

7 The Problems and Potential of Count-Based Population Viability Analyses

B.D. ELDERD, P. SHAHANI, and D.F. DOAK

7.1 Introduction

The field of conservation biology is focused on protecting species, and thus populations, from declines leading to extinction. This goal is a clear one; however, knowing when a population is in danger of extinction is the tricky first step to any process of species protection. To evaluate the conservation status of a population, biologists increasingly use a suite of methods collectively known as population viability analysis (PVA; Beissinger and Westphal 1998; Soulé 1987). With these mathematical models, we can use data from a population to predict whether it is on average declining, recovering, or persisting at a fairly constant size. By quantifying variability in population growth and decline, these models can also yield predictions of various measures of extinction risk, including mean time to extinction and the ultimate probability of extinction.

For the most part, traditional methods of PVA involve the use of age- or stage-structured matrix models to project populations forward through time and to estimate population growth rates (e.g., Crouse et al. 1987; Menges 1990; Chap. 6, this Vol.). These models are particularly useful for PVAs, because they are built upon detailed biological knowledge of a target population and thus support sensitivity analyses that can help inform decisions about the life-stages and vital rates on which to focus our time and resources. However, with these advantages come heavy data requirements that make proper parameterization of matrix models difficult, or at times impossible (Beissinger and Westphal 1998; Chap. 6, this Vol.). Estimating growth rates for each age or life stage of the population is laborious, requiring careful and detailed work to enumerate the fates of individual plants – tagging and measuring plants of a range of stage classes, and repeatedly revisiting them to estimate transition rates for several years. Worse, especially for long-lived species, mortality rates are often difficult to estimate accurately with sample sizes that are adequate for the study of growth and reproduction, requiring even larger numbers of

plants to be followed. Finally, estimating recruitment rates generally requires setting up further experimental plots (i.e., seed addition experiments). Assembled into a population matrix, these demographic data are extremely useful in guiding effective management. However, this utility hinges on pre-existing data being available, or on the resources and time to conduct the fine-scale studies needed to acquire diverse demographic data. This latter situation is most common for plant studies, since few rare plants have been studied thoroughly enough to allow a full demographic characterization without further work.

Thus, in many circumstances, data limitations severely hamper our ability to use the usual demographic approach to PVA. As an alternative to this approach, population count data can be used to predict future population trajectories and to evaluate extinction risks through the use of diffusion approximation PVA models (Dennis et al. 1991). These models are highly useful in that the type of data that they require – counts of relative population sizes through time – are more commonly available and are easier (though requiring no fewer years) to gather when not already in hand. With census data on changes in the number of individuals in the population or some subset of the population, we can estimate the mean and variance in stochastic growth rate. By approximating population growth as a diffusion process, we can then make predictions about extinction risk using metrics such as the mean, median, and modal times to extinction, the median population size at some time in the future, and the ultimate probability of extinction (Dennis et al. 1991; Gerber et al. 1999; Morris et al. 1999; Chap. 6, this Vol.).

This general density-independent diffusion-approximation (DA) method of PVA, elucidated by Dennis et al. (1991), holds considerable promise as a way to rigorously analyze population viability when demographic approaches are not feasible. However, its usefulness as a conservation planning tool relies upon numerous poorly explored factors, including the length of the time series available and the reliability of census estimates. Use of this method (Nicholls et al. 1996; Lima et al. 1998; Gerber et al. 1999), as well as attacks on its utility (Ludwig 1996, 1999; Fieberg and Ellner 2000), have become increasingly common but there are still few accessible reviews of the approach or syntheses of the method's problems and potential. In this chapter, we will first describe the basic DA approach, and then assess the quality of results it provides, evaluating and addressing some of the criticisms that it has faced in recent years. We will also ask how this approach performs when faced with a common problem for many plant species, the presence of an important but unseen life stage such as seeds in a seed bank.

7.1.1 A Genealogy of Count-Based PVA

The construction and use of population dynamic models has a long history, with many mathematicians and ecologists contributing advances and techniques that have enabled the development of diffusion-based extinction-time models. Here, we present a brief history of some of the work that contributed most directly to the formulation of the density-independent diffusion-based PVA models on which we focus. (We encourage readers who are totally unfamiliar with these methods and models to skip straight to the next section, which describes how to implement the approach.)

The first stochastic population model that seems to have contributed substantially to the formulation of current diffusion-based models was developed by Feller in 1939 (translation appears in Oliveira-Pinto and Conolly 1982). This model drew attention to the importance of considering temporal variation in birth and death rates for making population projections. Later models were used to predict extinction probabilities for populations with this kind of demographic stochasticity in birth and death rates (Kendall 1949).

Goel and Richter-Dyn (1974) demonstrated that, for unstructured populations, such discrete birth-death processes could be approximated by a continuous diffusion process (a random walk approximation with random deviations around a central tendency to grow or shrink), allowing more powerful mathematical analyses to bear on the prediction of extinction risk and timing. Several diffusion-based models were then developed that incorporated either environmental and/or demographic stochasticity into the population growth process (Gillespie 1972; May 1973; Capocelli and Ricciardi 1974; Karlin and Levikson 1974; Turelli 1978; Leigh 1981; Tier and Hanson 1981). Three of these models also included methods to derive extinction time estimates as a function of variance in either birth and death rates (Leigh 1981) or population size (Capocelli and Ricciardi 1974; Leigh 1981; Tier and Hanson 1981) and have contributed substantially to the development of diffusion process models used for PVAs today.

Parallel to this development of unstructured models (models that do not include age- or stage-based differences between individuals) to predict extinction times, a rich literature developed on how stochastic variation in age-specific demographic rates would influence the behavior of matrix models (Cohen 1977, 1979; Tuljapurkar and Orzack 1980; Tuljapurkar 1982). Of particular importance was work by Tuljapurkar (1982) that provided approximations for the mean and variance of stochastic population growth for matrix models. This development allowed the behavior of complex populations, with their stage-specific demographic rates (including means, variances, and correlations between the variability in these rates), to be summarized in the same measures of population change used by simple, unstructured models for extinction times.

Lande and Orzack (1988) used these more biologically realistic age-structured models to test how well unstructured diffusion process models represent the dynamics of populations with complex life histories. In particular, Lande and Orzack (1988) showed that the mean and variance in growth rate of an age-structured population, approximated by Tuljapurkar's method, are similar to the estimates derived if the population is "simplified" and modeled by a diffusion process such as that developed by Capocelli and Ricciardi (1974). The use of the diffusion process allows for the calculation of all the extinction risk measures previously computable for only very simple models of population growth. In other words, Lande and Orzack (1988) showed that an estimate of overall population dynamics, which can be derived from simple census data (repeated counts of all or part of a population across several years), could be used to give good approximations of the growth rate and extinction risk of a complex, stage-structured population.

7.1.2 The Basics of Count-Based PVA

Although the theoretical developments just described created the potential to use DAs of population growth to assess extinction risks from count data, a clear set of methods to do so was still lacking. Dennis et al. (1991) (and similar work by Braumann 1983) made these mathematical advances useful in conservation biology by showing how to arrive at unbiased maximum likelihood estimates of mean instantaneous stochastic growth rate (μ , the stochastic equivalent to r in a deterministic exponential growth model) and variance in stochastic growth (σ^2) using simple linear regression methods*. While the method of Dennis et al. (1991) ignores the effects of demographic stochasticity, it incorporates the generally more important effects of environmental stochasticity. Of particular importance is that the method can also handle complications arising from unequally spaced population counts, as well as other potential problems associated with real data sets (Dennis 1989). These developments have yielded a method of conducting PVA that is straightforward and uses the type of data that are most often collected on species of conservation concern (Morris et al. 1999).

Using a series of three steps, the DA method of Dennis et al. (1991) translates population count data into predictions of growth rate and extinction risk. As an example, consider a hypothetical population of Hooker's fairybell (*Disporum hookeri*), a common lily (Table 7.1). Values for μ and σ^2 are esti-

* In a technical sense, Dennis et al. (1991) uses a diffusion process based on simple Brownian motion to describe the population trajectory of a density-independent population for which numbers are driven by both an underlying growth rate and by environmental stochasticity. The method uses simple census counts and regression analysis to estimate the infinitesimal mean and variance of this diffusion process, defined as μ and σ^2 .

mated by first transforming census data (dates and population counts) so that they can be described by a linear model of the rate of population change across a time interval versus the length of the time interval. In particular, raw census data should be transformed using the following equations:

$$x = \sqrt{t_j - t_i}$$

$$y = \frac{\ln(N_j - N_i)}{x}$$

where N_i and N_j are adjacent census counts from years t_i and t_j . Thus, x is a measure of the time elapsed between two censuses and y is a measure of population growth over this interval (Table 7.1). These transformations are necessary to equalize the variances in population growth over intervals of different lengths, allowing a regression of y on x to fit the assumptions of a simple linear model. Indeed, the next step is to perform a linear regression of y on x (setting the y -intercept at zero; no growth can occur with no change in time), which yields estimates of μ and σ^2 . The slope of the best-fit line gives an estimate of μ , and the variance of the individual data points about this line gives an estimate of σ^2 (Fig. 7.1; Dennis et al. 1991). From a standard regression table, the slope, or μ , is thus given by the regression coefficient (or x -coefficient), and the variance, or σ^2 , is given by the mean square residual from the regression analysis. For the Hooker's fairybell data, $\mu=0.085$ and $\sigma^2=3.22$.

Table 7.1. Census data for a hypothetical population of *Disporum hookeri*. Here, x is a transformation of the time intervals between censuses ($x = \sqrt{t_j - t_i}$), and y is a log-transformation of population growth between two censuses ($y = \ln(N_j - N_i)/x$). Note the skipped years, which lead to larger values of x

| Year | Count | x | y |
|------|-------|----------|----------|
| 1982 | 129 | | |
| 1983 | 341 | 1 | 0.97207 |
| 1985 | 597 | 1.414214 | 0.396004 |
| 1986 | 172 | 1 | -1.24442 |
| 1989 | 356 | 1.732051 | 0.419986 |
| 1990 | 142 | 1 | -0.9191 |
| 1991 | 476 | 1 | 1.209591 |
| 1992 | 9 | 1 | -3.96819 |
| 1994 | 477 | 1.414214 | 2.80742 |
| 1995 | 934 | 1 | 0.67196 |
| 1996 | 198 | 1 | -1.55121 |
| 1997 | 465 | 1 | 0.85377 |

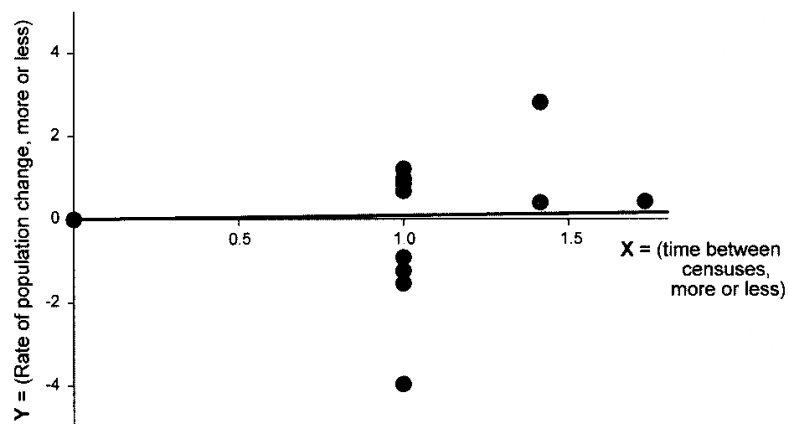


Fig. 7.1. Linear regression of y on x for Hooker's fairybell data, where y is the log-transformation of population growth between two censuses, and x is a transformation of time between censuses (equations given in text). The slope of the regression line gives an estimate of μ for the population, and the scatter of points about this line gives σ^2 ; these values are then used for further calculations in the diffusion approximation (DA) method

These values, together with a starting population size and pseudo-extinction threshold (the population size at which the population is considered critically endangered or essentially extinct), can be used to calculate various extinction risk measures. Incorporating information on the number of censuses and the length of the time series of data (in years) also allows calculation of confidence intervals about the estimates (Dennis et al. 1991). For Hooker's fairybell, we chose a starting population size of 465, which was the size of the population in the last census, and a pseudo-extinction threshold of four individuals. Conducting the various calculations described by Dennis et al. (1991) using these values yields an ultimate probability of extinction of 0.76, a mean time to extinction of 56 years, and a median time to extinction of 13 years for those trajectories in which the population does go extinct. Thus, this population has a fairly high probability of extinction, and extinction is likely to occur fairly soon; if this was a rare species, we might decide to invest effort into managing this population for recovery. The full results of the approach are best summarized by the cumulative distribution function (CDF) of extinction times (Fig. 7.2). Such a CDF can be used to infer values for multiple extinction measures, such as median time to extinction and the probability of extinction by a given time (100 years, for example). For more information on how to perform the calculations to yield these extinction risk estimates, see Dennis et al. (1991) and Morris et al. (1999). As noted above, the method of Dennis et al. (1991) yields not just these best-fit predictions, but also confidence intervals around all estimates, allowing careful assessment of

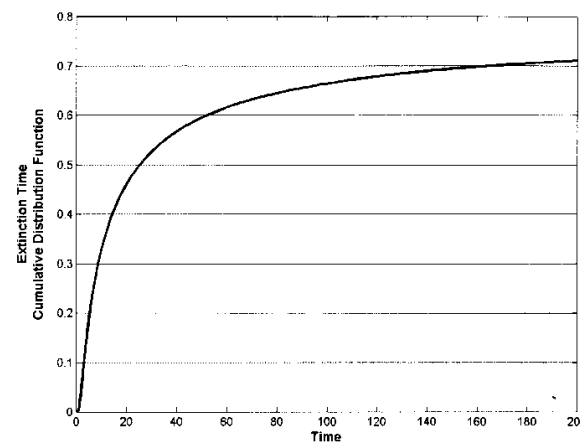


Fig. 7.2. Cumulative distribution function (CDF) for the probability of extinction for Hooker's fairybell. The line shows the probability of extinction on or before a certain time in the future. Here, we present the uncorrected CDF, which asymptotes at the ultimate extinction probability for the population (=0.76 in this case). Note that many authors present the conditional extinction time CDF, which shows the probability of extinction on or before a certain time *conditional* on extinction ever occurring. These conditional CDFs must asymptote to 1.0

our confidence in the extinction predictions generated by the DA (e.g., Gerber et al. 1999). Recent work by Holmes (2001) extended this method by providing new estimation methods for DA modeling when observation errors are especially high.

7.1.3 Problems and Criticisms of the DA Method of PVA

The minimum amount of data required and ease of parameterization of the DA model are major advantages that enable its use in the wide variety of situations in which only census data are available. The DA method is thus becoming increasingly popular, with rapid growth in the number of studies implementing it to estimate extinction risk. It has now been used to assess the viability of populations of over 60 different species in published studies (see Table 7.2), and many more in unpublished work. Interestingly, almost all of these applications have been restricted to mammalian and avian taxa; the only exceptions to this that we are aware of are its application to predict viability for a single plant population (Knowlton's cactus, Morris et al. 1999).

Despite this growth in popularity, there are a number of limitations to the DA method of PVA. The model assumes that annual population growth rates are log-normally distributed (or equivalently, that instantaneous per capita

Table 7.2. Examples of uses of the diffusion approximation (DA) method of population viability analysis (PVA) in recent studies

| Species | Years of data | Source |
|---------------------------------------------------|---------------|----------------------------|
| Mammals | | |
| Alabama beach mouse (2 populations) | 7–11 | Oli et al. (2001) |
| Blue wildebeest | 10 | Nicholls et al. (1996) |
| Cricetidae rodent (<i>Akodon olivaceus</i>) | 5 | Lima et al. (1998) |
| Cricetidae rodent (<i>Phyllostis darwini</i>) | 5 | Lima et al. (1998) |
| Didelphidae marsupial (<i>Thylamys elegans</i>) | 5 | Lima et al. (1998) |
| Eland | 10 | Nicholls et al. (1996) |
| Giraffe | 10 | Nicholls et al. (1996) |
| Grizzly bear | 29 | Dennis et al. (1991) |
| Impala | 10 | Nicholls et al. (1996) |
| Kudu | 10 | Nicholls et al. (1996) |
| North Pacific gray whale | 19 | Gerber et al. (1999) |
| Perdido Key beach mouse (2 populations) | 7 | Oli et al. (2001) |
| Roan antelope | 10 | Nicholls et al. (1996) |
| Sable antelope | 10 | Nicholls et al. (1996) |
| Tsessebe | 10 | Nicholls et al. (1996) |
| Warthog | 10 | Nicholls et al. (1996) |
| Waterbuck | 10 | Nicholls et al. (1996) |
| White rhinoceros | 10 | Nicholls et al. (1996) |
| Zebra | 10 | Nicholls et al. (1996) |
| Birds | | |
| Breeding birds (35 spp. in the UK) | 11–19 | Gaston and Nicholls (1995) |
| California condor | 16 | Dennis et al. (1991) |
| Central Florida Red-cockaded woodpecker | 12 | Morris et al. (1999) |
| Kirtland's warbler | 39 | Dennis et al. (1991) |
| Laysan finch | 20 | Dennis et al. (1991) |
| Lesser prairie chicken | 12 | Morris et al. (1999) |
| North Carolina Red-cockaded woodpecker | 11 | Morris et al. (1999) |
| Palila | 19 | Dennis et al. (1991) |
| Puerto Rican Parrot | 21 | Dennis et al. (1991) |
| White stork | 16 | Engen and Sæther (2000) |
| Whooping crane | 51 | Dennis et al. (1991) |
| Plants | | |
| Knowlton's cactus | 11 | Morris et al. (1999) |

growth rates are normally distributed) and that the “noise” of environmental stochasticity is small, without catastrophes or other large changes in population growth rates from year to year. However, the distribution that the growth rate takes will vary depending upon the biology of the species being studied and the range of environmental variation that it faces. In particular, assuming that population growth rates should conform to a normal distribution omits

the possibility of infrequent years that are catastrophes or bonanzas, which can have extreme effects on population dynamics, despite their infrequency (Mangel and Tier 1994; Ludwig 1996, 1999; but see Lande 1993 and Mangel and Tier 1993 for models that include catastrophes). Second, the model assumes that population growth in one time interval is not correlated with subsequent growth. However, in nature it is very common that environmental conditions correlate through time – for example, in many parts of the world droughts occur in prolonged sequences. Even more basic, the age or stage structure of a population provides a record of recent events that will always create some autocorrelation in population dynamics (Lande and Orzack 1988). Third, the model is density-independent, while either positive or negative density dependence clearly operates for many populations. Elaborations of the basic DA approach have been developed that deal with some of these problems. These include models that incorporate the effects of density dependence (Turchin and Taylor 1992; Turchin 1993; Dennis and Taper 1994; Foley 1994), catastrophes (Lande 1993; Mangel and Tier 1993), and spatial structure (Possingham and Davies 1995). Even though these models guard against some of the most obvious problems in the simple DA approach, they do so with the cost of heavier data demands and incomplete predictions of extinction-time distribution. Although some of these potential pitfalls have been addressed, particularly the use of bootstrapped simulations to provide parameter estimates for density-dependent populations (Dennis and Taper 1994), the limitations and complexity of these methods make them much more difficult to use or interpret with the sparse data usually available in conservation settings especially with respect to extinction time estimates. Due to these limitations, and given that many threatened species are likely to experience relatively density-independent growth, throughout the rest of this chapter we will focus solely on the use and analysis of the basic density-independent DA approach, evaluating its ability to accurately predict population growth rates and extinction times for plant populations.

A particular problem in using the DA method for plants is the invisibility of most seed banks. The DA method does not require absolute population counts, but does presume that a constant fraction of the total population is counted each year, so that measures of changes in the observed population accurately estimate rates of total population change. However, if a radically different fraction of the entire population is uncounted seeds versus counted adult plants in each year (as will be true for many annuals, in particular), the resulting estimates of population growth rates can be highly inaccurate, potentially skewing estimates of extinction risk. The challenges that seed banks may pose to PVA have been raised by previous authors (Higgins et al. 2000; Efford 2001; Doak et al. 2002; Chap. 6, this Vol.) but thus far, explorations of this issue have left more questions than answers.

While all of these issues are potentially important, it is not clear whether any of them doom the utility of the DA model. Like any other model, DA

approaches simplify the real complexity of population dynamics, but this does not necessarily make them less useful. However, more fundamental aspects of the DA model have recently received criticism, calling into question the general usefulness of this method for predicting extinction risk. As Ludwig (1996, 1999) pointed out, it is difficult to know how much variation in population growth rate from year to year is due to the effects of environmental stochasticity versus observation error. Ludwig (1999) condemned the DA method primarily for this reason, claiming that this problem creates extremely wide confidence intervals around extinction risk estimates, rendering them largely unusable. He also criticized the lack of density dependence in the DA model, claiming that this both biases estimates of the population growth rate and artificially decreases the breadth of the confidence intervals around these estimates (Ludwig 1999).

Fieberg and Ellner (2000) examined the DA model to determine how much data would be needed to derive useful estimates of extinction probability. They found that the model's predictions of extinction probability over 100 years are highly sensitive to changes in the mean population growth rate (r where r is stochastic population growth on the log scale, with mean μ and standard deviation σ). Because of this need for accuracy in estimates of r , they conclude that (even with perfect data) predictions of extinction probability can only be reliably made for very short time horizons – 10–20% of the number of years that censuses were conducted – making the DA model of extremely limited value in predicting extinction risk.

However, the work of other authors counters some of these criticisms. Meir and Fagan (2000) explored the impact of observation error in population counts in degrading the accuracy of extinction predictions. They partitioned this error into two types: bias in measurements (leading to systematic over- or underestimates) and random error in measurements. They found that overestimation bias has little effect on predictions of extinction dynamics, with 400% overestimation required to create significant error in predictions of extinction probability. The patterns for underestimation bias and for random observation error are also encouraging; it is only when both the population growth rate and the variance due to stochasticity are low that extinction probability predictions may deteriorate in quality. So, for scenarios in which there is little risk of extinction (high r), or a high risk of extinction (low r and high σ), predictions of extinction risk do not suffer when data includes random observation error. However, in more ambiguous cases (low r and low σ) we may need to be more cautious in our interpretation of model results, as they are much more sensitive to observation error. This difference in the results obtained by Fieberg and Ellner (2000) and Meir and Fagan (2000) is likely due to the specific scenarios that they examined and the questions they asked. Fieberg and Ellner (2000) focused on the more ambiguous cases, in which r is zero or close to zero, and σ is also low. Meir and Fagan (2000) examined a wider range of scenarios, and while they did find results similar to Fieberg

and Ellner's for populations with low r and low σ values, they found more positive results for other scenarios. In addition, Meir and Fagan only explored the effects of observation error on relative predictive power, and did not examine the absolute accuracy of extinction predictions (with or without observation errors).

In a second defense of PVA models, Brook et al. (2000) responded to critiques of Ludwig and others by analyzing the performance of demographic stage-structured PVA models, comparing model predictions to the actual trajectories of populations after the end of the data collection period used to parameterize the models. They found that, for the most part, true population trajectories correlate well with PVA predictions. This result is encouraging and suggests that, at least when comparing a range of populations with differing dynamics, PVA models may do a good job of ranking relative risk or general population trends. These demographic PVA models, while more complicated than DA models, share many of the same simplifying assumptions, and these results indicate that these features do not doom the resulting predictions to be hopelessly biased or imprecise.

Taken as a whole, the past literature provides some support for the utility of the DA approach, but still suggests that without a long time-series of data the predictions of DA models may either be uselessly broad or quite inaccurate. However, the analyses that have come to these conclusions have generally asked about the exact precision of the model predictions, which is at best a poor approximation to the way PVA results are most often, or at least most reasonably, used. More often than not, DA models have been used to make more qualitative judgements of risk, to assess relative risk of different populations, or to evaluate the effectiveness of conservation efforts on a whole host of species in a protected or managed area (Table 7.2). Additionally, efforts to ascertain the reliability of the method have only analyzed the forecasting of extinction risk based on estimation of μ and σ^2 . In doing so, these approaches have overlooked the fact that much of the variability in extinction risk comes from differences in initial population size, the third piece of information that comes from a set of count data. Finally, past work has generally not asked about specific life history features that may hinder or aid the utility of the DA method.

Next, we describe the modeling approach that we used to address these questions. Unlike past work that evaluates the absolute accuracy of DA estimates, we emphasize the comparative use of DA results (which of a suite of populations has the highest, and which the lowest, growth rate or extinction risk?). We also try to better simulate the use of data sets by real practitioners; in particular, we include initial population size (the final size of the census data available) as a piece of information to be gleaned from census data and used to project future risk. Finally, we look at the problem of unseen life history stages such as seed banks, that may alter the utility of DA-based PVAs for plants.

7.2 Methods

To examine whether the DA approach can provide useful information when based upon a reasonable amount of data, we constructed a simulation model to compare DA predictions with a known population process. This modeled or “true” population is stage-structured and is governed by a density-independent stochastic transition matrix. All simulations were initiated with 500 individuals arranged in the stable stage class vector for the mean matrix of that simulation. Both survival and fecundity rates were allowed to vary between years according to assigned means and variances. Matrix elements involving growth and survival were drawn from a beta distribution (i.e., a probability distribution bounded by 0 and 1), and fecundity rates from a log-normal distribution. In all simulations we bounded total survival in each year of each class by 1.0, proportionately rescaling the stochastically chosen matrix elements for a stage if their sum exceeded one. The correlations between the vital rates of the population were also varied. We report results for simulations using a correlation coefficient of either 0.08 or 0.80 between all variables.

Each simulation consisted of an initial 50-year “past” period, over all or part of which census data were collected to estimate future viability, followed by a “future” period in which we continued to simulate the population to observe its fate. The future period was set at 50 years, or until the population hit a pseudo-extinction threshold of four individuals, for all simulations. We chose a 50-year time horizon to predict population performance as this seems a reasonable period over which to make management decisions and over which useful predictions of population health might be possible.

All simulations reported here are based on survival and fecundity estimates for a perennial monocot, *Calochortus obispoensis* (Fiedler 1987), whose estimated vital rates yield a deterministic rate of increase (λ) of 1.02 (Table 7.3). To evaluate how well the DA method can predict extinction risk under a range of different circumstances, we tested its performance using “true” populations that spanned a range of growth rates but were all based upon *C. obispoensis* vital rates. To create differing population dynamics, we altered both the mean and variance of a single matrix element ($a_{2,2}$, the survival, without growth, of stage class 2; Tables 7.3, 7.4). The nine resulting matrices differ in both the mean and variability of population growth (Table 7.4). In particular, the range of variances used yielded populations that differed in their annual dynamics, from populations that experience very little change in stage 2 survivorship ($a_{2,2}$) from year to year, to others that experience high variation in stage 2 survivorship between years (with very good years and very bad years being more common than “moderate” years).

Each set of simulations consisted of 5,000 runs using a single combination of the mean and variance in $a_{2,2}$. We varied the number of annual censuses upon which viability predictions were made from 5 years to 50 years. To gen-

Table 7.3. The average matrix (± 1 standard deviation) for *Calochortus obispoensis* derived from Fielder (1987). The mean and variance of the $a_{2,2}$ matrix element (in bold) were varied away from these estimated values to create simulations with differing dynamics (see Table 7.4)

| | | From stage: | | | |
|-----------|---|--------------|----------------------|--------------|--|
| | | 1 | 2 | 3 | |
| To stage: | 1 | 0 | 0 | 1.73 (1.493) | |
| | 2 | 0.50 (0.490) | 0.95 (0.0141) | 0.60 (0.346) | |
| | 3 | 0.03 (0.045) | 0.03 (0.0141) | 0.38 (0.353) | |

Table 7.4. Parameters varied factorially (census period, demographic rate, and variance) for comparing diffusion approximation estimates to model growth rates and extinction times. The λ for the average matrix (a) as well as the population μ and σ^2 (b, c) are shown for all combinations of mean $a_{2,2}$ and $\text{Var}(a_{2,2})$

| a. | | | |
|------------------------|---------------------------------|--------------------------------|----------------------------|
| Census periods (years) | Mean demographic rate $a_{2,2}$ | Variance $\text{Var}(a_{2,2})$ | λ (average matrix) |
| 5 | 0.8750 | 0.0002 | 0.9605 |
| 10 | 0.9314 | 0.0054 | 1.0074 |
| 20 | 0.9596 | 0.0119 | 1.0314 |
| 50 | | | |

| b. | | | |
|----------------|---------------------------------|---------------------------------|---------------------------------|
| μ | | | |
| Mean $a_{2,2}$ | $\text{Var}(a_{2,2})$ 0.0002 | $\text{Var}(a_{2,2})$ 0.0054 | $\text{Var}(a_{2,2})$ 0.0119 |
| 0.8750 | -0.118 | -0.138 | -0.156 |
| 0.9314 | -0.012 | -0.045 | -0.065 |
| 0.9596 | 0.030 | -0.006 | -0.022 |

| c. | | | |
|----------------|---------------------------------|---------------------------------|---------------------------------|
| σ^2 | | | |
| Mean $a_{2,2}$ | $\text{Var}(a_{2,2})$ 0.0002 | $\text{Var}(a_{2,2})$ 0.0054 | $\text{Var}(a_{2,2})$ 0.0119 |
| 0.8750 | 0.072 | 0.125 | 0.177 |
| 0.9314 | 0.057 | 0.096 | 0.148 |
| 0.9596 | 0.048 | 0.083 | 0.143 |

erate the same distribution of population sizes at the junction of the past and future parts of the simulations (i.e., the initial population size for predictions of future viability), regardless of the census interval, we always simulated 50 past years, as noted above. Census data were collected for the appropriate number of years prior to year 50 of the simulation. For instance, a 5-year census would be conducted from year 46 to 50 in the simulation whereas a 10-year census period would include years 41 to 50.

During the census interval, the model stores accurate census data for the population each year. To estimate the population's growth rate, its probability of extinction for 50 years, as well as the population's mean, median, and modal times to extinction we used the techniques outlined by Dennis et al. (1991). These estimates were then compared to the "true" population's behavior for each simulation. Note that in estimating extinction risks we used the census data not only to calculate μ and σ^2 , but also to assign an initial population size (the final population size censused).

We also examined whether the DA method can accurately rank the relative viability of a suite of populations that do in fact differ in risk. To compare real and estimated rankings of viability, we simulated 5,000 sets of nine different populations whose growth rates were determined by separate combinations of the demographic and variance parameters in Table 7.4. We then used Spearman rank correlations to compare the ranks of the estimated stochastic population growth rates (μ) with the ranks of the realized growth rates and, similarly, the rankings of the predicted median extinction times and the realized extinction times. For all populations that did not go extinct during the simulation or whose predicted time to extinction was greater than the 50-year forecast period, we set extinction time to 51 years before conducting the Spearman rank analysis, making these values ties.

To explore the effect of unseen seed banks on the accuracy of extinction risk predictions, we ran further simulations treating the smallest size class (stage 1 in Table 7.3) as an invisible stage that could not be censused. In *Calochortus obispoensis* this smallest stage is in fact composed of small, grass-like plants, not seeds, but for our exploration of an unseeable stage, this difference is not important. In exploring the effects of an unseeable class on DA predictions, we first used the original parameter estimates from Fiedler (1987). We then tested four modifications of the basic matrix that included: (1) allowing persistence of stage 1 individuals by setting $a_{1,1}=0.5$ and reducing $a_{2,1}$ to 0.3; and/or, (2) decoupling variations in stage 1 demography from other stages by setting correlations between stage 1 rates ($a_{1,1}$, $a_{1,2}$, and $a_{1,3}$) and all other rates equal to zero.

7.3 Results

7.3.1 Predictions of Population Growth

We first asked whether the DA method would usually provide the correct *qualitative* prediction of population growth or decline. For most simulations, the DA provided a reasonable estimate of the "true" structured population's growth rate and thus its health. Figure 7.3 shows the results from a single set of population runs using the lowest demographic and variance rate. Areas in the upper right and lower left of the graph, delineated by the gray lines, correspond to regions where the model's prediction and results coincided. The upper left and lower right portion of the graph are areas where the model's prediction and results had opposite signs (e.g., the model predicted that the

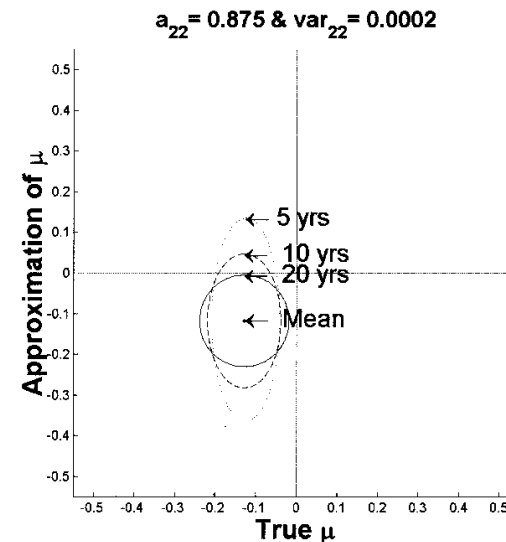


Fig. 7.3. The 95% confidence interval (CI) ellipses for the approximation of μ as calculated by the diffusion approximation compared to actual or "true" μ realized over 50 simulation years. This plot contains the results for the mean demographic rate $a_{2,2}=0.875$ and its variance ($v_{2,2}$)=0.0002. The ellipses show the combined CIs for the real and estimated variation in μ across all simulations. Ellipses are plotted for the 5-year (dotted ellipse), 10-year (dashed ellipse) and 20-year (solid ellipse) census periods, as is the mean (center asterisk) of the simulation. The gray horizontal and vertical zero lines are used for reference; areas within the ellipses in the upper right and lower left of the plots represent points where the approximation and "true" μ are equivalent in sign (i.e., either both are positive or both are negative). Thus, these are areas where the model correctly predicted whether the population is growing or declining

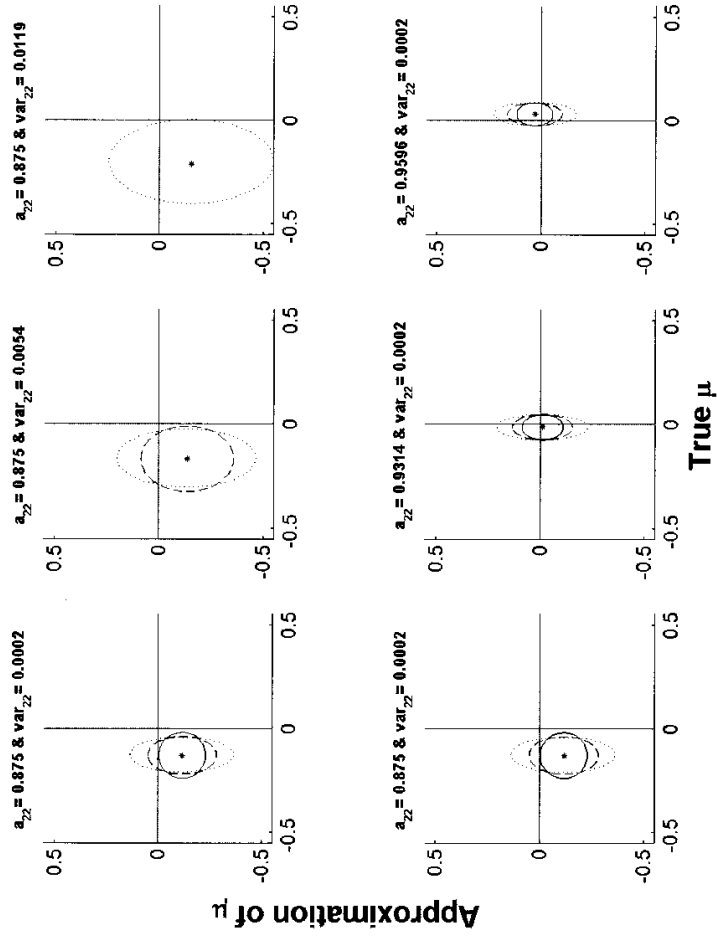


Fig. 7.4. The 95 % confidence interval (CI) ellipses for the approximation of μ as calculated by the diffusion approximation compared to actual or “true” μ realized over 50 simulation years. Within each subplot, the CI for the 5-year (dotted ellipse), 10-year (dashed ellipse) and 20-year (solid ellipse) census periods are shown along with the mean (center asterisk) of the simulation. The horizontal and vertical gray lines are zero lines used for reference; areas within the ellipses in the upper right and lower left of the plots represent points where the approximation and “true” μ are equivalent in sign (i.e., either both are positive or both are negative). The upper row of plots includes the results from simulations with mean $a_{2,2} = 0.875$ and three variance rates. The two upper right plots do not contain the 20-year census period and the far upper right plot does not contain the 10-year census period ellipse due to non-normal distributions caused by high extinction rates. The lower row of plots presents the results from simulations using three different mean $a_{2,2}$ values and a single variance rate

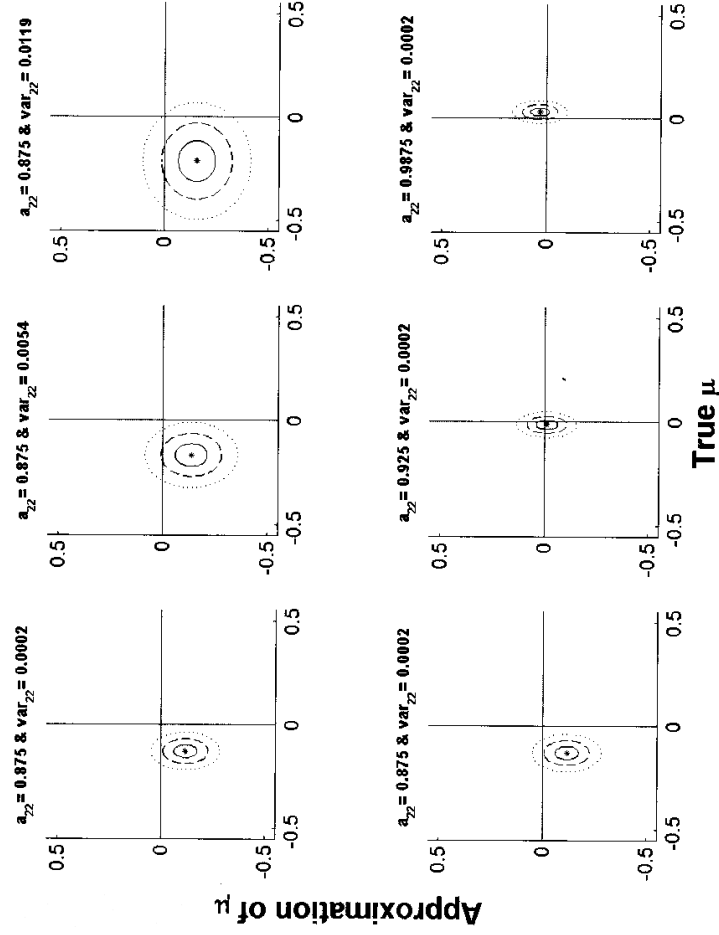


Fig. 7.5. The 95 % (dotted ellipse), 80% (dashed ellipse), and 50 % (solid ellipse) confidence interval (CI) ellipses and the mean (center asterisk) for the approximation of μ compared to actual or “true” μ for the simulation modeled. All ellipses assume a 10-year census period and are for the same mean and variance of $a_{2,2}$ used in Fig. 7.4

population should be growing; whereas the population was actually declining). Over the 5,000 replicate runs for all demographic and variance rates used, the mean predicted μ and the mean true (or realized) μ , for the 50 “future” years of the simulations, were almost identical (Fig. 7.4). Furthermore, the degree of uncertainty (difference in upper and lower confidence limits, or the confidence interval, CI) for estimated μ was comparable with the range of true uncertainty in future population trajectories (CIs of true μ) with even 10 years of data. More important is whether the 95% CIs of predicted values largely contain values of the same sign as that of the “true” μ , indicating good qualitative predictions about long-term population growth or decline. While this predictive power was weak with 5 years of census data, as the census period increased, the approximation did a good job of predicting population growth or decline, at least when the mean true μ was of large absolute value (Fig. 7.4). However, if “true” μ is close to zero, the DA predictions were much less reliable (i.e., the signs for the predicted μ and the “true” μ were switched). It is important to note, however, that over a 50-year future period, the true dynamics of these 5,000 populations from the different simulation runs range between growth and decline. Thus, predicting the health of a single population with $\mu \approx 0$ will always be difficult, not due so much to estimation problems as to the inherent uncertainty of vacillating dynamics over limited time horizons.

The 95% CIs encompass all but the most extreme predicted or realized population growth rates. In asking about the basic usefulness of forecasting using the DA method, it is also worthwhile to consider narrower confidence limits. In Fig. 7.5, we plotted 50, 80, and 95% CIs for 10 years of census data. The 80% CIs for most of our sets of simulations largely encompass only qualitatively correct values of μ . This was even true for populations that experience a considerable amount of variation; in the simulation with the largest variance, the 80% CI predictions were essentially all of the correct sign. This result further supports the utility of the DA method in making qualitative assessments of population viability (or the lack thereof).

7.3.2 Predictions of Extinction Risk

To examine how well the DA predicted extinction risk, we first conducted a logistic regression of whether or not the population went extinct over the 50-year “future” (or forecast) period versus the DA prediction of probability of extinction. Before this analysis was done, we examined the histograms generated by the data to verify that the assumptions of the logistic equation were not violated (e.g., most of the data points were located at either end of the distribution (i.e., they consisted mostly of ones and zeros)). Once verified, this analysis was done across all demographic and variance rates and repeated for each census period. The results show that, over many replicates,

the DA predicts the probability of extinction reasonably well (Fig. 7.6). However, it tended to underestimate the probability of extinction for populations that had an extremely low chance of extinction and overestimate extinction rates for all other situations. Those populations that had low probabilities of extinction likely went extinct due to a series of extremely bad years; this type of dramatic or catastrophic drop in population size and a population’s subsequent extinction were known beforehand not to be well predicted by DA (Dennis et al. 1991). As the probability of extinction rose above 10–20%, the DA yielded more conservative estimates of extinction probability for all census periods smaller than 50 years. Again, this inaccuracy is likely to be due to the inability of the DA approach to incorporate occasional extreme years (with good years having the largest effect in these cases). Not surprisingly, as the census period increased, estimated extinction probabilities became more accurate.

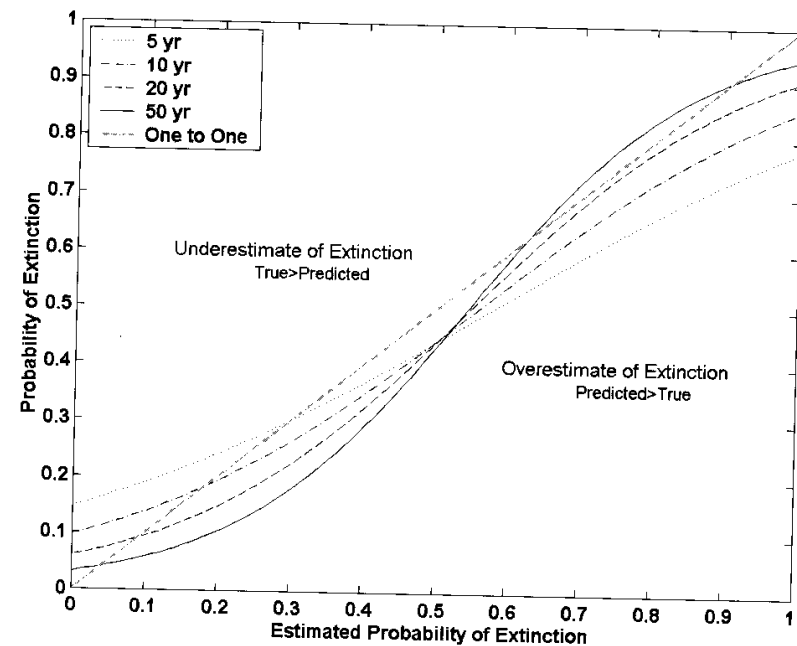


Fig. 7.6. The best fit lines of logistic regressions of the predicted probability of extinction according to the diffusion approximation versus whether or not the population went extinct over 50 years. The one-to-one line represents a perfect fit between “true” extinction probability and forecasted extinction probability. Areas above the one-to-one line represent regions where the model underestimated probability of extinction (i.e., liberal estimates) and areas below represent regions where the model overestimated the probability of extinction (i.e., conservative estimates)

Since the DA can, on average, give realistic estimates of extinction probabilities, how well did it predict extinction times? To answer this, we regressed the mean, median, and modal times to extinction for all populations that went extinct during the forecast period of the model against the “true” time to extinction. Although none of these three measures of extinction time relate exactly to the time to extinction, which is conditional on extinction occurring over a short time horizon (50 years for our simulations), they are the three most widely used measures of risk estimated from the DA method. The median and modal extinction time estimates were able to account for a considerable amount of variance in extinction times (Fig. 7.7). The amount of variance explained increases and asymptotes as the census period increased. However, the mean time to extinction, except when estimated with 50 years of census data, accounted for little of the variance in time to extinction. Although the predicted median and modal extinction times do provide useful estimates of extinction risk, it is worth noting that they do *not* provide good precision in estimating the “true” conditional extinction times we observed over our 50-year time horizon (personal observation). In particular, the median overesti-

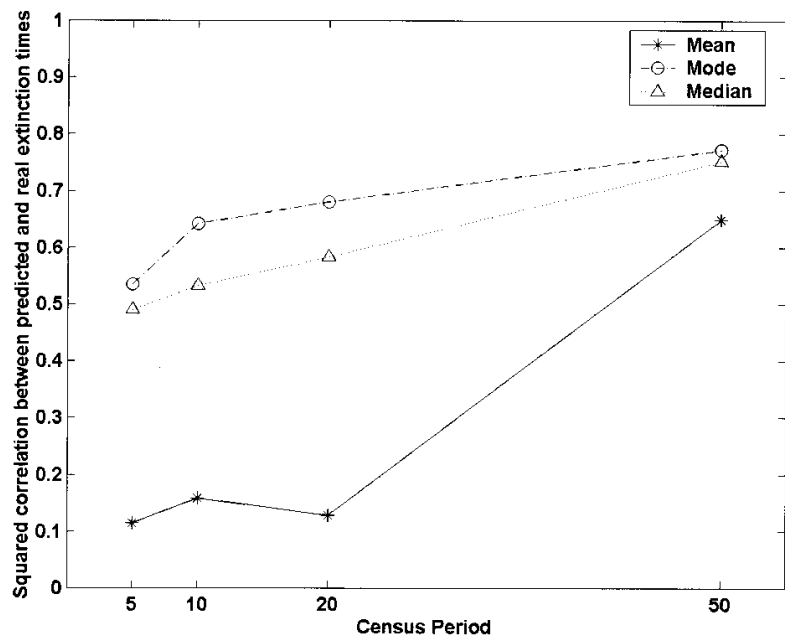


Fig. 7.7. The amount of variance explained (r^2) by a regression of “true” extinction time on either the mean, median, or modal predicted extinction time for populations that went extinct during the simulation. Values are plotted for all census periods

mates, and the mode underestimates, time to extinction. This is not surprising, given the typically skewed distribution of extinction times (Fig. 7.2), but it does show that the simple summary statistics derived from a DA analysis should be interpreted cautiously when assessing the likely timing of extinction over short time horizons.

7.3.3 Ranking Relative Risk

In addition to estimating μ for single populations, DA predictions can be used to rank populations with respect to the amount of extinction risk they face, relative to other populations. To gauge ranking accuracy, we correlated the ranking of “true” versus estimated μ s for sets of nine simulated populations, each with different combinations of the mean and variance of matrix element $a_{2,2}$ (Table 7.4). Correlation between true and estimated rankings were positive for over 75 % of samples for even a 5-year census period and increased with greater lengths of census data (Fig. 7.8A). Although these correlations are often far from perfect, they do suggest that even moderate amounts of census data can be useful in ranking populations for the potential for future growth. We replicated these simulations using a low correlation in variation of different demographic rates; the resulting decline in population variability substantially improves the power of the DA predictions to rank populations (Fig. 7.8B).

If the same correlation analysis is conducted for predicted and actual time to extinction (calculated from μ , σ^2 , and initial population size), the correlation between the DA estimates and “true” outcomes is much stronger (Fig. 7.9). Even with high correlations in matrix element variation and only 5 years of census data, the median rank correlation is over 0.75. With increases in census period or decreases in covariance, the DA method’s ability to correctly rank extinction times of populations increased even further. These results emphasize that the realistic use of initial population size estimates, along with μ and σ^2 , provides the DA method with considerable predictive power, even over time spans much longer than the period over which census data were collected.

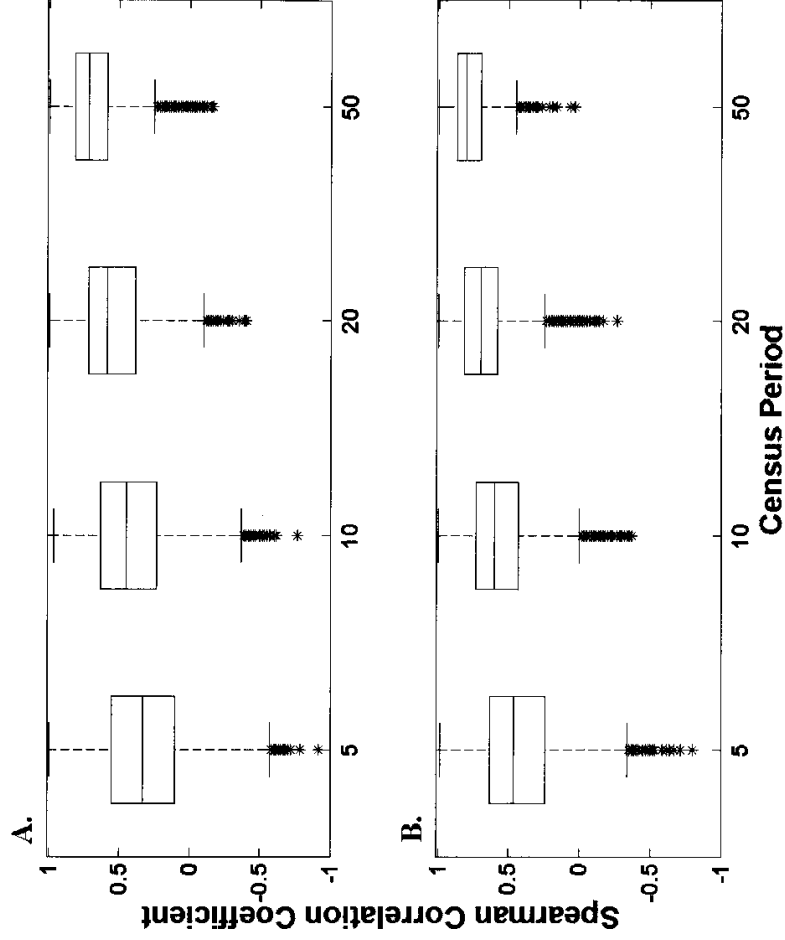


Fig. 7.8A, B. A box plot of Spearman rank correlation coefficients of "true" versus predicted μ for all census periods. Each *box* represents the upper and lower quartiles of data and is divided by a *line* representing the median. The box's whiskers extend to 1.5 interquartile ranges beyond the box's data. *Asterisks* mark all values beyond the whisker. The upper plot (A) contains data for simulations run with high correlation ($r=0.80$) between demographic rates. The lower plot (B) contains data for simulations run with low correlation ($r=0.08$) between demographic rates

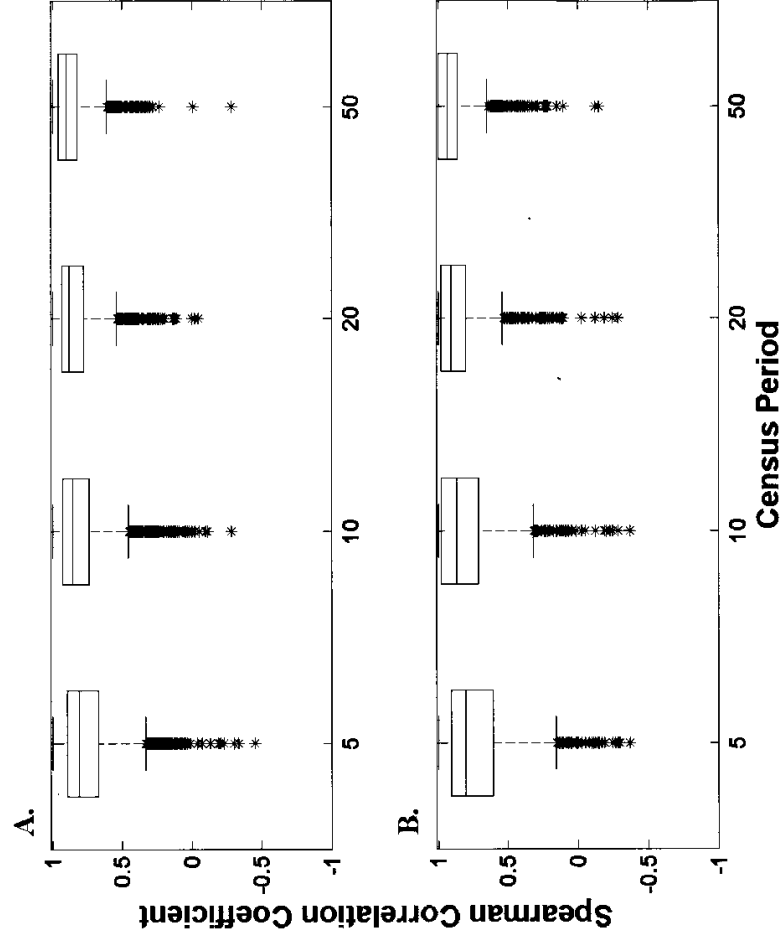


Fig. 7.9A, B. A box plot of Spearman rank correlation coefficients of extinction times (predicted versus actual) for all census periods. Each *box* represents the upper and lower quartiles of data and is divided by a *line* representing the median. The box's whiskers extend to 1.5 interquartile ranges beyond the box's data. *Asterisks* mark all values beyond the whisker. The upper plot (A) contains data for simulations run with high correlation ($r=0.80$) between demographic rates. The lower plot (B) contains data for simulations run with low correlation ($r=0.08$) between demographic rates

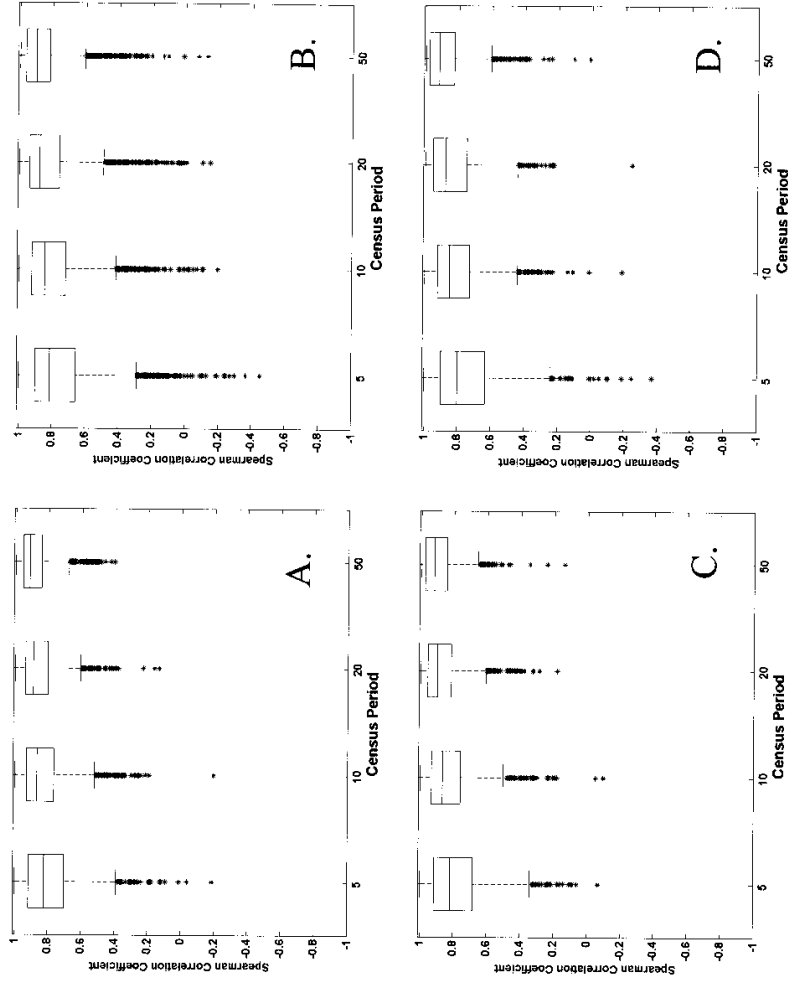


Fig. 7.10A, B. Box plots of Spearman rank correlation coefficients of extinction times for simulations in which seedlings (class 1) were not included in censuses. Plots A and B contain data for simulations run with a perennial class 1; B plot data are for simulations run with the original, annual class 1. C, D Plots contain data for simulations run with zero correlation ($r=0$) between class 1 demographic rates ($a_{1,1}$, $a_{1,2}$, $a_{1,3}$) and demographic rates for other stages, but high correlation ($r=0.80$) between all other rates. C Plot data are for simulations run with a perennial class 1; D plot data are for simulations run with the original, annual class 1

7.3.4 Effects of an Unseen Stage

For all of the simulations of different life history variations, the predictive power of the DA method was virtually unaffected by the ability to census individuals in the smallest size class. The different variants of the size class vital rates resulted in stable size class distributions that included anywhere from 14 to 18% of the population as part of the “seed bank.” Thus, even if up to one sixth of the population could not be censused, there was little difference in estimates of population health between simulations in which we were able to census this class versus those in which we were not. In particular, we found little change in the ability to rank either μ or extinction times when unable to census the smallest class (Fig. 7.10). This result held true for simulations run with the original transition matrix, and also for those in which stage 1 survivorship was increased, regardless of the level of correlation in demographic rates for seed bank stage with those for the other stages. Even making class 1 both perennial and uncorrelated in temporal variation with other stages did not change the lack of effect of seeing this stage (Fig. 7.10C). This rather surprising result seems to arise due to the high annual survivorship of the adult class (stage 3), which makes the observed part of the population the most stable. Clearly, this result needs to be tested for a range of different life histories, but it echoes Meir and Fagan’s (2000) analysis, showing that observation errors of population size must be large before they markedly degrade DA predictions.

7.4 Conclusion

Overall, our results indicate that in many circumstances the DA method can provide useful information for PVA practitioners with reasonable amounts of data. In particular, the DA approach does a good job of estimating μ when the true value is not near zero. In contrast, populations with a discrete growth rate near one (i.e., μ is near zero) will be highly affected by the vagaries of environmental stochasticity. In these situations, it would be difficult to have much faith in any prediction of μ or extinction probability, as the fate of the population will largely be determined by difficult-to-estimate variability. If one examines the confidence intervals around the mean (e.g., Fig. 7.4), it becomes evident that the predictive ability of the model should be called into question in these situations. Some critics of the DA method have focused on this weakness by analyzing populations with growth rates at or near equilibrium (Fieberg and Ellner 2000). For these situations, the DA method is indeed a poor predictor, although other methods are likely to be just as bad (Ludwig 1996, 1999; Chap. 6, this Vol.). It is also important to emphasize that part of

this poor predictive power arises from the inherent uncertainty of short-term outcomes when environmental variability is large. The key question to ask in a PVA is usually not what the true, long-term population behavior is, but rather what the range of likely outcomes is over a defined time horizon. With μ close to zero, these outcomes can span a wide range of values, just as can the estimated values (Fig. 7.5).

The DA method also does a reasonable job of predicting extinction risk. However, the estimates of extinction provided by the DA method are overly optimistic for populations that have an overall low probability of extinction. Thus, our results confirm that the method contains limitations when trying to forecast rare extinction events (Dennis et al. 1991). We also found that with limited data the method overestimates extinction probabilities for populations that have a high probability of extinction. Thus, the DA method overestimates extinction risk for the most endangered populations; however, it is also with regard to these populations that biologists would most want to be conservative or cautious in developing management strategies.

Not surprisingly, with more census data, predictions of extinction probability become more accurate. However, our results indicate that useful forecasts can be made without enormous amounts of data. Generally, 10 years of census data were sufficient to yield useful predictive power about extinction times (Fig. 7.7). This finding supports the results of Gerber et al. (1999), who studied the quality of DA predictions achieved with various amounts of census data, as compared with the known population dynamics from further censuses, for the North Pacific humpback whale. They found that predictions made with 11 years of census data were substantially more accurate than predictions made with even 8 years of data, but that the quality of predictions did not improve drastically when informed by further years of census data. Although their study focused on a rapidly recovering population with very low temporal variation in population growth, our results suggest that such limited data are useful in many other circumstances as well.

By far, our strongest results were from the ranking of the relative population growth and risk of extinction among a suite of populations with varying growth rates and variances. We found that the rankings of estimated μ values correlated reasonably well with the true rankings. More impressively, rankings of extinction predictions correlated extremely well with true rankings of extinction times. This result is in sharp contrast with more dismal analyses of the DA method (Ludwig 1996, 1999; Fieberg and Ellner 2000). The explanation for this difference is partly due to our emphasis on the ranking of risk rather than predictive precision. In addition, by tailoring our simulations closely to the real use of census data, we included the powerful effects of initial population size in determining extinction risk, which previous analyses have not.

However, in interpreting our ranking results, it is important to bear in mind the wide range of μ and σ^2 values of the populations we were ranking (Table 7.4). Attempts to rank the viability of populations with much more

similar dynamics will inevitably be less successful. Still, of the nine populations used for our ranking of relative risk, there were only three different deterministic growth rates, with the rest of the differences generated by changes in variability. Thus, our results show that the DA method can not only differentiate between populations that on average grow or decline, but also between populations that experience different amounts of variation. Critics have charged that the DA method can not reasonably assess population health when confronted with a range of environmental stochasticity. In contrast, we found that the method is robust, at least in assessing the relative health of a group of separate populations.

Although the DA approach is being used with increasing frequency (Table 7.2), it has rarely been applied to plants (but see Morris et al. 1999). The biggest challenge in applying the method to plant populations seems likely to be that population censuses will often not include all stages of the population, due to the difficulty of surveying a plant population's seed bank or other small stages (e.g., the cotyledon stage of *C. obispoensis*). Although limited to only one life history, our results indicate that the DA method can still perform quite well with this limitation. In this regard, our results confirm Meir and Fagan's (2000) finding that observation errors have to be fairly large before influencing DA predictions. Still, our robust findings are probably driven by the high adult survivorship of the particular life history we used. Not including the smallest size class in census counts is certain to have much greater effects on the quality of viability predictions when the larger (adult) size classes are less long-lived. Thus, the method should be used with great caution, if at all, for short-lived perennials or annuals that have seed banks containing a large and vacillating fraction of the population's individuals.

It is important to emphasize that we base our assessment of the "usefulness" of the DA method not on a 0.95 probability of rejecting hypotheses about population growth, but upon a looser standard more appropriate to conservation management. In particular, the ability of the DA approach to more often than not predict the right qualitative dynamics of a population, even with considerable uncertainty (Figs. 7.4, 7.5) indicates that while short periods of census data are not sufficient to make definitive conclusions, they do form a firm enough basis to improve conservation assessment. In this sense, we are highly pragmatic (or even optimistic) in our evaluation of the DA method and its potential to improve PVA and conservation planning.

In summary, the DA method is a useful PVA tool that can inform decisions about the best targets for conservation efforts. Ecologists have developed a number of models in order to understand the interaction of birth and death processes that lead to either a population's growth or its decline. In particular, matrix models and their many elaborations have become standard tools for PVA analysis (Chap. 6, this Vol.). However, these models require large amounts of data. As an increasing number of plant and animal populations have become threatened with extinction, the time available to collect the necessary

field data for parameterizing the more complex models is not necessarily available. The DA method employs a relatively simple technique to use count data to estimate population growth and extinction risk. For plants in particular, basic counts of individuals are easy and inexpensive to acquire, making DA methods an especially appealing way to utilize past data as well as current data from ongoing monitoring programs. While it is important to recognize the limitations and uncertainties in the results obtained from the DA method, we believe that it can serve a very useful function in the assessment of viability. Very short time-runs of data will not allow precise analyses of population dynamics, but even modest amounts of data can provide good estimates of qualitative dynamics and especially of relative risk of extinction. With its modest data needs and potential to substantially improve the biological basis of conservation decision-making, the DA approach to viability assessment deserves further use and development as an important conservation tool.

Acknowledgements. We thank Christy Brigham and Mark Schwartz for inviting us to contribute to this volume. Jennie Kluse provided crucial help and support during this project. Conversations with Bill Morris have helped to sharpen many of the ideas presented here. Brian Dennis and one anonymous reviewer provided thoughtful comments that greatly improved this manuscript. We are grateful for NSF awards to Doak, NSF IGERT support for Elder, and USDE GANN support for Shahani.

References

- Beissinger SR, Westphal MI (1998) On the use of demographic models of population viability in endangered species management. *J Wildl Manage* 62:821–841
- Braumann CA (1983) Population growth in random environments. *Bull Math Biol* 45:635–641
- Brook BW, O'Grady JJ, Chapman AP, Burgman MA, Akçakaya HR, Frankham R (2000) Predictive accuracy of population viability analysis in conservation biology. *Nature* 404:385–387
- Capocelli RM, Ricciardi LM (1974) A diffusion model for population growth in random environment. *Theor Popul Biol* 5:28–41
- Cohen JE (1977) Ergodicity of age structure in populations with Markovian vital rates, III: Finite-state moments and growth rate; an illustration. *Adv Appl Probab* 9:462–475
- Cohen JE (1979) Comparative statistics and stochastic dynamics of age-structured populations. *Theor Popul Biol* 16:159–171
- Crouse DT, Crowder LB, Caswell H (1987) A stage-based population model for Loggerhead sea-turtles and implications for conservation. *Ecology* 68:1412–1423
- Dennis B (1989) Stochastic differential equations as insect population models. In: McDonald L, Manly B, Lockwood J, Logan J (eds) Estimation and analysis of insect populations. Proceedings of a Conference, Laramie, Wyoming, 25–29 January 1988. Lecture notes in statistics 55. Springer, Berlin Heidelberg New York, pp 219–238
- Dennis B, Taper ML (1994) Density dependence in time series observations of natural populations: estimation and testing. *Ecol Monogr* 64:205–224

- Dennis B, Munholland PL, Scott JM (1991) Estimation of growth and extinction parameters for endangered species. *Ecol Monogr* 61:115–143
- Doak DF, Thomson DM, Jules ES (2002) PVA for plants: understanding the demographic consequences of seed banks for population health. In: Beissinger S, McCullough D (eds) Population viability analysis. University of Chicago Press, Chicago, pp 312–337
- Efford M (2001) Environmental stochasticity cannot save declining populations. *Trends Ecol Evol* 16:177
- Engen S, Sæther B (2000) Predicting the time to quasi-extinction for populations far below their carrying capacity. *J Theor Biol* 205:649–658
- Feller W (1939) Die Grundlagen der Volterraschen Theorie des Kampfes ums Dasein in wahrscheinlichkeitstheoretischer Behandlung. *Acta Biother* 5:11–40
- Fieberg J, Ellner SP (2000) When is it meaningful to estimate an extinction probability? *Ecology* 81:2040–2047
- Fiedler PL (1987) Life history and population dynamics of rare and common mariposa lilies (*Calochortus purshii*: Liliaceae). *J Ecol* 75:977–995
- Foley P (1994) Predicting extinction times from environmental stochasticity and carrying capacity. *Conserv Biol* 8:124–137
- Gaston KJ, Nicholls AO (1995) Probable times to extinction of some rare breeding bird species in the United Kingdom. *Proc R Soc Lond B* 259:119–123
- Gerber LR, DeMaster DP, Kareiva PM (1999) Gray whales and the value of monitoring data in implementing the U.S. Endangered Species Act. *Conserv Biol* 13:1215–1219
- Gillespie JH (1972) The effects of stochastic environments on allele frequencies in natural populations. *Theor Popul Biol* 3:241–248
- Goel NS, Richter-Dyn N (1974) Stochastic models in biology. Academic Press, New York
- Higgins SI, Pickett STA, Bond WJ (2000) Predicting extinction risks for plants: environmental stochasticity can save declining populations. *Trends Ecol Evol* 15:516–519
- Holmes EE (2001) Estimating risks in declining populations with poor data. *Proc Natl Acad Sci USA* 98:5072–5077
- Karlin S, Levikson B (1974) Temporal fluctuations in selection intensities: case of small population size. *Theor Popul Biol* 6:383–412
- Kendall DG (1949) Stochastic processes and population growth. *J R Stat Soc B* 11:230–264
- Lande R (1993) Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *Am Nat* 142:911–927
- Lande R, Orzack SH (1988) Extinction dynamics of age-structured populations in a fluctuating environment. *Proc Natl Acad Sci USA* 85:7418–7421
- Leigh E (1981) The average lifetime of a population in a varying environment. *J Theor Biol* 90:213–239
- Lima M, Marquet PA, Jaksic FM (1998) Population extinction risks of three neotropical small mammal species. *Oecologia* 115:120–126
- Ludwig D (1996) Uncertainty and the assessment of extinction probabilities. *Ecol Appl* 6:1067–1076
- Ludwig D (1999) Is it meaningful to estimate a probability of extinction? *Ecology* 80:298–310
- Mangel M, Tier C (1993) A simple direct method for finding persistence times of populations and application to conservation problems. *Proc Natl Acad Sci USA* 90:1083–1086
- Mangel M, Tier C (1994) Four facts every conservation biologist should know about persistence. *Ecology* 75:607–614
- May RM (1973) Stability and complexity in model ecosystems. Princeton University Press, Princeton
- Meir E, Fagan WF (2000) Will observation error and biases ruin the use of simple extinction models? *Conserv Biol* 14:148–154

- Menges ES (1990) Population viability for an endangered plant. *Conserv Biol* 4:52-62
- Morris W, Doak D, Groom M, Kareiva, P, Fieberg J, Gerber L, Murphy P, Thomson D (1999) A practical handbook for population viability analysis. The Nature Conservancy, Arlington, Virginia
- Nicholls AO, Viljoen PC, Knight MH, van Jaarsveld AS (1996) Evaluating population persistence of censused and unmanaged herbivore populations from the Kruger National Park, South Africa. *Biol Conserv* 76:57-67
- Oli MK, Holler NR, Wooten MC (2001) Viability analysis of endangered Gulf Coast beach mice (*Peromyscus polionotus*) populations. *Biol Conserv* 97:107-118
- Oliveira-Pinto F, Conolly BW (1982) Applicable mathematics of non-physical phenomena. Ellis Horwood, Chichester
- Possingham HP, Davies I (1995) ALEX - a model for the viability analysis of spatially structured populations. *Biol Conserv* 73:143-150
- Soulé ME (1987) Viable populations for conservation. Cambridge University Press, Cambridge
- Tier C, Hanson FB (1981) Persistence in density dependent stochastic populations. *Math Biosci* 53:89-117
- Tuljapurkar SD (1982) Population dynamics in variable environments. II. Correlated environments, sensitivity analysis and dynamics. *Theor Popul Biol* 21:114-140
- Tuljapurkar SD, Orzack SH (1980) Population dynamics in variable environments. I. Long-run growth rates and extinction. *Theor Popul Biol* 18:314-342
- Turchin P (1993) Chaos and stability in rodent population dynamics: evidence from non-linear time-series analysis. *Oikos* 68:167-172
- Turchin P, Taylor AD (1992) Complex dynamics in ecological time series. *Ecology* 73:289-305
- Turelli M (1978) A re-examination of stability in random varying versus deterministic environments with comments on the stochastic theory of limiting similarity. *Theor Popul Biol* 13:244-267