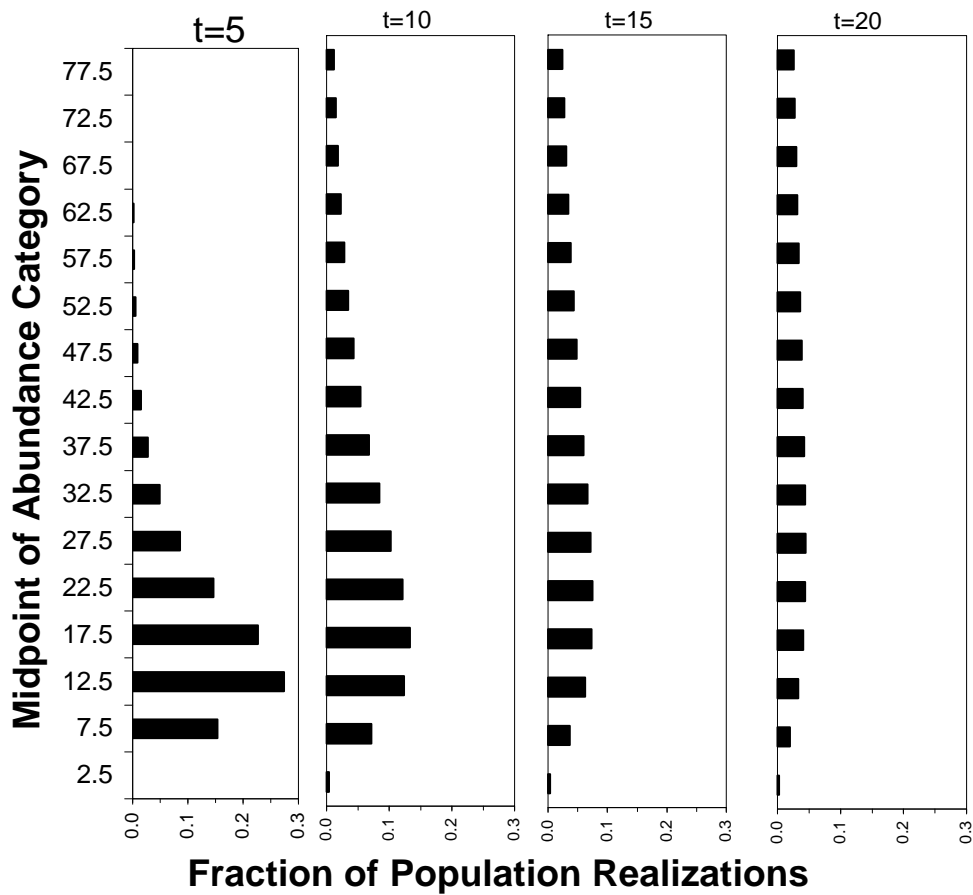
FIG. 3.4: Normal distributions of the log of population size, when the parameter μ is A) positive or B) negative. The size of the "red zone" gives the probability of extinction.

Log N(t)

A

Normal Distribution

σ^2

Initial Population Size

$\mu > 0$

Log N_0

Log N_e

Extinction Threshold

t_1 t_2 t_3 **t**

Red

Log N(t)

B

Log N_0
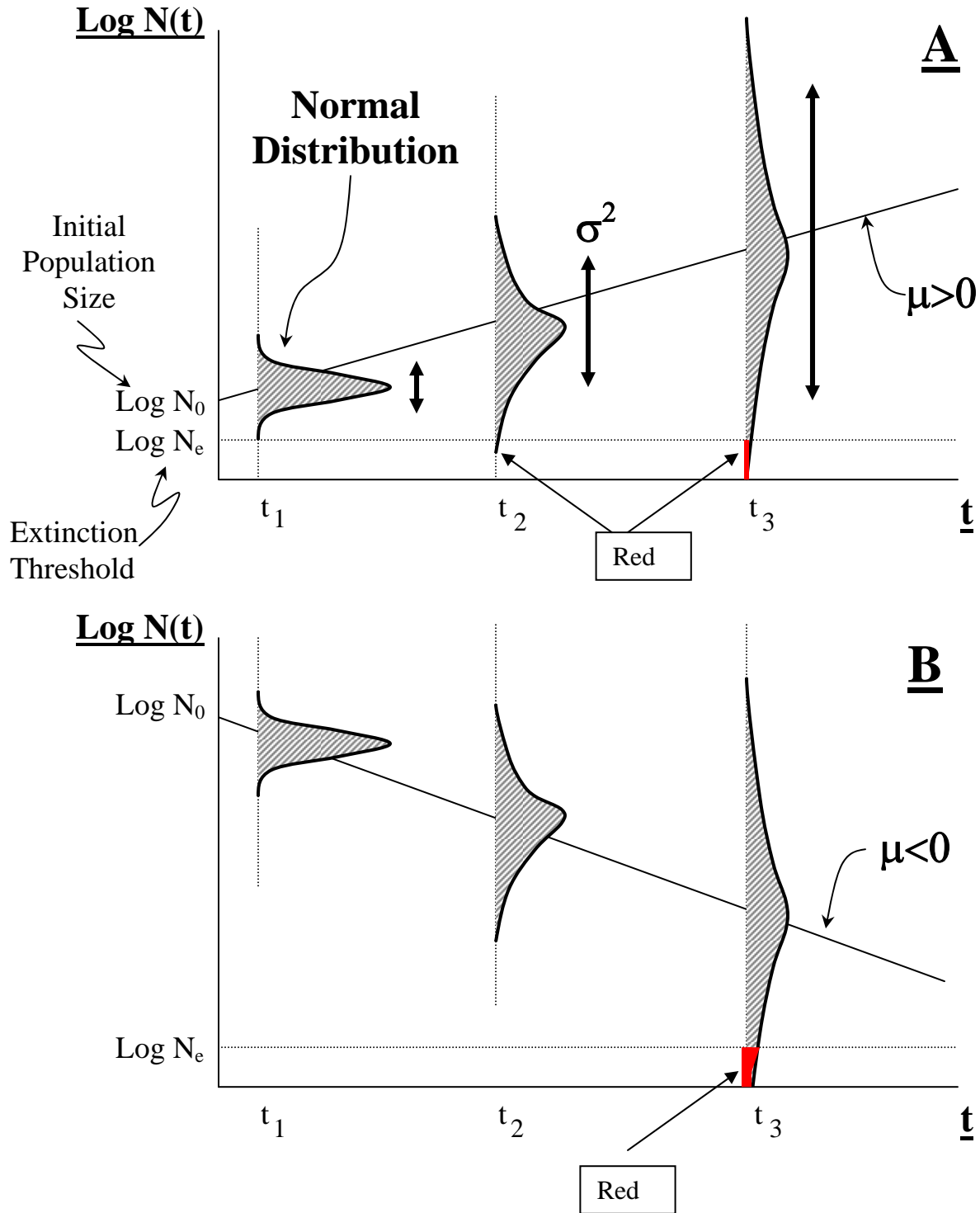
$\mu < 0$

Log N_e

t_1 t_2 t_3 **t**

Red

FIG. 3.5: The regression of y on x for the Knowlton's cactus data. The slope of the regression line is an estimate of μ, and the variance of the points around the line is an estimate of σ^2.
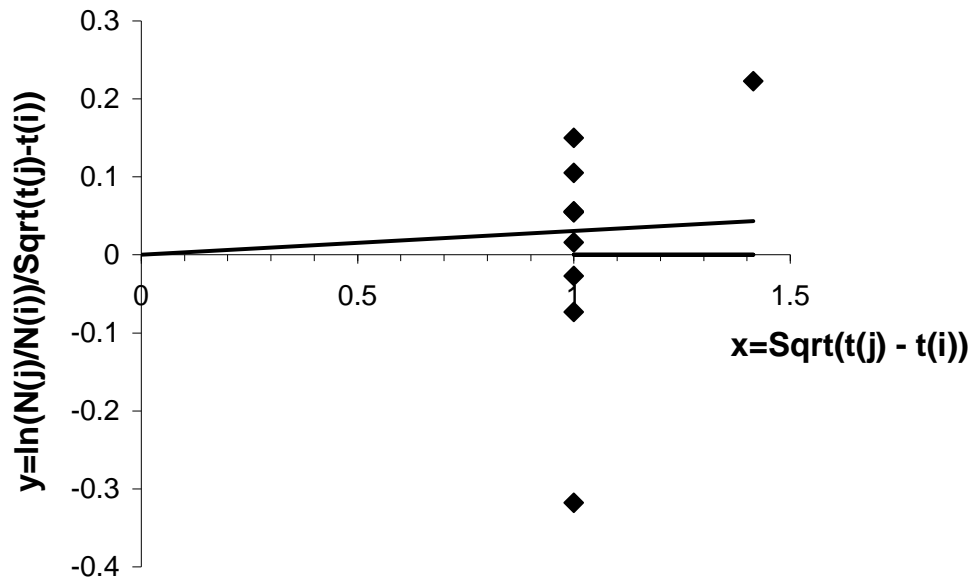
FIG. 3.6: The cumulative distribution function of extinction time for the lesser prairie chicken estimated from the data in Fig. 3.1E. Arrows indicate how the CDF can be used to calculate: A) the median time to extinction given that extinction occurs (note that the median, 29 years, is less than the mean time to extinction of 32.1 years); B) the probability of extinction by 100 years; and C) the number of years at which there is only a 5% chance of population persistence.

Lesser Prairie Chicken

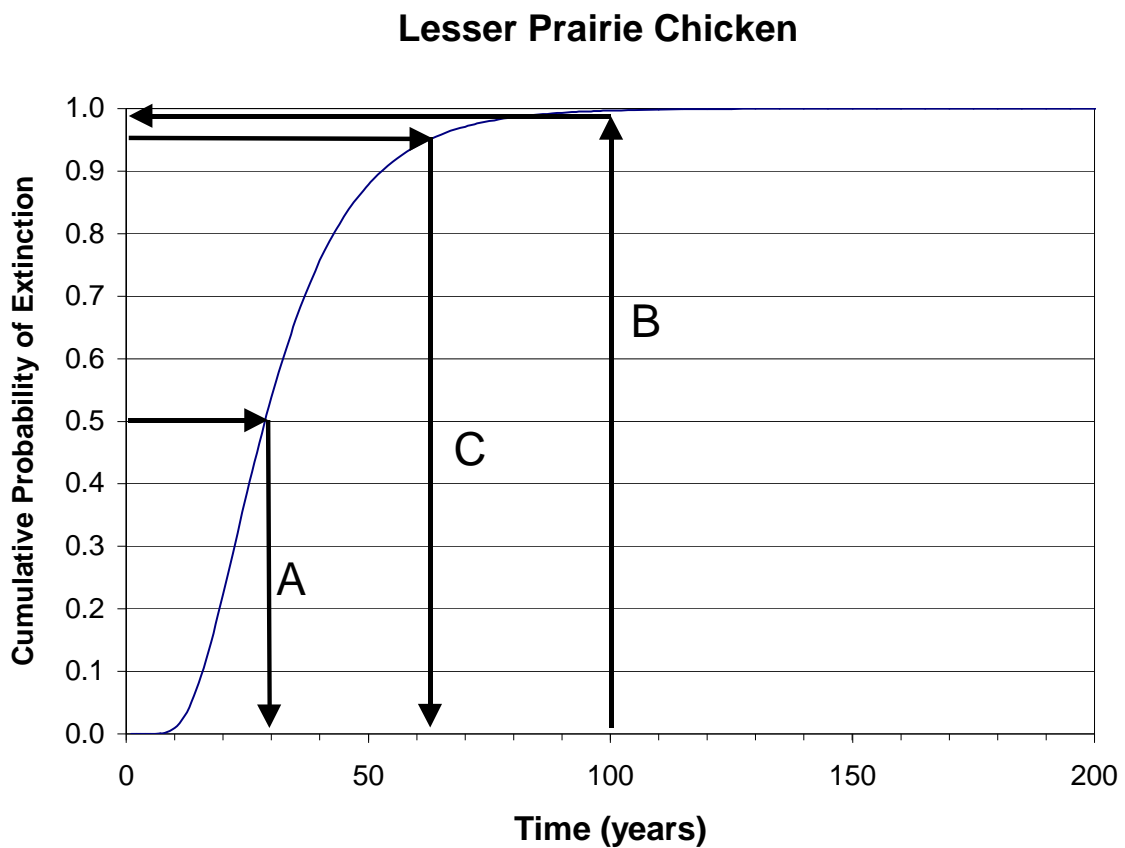FIG. 3.7: How to use the extinction time CDF in site-based and eco-regional planning. A) Comparing the CDF's for the two red-cockaded woodpecker populations in Fig. 3.1B,C (for both curves, initial population size equaled the last available count and the extinction threshold was 10 birds). B) CDF's for the Yellowstone grizzly bear (Fig. 3.1D) assuming initial population sizes of 10 or 47 females and an extinction threshold of 1 female; C) The effect of the variance parameter σ^2 on the CDF, using the data for the Yellowstone grizzly bear with the observed variance (σ^2=0.9) or one-half the observed variance (σ^2=0.45).

A. Red-Cockaded Woodpecker

FIG. 3.7 (cont).

B. Yellowstone Grizzly Bear

C. Yellowstone Grizzly Bear
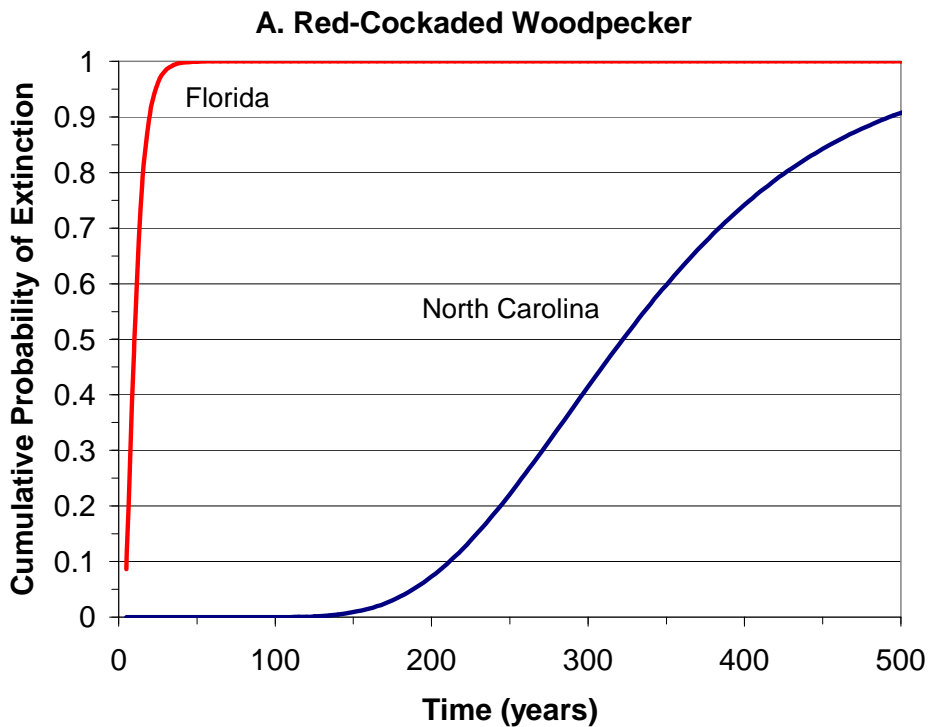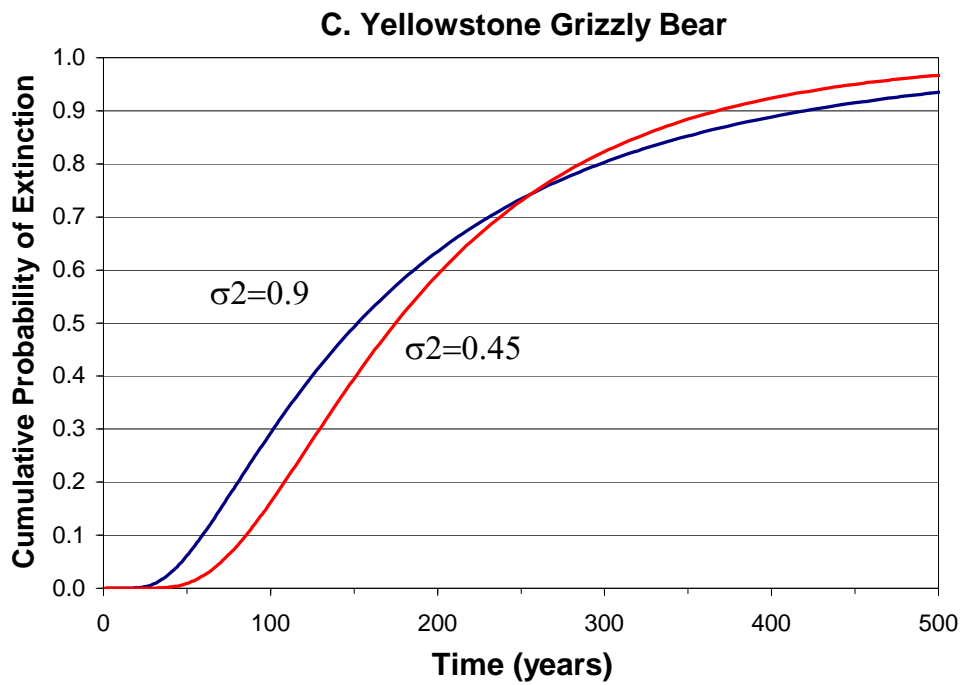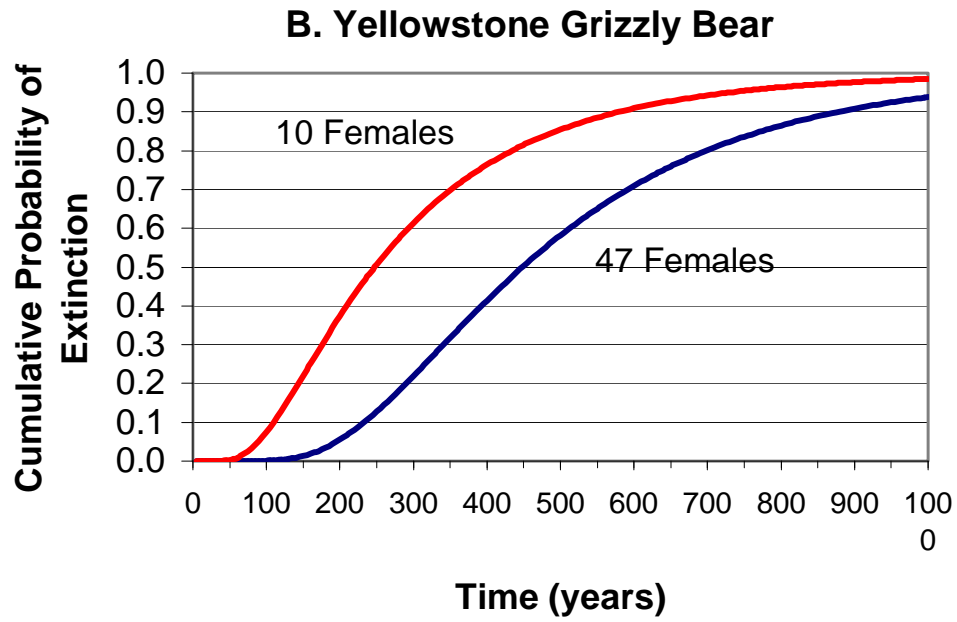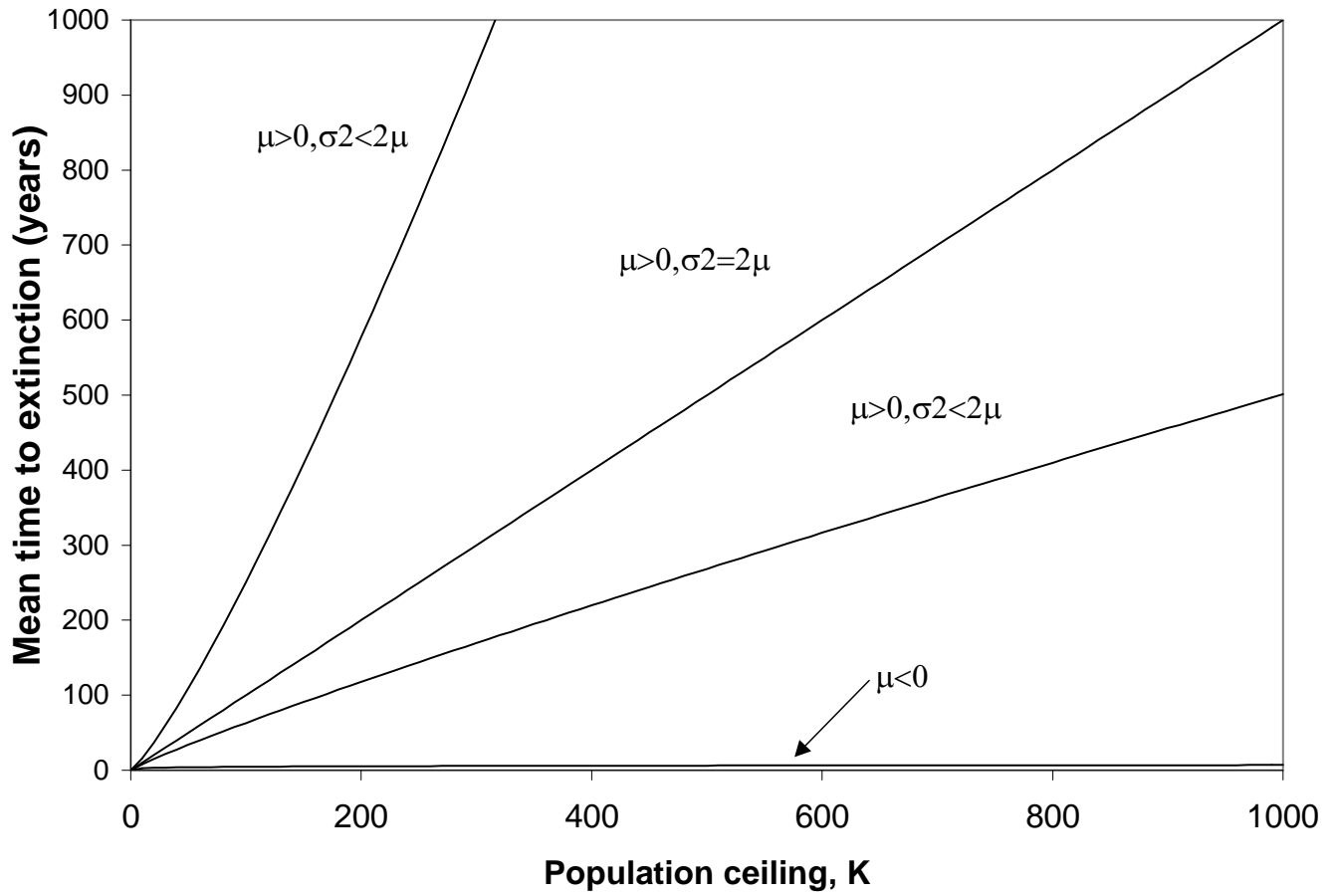
FIG. 3.8: The scaling of the mean time to extinction vs. the height of the population ceiling in a model of "exponential growth up to a ceiling" (after Lande 1993).

CHAPTER FOUR: PROJECTION MATRIX MODELS

While simple counts of the number of individuals in a population are more likely to be available (See Chapter 2, Fig. 2.1), for a few species of particular concern we may have access to detailed demographic information describing the rates of survival, reproduction, and growth of individuals that differ in size, age or other characteristics. Viability analyses that use such individual-based data most often rely upon population projection matrices. Matrix models predict long-term population growth rates, transient population dynamics, and probabilities of extinction over time. A basic requirement for constructing a projection matrix is that we must be able to classify individuals unambiguously into classes based on their age, size or life-history stage. We must then quantify the survival, growth, and reproduction of numerous individuals in each class over a minimum of 2 to 3 years, preferably longer. These data are used to calculate so-called "vital rates", or the class-specific annual rates of survival, growth and fecundity, as well as the degree of year-to-year variation in those rates. In turn, we use the vital rates to compute the entries in the projection matrix, which we then use to predict the likely future trajectory of the population and its risk of extinction.

Projection matrix models have three advantages over simpler models that track only the total number of individuals in a population, such as those we reviewed in Chapter 3. (The tradeoff that balances these advantages is that we require far more data to construct a projection matrix than we do to perform a count-based PVA.) First, projection matrices make it possible to assess the influence that the vital rates of particular classes have on the growth of the population as a whole. For example, it is possible in a matrix analysis to assess how much juvenile mortality (as distinct from the mortality of other life stages) drives population decline. In an analysis based on total population counts, we would not be able to discern whether juvenile mortality plays a role in the decline -- we would simply know that the population is declining. Yet if juvenile mortality is a key factor causing the decline, management efforts aimed at

improving juvenile survival should be more effective than efforts aimed at other vital rates or life stages.

A second advantage to a matrix model is that it may more accurately predict future population trends for a long-lived species that has undergone either recent changes in one or more vital rates (e.g. due to a novel human impact, or a recently-imposed management plan) or a perturbation in the population structure (i.e. the distribution of individuals among classes). For example, if the fecundity of adults suddenly drops, or if a large number of juveniles unexpectedly migrates from the population, counts of adults may show little change for several years, despite the fact that the adult population will certainly decline once the reduced juvenile cohort matures. Put another way, count data for long-lived species can reflect past conditions more than current ones. If recent changes in vital rates or population structure have occurred, more accurate predictions are possible with a matrix approach.

A third advantage of projection matrix models is that they are particularly well suited to evaluating management alternatives, provided demographic data from contrasting situations exist. For example, an experiment in which different management techniques are applied randomly to different plots or data from sites with different management histories would facilitate the construction of contrasting matrices for each management scenario. These matrices would serve to integrate the various effects of management on multiple vital rates into an overall effect on population growth. Moreover, manipulation of the parameters in matrix models allows one to perform computer "experiments" to predict the likely effects of proposed management practices. Importantly, these models can be informative about the magnitude of threats and the potential for improvements, and allow determination of how much effort will be necessary to rescue a declining population.

Like count-based models, projection matrix models can also be used to assess the relative viability of different EOs. The difficulty is that in order to do this, demographic data must be collected from several sites. Obviously, only very rarely will it be possible to undertake this type

of analysis, but at the end of this chapter we present one example of this comparative approach using a TNC data set for the rare plant *Aletes humilis*.

In this chapter, we describe the construction and analysis of projection matrix models, but we do not cover the topic comprehensively (thorough reviews are given by Caswell (1989) and Tuljapurkar and Caswell (1997)). There are a large number of complexities and nuances to this type of PVA; hence users would be well-advised to consult with a population modeller to go beyond the simpler uses of matrix models covered here. However, it is important to have an understanding of the principal issues in model construction and interpretation even if collaborating with a mathematical population biologist.

Constructing and using a projection matrix model

The most laborious and time-intensive step in matrix-based modeling is the collection of demographic data on known individuals over a number of years. The details of how to gather such data are well described in a variety of references (e.g. Southwood 1978, Krebs 1989), and we do not review them here. Instead, we describe in Box 4.1 the steps one must follow to use raw data on individuals to produce a projection matrix and to use the matrix to predict future population sizes. The basic steps are:

Step 1: Determine what feature of individuals (age, size, or life stage) best predicts differences in vital rates. Then divide the population into classes based upon the feature you have chosen.

Step 2: Use demographic data on known individuals to estimate the vital rates for each class, and use them to construct a population matrix, according to the rules specified in Box 4.1.

Step 3: Construct a population vector by specifying the initial number of individuals in each class in the population. A population vector is a list of the number of individuals in each class; the sum of the elements in the vector equals the total population size.

Step 4: Use the matrix and the population vector to project the population forward in time, thus predicting the future size of the population, the long-term population growth rate, λ, and the risk of future extinction. This step involves simple rules of linear algebra (Box 4.1, Step 4).

While these simple steps apply to any matrix-based PVA, there are a host of additional complexities that may be added to the models, and many additional analyses that could be performed. The most essential complexity to be included in a PVA, provided the data are available, is year-to-year variation in vital rates. We discuss this complexity in detail in the following section of this chapter. One additional analysis that is usually desirable is to perform "experiments" by looking at effects on λ and on extinction risk of altering matrix entries to reflect changes in the demographic rates of particular life stages resulting from differing forms of management. Often this is the most instructive step in using matrix models. After we review how to include stochastic variation into matrix models, we give an example of a matrix-based PVA using TNC data, illustrating how projection matrices can be used to explore management options.

Stochastic matrix models: incorporating variability and uncertainty

Matrix population models can be either deterministic (all vital rates are constants) or stochastic (vital rates vary over time). The long-term population growth rate in a matrix model is analogous to λ in the simple population growth model (see equation 3.1, Fig. 3.2). If environmental variation is low, or if we have no information regarding its magnitude, a deterministic matrix model is often used; in this case, the long-term population growth rate will be a constant. If environmental variation is incorporated into the model, then the annual change in population size will vary over some range of values, just as it does in the analysis of count data in Chapter 3. Projecting population growth in a stochastic matrix model involves the same rules of linear algebra as in Box 4.1; the only difference is that the matrix itself will vary from

year to year. In practice, stochastic matrix projections are usually performed with the aid of a computer. A number of PVA software packages (RAMAS, ALEX, Vortex, etc.) have been developed for this purpose (for a review of these packages, see Lindenmayer et al. 1995). The most commonly used way to present the results of stochastic simulations is to display both the average and the 95% confidence limits for a series of population realizations over some time interval of interest, say the next 20, 50 or 100 years (for example, see Fig 4.1; for methodology see Heyde & Cohen, 1985; Alvarez-Buylla & Slatkin, 1991). In this way, population size projections can be compared with new data from ongoing population censuses; deviations between actual and predicted trajectories would then suggest that changes in vital rates or population structure have occurred, or that there are errors in the model that need to be corrected.

In addition to projecting future population size, we can also use stochastic matrix models to quantify extinction risk. For a deterministic matrix model, only three outcomes are possible (stasis, growth to infinity or decline to extinction), just as in the simple geometric growth model of equation 3.1 (see Fig. 3.2). If the population is declining deterministically, it is a simple matter to project the population until the number of individuals falls below the threshold, thus determining the predicted time to extinction. For models that incorporate variation in vital rates, extinction is a stochastic event, and its probability will be related both to the average value of λ and to its variance. Just as in the simpler count models, when λ is more variable the risk of extinction tends to rise, even in populations whose average growth rate is greater than 1.

Most commonly, variability is added to a projection matrix in one of two ways: by constructing separate matrices that represent different environmental conditions (which we will call the "multiple matrices" approach) or by constructing a matrix whose entries are random variables (the "variable entries" approach). Below we briefly describe both approaches, and provide references to studies that have used each approach. Two studies that incorporated elements of both approaches addressed the viability and management of populations of endangered plants (Maschinski et al. 1997, Gross et al. 1998).

The multiple matrices approach involves constructing a separate matrix for each of several years of data, or from multiple situations, and then analyzing population trends based on either random draws or specified sequences of these matrices. For example, the extreme weather associated with El Niño events may be reflected in lower than average values for both survivorship and fecundity rates. Because of these concerted effects, we might best model this kind of variation by using two kinds of matrices, one for "normal" years, and another for El Niño years. Then, to build projections of the potential fate of the population, we could use the normal matrix as a default, and substitute the El Niño matrix at randomly chosen intervals that correspond to the typical frequency of El Niño events. Because the exact sequence of matrices used will differ among runs, it is necessary to repeat these simulations many times (at least 1000 runs is recommended, see Harris et al. 1987), and summarize the results of these runs in terms of the probable population trajectories, extinction risk, and population growth rate. This approach is also useful for modeling populations subject to periodic events such as controlled burns (Gross et al. 1998) or years of high rainfall that occur at regular intervals (Beissinger 1995); in this case, the sequence of matrices would be fixed, not random.

One limitation of the multiple matrices approach is that it captures only the specific relationships among vital rates that were observed in the years in which the demographic data were collected. For instance, in the example above, the specific combinations of values for survivorship and fecundity measured for El Niño and non-El Niño years will be the only combinations ever used to represent variation in environmental conditions. While the multiple matrices approach has the advantage that it does not stray beyond the observed data, it has the disadvantage that it thereby restricts (perhaps unrealistically) the possible combinations of vital rates that the stochastic model can generate. Using the multiple matrices approach is most appropriate when simulating the effect of discrete events (e.g., fires, hurricanes, floods, logging) on the population of interest, because such events typically result in large, strongly correlated changes in vital rates.

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The variable entries approach involves drawing each matrix element at random during each time step of the simulation. Unlike the multiple matrices approach in which a limited number of matrices are employed, the variable entries approach involves the assembly of a unique matrix at each time step, and thus explores a much wider range of combinations of vital rates than does the multiple matrices approach. As above, it is necessary to perform the simulation many times to account for variation among runs. PVAs employing the variable entries approach have been performed for desert tortoises (Doak et al. 1994) and northern spotted owls (Lamberson et al. 1992).

There are two ways that matrix entries can be drawn. First, each entry can be chosen at random from a list of discrete values, most likely those that were actually observed in the data set (note that individual entries are being drawn, not entire matrices as in the multiple matrices approach). Second, entries can be drawn from a continuous range of possible values specified by probability distributions whose means and variances are estimated from the demographic data. When using the second approach, we must first decide which of many probability distributions (e.g., uniform, normal, log normal, beta, gamma) to use. When insufficient data exist to clearly favor one probability distribution over others, one can explore several distributions in parallel models whose results are examined for shared predictions about extinction risk.

There is another major question that must be answered when building a stochastic matrix model: should we incorporate correlations in vital rates into the model? There are two types of correlation to consider: correlations among the different entries in the matrix, and correlations between the values of a single matrix entry in subsequent years. The first type of correlation arises because different vital rates will often change in a concerted fashion. For example, the fecundity values of *all* classes may increase in good years. Similarly, years of high survivorship may also be years of high fecundity, and thus survivorship values and fecundity values should be positively correlated. Furthermore, management efforts directed at a particular life stage may show correlated effects in multiple vital rates associated with that stage. Correlations among

vital rates will be automatically built in to the multiple matrices approach, but must be specified in the variable entries approach.

Correlation among the values of a single matrix entry can arise if the environment is correlated among years (e.g. good years may tend to be followed by good years). Environments may be periodic, having exceptional years (good or bad) occurring on a roughly predictable schedule (e.g., 10-year snowshoe hare cycles that affect food availability for predators such as lynx and owls). The decisions on whether and how to incorporate correlation structure into a model can have a large influence on predictions (Groom and Pascual 1998; for examples of how to include correlations among different matrix elements, see Doak et al. 1994 and Gross et al. 1998).

Before moving on to an example of a stochastic matrix model, we warn readers that ***extreme caution should be used in interpreting the results of stochastic matrix models that are based on only a few years of data***. With only 3 or 4 years of demographic data, it is unlikely that the true range of environmental conditions will have been observed, or an anomalous year will be included and given more weight than its actual prevalence in longer time series warrants. Such small samples of data also may show spurious correlations among vital rates (e.g., fecundity and subadult survival varying together by chance when in reality they are unrelated, or vice versa). Further, it is extremely difficult to identify a best-fit probability distribution for a particular vital rate when using small samples of data. It is preferable to work with at least 6-10 years of data, as we discussed in Chapter 3, and to be cautious in accepting results obtained with fewer years of data.

Population status of Aletes humilis*: an example based on real data*

Aletes humilis (Apiaceae) is a rare, endemic plant found in Larimer and Boulder counties, Colorado. The plant is an herbaceous perennial that most commonly inhabits crevices of north-facing granite cliffs, but is also found in some other habitats (Schulz & Carpenter, unpublished manuscript). The plant forms cushions 5-20 cm in diameter and rarely reaches more than 10 cm

in height. All populations of the plant are relatively small (50 to a few thousand individuals),
and patchily distributed (usually isolated from neighboring populations by several km), yet they
are composed mostly of reproductive adults.

The Nature Conservancy, concerned that this rare plant could slip into extinction, created
two small preserves for *A. humilis* at Phantom Canyon and Cap Rock in Larimer County. The
populations at Phantom Canyon and Cap Rock are small (roughly 1100 and 920 individuals
respectively), but appear to be relatively stable. At Phantom Canyon (elevation 6100-6600 ft),
an area of granitic outcrops typical of the species' habitat, the populations appear to be
constrained by their ability to disperse to empty "safe sites," cracks in the boulders with
sufficient soil. Once a plant colonizes a fissure in the rock, it typically grows rapidly to fill the
entire opening, and then remains at roughly this size until it dies. Thus, it is possible that in these
habitats, populations could be enhanced by distributing seeds to crevices. At Cap Rock
(elevation 7500 ft), however, the plant is found beneath ponderosa pine canopy, where its
recruitment may be inhibited by the thick layers of pine duff. Gopher disturbance may open sites
for *A. humilis* recruitment, although it can also harm established plants (Schulz & Carpenter, in
review).

Demographic data on *A. humilis* were collected on over 300 tagged individuals for 7
years at several sites within the Phantom Canyon Preserve and on 76 tagged plants for 5 years in
the Cap Rock Preserve (Schultz and Carpenter, unpublished data). Tagged plants were measured
each year (to obtain the two-dimensional area of each plant) and any fruiting was noted, as well
as any degeneration or death. Few seedlings were noted at either site, but those that appeared
were followed in a similar manner.

Constructing a population projection model from the demographic data collected by TNC
involves the steps outlined in Box 4.1. Based on the available data, a size-based model is most
appropriate. We do not know plant ages, and few discernable life stages are apparent for the
plant (although a very simple stage-based model with seeds, seedlings and adults would be
possible to construct). Division of the population into size classes makes sense only if the

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probability of surviving or reproducing differs according to size. Examination of the data on the tagged individuals revealed a few differences among the probabilities of survival and fruiting among individuals of different sizes. At Phantom Canyon, survivorship was lowest among the smallest individuals (2-4 cm^2 in area), low in somewhat larger individuals (4-50 cm^2), and highest in the largest individuals (>300 cm^2 in area).   Fruiting was rare in individuals smaller than 50 cm^2, moderate in individuals 50-100 cm^2, and highest in individuals >100 cm^2.   At Cap Rock, fewer obvious differences were apparent among individuals in different size classes, particularly among the larger-sized individuals. Nevertheless, in order to compare analyses between these sites, we decided to divide both populations into the same 4 size classes (2 - 4 cm^2; >4 - 50 cm^2; >50 - 100 cm^2; >100 cm^2). Clearly, this step in the process involves a great deal of judgement. It is always prudent to look at the effects of choosing different size categories to see if those decisions greatly influence the predictions of the model. In this case, we explored several different scenarios, but all produced similar results.

The vital rates and transitions among these 4 size classes can be calculated easily from the demographic data. As an example, Table 4.1 presents data from Phantom Canyon on the size of six individuals in each of the 7 years of the census. Plants can survive or die in any given year-to-year transition. If they survive, they can either grow, shrink or stay the same size. By following individual plants, one can trace their history of growth and survival. For example, individual #114 had a size of 50.27 cm^2 in the first year, and thus was categorized as a >4-50 cm^2 plant. Between 1989 and 1992 it survived and stayed in the same size class every year. Then in 1993 it grew to 70.88 cm^2, and thus made a transition into the next size class. Individuals #29 and #223 both shrank from the >100 cm^2 category to the >50-100 cm^2 category, and then died at the end of the sampling period. By tabulating the fates of all individuals in each size class each year, we calculated the "transition probabilities" or the fraction of plants in each size class that shrink by one size class, remain in the same size class, or grow into the next largest size class over one year. We entered these values directly into the matrix, as described in Box 4.1.

The final decision that must be made to model this population is how to represent the production of new individuals (i.e. fecundity). There are no data available on the demography of seeds once they are dispersed from the parent plant. Most seeds land directly below the parent plant, and if they germinate, are found as seedlings only if the parent dies and the space the parent occupied is made available. Thus to represent newborn individuals, we decided to add to the model a fifth category, "seedlings". Parentage was assigned to the plant occupying the site before the seedling was found, and the size of that individual was used to assign to a particular size class the successful production of a seedling. Plants at Cap Rock produced many more seedlings than those at Phantom Canyon.

From the available data it was possible to produce individual matrices for each pair of years in the data set (e.g., one for the 1994-95 transition: Table 4.2) for both populations, resulting in six matrices for Phantom Canyon and four for Cap Rock.

In projecting these matrices forward to calculate λ and extinction probabilities, we wrote a MATLAB program that took the multiple matrices approach. At each time step, the program selected one of the individual matrices calculated for each year-to-year transition in the data set. Each matrix had an equal probability of being drawn in any time step. We tried using the variable entries method, but with so few years of data with which to fit probability distributions, we felt that our efforts could lead to large inaccuracies with this approach.

Our analyses make different predictions about the viability of the Cap Rock and Phantom Canyon populations. We found an expanding population at Cap Rock (Fig. 4.1), that shows no risk of extinction over then next 50 or even 100 years (the model predicted a 0% probability of extinction in 100 years, and only a 10% probability of falling below 200 individuals). However, at Phantom Canyon the population appears to be in decline (Fig. 4.2). The model shows a 50% and 100% probability of falling below 45 or 200 individuals, respectively, over the next 100 years (Fig. 4.3).

This example illustrates how population viability analyses based upon projection matrices could be used to compare the relative viability of 2 or more occurrences. The models suggest

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that the Cap Rock population is likely to persist if the estimated vital rates prevail, but that we may need to consider management to improve the viability of the Phantom Canyon population.

"Experiments" with matrix models to determine best management practices

It is often instructive to conduct computer "experiments" to ask what effect particular changes in management may have on population growth rate or extinction risk. We can use the model to ask "how will population viability change in response to the expected change in a vital rate?" For example, if we planted seeds of *Aletes humilis* in empty crevices, with an expectation of doubling seedling recruitment, we could double that value in the matrix and determine how much the probability of extinction would decrease. Such experiments can serve as an indicator of the potential utility of specific management strategies. We can also ask the reverse question: "in order to have an extinction risk below 5% over 100 years (or an extinction risk of 100% over 5 years for an exotic we wish to control), how large must a given matrix element or elements be?" For example, we could determine how much greater seedling recruitment would have to be to obtain a positive growth rate for the Phantom Canyon population of *Aletes humilis*, and then ask whether such a rate is practically achievable. Because recruitment is limited by dispersal of seeds to sites not currently occupied by adults, we asked whether doubling seedling recruitment via seedling transplants performed at various time intervals would be sufficient to divert the population from its projected decline. After several trials, we learned that only if we planted seedlings every year would the population begin to increase, although a few of the simulation runs still decreased (see Fig. 4.4). After performing additional analyses to be sure of our result, and once sure that some intervention is warranted, we could then assess whether this type of intervention is feasible. This approach can be extremely helpful for guiding management decisions in many cases.

As we pointed out at the beginning of this chapter, an informative use of matrix models is to identify which life stage or which vital rates have the greatest influence on overall population growth. We can explore this question through a series of computer "experiments" akin to the

ones we just described. The idea is to systematically increase or decrease by a small amount each of the elements in the matrix, one at a time, and then examine the resulting rates of population growth (for an example, see Crouse et al. 1987). In this way we could ask, for example, whether it is more effective to manage populations of *A. humilis* by transplanting seedlings (i.e., enhancing fecundities) or reducing trampling of established plants (i.e., increasing survival of adults).

Finally, as our analysis of seedling transplantation for *A. humilis* indicates, one can use a matrix model to ask how frequently to apply a management regime. For example, if we have information on populations under two types of management, say burned and unburned plots, we could use a model to examine the effect of different burning cycles on population growth rates and thus determine the optimum burning cycle (see Gross et al. 1998).

Prospects for the use of matrix-based PVAs in TNC decision-making

Often, structured models are seen as impractical for application in TNC planning efforts due to the amount of effort that must be put into gathering sufficiently detailed data for analysis. At a bare minimum, three years of effort must be dedicated to marking, recapturing, and measuring individuals in a population to even construct a stochastic matrix model. However, three years of data would be insufficient to characterize the true degree of variation in a population's vital rates unless they are highly invariant -- put another way, the accuracy of these models will depend on how well a few years of data capture the range of variation the population experiences. For most populations many more years of data are required, especially when evaluating populations subject to long-term trends in vital rates or changes in management practices. In this sense, *projection matrix models are likely to require as many years of data as the count-based approaches, and of course much more effort is required to gather these more detailed data*. Because of their data requirements, matrix-based approaches will only rarely be of use in ranking EOs.

Yet, while it is certainly true that it will not be possible to perform projection matrix analyses for very many species or locations, there are cases in which this type of modeling will be more informative and useful than less data-intensive modeling efforts. Threatened and endangered species of particular prominence, species with large effects on ecosystems or on other species ("keystone" species), indicator species, umbrella species, or surrogates for a species of particular concern are all likely candidates for this type of PVA. When such species are long-lived, it will be particularly valuable to adopt a matrix-based approach to more accurately predict the population consequences of changes in vital rates and population structure. Results of matrix-based PVAs for taxa of special interest may help us to set goals for the size of particular reserves, or to judge the overall effect of a management practice. The analysis of matrix projection models can also help us to identify which life stages or vital rates most influence population growth rate, information that can be used to focus management and monitoring efforts. Similarly, by using the model to simulate different threats or by contrasting sites with different threats, it may be possible to evaluate which threats are most serious, and guide rescue efforts. Finally, because it is possible to test probable outcomes of different strategies by carrying out detailed "experiments" with the model, matrix-based approaches can serve an integral role in an adaptive context of reserve management.

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BOX 4.1 (Key): Constructing and Using a Matrix Model - A Step-by-Step Guide

<u>Step 1</u>. Decide if the population is best classified by age, size, or life stage.

To put together a model we must first divide the population into different classes. We can do this by AGE (e.g., all individuals a year old, all individuals 2 years old, etc.), SIZE (e.g., all individuals <10 cm long, all individuals 10-20 cm long, etc.), or STAGE (e.g., all seeds, all seedlings, all saplings, all adults). The choice of which type of classification to use depends on the life history of the organism and on the available data.

Age-structured populations: For many species the age of the individual is the best descriptor of how the vital rates react to the environment. For example, it could be that 1-yr olds survive worst, and 3-yr olds best. An age-structured matrix is often the method of choice when our data are taken from known-age individuals in a cohort analysis. Determinate growers (e.g. mammals and birds) are often modeled in this way, or with a modified formulation which adds a final adult stage. This simplification is only appropriate for species in which there is little variation in adult survival and fecundity rates as individuals age. Obviously, an age-based classification is restricted to species that are easy to age in the field.

Size-structured populations: If the exact age is not as important as the physical size of an individual in determining its vital rates, then a size-based model should be used. Examples include plants, for which size often influences how many seeds an individual can produce, and many fish species, in which size influences survival. Size may also be used when age is unknown, because size can be measured easily in the field. Typically, the divisions between size categories are determined by looking for critical sizes at which vital rates change abruptly, or by

assuring that the number of individuals in the data set that will fall into each size class will be adequate to estimate vital rates (see below).

Stage-structured populations: Organisms in which the life stage of an individual (such as simply being a newborn, a juvenile, or a reproductive adult, regardless of age or size within these stages) has the greatest influence on vital rates should be modeled as a stage-structured population. Stage-structured models can be the easiest to use because recognizing distinct stages may be more practical than determining age or size.

Next we must determine the number of classes to use. This decision must strike a balance between two opposing goals. First, each class should be as homogeneous as possible -- that is, all individuals within a class should be quite similar in terms of their vital rates, while differing from individuals in other classes. Second, the number of individuals in each class must be large enough to estimate vital rates accurately. Using too few classes will cause us to lump in a single class individuals that possess different demographic rates, whereas using too many classes means that some will contain too few individuals for accurate estimation of vital rates. See Vandemeer (1979) for one approach to balancing these two goals.

Step 2. Construct a projection matrix.

We are now ready to transform raw data into class-specific vital rates, and then put these into a matrix format. All projection matrices, regardless of the type of classification used, have the form:

FROM CLASS

$$
\begin{array}{c}
\text{TO} \\
\text{CLASS}
\end{array}
\quad
\begin{array}{c c c c c}
 & 1 & 2 & 3 & 4 \\
1 & a_{11} & a_{12} & a_{13} & a_{14} \\
2 & a_{21} & a_{22} & a_{23} & a_{24} \\
3 & a_{31} & a_{32} & a_{33} & a_{34} \\
4 & a_{41} & a_{42} & a_{43} & a_{44}
\end{array}
$$

Each matrix entry (a_{11} - a_{44}) has two subscripts, the first indicating its row and the second indicating its column in the matrix. Each entry corresponds to the annual rate of the transition FROM the class indicated by the column subscript TO the class indicated by the row subscript. Thus a_{32} is the annual rate of transition from class 2 to class 3. Fecundities are placed in the first row of the matrix because they represent contributions from adult classes to the newborn class (which by convention is class 1), and in this case correspond to entries a_{12}, a_{13}, and a_{14}. All other entries in the matrix represent class transitions of individuals other than newborns (for example a_{23}, a_{33}, and a_{43} give the fraction of class 3 individuals that shrink to class 2, remain the same size, and grow to class 4 in one year, respectively).

The details of taking raw data and calculating the probabilities that go into the matrix are discussed using two examples.

Example 1: A stage-structured matrix.   We will use as our first example a modified age-based matrix for the American Oystercatcher, a threatened shorebird that breeds along the eastern and gulf coasts of the U.S. (from Davis and Groom, unpublished manuscript). American Oystercatchers can be divided into three stages: juveniles, subadults, and adults. Data on the fates of banded oystercatchers and the success of known nests have been gathered by a variety of researchers for more than a decade. American oystercatchers have very low fecundity due to

high rates of nest loss to predators and storm events. Each adult oystercatcher nesting on South Core Banks, NC, produces an average of only 0.054 offspring that survive to the following year (Davis and Simons 1997). Juvenile survivorship is also low, estimated to be 66.5% per year. However, adult survivorship is high, and birds may live as long as 20 years. Annual adult and subadult survivorships are estimated to be 95% and 72.4%, respectively.

We have arranged these data on fecundity and survival rates of individuals in each stage into a matrix, **M** (see equation 4.1 below). Fecundity values are placed on the first row, and survival rates are placed in the other two rows so as to correctly represent transitions from one stage to another (e.g., survival from the subadult stage to the adult stage (0.724) goes in column 2 (FROM subadults) of row 3 (TO adults):

$$
\begin{array}{l}
\text{FROM:} \\
\begin{array}{l}
\text{TO:} \\
\text{juveniles} \\
\text{subadults} \\
\text{adults}
\end{array}
\begin{array}{ccc}
\text{juveniles} & \text{subadults} & \text{adults} \\
\begin{bmatrix}
0 & 0 & 0.054 \\
0.665 & 0 & 0 \\
0 & 0.724 & 0.95
\end{bmatrix}
\end{array}
= \mathbf{M} \qquad (4.1)
\end{array}
$$

Example 2: A size-structured matrix. Nantel et al. (1996) performed a PVA to determine the harvest potential of American Ginseng (*Panax quinquefolium*). Ginseng is a perennial plant that is difficult to age, but individuals vary in their survival and fecundity according to the number of leaves. Hence, plants are divided into 4 size classes, those with 1, 2, 3, and 4 leaves, and into seed and seedling classes.

In the case of a size-structured population, many more transitions among classes are possible than in an age-structured or even a stage-structured population, because individuals may grow one or more size classes in a single year, and may even drop from a larger to a smaller class (many plants, for example, may shrink between years). To measure the rates at which these numerous transitions occur in the population, it is best to perform a census of marked individuals in all size categories (as was done with *Aletes humilis*; see Tables 4.1 and 4.2). We do not have

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the original data that Nantel et al. used to construct their matrices, but we could imagine they followed 100 marked individuals in each size class (including seedlings, which are called the 0 size class) and obtained the following results:

SIZE NEXT YEAR:	SIZE CLASS WHEN MARKED:				
	0	1	2	3	4
0	0	0	0	0	0
1	16	25	0	0	0
2	2	59	52	6	0
3	0	0	40	85	19
4	0	0	3	5	74

Note that the numbers in each column do not sum to the initial number of marked individuals (due to mortality), that most individuals with 1 leaf grow if they survive, and that shrinkage occurs only rarely (6 individuals with 3 leaves shrank to having just two, and 19 individuals with 4 leaves shrank to having just 3). Fecundity values represent the production by aboveground plants of seeds in the soil (represented by size class "S"). Estimating fecundities is more complex than estimating other matrix elements; we discuss the estimation of fecundities in more detail in Box 4.2. In this example, counting the average number of seeds that each marked individual produces during the year is the most straightforward way of calculating fecundity (although these numbers must be corrected for the death of seeds between the time they are produced and the time of the next census; see Box 4.2). The estimated fecundities for ginseng are 0, 0, 1.35, 13.24, and 18.50 surviving seeds per year for classes 0 to 4, respectively. Nantel et al. estimated that 9% of seeds survive and emerge as seedlings in the following year. Using the fecundity estimates in the first row of the matrix, and dividing each number in the table

above by 100 (the initial number of marked ginseng plants in each size class) to get the corresponding matrix entries, yields the matrix:

	S	0	1	2	3	4
S	0	0	0	1.35	13.24	18.50
0	.09	0	0	0	0	0
1	0	.16	.25	0	0	0
2	0	.02	.59	.52	.06	0
3	0	0	0	.40	.85	.19
4	0	0	0	.03	.05	.74

Step 3. Construct an initial population vector.

The initial population vector is simply a column of the numbers of individuals currently in each class. For example, if the oystercatcher population in Example 1 above has 40 juveniles, 50 subadults, and 60 adults in year t, the population is described by the vector:

$$\mathbf{n_t} = \begin{bmatrix} 40 \\ 50 \\ 60 \end{bmatrix}$$

The total population size is obtained by adding together the numbers in the vector (so this population has a total of 150 individuals).

Step 4. **Project the population by multiplying the projection matrix by the population vector.**

Projecting the number of individuals in each class one year from now given a current population vector consists of multiplying the projection matrix by the population vector to generate a new population vector. Multiplication is achieved as follows. For each row of the matrix, take the product of the first entry of that row and the first entry of the vector, add that to the product of the second entry of that row and the second entry of the vector, and repeat for all other entries of the row and vector. The result is the first entry in the new population vector. Repeat this process for all other rows of the matrix. For example, to project the oystercatcher population, we multiply the matrix **M** (see equation 4.1 above) by the population vector $\mathbf{n}_t$:

$$\mathbf{M} \quad \text{x} \quad \mathbf{n_t} \quad = \quad \mathbf{n_{t+1}}$$

$$\begin{bmatrix} 0 & 0 & .054 \\ .665 & 0 & 0 \\ 0 & .724 & .95 \end{bmatrix} \text{x} \begin{bmatrix} 40 \\ 50 \\ 60 \end{bmatrix} = \begin{bmatrix} (0\text{x}40)+(0\text{x}50)+(0.054\text{x}60) \\ (.665\text{x}40)+(0\text{x}50)+(0\text{x}60) \\ (0\text{x}40)+(0.724\text{x}50)+(.95\text{x}60) \end{bmatrix} = \begin{bmatrix} 3.2 \\ 26.6 \\ 93.2 \end{bmatrix}$$

Note that the total population decreased from 150 individuals in year t (the sum of the entries in $\mathbf{n_t}$) to 123 individuals in year t+1. Thus we use information on vital rates embodied in the projection matrix **M**, and census figures on the numbers of individuals at time t, $\mathbf{n_t}$, to give us a projection of the number of individuals we will find in each class at time t+1, or $\mathbf{n_{t+1}}$. To project farther into the future, we simply continue to multiply the matrix by the newest population vector, as shown below for one more iteration:

$$
\begin{array}{ccccc}
\mathbf{M} & \mathbf{x} & \mathbf{n_{t+}} & = & \mathbf{n_{t+2}}
\end{array}
$$

$$
\begin{bmatrix} 0 & 0 & .054 \\ .665 & 0 & 0 \\ 0 & .724 & .95 \end{bmatrix}
\times
\begin{bmatrix} 3.2 \\ 26.6 \\ 93.2 \end{bmatrix}
=
\begin{bmatrix} (0\text{x}3.2)+(0\text{x}26.6)+(.054\text{x}93.2) \\ (.665\text{x}3.2)+(0\text{x}26.6)+(0\text{x}93.2) \\ (0\text{x}3.2)+(.724\text{x}26.6)+(.95\text{x}93.2) \end{bmatrix}
=
\begin{bmatrix} 5 \\ 2.1 \\ 107.8 \end{bmatrix}
$$

Now the population has declined further, to approximately 115 in year t+2. Ultimately, the population will take on a constant rate of population growth or shrinkage (or in rare cases, reach a constant size), and this rate will correspond to the so-called "dominant eigenvalue" of the matrix, λ ("lambda"; for methods to calculate λ, see Caswell 1989). Values of λ larger than 1 indicate population growth, while values smaller than one indicate population decline. This constant population growth rate will be achieved only if all the rates in the matrix remain constant (i.e., if the model is deterministic). The realized population growth rate that results when matrix elements vary is most easily determined by computer simulation, which may be performed using commercially available PVA software (RAMAS, Alex, Vortex, etc.), or by writing simple programs in mathematical software such as MATLAB or Mathematica.

Greater detail on the technical aspects of matrix model formulation and analysis can be found in Caswell (1989).

_____

BOX 4.2 (Key): Calculating Fecundity Values

Special care must be taken in calculating fecundity values because matrices are calculated and multiplied on an annual cycle. Thus, fecundity values that only account for the number of offspring produced per female per year will overestimate the true fecundity values because they fail to account for the mortality incurred either by reproductive females or the offspring themselves during each annual cycle. The timing of a census with respect to breeding will have different consequences for the calculation of fecundity. If we imagine that a census just occurred immediately after breeding (a post-breeding census), then to accurately predict the number of offspring that each female in our census will produce before the next census, we need to account for the mortality of those females before the next breeding event. It is likely that immediately prior to the next breeding event, most of the females that are fated to perish over the coming year will have already died. Hence when calculating F_i (the fecundity of class i females) for a post-breeding census, we discount the birth rate b_i by female survival P_i:

$$F_i = P_i \, b_i \, . \tag{4.2}$$

If instead the census occurs immediately before breeding (a pre-breeding census), we will need to account for the mortality of the offspring in our estimates, because certainly not all the young born immediately after the census will still be alive nearly a year later at our next census. The probability of producing offspring in a population censused prior to breeding is:

$$F_i = l_1 \, b_i \tag{4.3}$$

where l_1 is the first-year survival rate of offspring.

For many species, censuses will be conducted neither immediately before nor immediately after breeding, in which case both the mortality of offspring from the time of birth until the next census and the mortality of females prior to the next breeding event must be accounted for:

$$F_i = l_p P_i^{1-p} \, b_i \qquad\qquad (4.4)$$

where p is the amount of time (measured in a fraction of a year) between the time of birth and the next census and l_p is the proportion of offspring that survive for a time interval of length p.

These details are commonly ignored in the construction of matrix models, but must be adhered to in order to calculate fecundity correctly. See Caswell (1989) for more detail.

_____

Table 4.1. Sample data from the Phantom Canyon population of *Aletes humilis* (Schulz and Carpenter, unpublished data). Plants were tagged and measured, and re-censused yearly.

Plant size (cm^2):

Year:	1989	1990	1991	1992	1993	1994	1995
Tag #							
29	188.69	153.94	176.72	132.73	132.73	95.03	dead
51	9.26	9.26	14.19	17.73	19.66	23.76	12.57
56	3.14	21.65	33.18	38.48	28.27	44.18	7.07
114	50.27	50.27	50.27	50.27	70.88	78.54	50.27
223	194.83	153.94	182.65	132.73	63.62	50.27	dead
224	2.41	4.91	7.07	9.62	11.04	dead	

Table 4.2. Population matrix for the Phantom Canyon population of *Aletes humilis* for the year 1994-1995.

	Seedlings	2-4 cm^2	>4-50 cm^2	>50-100 cm^2	>100cm^2
Seedlings	0	0	0.060	0.046	0.044
2-4 cm^2	0.14	0.25	0.000	0.000	0.004
>4-50 cm^2	0.85	0.345	0.681	0.145	0.006
>50-100 cm^2	0	0.000	0.214	0.554	0.127
>100 cm^2	0	0.000	0.048	0.123	0.809

Fig 4.1. Trends in the Cap Rock population of the cushion plant *Aletes humilis* (Apiaceae) projected for 50 years using a stochastic projection matrix model. The solid line is the average of 100 independent runs of the simulation, and the dashed lines are the 95% confidence limits on the population size over this 50 year interval.
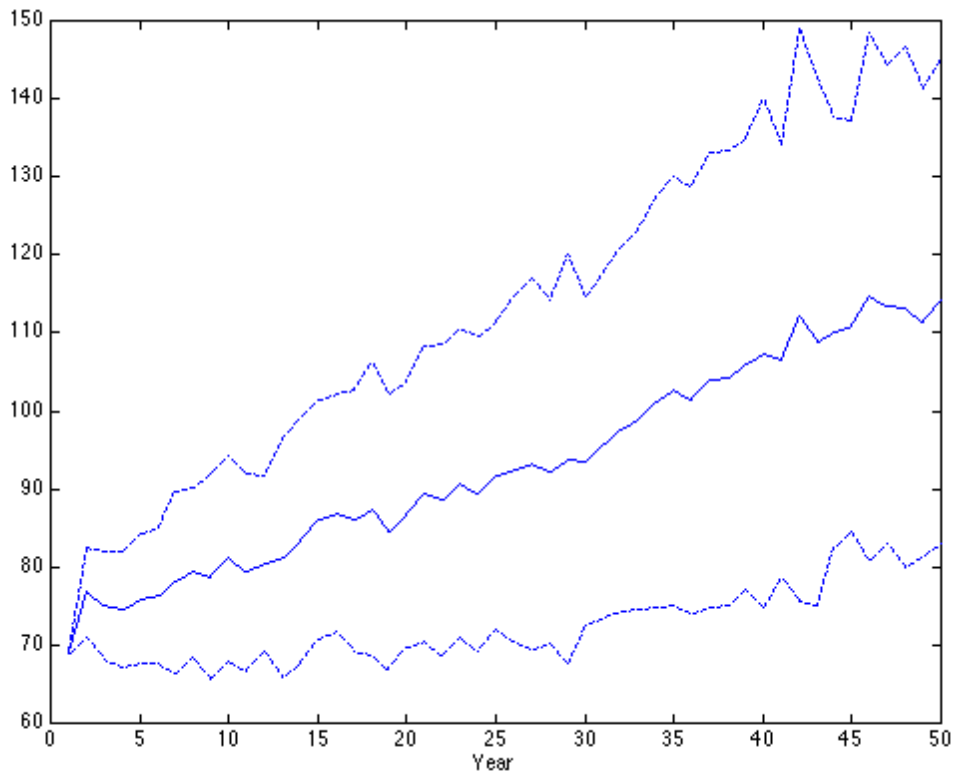
Population Size

Fig. 4.2. Population trajectory for the Phantom Canyon population of *Aletes humilis*. The projection based on field data shows a nearly 50% decline over 50 years. Solid line is the average trajectory taken over 100 simulations, and the dashed lines are the 95% confidence limits.
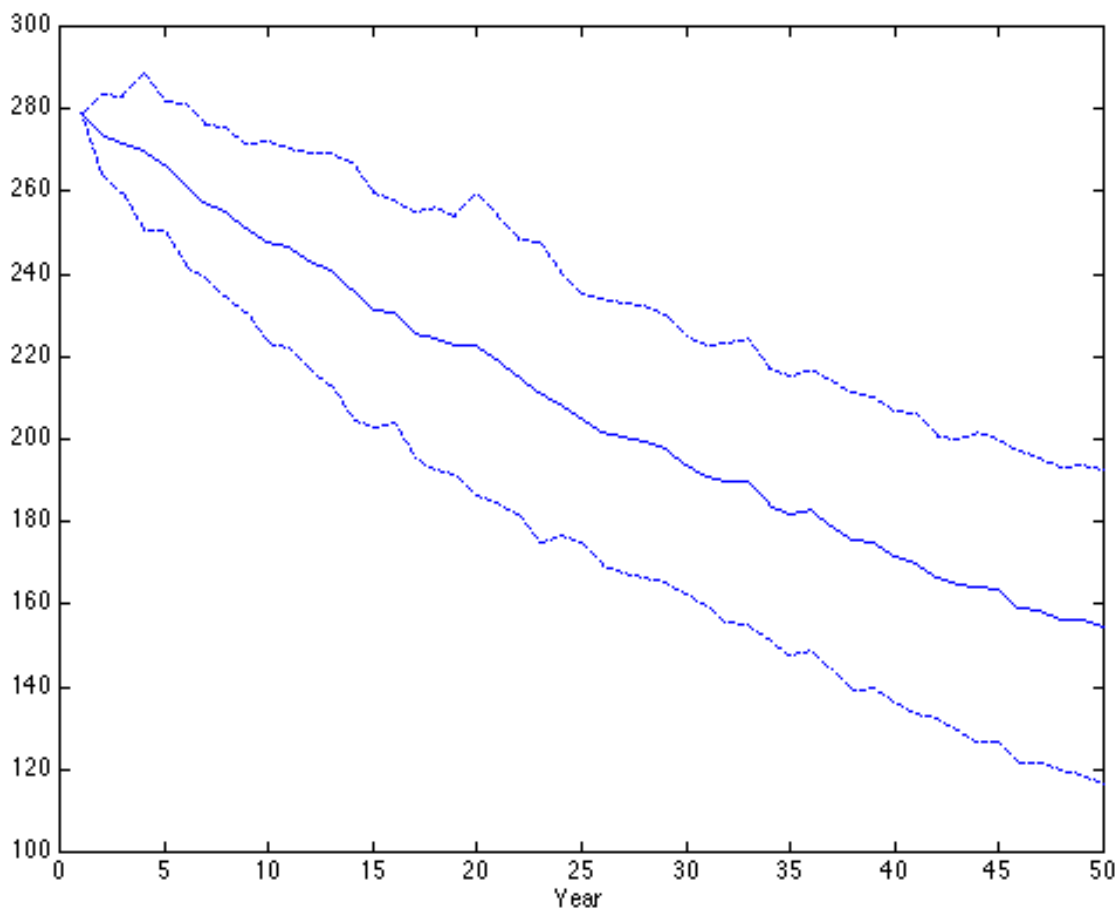
Population Size

Fig. 4.3. Extinction risk profile for the Phantom Canyon population of *Aletes humilis*. The probability of dropping below a threshold population size by 100 years is shown in the dark line, and the 95% confidence envelope is shown in the dotted lines.
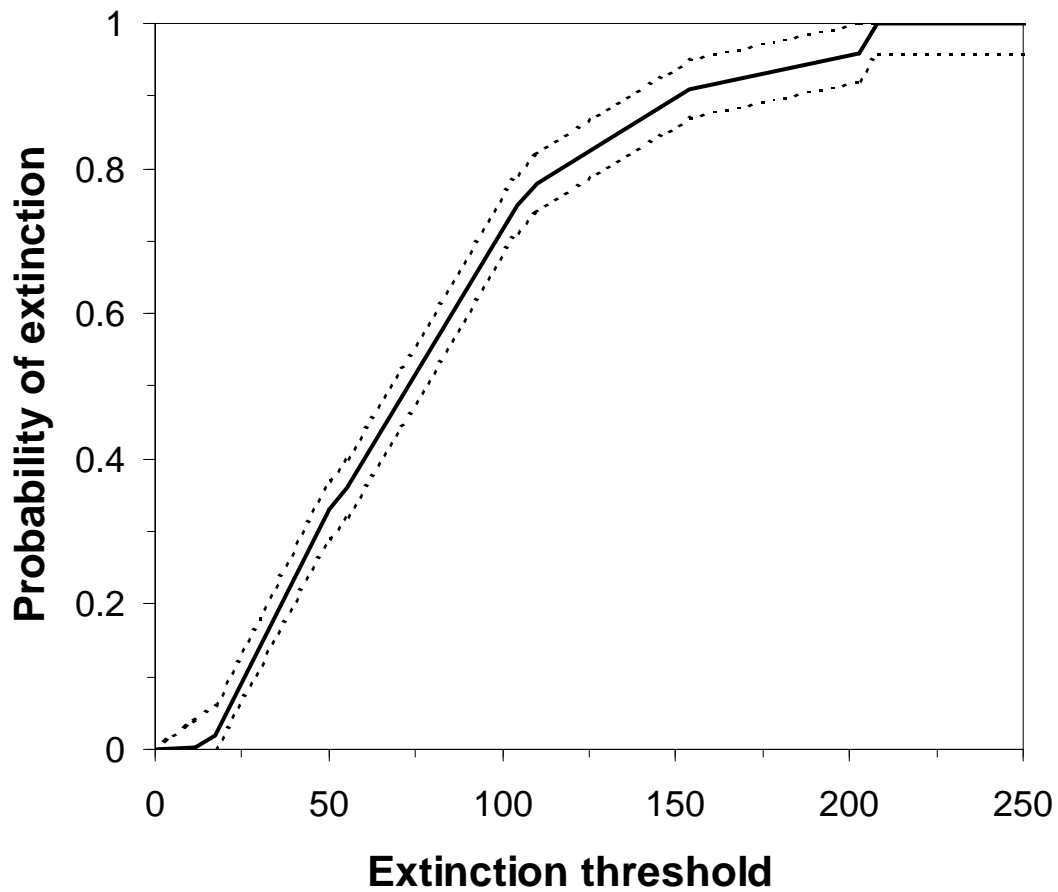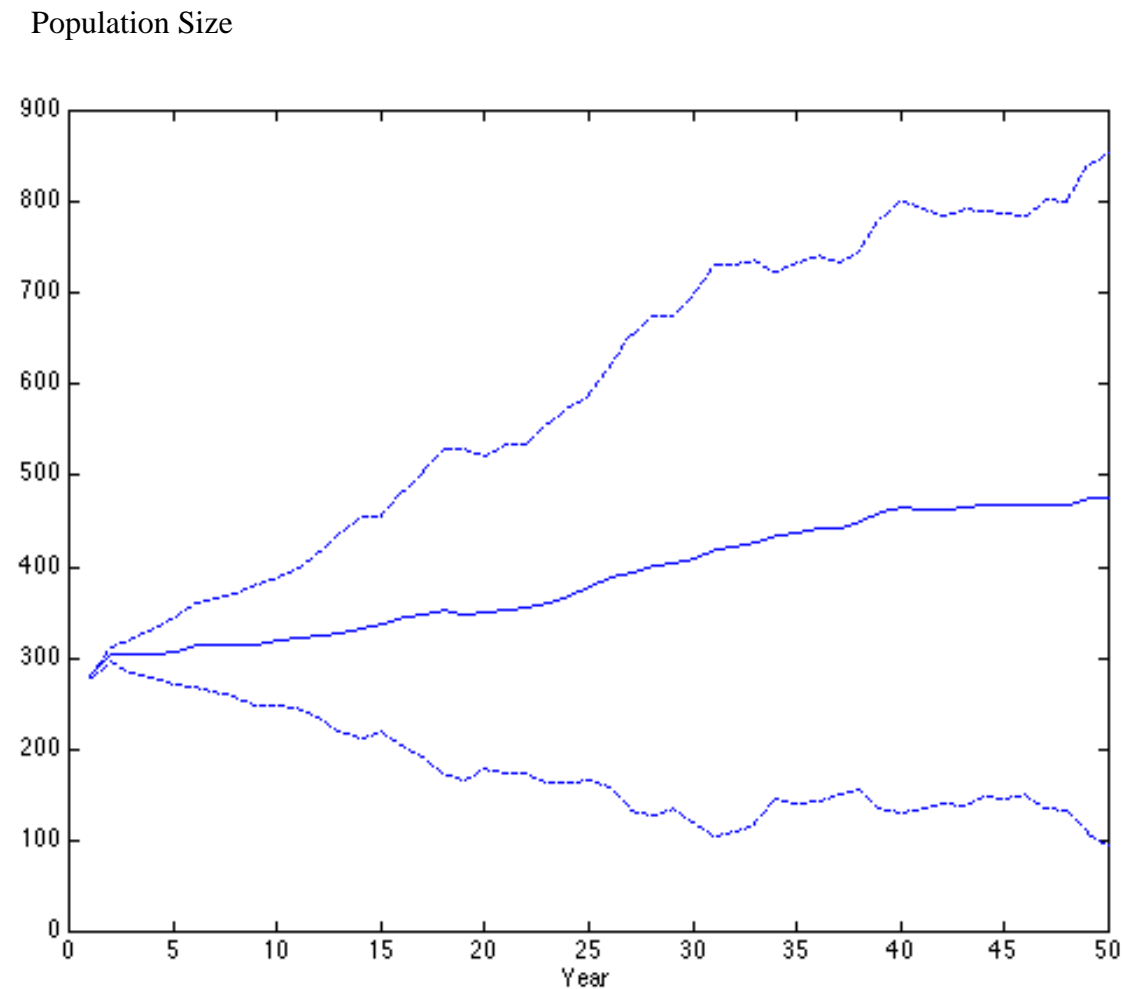
Fig. 4.4. A projection model "experiment" of doubling seedling recruitment via transplantation each year shows the average population increases in size over 50 years (although some replicates still decline - see lower confidence limit). Solid line is the average trajectory taken over 100 simulations, and the dashed lines are the 95% confidence limits.

Population Size

CHAPTER FIVE: POPULATION VIABILITY FOR MULTIPLE OCCURRENCES, METAPOPULATIONS, AND LANDSCAPES.

In Chapters 3 and 4, we considered the methods available for estimating population viability of single element occurrences, or single populations. Although the great majority of data available to both TNC and other ecologists was collected at only one site or population (Figure 2.1), many of the most pressing questions that PVA should help to address involve multiple occurrences. For example, how many populations are needed to ensure a high probability of survival for a species? To what extent should multiple occurrences be clumped versus spread apart? Can small and low quality element occurrences add significantly to regional viability of a species? Even among TNC's most highly prioritized species, many occur in more than one -- or even more than five -- sites (Figure 5.1); thus the question of how best to protect species from extinction nearly always involves the analysis of populations arrayed across multiple sites with particular spatial configurations. In this chapter, we address the analysis of these complicated situations.

Spatial population dynamics is an area of ecology rife with highly complex models. In particular, any conservation ecologist has probably read of the importance of "metapopulation dynamics" for population viability and landscape-level planning (e.g., Gilpin and Hanski 1991, Hanski and Gilpin 1997, Doak and Mills 1994, McCullough 1996). However, the data available for most species of concern do not include enough or the right kinds of information to justify these complicated modeling methods. For example, the data sets (see Fig. 2.1) submitted to the PVA workshop from which this handbook grew were completely devoid of information on dispersal rates or distances or even the spatial locations of individuals. Therefore, even more

than in previous chapters, we will take an approach here that distinguishes useful methods for viability assessment in the face of realistic data limitations from more ideal analyses that simply require too much information.

Data limitations are typically so severe for multiple site viability analyses that the word "analysis" is itself a little misleading. Often, when examining questions about multiple occurrences the best we can do is a structured form of thought experiment. It would be easy to read this chapter and conclude that there will *never* be enough data to rigorously perform viability analysis for multiple occurrences. However, data scarcity does not mean that we need to be paralyzed. Using the approaches we discuss below can often illuminate non-obvious tradeoffs or important questions that can improve viability planning. While the lack of data to perform multiple occurrence viability analysis correctly is a constant frustration, exploring the options using some fashion of quantitative reasoning can be highly useful.

We will begin by discussing the types of information that are ideally available to analyze the viability of multiple populations, then progress from simple to more complex methods of analysis. Finally, at the end of the chapter we will offer some general guidelines for multi-site considerations that should play a role in conservation planning.

Data Needed to Understand Multiple Sites and Populations

The primary reason that viability assessment for multiple sites is more complicated than single-site PVA is the need for more and different data. In particular, there are three distinct classes of data that are relevant for multiple site planning. Only very rarely will all three types of

data be available for a given species. However, before diving into how to proceed without this information, it is important to clarify what is needed for a full analysis, and why:

The quality of each population being considered. Essentially, 'quality' here means the results of a single site PVA, as discussed in Chapters 3 and 4. While there can be many aspects to an assessment of population quality (see Box 5.1), the most useful result for linking together multiple site analyses into a multiple occurrence PVA is some estimate of the probability of population persistence at each site over some clear time horizon.

Correlations of the fates of populations due to shared environments. The most important influence of spatial arrangement on overall viability is the extent to which populations at different sites will share the same fate at the same time. Thus, if two populations are in close proximity, they are likely to be similarly affected by variations in the environment, whether these variations are "normal" vacillations in rainfall, or "extreme" events such as fires and hurricanes. Other factors, such as elevation on a flood plain, can also generate correlations that are unrelated to simple physical proximity. There are many different ways -- in theory -- to estimate and measure the degree of correlation in the fates of populations. However, there are currently few good general methods with which to carry out such analyses, and we rarely have the data needed to use these rigorous estimation techniques. Only for the simplest types of catastrophes is it an easy matter to estimate correlations in the probabilities of extinction of two occurrences. However, using correlations in weather fluctuations, knowledge of the sizes of major disturbance events, and other less precise estimates of how much or how little each pair of sites will be correlated can still be highly informative, as we discuss below.

How much movement occurs between each pair of populations? Estimation of movement rates is important for several reasons, including the genetic effects of movement, the potential of spatially separated populations to 'rescue' each other from extinction (in the 'rescue effect', dispersers from other populations add numbers to a failing population and therefore rescue it from extinction), and the possibility that a population that goes completely extinct might be recolonized through immigration. While there are many methods available to estimate movement rates for different taxonomic groups (Turchin 1998), most are complex and are often extremely labor-intensive. As we discuss in the next section, the most important questions concerning movement of a target species may often be fairly easily answered with good knowledge of the basic natural history.

A Schematic Breakdown of Multiple Occurrence Scenarios.

Using a qualitative description of different degrees of movement and different correlations in the fates of populations, we can distinguish several distinct conservation scenarios (Table 5.1), each of which require somewhat different approaches to viability analysis.

High correlation in the fates of different populations (Cases A1, A2, A3): spatial analysis not required. When there is a high correlation in the fates of different populations, then there is little need to enter into the quagmire of spatial population analysis. It is easiest to understand this point by realizing that correlations of population-level fates are generated by correlations in the fates of individuals. The highest degree of population-level correlation that is likely to occur is when two individuals in separate populations are no less correlated in their fates than are two

individuals that are in the same population. For example, if essentially all the temporal variation in the environment is generated by large scale weather events (e.g., hurricanes or El Niño events), then individuals in populations separated even by dozens of kilometers may be thought of (more or less) as members of a single population, at least in terms of how their fates affect the risk of species extinction. In this circumstance, there is probably little benefit from having multiple populations other than a simple increase in the total number of living individuals and possible increases in local genetic diversity. Thus, the methods described above for single populations are all we need to adequately assess viability. Obviously, Cases A1, A2, and A3 do differ from one another, ranging from what is in fact a single intermating population (A3) to what are utterly distinct populations (A1). However, the key point is that for all these situations, we can avoid the complications of spatial population analysis and still do a good viability assessment.

Isolated, independent populations. When there is effectively no movement between populations *and* there is little or no correlation in the fates of populations (Case B), then the advantages of protecting multiple populations can be extremely large. Each population represents an *independent* chance of continued existence and the probability of global extinction will decline rapidly with the number of occurrences. Even better, the methods of analysis for this situation include some simple extensions of the approach presented in Chapter 3. The crucial question is how to determine the overall probability of extinction, over some time horizon, for a collection of independent populations (occurrences). Or, stated as the decision that must frequently be made: given that some populations of a species are already preserved, what will be gained by preserving additional populations? The method used to assess this question relies upon the

independence of the fates of each population. Given this independence, the probability of all M populations becoming extinct is simply the product of the probabilities that each individual population in the collection becomes extinct:

$$P_{global} = P_1 * P_2 * P_3 * P_4 * P_5 * _{...} * P_M \qquad (5.1)$$

where P_i is the probability that population i becomes extinct over some fixed time horizon, and where P_{global} is the probability that all M populations die out.

Using this simple formula, one can easily understand the assertions by various authors that preserving three or four populations will usually be enough to ensure a good chance of viability (Figure 5.2, $P_i = 0.2$ or 0.4). We can also see why these generalizations should not be taken too seriously (Figure 5.2, $P_i = 0.6$); while there is often a dramatic effect of adding additional populations on the safety of the whole set of occurrences, exactly how much additional safety is generated depends critically on the individual extinction probabilities of each occurrence. For example, adding many poor-quality (i.e., extinction-prone) populations to a set of occurrences already including two high-quality populations may have little effect on overall safety. In contrast, if all populations are relatively extinction prone, then there can be a substantial gain in safety from increasing numbers of occurrences (Figure 5.2, $P_i = 0.6$). Perhaps the most important message from this type of analysis is that the importance of different population occurrences for overall viability is highly dependent upon the quality of all sites. That is, there is no clear cut-off of single-population extinction probability below which a population can simply be dismissed as unimportant. In Box 5.2, we show how to use this method

to assess the overall viability of the set of isolated grizzly bear populations inhabiting the Lower 48 United States and British Columbia.

Clearly, situations in which there is no migration and no correlation in the factors affecting a set of populations are extremely unlikely. However, even when we know -- but do not have data to quantify -- that some inter-population movement and some correlation in fate exists, this simple approach is usually worth taking, simply because it gives a good starting point for analyzing the relative merits of protecting multiple sites. Furthermore, the results of this analysis can give much more meaning to our qualitative understanding of movement and correlation. If there is some correlation of population fates, but little or no movement, then the added safety of multiple protected sites will be weakened. Conversely, if there is some movement between sites, but little correlation in the effects of catastrophes on different populations, then there is likely to be more safety in numbers than the simple analysis shows. Having a clear, quantified benchmark against which to set these statements of 'more or less safety' gives them far more meaning and importance. We now turn to methods with which to analyze these complications directly.

No inter-population movement, but moderate correlation in fates of populations. When there is no direct interaction of populations (i.e., no movement of individuals between populations), but there are common factors influencing the growth, decline and extinction of separate populations, the safety gained by preservation of multiple sites can be substantially degraded (Case C). In theory, quantifying the gain in probability of overall extinction with correlated fates is a very simple extension of the last case. We modify equation 5.1 slightly to read:

$$P_{global} = P_1 * P_{(2|1)} * P_{(3|1,2)} * ..... * P_{(M|1,2,...,[M-1])} \tag{5.2}$$

where $P_{(i|1,2,...,[i-1])}$ is a conditional probability; in words, it is the probability that population i goes

extinct *given that* populations 1 through i-1 already have or will simultaneously become extinct.

The insertion of these conditional probabilities is a way of incorporating correlated risk into the

formula. For example, if the probability of extinction over 100 years is 0.2 for each of two

populations, then the probability that both become extinct independently is 0.04. However, if

extinctions are highly correlated -- perhaps due to fires that might spread through both

populations -- then the risk of extinction of the second population might be 0.8 *if* the first

population becomes extinct. Therefore, the overall risk of extinction is 0.2*0.8 = 0.16. In this

case, the gain in safety (= reduction in risk of extinction) that is realized by preserving two

versus one population is much more modest.

Adding correlation can strikingly reduce the effectiveness of multiple occurrences in

creating safety (Figure 5.3). However, the extent to which correlations counteract the gains from

multiple protected sites depends on the details of each situation. In particular, it is unlikely that

all populations are equally correlated in their fates. Especially if physical proximity results in

high correlation, it may be beneficial to preserve sites that are as distant as possible from one

another. In other words, when movement either doesn't occur, or is of relatively little

importance, the risks that proximity poses by increasing correlated extinctions is of paramount

importance and should be minimized. While this advice runs counter to standard conservation

recommendations, the reasoning is straightforward and likely to be as or more important than the

considerations of movement between populations that underlie recommendations to place

reserves close together (see next section).

How can we apply this abstract reasoning to real situations (that is, how do we estimate the conditional probabilities in equation 5.2)? Analysis of the extent to which conservation gains are eroded by correlations can either be quite complicated or fairly simple. As usual, the tractable case, with which we will start, is less realistic. The key assumption in making a correlated extinction problem simple is that the major factors causing population extinctions are discrete 'catastrophes' that can strike more than one population at a time: fires, floods, epidemics, and droughts are among the likely factors causing such correlated extinctions. In this case, we simply need to know the probability of each population succumbing to extinction given that others have or will also become extinct. This type of data is rarely available from real extinction records. However, physical data such as records of fire sizes and correlations in rare weather conditions across the range of populations can provide good guidelines for estimating the correlations in extinction risks from such discrete events.

A more complicated situation arises when factors other than catastrophes drive extinctions. In particular, "normal" environmental fluctuations, as discussed in Chapter 3, can result in extinctions that are driven by series of poor, but not catastrophic, years. In this case, shared environments still can drive correlated extinctions, but it is much more difficult to estimate the correlations, because they are the result of shared events over many years. There are as yet no clear analytical results that are comparable to those of Dennis et al. (1991) with which to analyze this situation. However, computer simulations of multiple populations reacting to correlated environmental fluctuations can be used to untangle correlations in extinction probabilities (Harrison and Quinn 1989); to apply these methods to a real situation will probably require collaboration with a modeler who can tailor a simulation to the specifics of a real system.

<u>Movement, although not extensive, is important, and populations are not highly correlated in</u> <u>fates</u>. Here we finally come to the situation that is usually the *only* one presented in discussions of multiple populations and conservation strategies: simple metapopulations (Case D; see Box 5.3 for a run-down on basic metapopulation ideas applicable to TNC problems). In this situation, multiple occurrences provide greater safety for the same reasons discussed above under Cases B and C, but there is also potentially a huge additional gain in safety from movement between populations. Movement can either result in recolonization of habitat patches in which populations have gone extinct, or prevent extinctions through 'the rescue effect'.

Before now we have dismissed movement, in spite of its potentially huge importance in determining the safety of multiple occurrences, simply because of the difficulty in acquiring good data on dispersal. Since we must usually make wild guesses at movement rates, our philosophy is that it is often better -- at least initially -- to pretend that it doesn't happen. This will give us both more conservative estimates, and also estimates that do not rely upon very suspect guesses. However, it is still worthwhile to consider metapopulation processes and their implications for multiple occurrence analysis, both because in some circumstances movement is relatively well-understood and important (Beier 1993) and because these ideas are so prevalent in the conservation literature.

In the simplest metapopulation situation, two processes counter one another: the extinction of local populations, and the recolonization of habitat patches. For this simple situation, the mean time to extinction depends upon four variables: the probability of local patch extinction, the rate of movement between patches, the number of habitat patches (not all of them occupied all the time), and the correlation in extinction probabilities (Figure 5.4). Each of these factors has the effect that one would expect, with the best possible combination being that: 1)

there is low probability that each local population becomes extinct; 2) rates of movement between populations are high; 3) the number of habitat patches is large; and 4) extinction of different populations is uncorrelated. In the extreme, these conditions mean that we don't have to consider a collection of populations as a 'metapopulation' at all (Table 5.1). However, as we have mentioned above, there is an important complication that is ignored in most treatments of simple metapopulation theory, the confounding of correlation in local population fate (extinction times) and movement rates. For almost all species and patch arrangements, there is likely to be a strong effect of the distance between patches on both movement rates and the shared chance of extinction. Thus, greater proximity will result in the opposing effects of higher movement rates and greater correlation in extinction, with an uncertain net outcome for global extinction risk.

Even incorporating the complications just mentioned, most metapopulation models are far too simplified for on-the-ground conservation planning. In particular, they rely on assumptions of equal immigration rates between all habitat patches, as well as equal population sizes and extinction risks in all habitat patches. To tailor these scenarios to specific problems and decisions requires more elaborate simulation models that take these basic ideas and apply them to more complicated situations. While these highly specific simulations are beyond the scope of this handbook, in Box 5.4 we outline three basic approaches to such an analysis. Unfortunately, only rarely will there be enough data available to perform such simulations with any confidence.

As we've repeatedly stated, the information needed to address Case D in our table of spatial situations is rarely available or obtainable without extended, intensive sampling. However, this is **not** to say that 'metapopulation-like' spatial situations are uncommon or unimportant. This leaves the obvious conundrum of how to analyze multi-site viability with the

usual mismatch between conservation needs and data availability. In the final section of this chapter we provide some thoughts on approaches to this problem.

Assessing Multi-population Viability with Realistic Constraints.

The basic problem in assessing multi-population viability is the need for three distinct types of information: everything needed to assess single population viability, movement rates between populations, and correlation in the factors influencing different populations. Without all this information, we are left with the question of how to actually proceed without knowing where in Table 5.1 we really are. We suggest the following way of approaching this all-too-typical set of limitations:

1. First, reclassify all occurrences of a species into sets. Each set should include sites that are likely to have enough movement and/or correlation in environments that they are best considered as one population unit for viability analysis (note that these groups of occurrences might be distant enough from one another spatially that they should certainly be considered as separate EOs in standard TNC protocols). However, different sets should be defined so that they are likely to be relatively independent population units.

2. Treat each set of highly correlated EOs as a single, unified population, estimating its viability using single-population methods. Then perform the simplest type of multi-population viability assessment (equation 1) on the sets rather than their component populations, assuming that no movement or correlation occurs between sets. While this type of analysis is clearly

oversimplified, it provides a starting point from which to guess at the importance of movement and correlation effects.

3. Use this simplest analysis to make initial guesses at the effects of keeping or removing different populations. However, do not accept these results as a final answer, but rather as a starting point, to which can be added further knowledge of the species' natural history. For example, while this type of analysis might suggest that a small population close to several others is unimportant, such habitat patches might be of known importance for the enhancement of movement between other populations, and this qualitative knowledge should be used to modify the conclusions of the formal viability assessment.

4. Finally, in using this type of simplified analysis to frame a preservation strategy, it can be helpful to think of the two usually unknowable spatial factors influencing viability -- correlations and movement -- as opposing forces. The closer together populations are, the higher movement is likely to be between them, generating more safety; the farther away they are, the less correlated they will be, generating more safety. This fundamental conundrum implies that a mixed strategy is often the best to pursue, with clustering of preserved areas at smaller scales to facilitate movement, and preservation of two or more clusters at larger scales in order to reduce the risk of simultaneous disasters. In our typical state of ignorance about the importance of movement and correlation in influencing overall risk, this mixed strategy is likely to be the most conservative and defendable.

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BOX 5.1 (KEY): Methods to Judge Single Site Quality

Ideally, when judging the importance of a site for a multi-occurrence viability plan, we would have the results from analyses like those presented in Chapters 3 and 4 for each and every site. In particular, using either the methods of Dennis et al. (1991), or stochastic simulations of projection matrix models, we would like to have an estimate of extinction probability (over some specified time horizon) for each population. However, even if we have good enough data from one population to perform such an analysis, we usually don't have sufficient information to do any analysis for most populations. This leaves three common choices:

1. The "Representative Sites" Method. Use data from one or two well-studied sites to make quantitative estimates of viability for other occurrences (see Fig. 3.7B and Box 5.2). While this is usually the most reliable way to proceed, we still have to be somewhat skeptical of these estimates, since the genetics and the environmental conditions (both natural and anthropogenic) that together control the demography of each population is unlikely to be identical. Nonetheless, such estimates provide a good starting point for multiple occurrence viability planning.

2. Wild (or Educated) Guesses. Without any good data on any population of our species, we must resort to guessing about the likelihood of extinction. These guesses can take many forms: a) modifications of quantitative viability estimates using data from other, related species; b) historical data on estimated population sizes and rates of extinction of a formerly common species (e.g., Berger 1990) ; c) natural history intuition and broad patterns of viability. This last

method is essentially using any available information to put brackets around extinction probabilities and the way that they are likely to vary with population sizes. Familiarity with a taxonomic group and the work that has already been done on other species within the taxon can yield valuable information upon which to build viability estimates. For example, Heppell (1998) has summarized work on multiple turtle species to arrive at generalizations about the demographic patterns of this group. **The key strategy in using this "anything goes" approach is to avoid making single estimates of extinction rates**. Rather the focus should be on making *minimum and maximum estimates* that bracket reality. We can often make such estimates even when we can't know the specifics of a population's chances of survival. Using *both* the minimum and maximum estimates in our calculations then gives us a range that, *to the best of the available knowledge*, bounds the likely viability. Surprisingly frequently, the practical answers for a conservation strategy do not require more than these "brackets."

One further point that should receive special attention here is the need to consider changing conditions in estimating single site quality or viability. Even if all the data needed for the Dennis et al. approach are in hand, the effects of future management (to improve a population's probabilities of survival) or future impacts (which may greatly reduce the chances of survival) should be weighed in making population viability estimates.

3. Despair. We do not encourage this approach. Although analyzing multiple occurrence viability is not simple, and we are always limited by the data at hand, it is much more profitable to go through the steps of a simple analysis with guesses than to not do it at all. Partly, this is because of the initially non-intuitive answers that often emerge from viability analysis (often 'non-intuitive' results become intuitive once they are reflected on). Partly, analysis is useful because it

can clarify the need for some kinds of information and the unimportance of other information.

One of the most useful outcomes of models in conservation is the setting of priorities for

information we need to gather.

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BOX 5.2 (Key): Analysis of multiple occurrence viability for the grizzly bear

While we did not find a data set from TNC that would clearly (and cleanly) serve as an illustrative example for multiple occurrence viability assessment, many such data sets do exist. Here, we use the results for the Yellowstone grizzly first described in Chapter 3 to show how such an assessment can be done. It is worth emphasizing at the outset that this question is not an abstract one; ongoing planning and litigation concerns the question of the overall viability of the small and scattered grizzly populations in the Lower 48 United States.

There are five known grizzly populations in the Lower 48 United States and adjacent parts of Canada, with minimum estimated population sizes ranging from 306 in the Northern Continental Divide Ecosystem to five in the North Cascades (United States Fish and Wildlife Service 1993; Table B5.2.1). Since each of these areas is distinct and fairly isolated from the others, we will proceed with an analysis that assumes both that there is no movement between the populations (which is almost certainly true) and that there is no correlation in the fates of the populations. This second assumption is not correct; there is good evidence of widespread environmental factors, including weather and masting of white-bark pines (Mattson et al. 1992), that will create at least some correlations in the fates of bear populations in the inter-mountain West. However, since we can't clearly evaluate the strength of such correlations, we will proceed here with the simplifying assumption of totally independent fates. We discuss the issues of correlated fates in more detail in the body of the chapter.

To estimate the viability of each population, we used the Dennis et al. method described in Chapter 3. Since not all of the five grizzly populations have enough data to estimate μ and σ^2, we instead use estimates from the very extensive Yellowstone data set (Dennis et al. 1991; μ

= -0.007493 and $\sigma^2 = 0.008919$). Using these values, we calculated the probability of extinction at 500 years, assuming an extinction threshold of 2 bears (Table B5.2.1; for methods, see Box 3.3).

Given our estimates of single population viability, we can ask a variety of questions about the advantages for overall viability of protecting different combinations of the five populations. First, what are the gains of adding sequentially smaller populations to a collection of occurrences for this species? For the 500 year time span, protecting the Yellowstone population in addition to that of the Northern Divide decreases the probability of extinction from 0.342 (for the Northern Divide alone) to the product of the two populations' extinction probabilities: 0.342*0.392 = 0.134. While this dramatic gain in safety may not seem surprising, there is also a substantial lessening of extinction risk from adding the much smaller Selkirk population to the first two: 0.342*0.392*0.823= 0.110. Figure B5.2.1 illustrates that adding the remaining two populations to the portfolio of sites yields diminishing benefits.

Another question is whether the three smallest populations together can guarantee as little risk of extinction as either of the two largest populations. The answer is no: the three small areas together have a combined extinction risk about double that of either of the two larger populations alone: 0.892*0.890*0.974 = 0.713. However, in terms of bears alive at the present time, this is a surprisingly small extinction risk, since these three populations together harbor only 45 individuals, less than a fifth the number in either of the two large populations.

Finally, one way to view the results of this type of analysis is simply to ask about the safety from regional extinction under the very best scenario of maintenance of all current populations. For 500 years, we would predict only a 9.6% chance of extinction of all populations (100*0.342*0.392*0.823*0.890*0.974). While reasonably small, this risk is still greater than the

1% chance of extinction over reasonable time horizons that is frequently called for in

conservation. Worse, we know that it is certainly a low estimate, since the two largest

populations are relatively close together and thus will share correlated fates. By showing that our

optimistically simple analyses yield inadequate safety, an analysis like this one can support the

need for more proactive conservation measures.

Table B5.2.1. Single population viability estimates for five grizzly populations. *Current size is a

minimum estimate of current population size. Data from United States Fish and Wildlife Service

1993.

Population	Current Size*	Probability of extinction (500 years)
Northern Divide	306	0.342
Yellowstone	236	0.392
Selkirks	25	0.823
Cabinet/Yaak	15	0.890
North Cascades	5	0.974

Figure B5.2.1. Extinction risk for sets of grizzly bear populations over 500 years. From left to right, each bar plots the global extinction probability obtained by adding sequentially smaller populations to a collection of protected areas.
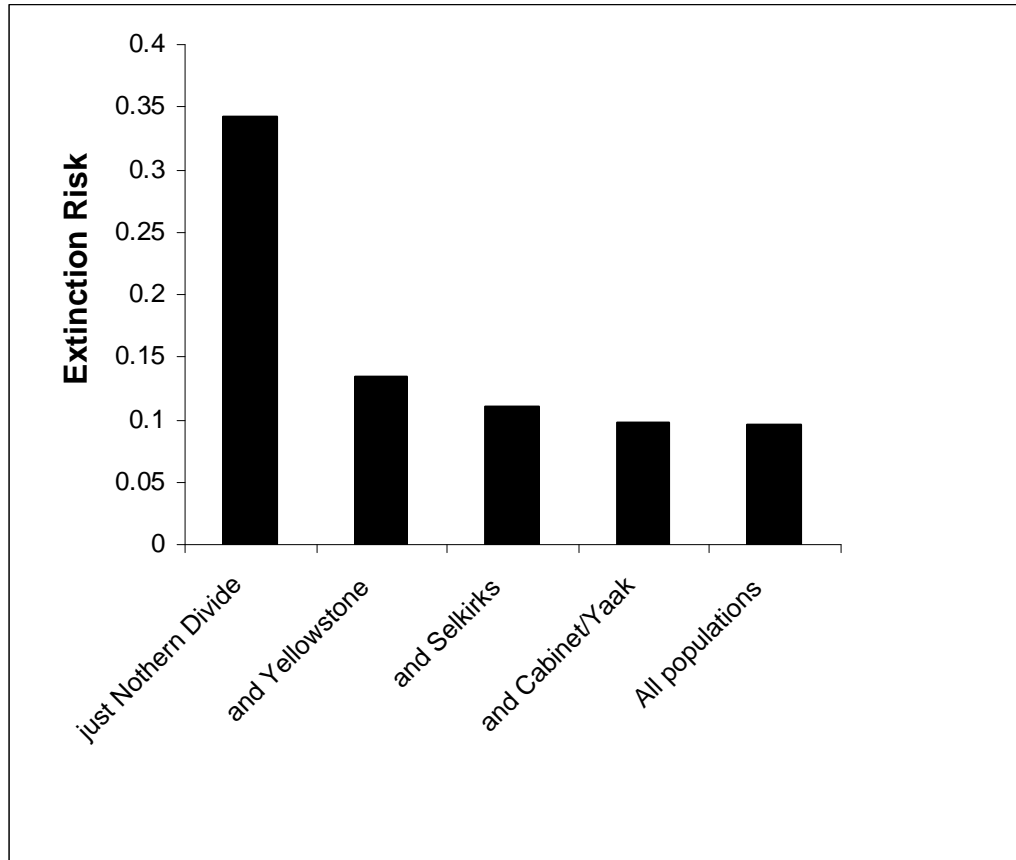
BOX 5.3 (Key): The Basics of Metapopulations

While a great deal has been written about metapopulation dynamics (Levins 1969, Gilpin and Hanski 1991, Hanksi and Gilpin 1991, 1997), it is worthwhile here to provide a quick review of basic metapopulation models. In part this is because most of the general statements about conservation of multiple occurrences come directly from the simplest metapopulation models, and in part because most of the more elaborate models are built directly on the framework of Levins' original ideas.

In large part, the influence of the original metapopulation model (Levins 1969) comes from its simplicity. In this model, only two parameters are assumed to control the metapopulation: the rate at which occupied habitat patches become extinct (*e*) and the rate of recolonization, or founding of populations on unoccupied habitat patches (*m*). Most simply, the measure of the metapopulation's size or health is the proportion of suitable habitat patches with an extant population (*p*). Thus, *p* ranges from 0 to 1 (i.e., from no patches occupied to all occupied). The change in this proportion is a function of *e* and *m*:

$$\frac{dp}{dt} = mp(1-p) - ep$$

Several assumptions are implicit in this model. First, it is assumed that colonization arises solely due to immigration from currently occupied patches in the metapopulation (i.e., not from populations outside the metapopulation being considered). Thus, *m* is the rate at which colonists from extant patches find and successfully colonize empty patches, and *mp(1-p)* is the overall rate of colonization, given *p*. Furthermore, this model assumes that all patches are equally likely to provide colonists to any other patch. This is equivalent to assuming that all patches are equally far apart and that they are all of the same size and quality. The loss of populations due to

extinction is represented by $-ep$. Thus, e is a simple rate of local population extinction, and there is again the implicit assumption that all populations are identical – that they all share the same probability of extinction per unit time – as well as that these extinction probabilities are completely uncorrelated with one another. Finally, Levins' model does not include rescue effects; each population's probability of extinction is independent of how many other habitat patches are occupied. For clear but more detailed reviews of this model and its basic modifications, see Gotelli (1991, 1995).

One crucial point to make is that, as presented above, simple metapopulation models do not include any explicit term for the number of habitat patches that might support populations. Indeed, the theory relies on the assumption that there are enough patches that we can summarize average behavior using just the proportion of occupied patches. However, to make any useful predictions for rare species, with finite numbers of populations and habitat areas, we need to explicitly include the number of patches in our model. Nisbet and Gurney (1982) have produced such a model, allowing the estimation T_M , the mean time to extinction for a metapopulation with a total of H patches:

$$ T_M = T_L \exp\left\{ \frac{H}{2}(mT_L + \frac{1}{mT_L} - 2) \right\} \qquad\qquad (B5.3.1) $$

where T_L equals $1/e$, the mean time to local population extinction, and m is again the rate of colonization of empty patches. In Chapter 3 we have emphasized that mean time to extinction is usually a rather poor measure of viability for a single population. The same is true for a metapopulation. However, with far less theory done for multiple occurrence viability, this result of Nisbet and Gurney is one of the only useful, mathematically explicit results to link patch

number to viability. Figure 5.4 shows results from this formula, illustrating how extinction time varies with patch number, as well as with e and m.

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BOX 5.4 (Optional): Methods for quantitative analysis of complicated multiple occurrence situations

Three general approaches have been developed to deal with the complications of multiple occurrence patterns. While all have limitations, each adds reality to the bare-bones assumptions of the simplest metapopulation models reviewed in Box 5.3. Below, we simply provide a thumbnail sketch of each approach, along with references for further reading.

More complicated metapopulation approaches. Numerous papers have been published that directly elaborate on the basic Levins metapopulation model. Perhaps the most promising of these approaches is the "incidence function" method of Hanski (Hanski 1991, Hanski et al. 1996). The essential idea of this approach is to use data that are relatively easy to collect for separate populations to estimate the more difficult to obtain extinction and colonization rates needed for a metapopulation model. These models add reality to the metapopulation approach by estimating how extinction and colonization rates vary with habitat patch sizes, distance from other patches, etc. Most commonly, the data used to estimate the metapopulation parameters involve patterns of current patch occupancy (is there a population on a suitable habitat patch, or is it extinct, right now?). Making certain assumptions about how distance and patch size are likely to influence extinction and colonization, this occupancy data can then be used to estimate occurrence-specific extinction and colonization rates. This in turn allows a much more realistic assessment to be made of metapopulation structure, the importance of each habitat patch for metapopulation survival, and, through simulation, the probability of metapopulation extinction (Hanski et al. 1996). However, while this method has clearly given powerful results for species

with large numbers of separate patches and populations, for species with a small number of

occurrences and only a few years of observations, it is dubious that the results of incidence

function analysis will be reliable. Two other problems also may limit this approach to viability

estimation. First, to use the approach we must assume that a metapopulation has not been

perturbed by any substantial changes in the number or arrangement of habitat patches, or in the

magnitudes of colonization or extinction rates, in the recent past. Second, the method requires

comprehensive surveys of all extant populations and also all suitable, but unoccupied, habitat

patches within the area of concern.

Spatial Demography Methods. It is not difficult to expand the matrix models we reviewed in

Chapter 4 to include different subpopulations linked by movement. In this way, spatial structure

can be incorporated into the framework of demographic analysis. Examples of this approach

include Wootton and Bell's (1992) analysis of peregrine falcons in California, and Horvitz and

Schemske's (1995) study of the demography of a tropical shrub through different stages of

succession. The advantage of this approach is its ability to very flexibly combine information on

within-population demography of individuals with between-population differences in rates. For

example, a simplified form of this approach is the basis for most 'source-sink' models, which

classify habitats into just two types (demographically good "source' habitat and demographically

poor "sink" habitat) linked by movement (Pulliam 1988, Doak 1995). Furthermore, it allows

great flexibility in defining the ease of movements of different types of individuals (e.g., adults

versus juveniles) between different subpopulations. While it is easy to use these spatial

demography models to estimate overall metapopulation growth rates, they must be simulated

stochastically to generate extinction time estimates (as was the case for single population

demography models; see Chapter 4). An additional limitation is that they require estimates for a

large number of parameters – in particular, the rates of movement of individual in each size or

age class between each pair of habitat patches.

Spatially Explicit, Individually-Based (SEIB) Simulations. A growing class of simulation models

is capable of simulating the movements of individual animals (or seeds) across complicated

landscapes with varying habitat types that are defined by nuanced differences in the demography

and movement rules of individuals in them. There are numerous examples of programs written

for single applications of this type (Pulliam et al 1992, Lamberson et al. 1994, Liu et al. 1995), as

well as commercially available packages (e.g., RAMAS, PATCH; see Schumaker 1998 for

probably the best and least expensive model of this type (it's free)). Most of these models use

GIS outputs to construct complicated landscapes that can be based upon classifications of real

land patterns. While these programs are capable of the most 'realistic' spatial population

dynamics by far, they are also the most prey to the problem of parameter estimation. In

particular, by incorporating movement between suitable habitats through individual movement,

they require knowledge of movement behavior that is essentially never known for rare species;

furthermore, this ignorance can have dramatic consequences for the predictions of such models

(Ruckelshaus et al. 1997). However, these models are still quite new, and more work may be

able to define how useful their predictions can be within the limits of our usual ignorance about

real species in real landscapes.

All these methods have the general advantage of being able to include substantially more

biological detail than do simple metapopulation approaches. Thus, they are far more appealing

than the much simplified treatments of multiple occurrence viability that we mostly discuss in

this chapter. However, the real key to making these methods useful is having the information to estimate a majority of their many parameters, and being willing to carefully explore the consequences of having poorly estimated parameters. However, even with poor data, trying to fit a complicated model to a particular situation can also be informative as a check on a much simpler analysis: if the complex simulation confirms the conclusions of a simple analysis, we can place greater confidence in the results and their use as a basis for conservation planning.

Table 5.1. Six combinations of movement rates and correlations in fates are likely to actually occur. If movement rates are high between two populations, it is difficult for their fates to be less than highly correlated, thus two of the cells will never occur. In addition, low to medium movement is expected to cause at least *some* interpopulation correlation, so one cell is unlikely to occur. We also include examples of species that appear to exemplify each combination; for these examples, we have picked relatively well-known species and made judgement calls about the correlation categories into which each would fit. In most of these cases, data that would allow the correlations to be calculated are lacking.

Correlation in Population Fates:	Movement between Populations:		
	None	**Low to Medium**	**High**
None	*Case B* Plants on scattered Chicago prairie fragments (Panzer and Schwartz 1998)	Unlikely to exist	Can't exist
Low to Medium	*Case C* Endemic annuals on scattered serpentine outcrops in California (Kruckeberg 1984) Birds in San Diego chaparral fragments (Bolger et al. 1991)	*Case D* Furbish's Lousewort in Maine (Menges 1990)	Can't exist
High	*Case A1* Insects in scattered Chicago prairie fragments (Panzer and Schwartz 1998)	*Case A2* Bay Checkerspot Butterflies (Harrison 1989)	*Case A3* Acorn Woodpeckers in Southwest (Stacey and Taper 1992)

Figure 5.1. Number of known occurrences for TNC priority G1 and G2 species. Histograms show the number of occurrences per species, grouped for single numbers of occurrences below 40 occurrences, and in groups of ten (e.g., 50-59 occurrences) above 40.
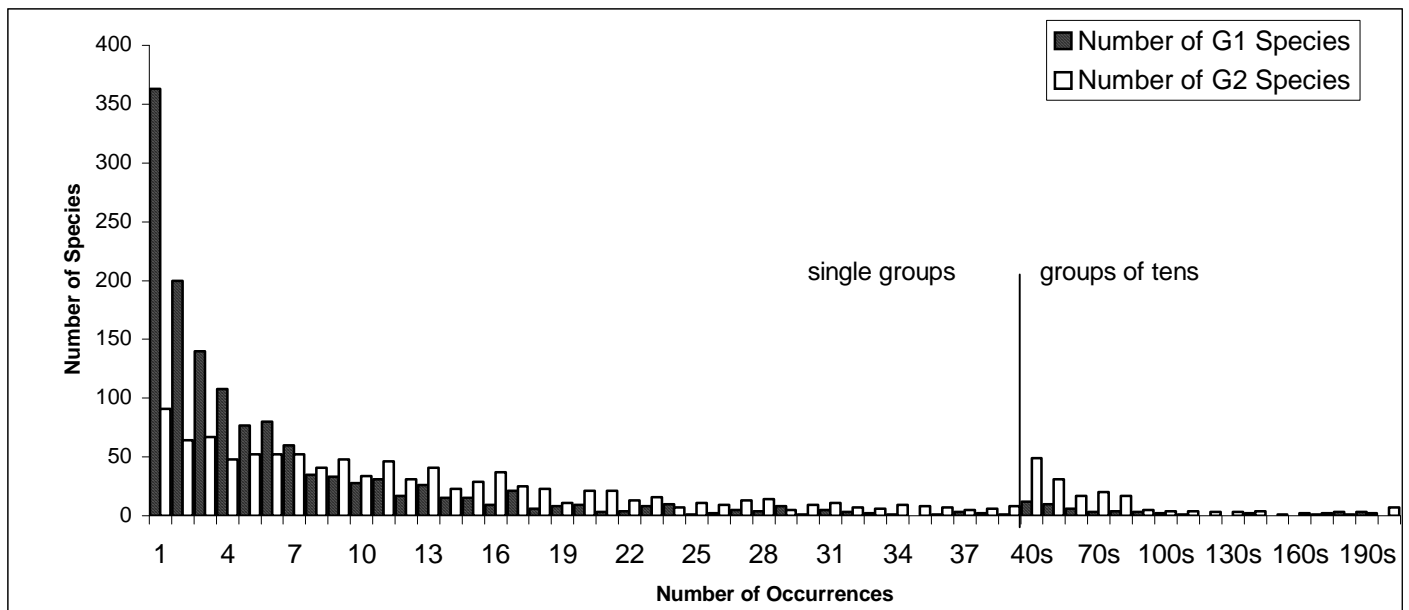
Figure 5.2. Changing risk of extinction with increasing numbers of populations. These probabilities are calculated using equation 5.1, assuming that extinction risk is uncorrelated and that all populations have the same probability of extinction, P_{ex}. Each line shows changing risk of total extinction, as a function of the number of populations, for a different per-population extinction probability.
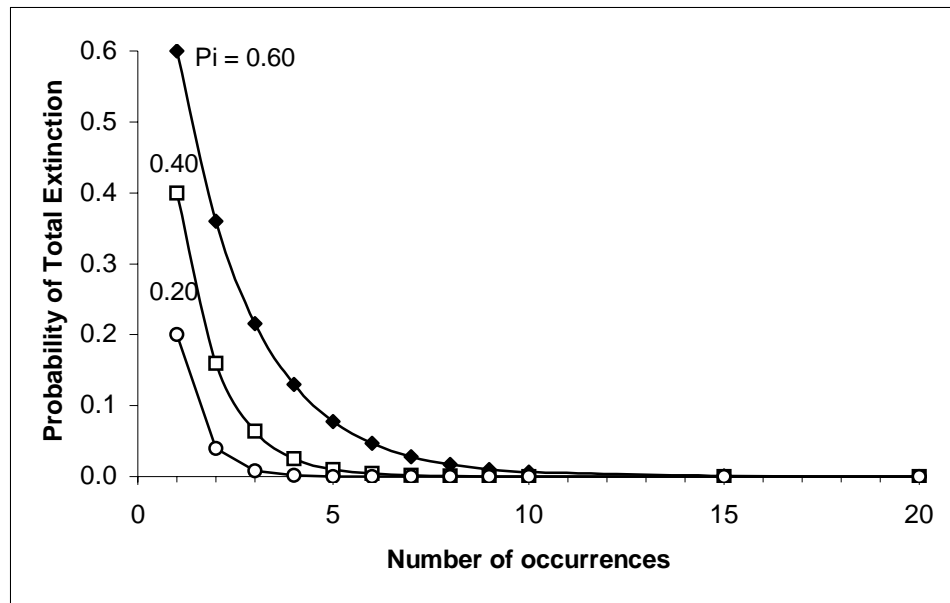
Figure 5.3. The safety of multiple occurrences given correlation in extinction rates. The probability of extinction over all populations is plotted versus the number of patches, for no correlation (open circles) and low (open squares), medium (filled diamonds) and high correlation (crosses). The probability that a single patch becomes extinct is 0.1 for all lines. Note that there is no single best way to add correlation in extinction rates; the degree of correlation and its pattern are outcomes of the biological and physical forces that cause extinction in each situation. For this example, we have used a simple functional form to add correlation in extinction risk[*]. However the pattern shown in the figure is very general; it doesn't depend upon the exact function used.
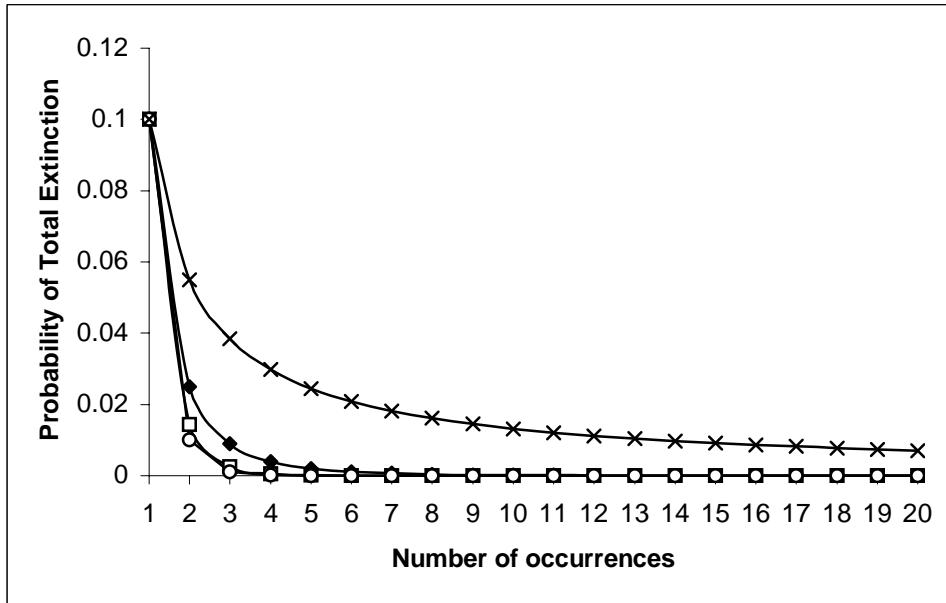
[*] In making this figure, we have assumed that the probability of extinction for a patch increases if other patches have already gone extinct. We estimate the extinction probability of M patches as: $P_{global} = \prod_{n=1}^{M} \left[1 - \frac{(1-P_1)}{1+a(n-1)^b} \right]$ (see equation 5.2). Here, P_1 is the probability that a single, isolated patch becomes extinct. The parameter a controls the overall strength of correlation, while b is a shape parameter, affecting the pattern of correlations (i.e., if more and more patches suffer extinction, is there a diminishing, linear, or accelerating influence on the extinction probabilities of remaining populations?). In this figure, we have assumed that b = 1 for all lines, while $a = 0$ for no correlation, and 0.05, 0.2 and 1 for low, medium, and high correlation, respectively.

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Figure 5.4. Factors influencing the extinction times of metapopulations with a finite number of local populations. A,B,C) In the simplest case (as described by equation B5.3.2), three factors influence the mean time to metapopulation extinction: A) mean lifetime of a local population (conversely, the probability of individual patch extinction); B) probability of colonization of empty patches; and, C) the number of habitat patches. (For each of these graphs, parameters that are not explicitly varied are held constant as: Colonization rate = 0.1, number of populations = 5, mean population lifetime = 20 years). D) Adding temporal correlation in the extinction probabilities for local populations can strongly influence metapopulation extinction times, with higher correlation (dark triangles) leading to much more rapid extinction even with a large number of local populations (modified from Harrison and Quinn 1989, figure 4).
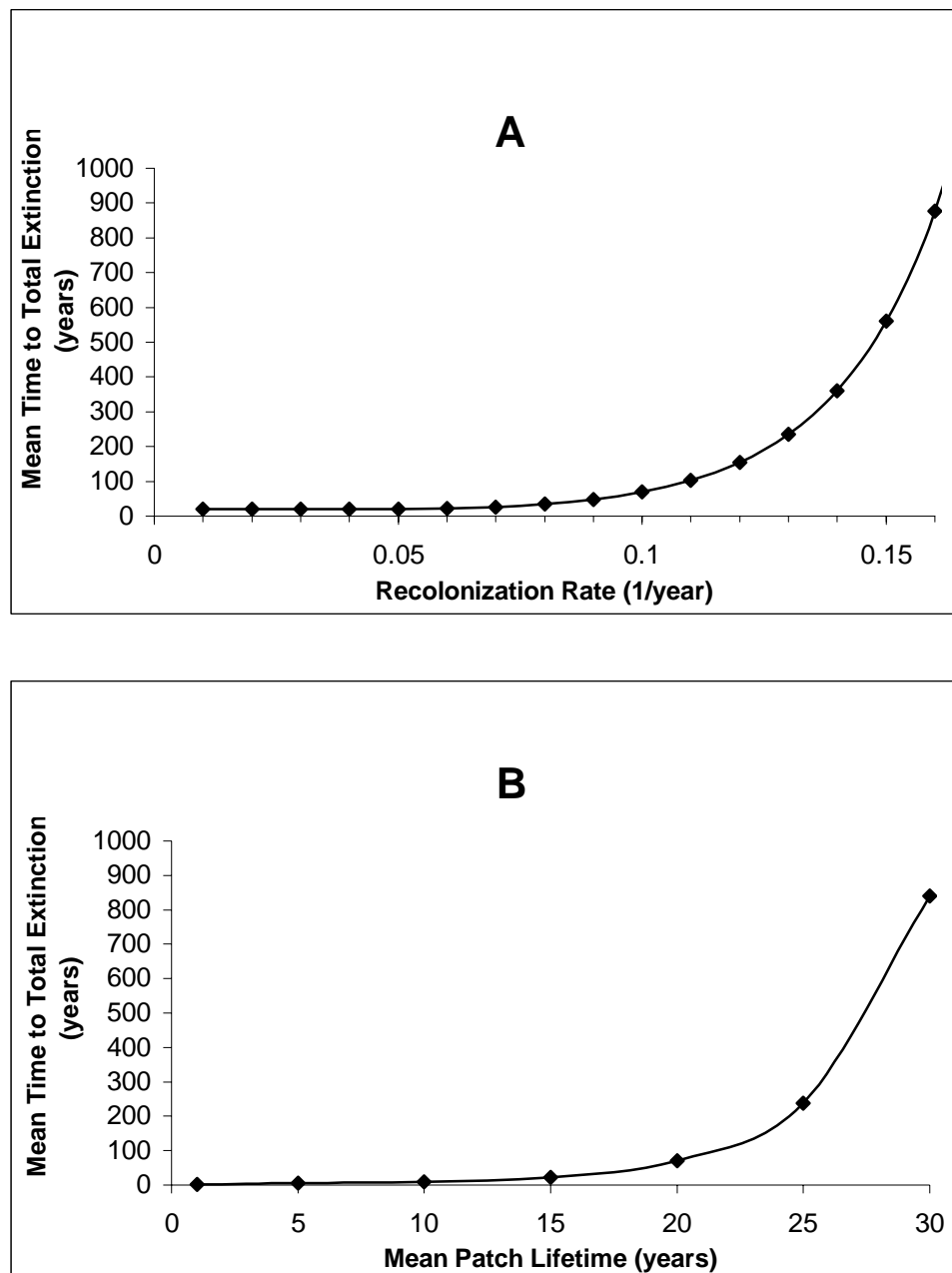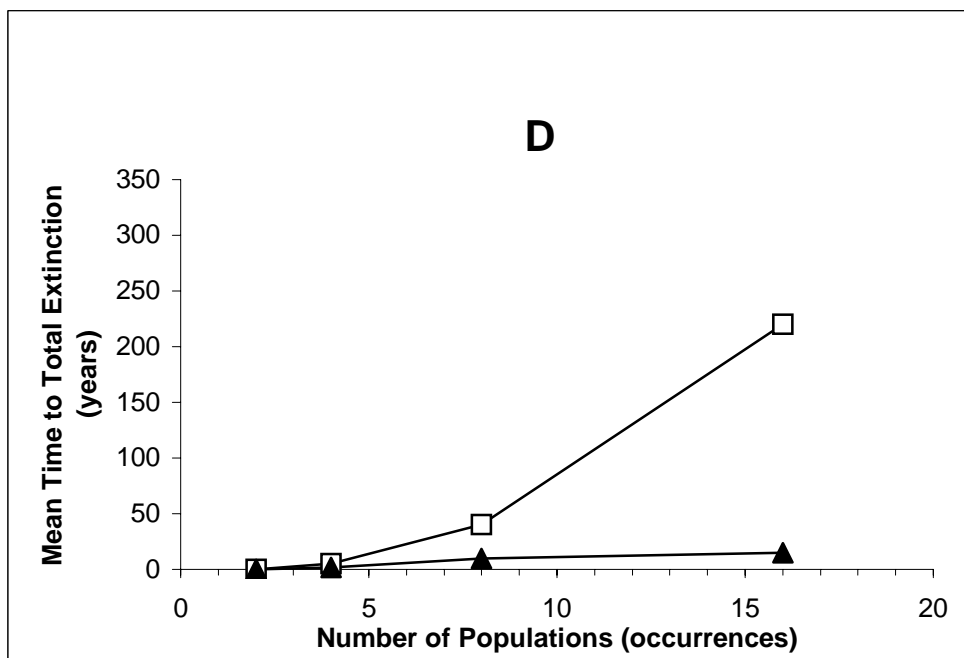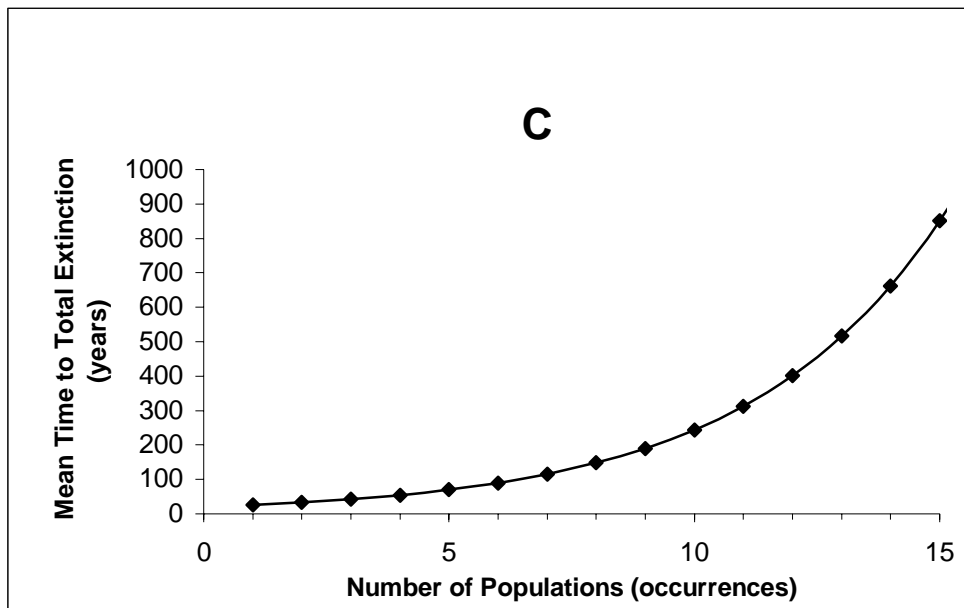
Fig. 5.4 (cont).

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CHAPTER SIX: MAKING MONITORING DATA USEFUL FOR VIABILITY ANALYSIS.

A recurrent problem in viability analysis is the difficulty of reaching clear conclusions based upon the data available. This is not a problem restricted just to TNC, North America, or even terrestrial habitats: the basic fact of rarity, plus the limited funding available for monitoring, make the collection of reliable ecological data on rare species difficult. However, the utility of monitoring data is often also limited because there is little thought given to how this information will or could contribute to viability assessment. This short-coming probably occurs because most discussions of monitoring strategies in the ecological literature are motivated by statistical considerations (e.g. reducing bias in estimates of population size) rather than by questions about the ecological processes, especially those generating variability through time, that will determine viability. Below, we discuss six points to consider in designing and implementing a monitoring program for species of concern. While we recognize that most monitoring plans are seeking data to fulfill a diversity of goals, the points and recommendations we give should for the most part be compatible with other goals, while also increasing the utility of data for viability assessment.

1) Especially when collecting census data, design a regular scheme for sampling across both time and space. As emphasized in Chapters 3 and 4, temporal variation is the driving force behind many extinctions, and thus monitoring data should allow a good estimate of temporal variation in population sizes. Additionally, for the viability of species with multiple occurrences, it is crucial to know how highly correlated fluctuations are across space (Chapter 5). A problem with many monitoring schemes is the inability to statistically untangle the spatial and temporal components

of population change. The easiest way to ensure that this dissection can be done is to have a regular sampling scheme (Figure 6.1). Generally, the ideal is to census every population every year. Given that this ideal is expensive, there are two reasonable alternatives: first, target some populations for sampling every year, and for all others have a regularly spaced, multi-year sampling plan (Figure 6.1A; note that the method of quantifying extinction risk we reviewed in Chapter 3 does not require censuses to be taken every year). This is the best plan if there are a few populations that are of particular importance, or that are undergoing important management that warrants more intensive sampling effort. Alternatively, put all populations on a multi-year plan (Fig. 6.1B). Note one important aspect of both the multiyear plans: *some* populations are sampled each year and each population is sampled at a regular interval. These features allow the monitoring to catch the effects of rare years that will affect some or all populations. Both these alternative scheme have obvious costs in terms of their ability to detect important events that will not affect all populations equally, or to provide accurate estimates of viability for each population. To minimize these costs, it is important to stratify the sampling regime over any known determinants of demography, such that some populations are sampled in each year that are both near and far from one another, that occur on each important substrate type, and in each microhabitat or geographic region.

2) Design short-term monitoring 'experiments' to estimate observation errors. To use monitoring information to estimate the temporal or spatial variation in population size or demographic rates, we must either know that there is very little observation error or, more realistically, have some estimate of this source of variation. By subtracting such an estimate from observed variation in census or demography data, we can make much more accurate estimates of true variation and

hence real extinction risks. The most practical way to quantify uncertainty in monitoring data is to occasionally perform several independent censuses in quick succession (say, over the course of a week); differences in the estimates over such a short time give an estimate of the variation due to observation uncertainty, which can then be removed from estimates of 'true' variation in population sizes from year to year or place to place. This error-checking procedure need not be performed often, but should be repeated at least once for both high density and low density populations, as observation errors can be proportionally much larger for sparser populations. While these rapid resamplings require extra time and effort, they can be combined with the field-training of new employees or volunteers in order to decrease this cost.

3) Question the trade-off of sampling accuracy versus number of sampling sites. With limited resources, all populations cannot be sampled with high accuracy all the time. However, this does not always mean that the most information will be gained by sampling only a few sites carefully. In many situations, the best monitoring program may involve less accurate sampling over more sites, increasing knowledge about the range of population numbers, demographic rates, etc. at the cost of less precise estimates at any one locale. This is particularly true if, following the last suggestion, some effort goes into the estimation of observation error, allowing its effects to be explicitly accounted for in estimates of true population variation and hence viability. However, even for quick and dirty monitoring, it is crucial for viability analysis to make clear quantitative estimates, rather than simply saying that "tens' or "hundreds" of individuals are present.

4) Combine initial, intensive demographic monitoring with subsequent, continuing population censusing. Much of the frustration and uncertainty over viability analyses that rely on population

count data comes because of all the biology that is ignored by such information. Furthermore, much of the difficulty of maintaining monitoring programs comes because of the expense of monitoring several different variables (e.g. seedling abundances as well as numbers of reproductive plants; number of singing males plus numbers of fledglings). Both these problems can be helped by combining initial demographic sampling with subsequent population monitoring. While not enough for a full demographic analysis, even two or three years of demographic data collection can greatly inform later, less intensive monitoring effort. Such demographic data collection will help one to pick the most informative variables for later monitoring. For example, such an analysis may show that flowering individuals are far more accurately counted and account for more variation in population growth than do seedlings, allowing subsequent data collection to be limited to a single, informative life history stage. Similarly, a small set of demographic data may show that it is easier, faster and more informative to monitor, say, the relative numbers of adults to subadults than it is to estimate the absolute numbers of either, making for more efficient long-term monitoring. Finally, intensive initial data collection provides what is essentially mechanistic information with which to understand future population patterns. For example, if later monitoring shows very high correlations in fluctuations between some populations, demographic knowledge can often lend insight into what life stages are being affected to create these correlations.

This type of combined strategy is of particular importance when performing management experiments, such as initiating experimental burn treatments, for two reasons. First, a change in the population's growth rate may be delayed in time relative to the onset of management, because the population's size or age structure will take time to adjust to the new demographic rates. Detailed demographic information would allow us to anticipate this delay, and not be

surprised when count data do not show a response to management over the short term. Second, combining the initiation of a management intervention with intensive demographic sampling can generate a great deal of knowledge about why a treatment does or does not work, while less-costly longer-term sampling can give the data needed to assess whether short-term effects translate into longer-term gains. In particular, this type of longer-term monitoring, with a regular pattern of temporal and spatial sampling, keeps attention on the interaction of management with natural environmental variations, crucial to the assessment of how management will influence viability.

5) Carefully quantify sampling effort. While this hackneyed admonition is by no means original, it is still important. Furthermore, the challenges of keeping track of sampling effort when using volunteers and a combination of highly trained and novice employees is not at all simple. The advice of many statisticians is to simply ignore information gained outside of a clearly defined sampling plan: this advice is foolish, which is why most field biologists ignore it. However, what can be done is to keep records of observations that clearly distinguish the hours put into monitoring by individuals of different experience levels, and to distinguish haphazard observations from structured ones. Just as important as quantifying overall monitoring effort is to keep separate the actual observations made by different types of individuals or methods of observation. Thus, it is better to distinguish who saw each individual turtle over a year of observations than to separately record which individuals were seen and the total effort of all kinds expended (e.g. if a visiting 5 year old sees an individually-marked turtle that has not been observed in 10 years of regular censuses, note that this is the circumstance that led to the

observation). This type of breakdown allows tests to see if sampling effort matters, or whether it is important to distinguish the type of observer.

6) Don't concentrate monitoring effort in only the best habitats. It is normal to set up monitoring plans that concentrate solely, or at least disproportionately, on the densest, apparently "best" parts of a population. There are at least three problems with this almost universal bias of ecologists. First, it implicitly assumes that areas with more individuals are those that are the best habitat -- the 'source' areas for a population. As Van Horne pointed out fifteen years ago (Van Horne 1983) this is likely to be untrue for many species. For animal species, areas with large numbers of successful, territorial adults may support lower densities than areas with "floater" juveniles. For plants, areas with high seedling establishment are not necessarily those areas with the highest subsequent survival and seed production. Second, monitoring only the best habitats can prevent us from obtaining any understanding of how population performance (growth rates and fluctuations) vary with habitat. This knowledge is obviously key to the design of restoration and recovery plans, and to deciding whether "marginal" EOs contribute significantly to regional persistence. A related idea is that we often don't know the full range of habitats for a species when a monitoring plan is established, and fully sampling the widest range of potential habitats stands the best chance of allowing later extrapolation to unsampled areas. Finally, concentrating sampling within the currently best habitat assumes that current patterns are static. If density and habitat quality vary over space and time, we may miss important information by an overly-concentrated sampling plan. While all these points suggest a more widely dispersed sampling plan than is usually implemented, there can be little point in a great deal of sampling in what

prior experience says are truly poor habitat areas. In this case, it may still be appropriate to sample low density areas through the use of quick presence-absence surveys.

Summary

Perhaps the most important point in trying to make monitoring programs more compatible with the estimation of population viability is to emphasize the estimation of *variation* as well as averages. This includes both spatial and temporal variation, as well as their interactions. A second point is to use a variety of sampling methods and intensities over time in order to direct and allow better interpretation of longer term monitoring. Because most of us have an intimate familiarity with only a handful of sampling and data analysis methods, we tend to formulate monitoring programs that use only one or two methods. Trying to broaden the set of tools used in monitoring can often greatly increase the usefulness of the data generated, as well as lessen the cost of the knowledge gained.

Figure 6.1. Two alternative monitoring plans, each with approximately the same total number of censuses performed, that ensure good estimation of temporal and spatial variation for viability analysis. In A, a single, presumably important, population (Population A) is singled out for monitoring every year, while all others are monitored every 3 years. In B, an equal number of populations are monitored each year, but each population is monitored every 2 years. Note that the first scheme still allows for regular, consistent sampling of all "less-critical" populations, even though this sampling is less frequent. This regularity is crucial for the estimation of variation patterns.

A.   Population:

Year:	A	B	C	D	E	F	G
1	X			X			X
2	X	X			X		
3	X		X			X	
4	X			X			X
5	X	X			X		
6	X		X			X	
7	X			X			X
8	X	X			X		
9	X		X			X	

Figure 6.1 (cont.)

B. Population:

Year:	A	B	C	D	E	F	G
1	X		X		X		X
2		X		X		X	
3	X		X		X		X
4		X		X		X	
5	X		X		X		X
6		X		X		X	
7	X		X		X		X
8		X		X		X	
9	X		X		X		X

CHAPTER SEVEN: REALITY CHECK: WHEN TO PERFORM (AND WHEN NOT TO PERFORM) A POPULATION VIABILITY ANALYSIS

Rare species are difficult to study, but as conservationists we are interested in them precisely because they are rare. Thus we constantly face the "Catch-22" that we have chosen to operate in an arena with limited data, yet we require *some* information upon which to base conservation decisions. Population viability analysis is only one way to arrive at such decisions (others include identifying and preserving critical habitat for species of interest, "rules of thumb" for the number of occurrences to conserve, expert opinions regarding population health, extrapolation based on historical extinctions of similar species, etc.). Given the urgent need to choose among these decision-making strategies, two questions arise: how much data do we need to perform a population viability analysis, and how often (that is, for how many species or EOs) will a critical amount of data exist to warrant a PVA?

Ballpark estimates for the minimum amount of data needed to justify a population viability analysis are given in Table 7.1. We admit up front that the data requirements in the table are largely a matter of opinion, and other population biologists would likely take issue with our particular choices. But all would likely agree that there is a continuum joining cases in which PVA is impossible and cases in which PVA is highly informative. Note that this table lacks a column entitled "Abundant Data", because this scenario is likely to be as rare as are the species we are trying to conserve. Two columns in the table are self-explanatory: the case of no data and the case in which sufficient data are available that most would agree PVA is useful. The other two columns are more challenging. First, we acknowledge that there will be cases (in fact, it's likely to be a large majority of cases – see below) in which sparse data exist but a

formal population viability analysis is simply not worth doing, and may even be detrimental. For example, if we have only 3 or 4 counts from a population, we could in principle use the method of Dennis et al. (1991) to estimate the parameters μ and σ^2, with which we could calculate measures of extinction risk (see Chapter 3). However, with only 3 censuses, the linear regression we would perform would use only 2 data points (the change in the counts over 2 inter-census intervals) to estimate 2 parameters. The estimates of μ and σ^2 that such a regression would yield would be highly uncertain, as would the resulting estimates of population viability. Using a quantitative analysis in this case is extremely risky, because it invites us to view as mathematically rigorous a viability assessment that is really not much better than a guess. But we also claim that where some data exist (the 3rd column in Table 7.1), we may gain more insight by performing a PVA than we do by forgoing formal quantitative analyses, provided that we view its conclusions as tentative and subject to updating as additional data become available. We discuss the reasons why below.

How frequently will sufficient data on a species or EO be available to make PVA a worthwhile pursuit according to our criteria (i.e. how common are the 3rd and 4th cases in Table 7.1)? The answer is, we don't really know. But we suspect that fewer than 5% of the species and EOs that must be considered in ecoregional planning efforts have been well-enough studied to allow quantitative analyses, and that the 3rd case in our table will be far more common than the 4th. Despite this speculation, we remain optimistic that population viability analysis can play a useful role in ecoregional planning efforts, for six reasons:

1) Sufficient data *do* sometimes exist. While data relevant to conservation will be perennially scarce, the despairing view that lack of data dooms all quantitative analysis is unwarranted. At least 5 of the 20 data sets submitted to the PVA workshop (see Table 2.1, Fig. 2.1) meet our

criteria for justifying a formal viability assessment (Table 7.1). Moreover, many participants in

the workshop stated that they knew of additional data sets in Heritage databases or personal files

that would meet the criteria, but had not previously considered them to be of use for quantitative

analyses. Indeed, one hope we have in preparing this handbook is that conservation practitioners

will realize that some analyses are in fact possible with limited data sets, and that they will scour

their data files and field notes for previously overlooked data.

2) Some PVA methods are quite easy to implement. Doing population viability analysis does

not require one to become initiated into the priesthood of mathematical population biology. For

example, all the analyses discussed in Chapter 3 can be handled by a few simple procedures in a

spreadsheet program such as Microsoft Excel. The speed and ease of such analyses make it hard

to justify *not* doing them to gain some insight into population viability when some data exist.

3) PVAs can be updated. Additional data are constantly being accumulated, in part as a result of

basic monitoring for rare species. Thus not only is the number of species that can be subjected to

quantitative analysis likely to increase, but the quality of previously-performed viability

assessments is likely to improve as additional information is incorporated. As we have

repeatedly emphasized, a strength of quantitative measures of viability not possessed by more

intuitive measures is that we can easily evaluate how the measures are affected by changes in our

assumptions (for example, if separate EOs are linked by migration, then viability assessments

made by assuming they are isolated will overestimate the risk of collective extinction; see

Chapter 5). Thus modest amounts of additional data (such as the discovery that there is *some*

migration among EOs, even if we lack estimates of its magnitude) quickly tell us at least the

direction in which to modify a previously calculated viability measure. Of course, more detailed

information (e.g. estimates of migration rates, or additional census counts) would allow us to actually update the quantitative measures directly.

4) <u>PVA informs the design of monitoring schemes</u>. Not only do monitoring data improve the quality of PVAs, but as we have emphasized in Chapter 6, PVAs can suggest ways to improve the usefulness and efficiency of monitoring. For example, projection matrices can tell us which life stages contribute the most to population growth; targeting those stages to the exclusion of less-important ones may be the most efficient sampling strategy.

5) <u>Viability assessment and management are connected</u>. The quantitative methods we use to conduct population viability assessment can do double duty by helping us to make management decisions. Projection matrices are the most useful in this regard, because they can tell us not only whether the population is on the decline, but which life stages and which demographic rates should be the foci for management efforts.

6) <u>PVAs have "strength in numbers"</u>. Quantitative analyses of well-studied species or EOs can inform us about related species or similar locations about which we have little or no data. The idea is that by building up a "library" of viability analyses, we may eventually be able to place rough bounds on population parameters (e.g. μ and σ^2, see Chapter 3) for groups of species that share similar life histories, or inhabit similar environments. We could then ask: "if we know only the current size of a population of interest, but we assume its parameters to be similar to those of ecologically similar species, what is its relative risk of extinction?" With such comparative approaches, viability assessments for relatively well-studied populations may aid us in making decisions about other, less-studied populations. With enough estimates of μ and σ^2 in our database, we may one day be able to bring more quantitative rigor to the process of assigning

EO ranks (A, B, C, and D) for populations about which we know only the life history of the organism, the environmental conditions, and the current population size.

While we are sanguine about PVA's potential, our concern is genuine that users of PVA must not be blind to the important caveats we have tried to raise throughout this handbook. To drive this point home, we review the most important ones below.

Important Caveats for Users of PVA:

1) *Viability assessments made with limited amounts of data will have wide confidence limits (i.e., low precision)*

Although in this handbook we have mainly discussed how to calculate direct viability measures (such as the probability of extinction over 100 years or the mean time to extinction), it is critical to remember that these are only estimates, and that associated with each estimate is a confidence interval that portrays the most likely *range* of values in which the "true" value lies, given the level of uncertainty in the available data. In general, the smaller the number of data points that went into the estimate, the wider the confidence interval will be. To have a true sense of what the data do (and do not) say about extinction risk, we should calculate and examine confidence intervals for our viability measures. While they lie outside of the scope of this handbook, some methods to calculate these confidence limits have been developed for count-based analyses (see Dennis et al. 1991) and for projection matrix models (see Chapter 7 in Caswell 1989).

2) *Observation errors in the data used to construct a PVA will influence its predictions.*

Errors in counting the number of individuals in a population, or in measuring demographic rates, will tend to inflate our estimates of year-to-year variability, and variability has a major effect on population persistence (see Chapter 3). In some cases, we may be able to partition the total variability in the data into observation error and true environmental variability (for example, if at

each census the population was sampled several times over a short period of time; see Chapter 6). But in most cases, the best we may be able to do is to be aware of the influence of observation error on our viability estimates, and to design future monitoring schemes in such a way that the magnitude of observation error can be estimated.

3) ***Rare events (either good years or catastrophes), although usually omitted from viability analyses, will affect a population's extinction risk.***

Most quantitative measures of viability ignore rare events, because there is simply no way to estimate their frequency or magnitude with limited data. When presenting viability estimates, we will almost always need to include the qualifier that we have not accounted for the potential impact of floods, fires, extreme storms, unusually favorable growing seasons, and other rare events.

4) ***Real density dependence, if ignored, will cause resulting viability assessments to be in error.***

Many viability assessments assume that the average population growth rate (e.g. λ in equation 3.1) is not influenced by population density (this is as true of the matrix models reviewed in Chapter 4 as it is of the simple count-based models in Chapter 3). At some level, this must be false; no population can grow forever without straining its resource base and thereby reducing its own growth rate. At the opposite end of the density spectrum, low-density populations may experience higher growth rates because competition for resources is weak, or lower growth rates if finding mates becomes difficult. The most common justifications for omitting density dependence are lack of sufficient data to fit a density-dependent model and the greater difficulty of deriving analytical expressions for extinction measures in models with density dependence. These and other justifications are summarized by Groom and Pascual (1998). Recent theoretical work (e.g. Middleton et al. 1995) is helping to address the second problem. But when lack of

data prevents us from evaluating density dependent models, we should at least be explicit about this potential source of error.

5) *Migration and environmental correlation among a set of populations will cause the extinction risk to differ from that of a suite of isolated, independent populations*.

If our data do not allow us to estimate rates of migration among populations, or the degree to which population fluctuations are correlated among populations due to shared environmental factors, we may be forced to ignore these complications (see Chapter 5), but we should *not* ignore how this omission might influence the predicted likelihood of collective extinction.

6) Genetics may exert strong effects on population viability.

As we noted in Chapter 2, while much of the literature on population viability has emphasized genetic problems and concerns, data sets for rare species almost never include genetic information. In most cases ignoring genetic processes will yield optimistic estimates of viability, since if inbreeding and inbreeding depression are significant they will act synergistically with environmental variation in driving small populations extinct (Gilpin and Soule 1986, Mills and Smouse 1994). However, the past tendency to dismiss some small populations as inherently inviable because of predicted genetic consequences is not justified (Lesica and Allendorf 1992, Lande and Barrowclough 1987). In the absence of genetic information, being aware of the optimistic effect on viability estimates of ignoring genetic effects may be the best we can do.

The Last Word:

Population viability analysis is attractive because it forces us to define what we mean by phrases such as "the long-term survival of all viable native species" (see TNC's mission statement, Conservation by Design), and because it provides a way to assess the likelihood of "long-term

survival" using current population data. But PVA does not provide answers to all of the

questions that will need to be addressed in designing ecoregional plans. We will often lack

sufficient data to avoid the simplifying assumptions discussed in the caveats above, and for many

species, population-level data will be completely absent. Nonetheless, PVA will help us to gain

insight into the extinction risks faced by populations for which we do have data, and those

analyses will help us to assess the viability of less well-studied populations and species.

Ongoing work in theoretical population biology is constantly leading to new tools for population

viability analysis. By using the tools of population viability analysis when data are available,

conservation practitioners might create a "demand" for new methods and techniques that would

spur theoretical population biologist to improve existing approaches.

TABLE 7.1: Approximate guidelines for when to perform a population viability analysis.

Type of data:	Description of available data:			
	No Data:	Sparse Data:	"Some" Data:	Moderate Data:
Census counts:	-	<6 years of counts	6-10 years of counts	>10 years of counts
Demographic information on individuals:	-	Demographic data on a *subset* of life stages for only 1-2 years	Demographic data on most life stages for 2-3 years	Demographic data on all life stages for 4 or more years
RECOMMEN-DATION:	**PVA NOT POSSIBLE**	**PVA NOT RECOMMEN-DED**	**PVA MAY OFFER SOME PROVISIONAL GUIDANCE**	**PVA PROFITABLE**

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