

NOAA Technical Memorandum NMFS-F/NWC-198



**Determining Minimum
Viable Populations
under the
Endangered Species Act**

by
Grant G. Thompson



National Marine Fisheries Service
Alaska Fisheries Science Center
Resource Ecology and Fisheries Management Division
7600 Sand Point Way NE, Bin C15700
Seattle, WA 98115-0070

June 1991

**U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
National Marine Fisheries Service**

NOAA NMFS F/NWC-198: Determining Minimum Viable Populations under the Endangered Species Act

NOAA Technical Memorandum NMFS Series

The Northwest Fisheries Science Center of the National Marine Fisheries Service, NOAA, uses the NOAA Technical Memorandum NMFS series to issue informal scientific and technical publications when complete formal review and editorial processing are not appropriate or feasible due to time constraints. Documents published in this series may be referenced in the scientific and technical literature.

The NMFS-NWFSC Technical Memorandum series of the Northwest Fisheries Science Center continues the NMFS-F/NWC series established in 1970 by the Northwest & Alaska Fisheries Science Center, which has since been split into the Northwest Fisheries Science Center and the Alaska Fisheries Science Center. The NMFS-AFSC Technical Memorandum series is now being used by the Alaska Fisheries Science Center.

Reference throughout this document to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.

This document should be cited as follows:

Thompson, G.G. 1991. Determining Minimum Viable Populations under the Endangered Species Act. U.S. Dep. Commer., NOAA Tech. Memo. NMFS F/NWC-198. 78 p.

This document is available to the public through:

National Technical Information Service
U.S. Department of Commerce
5285 Port Royal Road
Springfield, VA 22161
1-800-553-8647
orders@ntis.fedworld.gov

INTRODUCTION

The task of determining whether a population is in danger of extinction is usually accomplished by conducting a population viability analysis. Stated simply, the central questions of population viability analysis are, "What, where, when, and how many?" The first three of these are questions of population distribution. "What" refers to the distribution of qualitative characteristics within a population, reflecting the fact that the presence or absence of certain kinds of individuals can affect a population's viability. For example, if a particular species' life history exhibits a maximum age of reproduction, then a population composed entirely of individuals older than that maximum age will not be viable. "Where" and "when" refer to the distribution of a population in space and time, which can also affect population viability. For example, if males segregate from females consistently in space or time, the population that they comprise will not be viable. The fourth question, "how many," refers to the size of a population. Generally, it is assumed that population viability decreases as population size becomes small. At the extreme, a sexually reproducing population that is reduced to a single individual will not be viable. While all four of these questions are important, this paper will focus mainly on the fourth ("how many").

More specifically, the primary purpose of this paper is to review the state of the art in conservation biology as it pertains to the determination of minimum viable populations (MVPs), at least within the context of populations that are qualitatively and spatiotemporally well distributed. The secondary purpose is to provide recommendations for conducting population viability analyses pursuant to petitions filed under the U.S. Endangered Species Act (ESA). The paper was prompted by five petitions directed to the National Marine Fisheries Service in the spring of 1990 for protection of certain stocks of Pacific salmon (*Oncorhynchus* spp.), and so may be biased to some extent toward methods or results of particular relevance to conservation of salmon stocks. For example, models that focus on individual territories or home ranges (e.g., Lande 1987) have been ignored.

One technical point should be noted early on: When the ESA refers to "species," it does not refer to true (i.e., taxonomic) species only, but also to subspecies and even to "distinct population segments." The problem of what constitutes a "species" under the ESA is addressed by Waples (1991), and will not be reconsidered here. The reader should note that the present paper's use of the term "species" in the context of the ESA should be interpreted in the legal, not the biological, sense.

Among the other terms used in the ESA, two of the most important are "endangered" and "threatened." The ESA defines an endangered species simply as one which is "in danger of extinction," while a threatened species is one which is "likely to become an endangered species within the foreseeable future." This language leaves a key

question unanswered: What constitutes danger of extinction? According to Webster's dictionary, danger is a generic term implying "exposure or liability to injury, loss, pain, or other evil." It is distinguished from *peril* in that danger does not necessarily imply a sense of immediacy; in other words, danger can encompass events far in the future. Unfortunately, this makes it possible to argue that all species are in danger of extinction. Absent divine intervention, eventual extinction of all species is more of a certainty than a danger (den Boer 1968, Soule and Simberloff 1986). Obviously, this is not what Congress had in mind when it passed the ESA, but it leaves open the question of how soon and how likely extinction must be before a finding of endangerment is warranted.

Beginning with Hooper (1971), Shaffer (1981), and Ginzburg et al. (1982), conservation biologists have argued that the process of extinction is best viewed as stochastic, and that endangerment should therefore be defined probabilistically, that is, in terms of the probability of persistence (p) over time (t). Such a definition could take the form of some measure of central tendency of extinction time (as in the birth-and-death process model described below), or by specifying a threshold probability of persistence p^* over a specified time horizon t^* (as suggested by Shaffer). For example, MVP might be defined as the population size (N) at which the probability of persistence over the next 100 years is 95%. Determining appropriate p^* and t^* values, however, is not a trivial undertaking (Appendix A discusses some of the difficulties involved).

Conservation biologists have attempted to simplify the task of understanding population stochasticity by dividing it into a number of components. May (1973) first distinguished between demographic and environmental stochasticity, and Shaffer (1981) suggested that stochastic effects due to genetics and catastrophes should also be considered separately. Demographic stochasticity arises from the fact that populations consist of individuals, each of which is subject to demographic processes that can be treated probabilistically (e.g., each individual faces a certain probability of death in any given year). Environmental stochasticity is a means of interpreting unpredictable changes in vital rates. Genetic stochasticity is used to account for the impacts of founder effect, genetic drift, or inbreeding. Catastrophes are extreme events (e.g., floods, fires, and droughts) that can be thought of as occurring randomly.

Unfortunately, to date no model has been developed that integrates all four components satisfactorily (Shaffer 1987). While models that emphasize demographic and environmental stochasticity typically define an MVP directly in terms of probability of persistence, this relationship is only implicit in models that emphasize genetic stochasticity, which tend to relate MVP directly to threshold levels of inbreeding or genetic variability (Ewens et al. 1987). Undoubtedly, there is a relationship between these two approaches, but it has yet to be made explicit.

Although it has so far proven infeasible to incorporate the four sources of stochasticity into a single model, it does appear that some consensus exists regarding their relative importance, except for catastrophes. Of the other three sources, the conclusion seems to be that environmental stochasticity is the most important and genetic stochasticity is the least, except in very small ($N < 100$) populations (Shaffer 1987, Lande 1988).

Catastrophe-related stochasticity is somewhat problematic, and has not always been handled uniformly in the literature. Usually, data limitations cause catastrophes to be ignored or treated on an *ad hoc* or subjective basis (e.g., Marcot and Holthausen 1987), although a few theoretical modeling efforts have been attempted (Hanson and Tuckwell 1978, Ewens et al. 1987). Goodman (1987a) and Simberloff (1988) suggest that it is not clear how catastrophes are to be distinguished from outliers along the spectrum of environmental variability. Simberloff (1988) and Thomas (1990) contend that the idiosyncratic nature of true catastrophes effectively precludes their inclusion in predictive models.

As the above discussion indicates, the process of extinction is not yet fully understood. To some extent, the explanation for this can be found in the fact that the discipline of conservation biology is quite new. Although many of the concepts used in conservation biology have existed for some time, Brussard (1991) has suggested that the discipline per se began in 1980 with the publication of *Conservation Biology: An Evolutionary-Ecological Perspective* by Soule and Wilcox. It is also interesting to note that the Society for Conservation Biology did not even exist until 1986.

OVERVIEW OF APPROACHES TO POPULATION VIABILITY ANALYSIS

Quantitative approaches to population viability analysis can be categorized conveniently into three groups: 1) "rules of thumb," 2) analytic approaches, and 3) simulation approaches. Obviously, there is a degree of subjectivity involved in this classification, but establishing some sort of systematization helps to clarify the relationships between different approaches.

Before discussing these approaches further, it will prove helpful to establish some notational conventions. Generally, notation will follow standard usage wherever possible. For the most part, random variables will be denoted by uppercase Roman letters, with specific values of such variables represented by lowercase Roman letters. Other variables, functions, and constants may be designated by either Roman or Greek letters, and may be either uppercase or lowercase. It should be noted that some quantities such as population size N are treated as random variables in some contexts but not in others. Expected values and variances of random variables will be denoted $E(\bullet)$ and $Var(\bullet)$, respectively. Probability density functions will be designated $P(\bullet)$, with the symbol " p " reserved for the probability of persistence.

Rules of Thumb

A number of authors have noted the impossibility of establishing a "magic number" above which populations are "safe" and below which they face an unacceptable risk of extinction (Gilpin and Soule 1986, Soule and Simberloff 1986, Ewens et al. 1987, Goodman 1987a, Simberloff 1988, Thomas 1990). Nevertheless, it has also been argued that "scientists owe it to the rest of society to provide rules of thumb, even when they know that sometimes the rules will be misunderstood and misused" (Soule 1987).

The "50/500" rule of thumb initially advanced by Franklin (1980) and Soule (1980) comes the closest of any to attaining "magic number" status (Wilcox 1986). This rule prescribes a short-term effective population size (N_e) of 50 to prevent an unacceptable rate of inbreeding, and a long-term N_e of 500 to maintain overall genetic variability. The $N_e=50$ prescription (termed "the basic rule" by Soule 1980) corresponds to an inbreeding rate of 1% per generation, approximately half the maximum rate tolerated by domestic animal breeders (Franklin 1980). The $N_e=500$ prescription is an attempt to balance the rate of gain in genetic variation due to mutation with the rate of loss due to drift, and is based on a genetic study of bristles in *Drosophila* (Franklin 1980).

It should be emphasized that these prescriptions are classified here as rules of thumb not because they are based on primitive or inelegant science (they are not), but because they have been suggested for use in an across-the-board, "one size fits all" fashion. Practical applications of the 50/500 rule have been made by Foose (1983), LaCava and Hughes (1984), Lehmkuhl (1984), the U.S. Fish and Wildlife Service (1985), Allendorf and Servheen (1986), Reed et al. (1986), Dawson et al. (1987), Reed et al. (1988), and Allendorf et al. (in press).

It is important to note that the 50/500 rule is cast in terms of effective population size, a concept introduced by Wright (1931). The effective population size refers to an ideal population of breeding individuals produced each generation by random union of an equal number of male and female gametes randomly drawn from the previous generation. To the extent that this ideal is violated in nature, effective population size N_e differs from actual (or census) population size N , the total number of mature individuals in the population.

Thus, even if the 50/500 rule can be used as a rule of thumb for the minimum viable *effective* population, the minimum viable *census* population must still be determined. This problem can be addressed in two ways. One way is to devise a second rule of thumb that gives a single, invariant translation of N_e into N . Such rules generally take the form of an average value for the N_e/N ratio. For example, Soule (1980) indicates that the N_e/N ratio is commonly 25-33%, giving short- and long-term

MVPs of 150-200 and 1500-2,000, respectively. Salwasser and Marcot (1986) use 50%, corresponding to short- and long-term MVPs of 100 and 1,000, respectively. Wilcox (1986) suggests that 25% is "a good guess" for the N_e/N ratio in most natural populations, corresponding to the low end of Soule's (1980) range. More conservatively, Nelson and Soule (1987) indicate that the N_e/N ratio might be in the neighborhood of 10% for fish populations, giving a short-term MVP of 500 and a long-term MVP of 5,000. Shaffer (1987) suggests that "the actual number of individuals necessary to provide effective populations of several hundred will range from the upper 100s to the 1000s, perhaps rarely to the 10 000s."

The MVP values resulting from the above translations of the 50/500 rule and those resulting from other rules of thumb tend to fall within an order of magnitude of each other. Salwasser et al. (1984) prescribe an average population of at least 1,000 adults. Belovsky (1987) indicates that an MVP in the range of 1,000-10,000 adults should be sufficient for a mid-sized vertebrate species. Soule (1987) suggests that MVPs for vertebrate species should be in the "low thousands" or higher (although he also insists that this "is not a rule of thumb"). Thomas (1990) offers $N=5,500$ as "a useful goal," but suggests that where uncertainty is extreme "we should usually aim for population sizes from several thousand to ten thousand." Appendix B presents an approach based on the concept of extinction time elasticity wherein $N=5,000$ again emerges as a reasonable MVP.

The other method for computing MVP on the basis of the 50/500 rule of thumb is to use analytical formulae for translating N_e into N (or vice versa) on a case-by-case basis. However, this takes the approach out of the pure "rule of thumb" category and merges it into the "analytical" category, discussed below.

Analytic Approaches

Three methods have received by far the most attention of the various possible analytic approaches: population genetic models, the birth-and-death process model, and diffusion models.

Population Genetic Models

Population genetics provides a means of translating the N_e values given by the 50/500 rule into equivalent census population sizes. A standard text is Crow and Kimura (1970). Franklin (1980), LaCava and Hughes (1984), Lehmkuhl (1984), Reed et al. (1986), Lande and Barrowclough (1987), and Simberloff (1988) also present accessible introductions to the subject from the perspective of the 50/500 rule. The notation used here will follow that of Crow and Kimura for the most part. Another convention: Although in general the census population may vary from generation to

generation, the default assumption here will be that only the current value of N is known (the effect of relaxing this assumption is given in Equation [6]).

One factor that can cause N_e to diverge from N is skewness in the sex ratio. If the proportion of males in the population is designated m ,

$$N_e = 4m(1 - m)N. \quad (1)$$

When $m=0.5$, Equation (1) indicates that N_e and N are the same. At all other values of m , N_e is smaller than N .

Another factor that can cause N_e to diverge from N is variance in progeny number. For a sexually reproducing population, let the random variable K represent the number of offspring produced by a mating pair. Then,

$$N_e = \frac{2N - 2}{E(K) - 1 + \frac{Var(K)}{E(K)}}, \quad (2)$$

where $E(K)$ denotes the mean of K , and $Var(K)$ represents the variance of K .

Some special cases are of interest. In an ideal population, the number of progeny follows a binomial distribution, giving

$$P(k) = \binom{E(K)N/2}{k} \left(\frac{2}{N}\right)^k \left(1 - \frac{2}{N}\right)^{E(K)N/2 - k} \quad (3)$$

and

$$Var(K) = E(K) \left(1 - \frac{2}{N}\right), \quad (4)$$

where $P(k)$ is the probability density function of K , and the appearance of "2" in both equations results from the fact that all progeny have two parents.

Substituting Equation (4) into Equation (2) gives the special case

$$N_e = \frac{(2N - 2)N}{E(K)N - 2}. \quad (5)$$

In the even more special case of an equilibrium population (i.e., where K has a mean value of 2.0), Equation (5) reduces to $N_e=N$.

A third factor that can cause N_e to diverge from N is change in population size. Here, let census population size be indexed by generation, with the current census population designated $N(q)$, and assume that census data are available for $q+1$ generations. Even if the sex ratio is 1:1 and K is binomially distributed with a mean of 2.0, N_e will not generally equal $N(q)$, as shown below:

$$N_e = \frac{q + 1}{\sum_{i=0}^q \left(\frac{1}{N(i)} \right)} \quad (6)$$

(Actually, Equation (6) is only an approximation of the exact expression, but it tends to be the form most commonly used.)

Generally, all three factors discussed above (skewed sex ratio, nonbinomial distribution of K , change in population size) may play a role in determining N_e . Simon et al. (1986) demonstrated this in a study of coho salmon (*Oncorhynchus kisutch*), for example.

Although most research on the subject of effective population size (including the above equations) has been based on an assumption of discrete generations, the case of overlapping generations has also been considered. Hill (1972, 1979), for example, showed that the above equations need only be adjusted for appropriate units in order to hold for the overlapping generation case, so long as population size, sex ratio, and age distribution remain constant. Under less restrictive assumptions, however, the distinction between discrete and overlapping generations can be complicated. Waples and Teel (1990) and Waples (in press) note that the life history of Pacific salmon is a special case that fits neither the discrete generation nor overlapping generation models (the exception being pink salmon, *Oncorhynchus gorbuscha*, which tends to exhibit discrete generations). In the case of Pacific salmon, the effective number of breeders in any given year (N_b) represents only a portion of the total effective population size. Waples (in press) suggests that multiplying N_b by the average age of reproduction gives a suitable estimate of N_e .

It should also be noted that effective population size can be defined either in terms of the decrease in homozygosity due to common ancestry ("inbreeding effective size") or the random drift in allele frequencies due to sampling variance ("variance effective size"). Crow and Kimura (1970), Ewens (1982), and Crow and Denniston (1988) provide formulae for looking at N_e within these different contexts. In general,

distinguishing between the two types of effective size is a complicated exercise, although they converge in the special case where population size is constant.

The Birth-and-Death Process Model

The basic assumption of the birth-and-death process model is that the numbers of births and deaths occurring within a population (over a sufficiently short time increment) can be thought of as independent Poisson distributed variables. For a population of size N , the probabilities of a birth or a death occurring during a short time increment Δt are $b_N N \Delta t$ and $d_N N \Delta t$, respectively, where b_N and d_N are density-dependent per capita birth and death rates.

The expected time to extinction for a population of size N , $E(T_N)$, is equal to the mean time needed to reach a size of either $N-1$ or $N+1$, plus a weighted sum of the expected times to extinction corresponding to populations of size $N-1$ and $N+1$:

$$E(T_N) = \frac{1}{(b_N + d_N)N} + \left(\frac{b_N}{b_N + d_N} \right) E(T_{N+1}) + \left(\frac{d_N}{b_N + d_N} \right) E(T_{N-1}). \quad (7)$$

The recursive nature of Equation (7) allows it to be solved as follows:

$$E(T_N) = \sum_{i=1}^N \sum_{j=i}^{N_{\max}} \frac{1}{j d_j} \prod_{k=i}^{j-1} \frac{b_k}{d_k}, \quad (8)$$

where N_{\max} is an upper reflecting barrier that may or may not be finite (note that N_{\max} is not simply carrying capacity; it is an absolute upper limit to population size).

The birth-and-death process model dates from the work of Feller (1939), who treated the birth and death rates as density-independent constants and set N_{\max} at infinity. Kendall (1948) introduced the idea of variable birth and death rates, but viewed them as time- rather than density-dependent. Bartlett (1960) introduced the idea of density-dependent birth and death rates. MacArthur and Wilson (1967) introduced the concept of finite N_{\max} , but again viewed the birth and death rates as being density-independent below this ceiling. Richter-Dyn and Goel (1972) and Goel and Richter-Dyn (1974) presented a particularly thorough analysis of the model in its general form.

Leigh (1981) and Goodman (1987a, 1987b) noted that the treatment of births and deaths as independent Poisson distributed variables permits b_N and d_N to be reparametrized in terms of the expectation and variance of an instantaneous growth rate R :

$$E(R_N) = b_N - d_N, \quad (9)$$

and

$$Var(R_N) = \frac{b_N + d_N}{N}. \quad (10)$$

Substituting Equations (9) and (10) into Equation (8) gives

$$E(T_N) = \sum_{i=1}^N \sum_{j=i}^{N_{max}} \left[\frac{2}{j [j Var(R_j) - E(R_j)]} \right] \prod_{k=i}^{j-1} \frac{h Var(R_k) + E(R_k)}{h Var(R_k) - E(R_k)}. \quad (11)$$

Although Equations (8) and (11) are formally identical (via Equations [9] and [10]), the formulation given by Equation (11) is generally credited with taking the model out of the realm of mere demographic stochasticity by emphasizing the role of environmental stochasticity in determining the instantaneous growth rate (Goodman 1987a and 1987b, Shaffer 1987).

Because the probability density function (pdf) of persistence time is usually highly skewed, the mean time to extinction is sometimes not a particularly intuitive indicator of overall persistence (Goodman 1987b, Lande and Orzack 1988, Ferson et al. 1989, Dennis et al. in press). The main reason for characterizing the birth-and-death process model by $E(T_N)$ rather than p^* and t^* is that an explicit formula for the pdf of extinction time is unavailable for this model (although Richter-Dyn and Goel [1972] did give formulae for an arbitrary moment of the pdf, the possibility of constructing the full pdf from its moments apparently has not been explored in depth [Shaffer and Samson 1985]).

Diffusion Models

Precursors to the diffusion approach include works by Kerner (1957 and 1959), and Lewontin and Cohen (1969). In the diffusion approach, a deterministic differential equation is modified by incorporating a term that represents Gaussian white noise. Density-dependent models have been considered by Levins (1969), Goel et al. (1971), May (1973), Goel and Richter-Dyn (1974), Tuckwell (1974), Feldman and Roughgarden (1975), Ludwig (1975), Beddington and May (1977), Turelli (1977), Hanson and Tuckwell (1978), May et al. (1978), Polansky (1978), Roughgarden (1979), Tier and Hanson (1981), Ginzburg et al. (1982), Braumann (1983), and Dennis and Patil (1984). Although the stationary pdfs of many density-dependent models have been derived, the pdfs of extinction time are not typically obtainable in

explicit form (an exception is the logistic model with random variation in the intrinsic growth rate, as shown by Goel and Richter-Dyn [1974], Tuckwell [1974], Tier and Hanson [1981], and Ginzburg et al. [1982]).

The simple case of stochastic exponential growth was considered by Levins (1969), Goel et al. (1971), Capocelli and Ricciardi (1974), Tuckwell (1974), Keiding (1975), Turelli (1977), Ginzburg et al. (1982), Braumann (1983), and Lande and Orzack (1988). Most recently, it has been explored thoroughly by Dennis et al. (in press). The main assumption in the density-independent diffusion model is that $X(t)=\ln[N(t)]$ can be modeled as a Wiener process (Brownian motion) with drift. The process is characterized by an infinitesimal mean μ and an infinitesimal variance σ^2 that define a normal transition pdf for $X(t)$. Specifically, the pdf of $X(t)$ given an initial condition x_0 is normal with mean $x_0+\mu t$ and variance $\sigma^2 t$.

The diffusion process can also be expressed as a stochastic differential equation:

$$dN(t) = r N(t) dt + \sigma N(t) dW(t), \quad (12)$$

where $dW(t) \sim \text{normal}(0, dt)$, and the instantaneous rate of increase r is given in the Ito calculus (e.g., Turelli 1977) by

$$r = \mu + \frac{\sigma^2}{2}. \quad (13)$$

The pdf of extinction ("first passage") time can be written explicitly: It is the inverse Gaussian distribution (e.g., Johnson and Kotz 1970), which is very similar to the lognormal distribution for a given mean and variance. The name "inverse Gaussian" is somewhat unfortunate, since the distribution it describes is not the inverse of the Gaussian distribution. If x_E is the log population size corresponding to effective extinction (e.g., a single individual), and $x_d = x_0 - x_E$, then the pdf of first passage time is given by

$$P(t) = \frac{x_d}{\sigma t} \left(\frac{1}{\sqrt{2\pi t}} \right) \exp \left(-\frac{(x_d - |\mu|t)^2}{2\sigma^2 t} \right). \quad (14)$$

The mean of Equation (14) is

$$E(T) = \frac{x_d}{|\mu|}, \quad (15)$$

and the variance is

$$\text{Var}(T) = \frac{x_d \sigma^2}{|\mathcal{A}|^3}, \quad (16)$$

with a mode at

$$t_m = \left(\frac{x_d}{|\mathcal{A}|} \right) \left(\sqrt{l + \left(\frac{3}{2x'} \right)^2} - \frac{3}{2x'} \right), \quad (17)$$

where

$$x' = \frac{x_d |\mathcal{A}|}{\sigma^2}. \quad (18)$$

One of the most important contributions of the paper by Dennis et al. (in press) is its presentation of methods for obtaining maximum likelihood estimates of μ and σ^2 :

$$\hat{\mu} = \frac{\ln \left(\frac{n_q}{n_0} \right)}{t_q - t_0}, \quad (19)$$

and

$$\hat{\sigma}^2 = \sum_{i=1}^q \frac{[\ln(n_i) - \hat{\mu}(t_i - t_{i-1})]^2}{q(t_i - t_{i-1})}, \quad (20)$$

where n_i is the size of the population at time t_i , 0 is the index of the initial observation in the time series, and q is the index of the terminal observation in the time series.

Dennis et al. (in press) also present an algorithm for calculating the cumulative form of Equation (14), along with methods for conducting a variety of statistical tests. With these tests, one can evaluate a number of hypotheses, such as the hypothesis that μ is significantly different from zero, or the hypothesis that different parameter values were operative during separate subsets of the time series. For example, in the case of Pacific salmon in the Columbia River, the construction of several hydroelectric dams during the past few decades may have altered the parameters governing the stocks' dynamics. The tests described by Dennis et al. can be used to determine if μ or σ^2 changed significantly following construction of a particular dam.

Simulation Approaches

Included in this category are a number of fairly generic computer programs. Among these is the ONEPOP model (Gross et al. 1973), which has been applied to populations of elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), and bighorn sheep (*Ovis canadensis*) (Pojar 1981). The POPDYN model of Samson et al. (1985) has been applied to species as diverse as grizzly bear (*Ursus arctos*), gopher tortoise (*Gopherus polyphemus*), and northern spotted owl (*Strix occidentalis caurina*) (Simberloff 1988). The RAMAS model (Ferson et al. 1988) has been applied to populations of brook trout (*Salvelinus fontinalis*, Ferson et al. 1989), Atlantic cod (*Gadus morhua*, Ginzburg et al. 1990), and giant kelp (*Macrocystis pyrifera*, Burgman and Gerard 1990). The VORTEX model (Lacy 1991) and its predecessor (Grier 1980a) have been applied to bald eagle (*Haliaeetus leucocephalus*, Grier 1980b), Florida panther (*Felis concolor coryi*, Seal and Lacy 1989, Fergus 1991), Puerto Rican parrot (*Amazona vittata*, Lacy et al. 1989), eastern barred bandicoot (*Perameles gunnii*, Lacy and Clark 1990), Florida key deer (*Odocoileus virginianus clavium*, Seal and Lacy 1990), and Leadbeater's possum (*Gymnobelideus leadbeateri*, Lindenmayer et al. 1991).

In addition to these more-or-less generic models, many simulations have been developed for specific populations, for example, Yellowstone grizzly bear (Shaffer 1978, 1983; Knight and Eberhardt 1985, Shaffer and Samson 1985), New Mexico bighorn sheep (*Ovis canadensis mexicana*, Watts and Conley 1981), northern spotted owl (Marcot and Holthausen 1986), Wichita Mountains bison (*Bison bison*, Shull and Tipton 1987), and Snake River chinook salmon (*Oncorhynchus tshawytscha*, Lee and Hyman 1991).

Since each of the above models is slightly different from the others, it is probably not instructive to summarize the details of any particular model here. Instead, it might be more helpful to consider a generic example of how different types of stochasticity are dealt with in a typical simulation approach. The treatment of survival rates provides such an example. To begin with, an expected survival rate $E(S)$ is defined. In a deterministic model, the number of survivors N_S is obtained simply by multiplying $E(S)$ by the premortality number N , as if the survival rate were acting on the population en masse.

One way to stochasticize this simple process is to assume that the given survival rate acts as a probability of survival applied to *each individual* (as opposed to the aggregate population). In this case, N_S becomes a binomially distributed random variable (e.g., Deriso and Parma 1988):

$$P(n_s) = \binom{N}{n_s} E(S)^{n_s} [1 - E(S)]^{N-n_s}, \quad (21)$$

where $P(n_s)$ is the probability density function of N_s .

Basically, this approach incorporates demographic stochasticity into the model. Although the expected number of survivors is the same as in the deterministic model, the variance is no longer zero but

$$Var_B(N_s) = E(S) [1 - E(S)] N. \quad (22)$$

Alternatively, one could incorporate environmental stochasticity into the model by defining the survival rate as a random variable S that fluctuates from year to year (where the survival rate is once again applied to the aggregate population). Since by definition S ranges between zero and one, a natural way to incorporate environmental stochasticity into the survival process is to define S by a beta distribution:

$$P(s) = \frac{s^{a-1} (1-s)^{b-1}}{\beta(a,b)}, \quad (23)$$

where $P(s)$ is the probability density function of S , a and b are nonnegative parameters, and $\beta(\bullet)$ is the beta function (e.g., Johnson and Kotz 1970). The mean and variance of the number of survivors in this model are

$$E_B(N_s) = \frac{a N}{a + b} \quad (24)$$

and

$$Var_B(N_s) = \frac{a b N^2}{(a + b + 1)(a + b)^2}, \quad (25)$$

respectively.

By appropriate choice of the parameters a and b , the expected number of survivors can be set equal to the value obtained in the binomial or deterministic cases. If the means are so identified, however, the variances given by the beta and binomial treatments will generally be different, as indicated by the following ratio:

$$\frac{Var_{\beta}(N_s)}{Var_B(N_s)} = \frac{E(S)N}{a + E(S)}. \quad (26)$$

Yet again, one could incorporate both demographic and environmental stochasticity into the model by viewing the pdf of survivorship as a binomial-beta distribution (e.g., Boswell et al. 1979), wherein the rate term in the binomial distribution is mixed via a beta distribution, giving

$$P(n_s) = \binom{N}{n_s} \left(\frac{\mathcal{A}(n_s + a, N - n_s + b)}{\mathcal{A}(a, b)} \right). \quad (27)$$

For example, this is the approach used by Lee and Hyman (1991). In the special case where the a and b parameters of the beta distribution take integer values, the binomial-beta distribution is equivalent to the negative hypergeometric (Boswell et al. 1979). The binomial-beta has mean and variance equal to

$$E_{BB}(N_s) = \frac{aN}{a+b} \quad (28)$$

and

$$Var_{BB}(N_s) = \frac{ab(a+b+N)N}{(a+b+1)(a+b)^2}, \quad (29)$$

respectively.

As with the beta treatment, the mean of the binomial-beta can be set equal to the binomial or deterministic cases by appropriate choice of the a and b parameters. However, the binomial-beta variance will always be greater than either the binomial or beta, as shown by the following ratios:

$$\frac{Var_{BB}(N_s)}{Var_B(N_s)} = \frac{a + E(S)N}{a + E(S)} \quad (30)$$

and

$$\frac{Var_{BB}(N_s)}{Var_{\beta}(N_s)} = \frac{a + E(S)N}{E(S)N}. \quad (31)$$

An alternative to the above methods is to treat the survival rate as constant and apply a multiplicative, lognormal error term (e.g., Peterman 1981). However, using any of the above methods has a logical advantage over the lognormal noise approach in that the above methods prevent the number of survivors from exceeding N .

Finally, it is important to remember that although the discussion here has focused on a single survival rate, in principle every parameter governing every population process (e.g., growth, fecundity, migration, survival, etc.) could be considered probabilistically. One could even treat the variance estimates themselves probabilistically.

DISCUSSION

Evaluation of Alternative Approaches

The relative merits of the three general quantitative approaches outlined above (rules of thumb, analytic approaches, and simulation approaches) have been argued in the literature at some length. A brief summary of these evaluations follows.

Evaluation of Rules of Thumb

In terms of its ability to provide a "magic number," the 50/500 rule suffers from the lack of any single, broadly applicable ratio between effective and census population size. Even if such a ratio existed, however, the rule is open to question. The $N_e=50$ prescription is based on a threshold inbreeding rate of 1% per generation, but as Hooper (1971) notes, "There is no truly critical coefficient of inbreeding any more than there is a minimum genetically effective population size above which inbreeding does not occur." Likewise, Lacy (1987) states, "Unfortunately, the maximum acceptable level of inbreeding almost certainly differs among species. Currently, information does not exist for any species that would allow accurate determination of the degree of inbreeding that would jeopardize long-term survival." The $N_e=500$ prescription is equally problematic, being based on a model that assumes no natural selection, using a single experiment that examined a single characteristic (bristle number) in a single species (*Drosophila*) (Dawson et al. 1987, Simberloff 1988).

More generally, rules of thumb are routinely criticized on the grounds that they might not apply particularly well in specific cases (e.g., Shaffer 1981, Ligon et al. 1986, Dawson et al. 1987, Ewens et al. 1987, Soule 1987, Burgman et al. 1988, Lande 1988). Critics argue that population-specific viability analyses need to be conducted on a case-by-case basis. On the other hand, the plight of endangered species is so urgent and widespread that it may be logistically impossible to undertake viability analyses on more than a relative few of them in the time available (Diamond 1984,

Groves and Clark 1986, Gilpin 1987). In a triage-type situation, rules of thumb may be the only practical option (an example focusing on Pacific salmon is given by Nehlsen et al. 1991).

Depending on the degree of precision desired, it can be either disconcerting or reassuring to note that most rules of thumb fall within an order of magnitude of each other (Soule 1987), giving a generic MVP of 1,000 to 10,000 adults.

Evaluation of Analytic Approaches

Analytic approaches have also been criticized, for example by Shaffer and Samson (1985). Criticisms include lack of realism (as in the simpler diffusion models' assumption of density independence), exclusion of environmental stochasticity (as in early versions of the birth-and-death process model), and problems of interpretation (as in the Ito vs. Stratonovich solutions to stochastic differential equations, e.g., Turelli 1977). A problem with population genetic models is that the equations relating N_e to N require data that are often unavailable (Nelson and Soule 1987, Allendorf et al. in press).

While all of these criticisms have some merit in principle, it is not so clear that they have merit in practice (Simberloff 1988). Several studies have shown that simple analytical models can model complex age-structured dynamics with reasonable accuracy (Tuljapurkar and Orzack 1980, Heyde and Cohen 1985, Goodman 1987b, Lande and Orzack 1988). While the exclusion of density dependence in the simpler diffusion models may be unrealistic, extinction risks seem generally to be higher in density-independent models than in density-dependent ones, at least when the density dependence is compensatory (Ferson et al. 1989, Ginzburg et al. 1990). Thus, exclusion of density dependence may not pose a problem in terms of conservation (i.e., an MVP prescribed by a density-independent model may likely be higher than it needs to be). When data are insufficient to estimate the parameters used in population genetics models, plausible ranges of values can be explored to determine whether the missing data are truly critical (e.g., Simon et al. 1986, Allendorf et al. in press). Of course, analytic models also have the advantages of tractability, reliance on a relatively small number of parameters, and compactness of solution.

Evaluation of Simulation Approaches

Models of this type typically contain a large number of parameters, some or all of which are drawn from probability distributions with specified means and variances. Shaffer (1981) states, "At a minimum, such models (for vertebrates) require knowledge of the mean and variance of age and sex-specific mortality and fecundity rates, age structure, sex ratios, dispersal, and the relationship of these various

parameters to density." Estimation of these parameters is usually considered to be difficult at best (see Ferson et al. 1989 for a contrary opinion).

In particular, variances in these models can be so difficult to estimate that it is often necessary to specify them on a purely subjective basis (Dennis et al. in press). This practice disturbed the spotted owl scientific advisory panel to such an extent that the panel rejected all simulation results that were based on subjectively estimated variance parameters (Dawson et al. 1987). The estimation problems that tend to accompany the simulation approach can be illustrated by the model of Lee and Hyman (1991), which uses 32 parameters (only three of which are variances or coefficients of variation). In the sample configuration given by the authors, it was not uncommon to find an estimate described as "an outright guess" or a value that "seems reasonable."

Rigorous estimation of parameters often requires large amounts of both time and money, and even then acceptable results are not always forthcoming, even for the most basic vital rates. For example, Brussard (1991) notes, "Tens of millions of dollars are spent annually on grizzly bear research, but there are no reliable data on male mating success in this species."

Computational requirements can pose at least a minor problem for the simulation approach. Typically, a large number of runs is necessary to achieve convergence on the pdf of extinction time. At the low end, Harris et al. (1987) say that a minimum of 200 runs is necessary, while Lande and Orzack (1988) contend that a reliable analysis "must involve many thousands of independent simulations."

Finally, the simulation approach is problematic because it typically is not subject to independent validation. The source code is almost never published, and even when it is, thorough validation is an extremely time-consuming task (Simberloff 1988).

On the other hand, the simulation approach profits from its extreme flexibility (Shaffer 1981, Shaffer and Samson 1985). Any quantifiable assumption can be built into the model, and the model can be tailored to suit the needs of particular situations. Simulation models also permit separating known sources of variation from those that are unknown. Although models with large numbers of coefficients are the norm, smaller models can be constructed if overparametrization becomes a critical concern. As with the analytic approaches, it is often possible to address the problem of insufficient data by exploring ranges of parameter values. As a result, the simulation approach is fast becoming the method of choice (Simberloff 1988).

The Use of Models in Population Viability Analysis

Part of the problem in evaluating the various approaches can be traced to confusion regarding the role that models should play in population viability analysis or in management decisions based on population viability analysis. These roles are defined to a large extent by how scientists and managers view models in general. For example, if models are interpreted as literal representations of reality, it is easy to abdicate all responsibility for decision-making to the model. While this view certainly has its advocates, it is by no means universal. When dealing with a model of some natural system, it is important to realize that the model is not the natural system itself (or, in the words of Rosenblueth and Wiener [1945], "The best material model for a cat is another, or preferably the same cat"). Given this, it is not at all obvious that nature should possess any literal equivalent in mathematics or anyplace else (Wigner 1960). An alternative to the literalist perspective is to view models as scientific metaphors (Black 1962, Hesse 1965, Poythress 1983). In such a view, models are things to be used, involving interaction between model, scientist, and nature. This type of approach would find sympathy with Soule's (1987) contention that "models are tools for thinkers, not crutches for the thoughtless."

It has been argued that scientific understanding inevitably involves information that exists independently of any formal model (Polanyi 1962). By emphasizing the nonliteral nature of models, the metaphoric view also speaks to the legitimate role of subjective judgment in the scientific process. Marcot and Holthausen (1987) address this idea in the context of conservation biology, stating, "There is much to be said for using subjective assessments and professional judgments for evaluating population viability, as the basic quantitative tools are still being hewn." Soule and Simberloff (1986) argue similarly, writing, "Intuition, common sense and the judicious use of available data are still the state of the art." Likewise, Zimmerman and Bierregaard (1986) advocate reliance on "intuitive guessing . . . made by the field biologists involved."

This point is particularly important in an area such as conservation biology, where crisis is the norm rather than the exception. "In crisis disciplines, one must act before knowing all the facts" (Soule 1985). Stated alternatively, "The luxuries of confidence limits and certainty are ones that conservation biologists cannot now afford" (Soule 1980). Roughgarden (1983) describes the scientific process as one of building a convincing case, as distinguished from establishing proof by formal rules. In this context, the relevant question is not whether a state of endangerment can be *proven*; rather, the question concerns the appropriate response to whatever amount of information exists (or can be gathered expeditiously) (Maguire 1991). If this view is accepted, it becomes clearly inappropriate to require that a finding of endangerment be corroborated by any particular model before taking action.

Determining Appropriate Persistence Criteria

Shaffer's (1981) original definition of MVP was the population size that gives a 99% chance of persistence over a time horizon of 1000 years. However, he noted that this suggestion was made "tentatively and arbitrarily" and that other values (e.g., $p^*=0.95$, $t^*=100$) could be just as useful. He also emphasized, "I have offered one tentative definition in this paper, but it is not to be taken literally. It is intended as an example for consideration, not a standard for application." Thus, it is not clear that the (0.99,1000) standard has normative significance, but the same could be said just as well for a variety of other possible candidates.

Appendix A illustrates one problem common to any choice of threshold (p,t) values. In brief, any given (p^*,t^*) combination will fall onto a locus defined by some common level of social utility (a social indifference curve). The problem arises from the fact that the nominal utility associated with the threshold (p,t) value will almost certainly be different than the expected utility of the corresponding MVP. Fortunately, the error resulting from equating the two may be likely to fall on the side of conservation if the p^* value is sufficiently high (i.e., greater than about 90%).

Even if p^* values are restricted to the upper end of the possible range, however, another problem presents itself: MVP estimates resulting from thresholds within this range can still be radically different. For example, MVPs resulting from thresholds of (0.95,100) and (0.99,1000) can differ by orders of magnitude. Therefore, the choice between these two (or other) thresholds should not be made lightly. It has been suggested that risk analysis or decision theory might be helpful in evaluating tradeoffs between protection against extinction and the cost of obtaining such protection (Thibodeau 1983, Maguire 1986 and 1991, Marcot 1986, Salwasser et al. 1986). However, since costs will likely vary on a case-by-case basis, a decision-theoretic approach might likely require that p^* and t^* values be established on a case-by-case basis as well (Marcot et al. 1986). Although theoretical grounds for a single choice of p^* and t^* values appear to be lacking, perhaps some guidance can be taken from the relatively frequent use of the (0.95,100) standard, which has been employed (at least approximately) by Shaffer (1983 and 1987), Shaffer and Samson (1985), Suchy et al. (1985), Belovsky (1987), Marcot and Holthausen (1987), Lande (1988), and Soule and Kohm (1989).

Recommendations

Perhaps the best advice is to use all of the information and methods available to the maximum extent feasible. If a variety of approaches or models yield confirmatory results, their conclusion is obviously strengthened. Although the above discussion indicates that all of the common approaches have shortcomings, it is just as true that all can be a useful part of population viability analysis. For example, viability analysis should include a simulation approach whenever time and data permit. If time or data

constraints are so severe that a simulation approach is precluded during the first stages of analysis, it is advisable to include such an approach as soon as possible thereafter.

Unfortunately, lack of time or data can sometimes be a major limiting factor. The phenomenon of multiple filings under the ESA provides an example: Williams (1991) reports that one conservation group is considering filing 195 petitions for protection of Pacific salmon stocks. If all 195 stocks were to qualify as "species," the

1-year time limit prescribed in the ESA (less a reasonable allowance for administrative processing of the petitions) implies that such a filing would require conducting population viability analyses at the rate of about one per working day.

Although conducting complete viability analyses at the rate of one per day is out of the question, some constructive analysis can be undertaken in a relatively short amount of time if necessary. For example, the available rules of thumb can provide a preliminary, order-of-magnitude diagnosis. If a population contains more than, say, 10,000 individuals, it would probably take some fairly extreme extenuating circumstances to consider it endangered. Examples of such extenuating circumstances might be a continuing and severe rate of decline, or extreme variability in population numbers.

Likewise, the various analytic approaches can provide useful information with a minimum of time and data. As an example of how such approaches can be used, the density-independent diffusion model and estimation procedures described by Dennis et al. (in press) will be considered below in some detail. It should be made clear, however, that the special attention given to this model is for illustrative purposes only, and is not intended to discount the importance of other analytic approaches, simulation approaches, or rules of thumb.

Using a Diffusion Model to Estimate MVP

The only empirical information needed to implement the model of Dennis et al. (in press) is a time series of abundance estimates (or indices of relative abundance). Once a data set has been specified, some decisions need to be made regarding how the model treats the data and how the results are to be interpreted. First, it may be important to use a running sum as the index of abundance, rather than the raw data themselves. In their examination of the Yellowstone grizzly bear population, for example, Dennis et al. used a 3-year running sum of the number of observed mothers with cubs because grizzlies are unlikely to reproduce any more frequently than once every 3 years. Pacific salmon would be another example where running sums are appropriate, perhaps basing the interval on the average maximum spawning age of the

population, which would help minimize the extent to which the Markovian assumption underlying the diffusion model is violated (Waples in press).

Second, it is necessary to specify an abundance index value corresponding to extinction, N_E . Zero is not a possibility, since the model operates in terms of $\ln(N)$. If the abundance index is thought to be a good estimate of total population size, setting $N_E=1$ makes some biological sense, at least for sexually reproducing species. However, if the index measures only relative population size, setting $N_E=1$ is not quite so logically compelling. It is also important to remember that the model assumes density-independent dynamics; that is, it assumes that parameter values do not change at small (or large) population sizes. Such an assumption is likely to be most useful if N_E is restricted to the range above some critical population size where parameter values are likely to change (Capocelli and Ricciardi 1974, Dennis et al. in press). This is good advice for some applications, but where the goal is to estimate MVP, it begs the question (i.e., it tends to view the minimum viable population as a function of the *really* minimum viable population). Given that the ESA defines endangerment in terms of extinction (not just low numbers), perhaps the best alternative is to set $N_E=1$, at least for indices that measure the total population. Even when the index measures only relative abundance, using $N_E=1$ as a default definition would have the benefit of providing some standardization.

Once N_E has been established, the model provides a straightforward estimation of the pdf of extinction time for any given N . However, it should be emphasized that while this estimate is the product of a rigorous and well-developed theory, it is still only a point estimate. Unfortunately, the confidence intervals around the estimated pdf of extinction time tend to be quite broad. For example, in examining the dynamics of the California condor (*Gymnogyps californianus*), Dennis et al. (in press) estimated that the wild population censused in 1980 had a 22% chance of extinction by 1995, with a 95% confidence interval ranging from 2% up to 86%. (For simulation studies, the problem of establishing confidence intervals around MVP estimates is addressed by Harris et al. [1987].)

Finally, implementation of this or any other model requires choosing p^* and t^* values. Actually, two sets of threshold values are required in the context of the ESA, since the Act defines two levels of jeopardy (endangered and threatened). As noted in the Introduction, it is unfortunate that the ESA does not define endangerment with much precision. In the absence of further guidance, perhaps the best decision for "endangered" p^* and t^* values is to accept the conventional wisdom that sets $p^*=0.95$ and $t^*=100$. In other words, at the "endangered" level, MVP is the population size that gives a 95% chance of extinction over the next 100 years.

While the ESA is decidedly vague regarding the definition of endangerment, it does give some indication of how "threatened" p^* and t^* values should relate to their "endangered" counterparts. Since a threatened species is defined as one which is "likely to become endangered within the foreseeable future," one need only interpret the terms "likely" and "foreseeable future" to relate the "threatened" MVP to the "endangered" MVP. A reasonable interpretation of a "likely" event would be one which has at least a 50% chance of occurring. Quantifying "foreseeable future" is not so straightforward, but perhaps something like 10 years would be satisfactory. In other words, the "threatened" MVP is the population size that gives a 50% chance of reaching the "endangered" MVP within 10 years.

Other Considerations

As discussed in the Introduction, this paper has focused on the topic of MVP determination under the assumption that the population in question is qualitatively and spatiotemporally well distributed. In practice, of course, it will be necessary to determine whether this assumption holds and to adjust the analysis accordingly if it does not. Specific factors to be considered include genetic integrity (e.g., are there threats to the genetic traits that make a particular population worth preserving in the first place?) and population density (e.g., is the population distributed across its habitat in a way that makes finding a mate unlikely?). Additionally, the role (if any) of artificial propagation in maintaining the population should be addressed. Although artificial propagation can be used in a recovery plan, it should not be viewed as a permanent substitute for the population's natural capacity for self-maintenance (Waples 1991).

Furthermore, whenever a viability analysis includes formal modeling, model results should be checked against any other available indicators of population viability. If model results seem to imply a different conclusion than other indicators, both should be checked carefully to determine an explanation for the inconsistency. In addition to the rules of thumb described above, possible indicators of population viability include the ratio of current abundance to carrying capacity or historical abundance, abundance trends, and recent or likely future changes in factors that influence abundance trends. As an example of the last type of indicator, the construction of several hydroelectric dams on the Columbia River during the past few decades has been suggested as a primary cause for the decline of several naturally spawning stocks of Pacific salmon. However, it is not clear that the abundance trends observed during the period of dam construction are the best indicators of future abundance trends, since it is unlikely that dam construction will proceed at the same rate as in past years.

Another problem to consider is the role that an MVP should play in a recovery plan. In other words, suppose that MVP is estimated for a given population at 5,000

individuals, and that current N is estimated to be 2,000, thereby prompting an ESA listing. Is the goal of a recovery plan simply to achieve $N > MVP$? To answer this question, consider the density-independent diffusion model, where MVP is defined (for given p^* and t^* values) by the parameters μ and σ^2 . If the management regime changes significantly in response to a listing under the ESA (as is required), this will undoubtedly cause μ or σ^2 to change as well, in which case MVP will also change. For example, if a management action caused μ to increase (thus tending to slow or reverse a long-term decline), MVP would decrease, assuming that σ^2 did not increase along with μ . Thus, if a population viability analysis determines that $N < MVP$, the focus should shift immediately from that particular MVP to μ and σ^2 . In other words, when using a model of this type, the focus should not be so much on achieving MVP as on changing it (via μ and σ^2).

This leads to the question of whether "delisting" criteria should be specified at the time of an initial ESA listing. If these criteria include only policy decisions such as p^* and t^* values or statistical significance levels, the suggestion to make these explicit is worthwhile. This would help prevent the possibility of delisting occurring as a result of a change in listing criteria, and it would tend to reinforce the idea that the purpose of a listing is to effect recovery, not to guarantee special protection forever. However, if delisting criteria also include such things as particular models or a particular MVP, the suggestion is more problematic because it tends to place constraints on the role of information that might become available after the initial listing. For example, what seems like a reasonable MVP today might seem either needlessly conservative or recklessly optimistic 10 years from now.

A final cautionary note: Endangerment is not necessarily the same as depletion. In the case of harvested fish stocks, for example, the fact that a stock may be below the abundance level corresponding to maximum sustainable yield does not necessarily mean that an ESA listing is in order. A population can be depressed and still be relatively stable. In the context of the ESA, the question is not whether the stock could be managed better, but whether the stock is in danger of extinction.

ACKNOWLEDGMENTS

The following individuals provided helpful comments on an earlier draft of the manuscript: Nic Bax (Pentec Environmental), Jim Berkson (Columbia River Inter-Tribal Fish Commission), Mitch Friedman (Greater Ecosystem Alliance), Jim Lannan (Oregon State University), Bruce Marcot (U.S. Forest Service), Ben Sandford and Robin Waples (National Marine Fisheries Service), and Hal Weeks (Oregon Department of Fish and Wildlife).

CITATIONS

Allendorf, F. W., R. B. Harris, and L. H. Metzgar. In press. Estimation of effective population size of grizzly bears by computer simulation. *In* T. R. Dudley (editor), *Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology*, July, 1990, College Park, MD. Dioscorides Press, Portland, OR.

Allendorf, F. W., and C. Servheen. 1986. Genetics and the conservation of grizzly bears. *Trends Ecol. Evol.* 1:88-89.

Bartlett, M. S. 1960. *Stochastic population models in ecology and epidemiology*. Methuen, London, 90 p.

Beddington, J. R., and R. M. May. 1977. Harvesting natural populations in a randomly fluctuating environment. *Science* 197:463-465.

Belovsky, G. E. 1987. Extinction models and mammalian persistence. *In* M. E. Soule (editor), *Viable populations for conservation*, p. 35-57. Cambridge Univ. Press, Cambridge.

Black, M. 1962. *Models and metaphors: Studies in language and philosophy*. Cornell Univ. Press, Ithaca, NY, 267 p.

Boswell, M. T., J. K. Ord, and G. P. Patil. 1979. Chance mechanisms underlying univariate distributions. *In* J. K. Ord, G. P. Patil, and C. Taillie (editors), *Statistical distributions in ecological work*, p. 3-156. International Co-operative Publishing House, Fairland, MD.

Braumann, C. A. 1983. Population growth in random environments. *Bull. Math. Biol.* 45:635-641.

Brussard, P. F. 1991. The role of ecology in biological conservation. *Ecol. Appl.* 1:6-12.

Burgman, M. A., H. R. Akcakaya, and S. S. Loew. 1988. The use of extinction models for species conservation. *Biol. Conserv.* 43:9-25.

Burgman, M. A., and V. A. Gerard. 1990. A stage-structured, stochastic population model for the giant kelp *Macrocystis pyrifera*. *Mar. Biol.* 105:15-23.

Capocelli, R. M., and L. M. Ricciardi. 1974. A diffusion model for population growth in random environment. *Theor. Pop. Biol.* 5:28-41.

Crow, J. F., and C. Denniston. 1988. Inbreeding and variance effective population numbers. *Evol.* 42:482-495.

Crow, J. F., and M. Kimura. 1970. An introduction to population genetics theory. Harper and Row, New York, 591 p.

Dawson, W. R., J. D. Ligon, J. R. Murphy, J. P. Myers, D. Simberloff, and J. Verner. 1987. Report of the scientific advisory panel on the spotted owl. *Condor* 89:205-229.

den Boer, P. J. 1968. Spreading of risk and stabilization of animal numbers. *Acta Biotheor.* 18:165-194.

Dennis, B., P. L. Munholland, and J. Michael Scott. In press. Estimation of growth and extinction parameters for endangered species. *Ecol. Monogr.*

Dennis, B., and G. P. Patil. 1984. The gamma distribution and weighted multimodal gamma distributions as models of population abundance. *Math. Biosci.* 68:187-212.

Deriso, R. B., and A. M. Parma. 1988. Dynamics of age and size for a stochastic population model. *Can. J. Fish. Aquat. Sci.* 45:1054-1068.

Diamond, J. M. 1984. Distributions of New Zealand birds on real and virtual islands. *N. Z. J. Ecol.* 7:37-55.

Ewens, W. J. 1982. On the concept of the effective population size. *Theor. Pop. Biol.* 21:373-378.

Ewens, W. J., P. J. Brockwell, J. M. Gani, and S. I. Resnick. 1987. Minimum viable population size in the presence of catastrophes. *In* M. E. Soule (editor), *Viable populations for conservation*, p. 59-68. Cambridge Univ. Press, Cambridge.

Feldman, M. W., and J. Roughgarden. 1975. A population's stationary distribution and chance of extinction in a stochastic environment with remarks on the theory of species packing. *Theor. Pop. Biol.* 7:197-207.

Feller, W. 1939. Die Grundlagen der Volterraschen Theorie des Kampfes ums Dasein in Wahrscheinlichkeitstheoretischer Behandlung. *Acta Biotheor.* 5:11-40.

Fergus, C. 1991. The Florida panther verges on extinction. *Science* 251:1178-1180.

Person, S., L. Ginzburg, and A. Silvers. 1989. Extreme event risk analysis for age-structured populations. *Ecol. Model.* 47:175-187.

Ferson, S., F. J. Rohlf, L. R. Ginzburg, and G. Jacquez. 1988. RAMAS/a user manual: Modeling fluctuations in age-structured populations. Exeter Publishing, Setauket, NY.

Foose, T. J. 1983. The relevance of captive populations to the conservation of biotic diversity. *In* C. M. Schonewald-Cox, S. M. Chambers, B. MacBryde, and W. L. Thomas (editors), *Genetics and Conservation*, p. 374-401. Benjamin/Cummings Publishing, Menlo Park, CA, 722 p.

Franklin, I. R. 1980. Evolutionary change in small populations. *In* M. E. Soule and B. A. Wilcox (editors), *Conservation biology: An evolutionary-ecological perspective*, p. 135-149. Sinauer Assoc., Sunderland, MA.

Gilpin, M. E. 1987. Theory versus practice. *Trends Ecol. Evol.* 2:169.

Gilpin, M. E., and M. E. Soule. 1986. Minimum viable populations: Processes of species extinction. *In* M. E. Soule (editor), *Conservation biology: The science of scarcity and diversity*, p. 19-34. Sinauer Assoc., Sunderland, MA, 584 p.

Ginzburg, L. R., S. Ferson, and H. R. Akcakaya. 1990. Reconstructibility of density dependence and the conservative assessment of extinction risks. *Conserv. Biol.* 4:63-70.

Ginzburg, L. R., L. B. Slobodkin, K. Johnson, and A. G. Bindman. 1982. Quasiextinction probabilities as a measure of impact on population growth. *Risk Anal.* 2:171-181.

Goel, N. S., and N. Richter-Dyn. 1974. *Stochastic models in biology*. Academic Press, New York, 269 p.

Goel, N. S., S. C. Maitra, and E. W. Montroll. 1971. On the Volterra and other nonlinear models of interacting populations. *Rev. Mod. Phys.* 43:231-276.

Goodman, D. 1987a. Consideration of stochastic demography in the design and management of biological reserves. *Nat. Res. Model.* 1:205-234.

Goodman, D. 1987b. The demography of chance extinction. *In* M. E. Soule (editor), *Viable populations for conservation*, p. 11-34. Cambridge Univ. Press, Cambridge.

Grier, J. W. 1980a. Ecology: A simulation model for small populations of animals. *Creative Computing* 6(7):116-121.

Grier, J. W. 1980b. Modeling approaches to bald eagle population dynamics. *Wildl. Soc. Bull.* 8:316-322.

Gross, J. E., J. E. Roelle, and G. L. Williams. 1973. Program ONEPOP an information processor: a system modeling and communication project. Progress report, Colorado Cooperative Wildlife Research Unit, Colorado St. Univ., Ft. Collins, 327 p.

Groves, C. R., and T. W. Clark. 1986. Determining minimum population size for recovery of the black-footed ferret. *Great Basin Nat. Mem.* 8:150-159.

Hanson, F. B., and H. C. Tuckwell. 1978. Persistence times of populations with large random fluctuations. *Theor. Pop. Biol.* 14:46-61.

Harris, R. B., L. A. Maguire, and M. L. Shaffer. 1987. Sample sizes for minimum viable population estimation. *Conserv. Biol.* 1:72-76.

Hesse, M. 1965. The explanatory function of metaphor. *In* Y. Bar-Hillel (editor), *Logic, methodology, and philosophy of science: Proceedings of the 1964 International Congress*, p. 249-259. North Holland Publishing, Amsterdam.

Heyde, C. C., and J. E. Cohen. 1985. Confidence intervals for demographic projections based on products of random matrices. *Theor. Pop. Biol.* 27:120-153.

Hill, W. G. 1972. Effective size of populations with overlapping generations. *Theor. Pop. Biol.* 3:278-289.

Hill, W. G. 1979. A note on effective population size with overlapping generations. *Genetics* 92:317-322.

Hooper, M. D. 1971. The size and surroundings of nature reserves. *In* E. Duffey and A. S. Watt (editors), *The scientific management of animal and plant communities for conservation*, p. 555-561. Blackwell Scientific Publications, Oxford.

Johnson, N. L., and S. Kotz. 1970. *Distributions in statistics: continuous univariate distributions*, vol. 1. John Wiley and Sons, New York, 300 p.

Keiding, N. 1975. Extinction and exponential growth in random environments. *Theor. Pop. Biol.* 8:49-63.

Kendall, D. G. 1948. On the generalized "birth-and-death" process. *Ann. Math. Stat.* 19:1-15.

Kerner, E. H. 1957. A statistical mechanics of interacting biological species. *Bull. Math. Biophys.* 19:121-146.

Kerner, E. H. 1959. Further considerations on the statistical mechanics of biological associations. *Bull. Math. Biophys.* 21:217-255.

Knight, R. R., and L. L. Eberhardt. 1985. Population dynamics of Yellowstone grizzly bears. *Ecol.* 66:323-334.

LaCava, J., and J. Hughes. 1984. Determining minimum viable population levels. *Wildl. Soc. Bull.* 12:370-376.

Lacy, R. C. 1987. Loss of genetic diversity from managed populations: Interacting effects of drift, mutation, immigration, selection, and population subdivision. *Cons. Biol.* 1:143-158.

Lacy, R. C. 1991. VORTEX: Simulation model of stochastic population change. Unpubl. manuscript, 5 p. Chicago Zoological Society, Brookfield, IL 60513.

Lacy, R. C., and T. W. Clark. 1990. Population viability assessment of the eastern barred bandicoot in Victoria. *In* T. W. Clark and J. H. Seebeck (editors), *The management and conservation of small populations*, p. 131-146. Chicago Zoological Society, Brookfield, IL 60513.

Lacy, R. C., N. R. Plesness, and U. S. Seal. 1989. Puerto Rican parrot population viability analysis. Report to the U.S. Fish and Wildlife Service. Captive Breeding Specialist Group, Species Survival Commission, International Union for the Conservation of Nature, Apple Valley, MN.

Lande, R. 1987. Extinction thresholds in demographic models of territorial populations. *Am. Nat.* 130:624-635.

Lande, R. 1988. Genetics and demography in biological conservation. *Science* 241:1455-1460.

Lande, R., and G. F. Barrowclough. 1987. Effective population size, genetic variation, and their use in population management. *In* M. E. Soule (editor), *Viable populations for conservation*, p. 87-123. Cambridge Univ. Press, Cambridge.

Lande, R., and S. H. Orzack. 1988. Extinction dynamics of age-structured populations in a fluctuating environment. *Proc. Natl. Acad. Sci.* 85:7418-7421.

Lee, D. C., and J. B. Hyman. 1991. The stochastic life-cycle model (SLCM): A tool for simulating the population dynamics of anadromous salmonids. Unpubl. manuscript, 27 p. Resources for the Future, 1616 P Street NW, Washington, DC 20036.

Lehmkuhl, J. F. 1984. Determining size and dispersion of minimum viable populations for land management planning and species conservation. *Env. Manage.* 8:167-176.

Leigh, E. G. 1981. The average lifetime of a population in a varying environment. *J. theor. Biol.* 90:213-239.

Levins, R. 1969. The effect of random variations of different types of population growth. *Proc. Nat. Acad. Sci.* 62:1061-1065.

Lewontin, R. C., and D. Cohen. 1969. On population growth in a randomly varying environment. *Proc. Nat. Acad. Sci.* 62:1056-1060.

Ligon, J. D., P. B. Stacey, R. N. Conner, C. E. Bock, and C. S. Adkisson. 1986. Report of the American Ornithologists' Union committee for the conservation of the red-cockaded woodpecker. *Auk* 103:848-855.

Lindenmayer, D. B., V. C. Thomas, R. C. Lacy, and T. W. Clark. 1991. Population viability analysis (PVA): The concept and its applications, with a case study of Leadbeater's possum, *Gymnobelideus leadbeateri* McCoy. Report to the Forest and Timber Inquiry (Resource Assessment Commission), Canberra, Australia, 170 p.

Ludwig, D. 1975. Persistence of dynamical systems under random perturbations. *SIAM Rev.* 17:605-640.

MacArthur, R. H., and E. O. Wilson. 1967. The theory of island biogeography. Princeton Univ. Press, Princeton, NJ, 203 p.

Maguire, L. A. 1986. Using decision analysis to manage endangered species populations. *J. Env. Manage.* 22:345-360.

Maguire, L. A. 1991. Risk analysis for conservation biologists. *Cons. Biol.* 5:123-125

Marcot, B. G. 1986. Concepts of risk analysis as applied to viable population assessment and planning. *In* B. A. Wilcox, P. F. Brussard, and B. G. Marcot (editors), The management of viable populations: Theory, applications, and case studies, p. 89-101. Center for Conservation Biology, Department of Biological Sciences, Stanford Univ., Stanford, CA 94305.

- Marcot, B. G., D. Carrier, and R. Holthausen. 1986. The northern spotted owl (*Strix occidentalis caurina*). In B. A. Wilcox, P. F. Brussard, and B. G. Marcot (editors), *The management of viable populations: Theory, applications, and case studies*, p. 123-145. Center for Conservation Biology, Department of Biological Sciences, Stanford Univ., Stanford, CA 94305.
- Marcot, B. G., and R. Holthausen. 1987. Analyzing population viability of the spotted owl in the Pacific Northwest. *Trans. N. Am. Wildl. Nat. Res. Conf.* 52:333-347.
- May, R. M., J. R. Beddington, J. W. Horwood, and J. G. Shepherd. 1978. Exploiting natural populations in an uncertain world. *Math. Biosci.* 42:219-252.
- May, R. M. 1973. *Stability and complexity in model ecosystems*. Princeton Univ. Press, Princeton, NJ, 235 p.
- Nehlsen, W., J. E. Williams, and J. A. Lichatowich. 1991. Pacific salmon at the crossroads: Stocks at risk from California, Oregon, Idaho, and Washington. *Fisheries* 16:4-21.
- Nelson, K., and M. Soule. 1987. Genetical conservation of exploited fishes. In N. Ryman and F. Utter (editors), *Population genetics and fishery management*, p. 345-368. Univ. Washington Press, Seattle.
- Peterman, R. M. 1981. Form of random variation in salmon smolt-to-adult relations and its influence on production estimates. *Can. J. Fish. Aquat. Sci.* 38:1113-1119.
- Pojar, T. M. 1981. A management perspective of population modeling. In C. W. Fowler and T. D. Smith (editors), *Dynamics of large mammal populations*, p. 241-261. John Wiley and Sons, New York.
- Polansky, P. J. 1978. Two-dimensional stochastic exponential growth models. *J. Math. Biol.* 6:333-342.
- Polanyi, M. 1962. *Personal knowledge*. Univ. Chicago Press, Chicago, 428 p.
- Poythress, V. S. 1983. Science as allegory. *J. Am. Sci. Affil.* 35:65-71.
- Reed, J. M., P. D. Doerr, and J. R. Walters. 1986. Determining minimum population sizes for birds and mammals. *Wildl. Soc. Bull.* 14:255-261.
- Reed, J. M., P. D. Doerr, and J. R. Walters. 1988. Minimum viable population size of the red-cockaded woodpecker. *J. Wildl. Manage.* 52:385-391.

Richter-Dyn, N., and N. S. Goel. 1972. On the extinction of a colonizing species. *Theor. Pop. Biol.* 3:406-433.

Rosenblueth, A., and N. Wiener. 1945. The role of models in science. *Phil. Sci.* 12:316-321.

Roughgarden, J. 1979. *Theory of population genetics and evolutionary ecology: An introduction.* MacMillan Publishing, New York, 634 p.

Roughgarden, J. 1983. Competition and theory in community ecology. *Am Nat.* 122:583-601.

Salwasser, H., R. S. Holthausen, and B. G. Marcot. 1986. Viable population policy in the national forests: Of laws and regulations. *In* B. A. Wilcox, P. F. Brussard, and B. G. Marcot (editors), *The management of viable populations: Theory, applications, and case studies*, p. 41-48. Center for Conservation Biology, Department of Biological Sciences, Stanford Univ., Stanford, CA 94305.

Salwasser, H., and B. G. Marcot. 1986. Viable population planning: A planning framework for viable populations. *In* B. A. Wilcox, P. F. Brussard, and B. G. Marcot (editors), *The management of viable populations: Theory, applications, and case studies*, p. 63-71. Center for Conservation Biology, Department of Biological Sciences, Stanford Univ., Stanford, CA 94305.

Salwasser, H., S. P. Mealey, and K. Johnson. 1984. Wildlife population viability: A question of risk. *Trans. N. Am. Nat. Res. Conf.* 49:421-439.

Samson, F. B., F. Perez-Trejo, H. Salwasser, and M. L. Shaffer. 1985. On determining and managing minimum population size. *Wildl. Soc. Bull.* 13:425-433.

Seal, U. S., and R. C. Lacy. 1989. Florida panther population viability analysis. Report to the U.S. Fish and Wildlife Service. Captive Breeding Specialist Group, Species Survival Commission, International Union for the Conservation of Nature, Apple Valley, MN.

Seal, U. S., and R. C. Lacy. 1990. Florida Key deer (*Odocoileus virginianus clavium*) population viability assessment. Report to the U.S. Fish and Wildlife Service. Captive Breeding Specialist Group, Species Survival Commission, International Union for the Conservation of Nature, Apple Valley, MN.

Shaffer, M. L. 1978. Determining minimum viable population sizes: A case study of the grizzly bear (*Ursus arctos* L.). Ph.D. thesis, Duke Univ., Durham, NC, 190 p.

Shaffer, M. L. 1981. Minimum population sizes for species conservation. *BioScience* 31:131-134.

Shaffer, M. L. 1983. Determining minimum viable population sizes for the grizzly bear. *Intl. Conf. Bear Res. Manage.* 5:133-139.

Shaffer, M. L. 1987. Minimum viable populations: Coping with uncertainty. *In* M. E. Soule (editor), *Viable populations for conservation*, p. 69-86. Cambridge Univ. Press, Cambridge.

Shaffer, M. L., and F. B. Samson. 1985. Population size and extinction: a note on determining critical population sizes. *Am. Nat.* 125:144-152.

Shull, A. M., and A. R. Tipton. 1987. Effective population size of bison on the Wichita Mountains Wildlife Refuge. *Conserv. Biol.* 1:35-41.

Simberloff, D. 1988. The contribution of population and community biology to conservation science. *Ann. Rev. Ecol. Syst.* 19:473-511.

Simon, R. C., J. D. McIntyre, and A. R. Hemmingsen. 1986. Family size and effective population size in a hatchery stock of coho salmon (*Oncorhynchus kisutch*). *Can. J. Fish. Aquat. Sci.* 43:2434-2442.

Soule, M. E. 1980. Thresholds for survival: Maintaining fitness and evolutionary potential. *In* M. E. Soule and B. A. Wilcox (editors), *Conservation biology: An evolutionary-ecological perspective*, p. 151-169. Sinauer Assoc., Sunderland, MA.

Soule, M. E. 1985. What is conservation biology? *BioScience* 35:727-734.

Soule, M. E. 1987. Where do we go from here? *In* M. E. Soule (editor), *Viable populations for conservation*, p. 175-183. Cambridge Univ. Press, Cambridge.

Soule, M. E., and K. A. Kohm. 1989. *Research priorities for conservation biology*. Island Press, Washington, DC, 97 p.

Soule, M. E., and D. Simberloff. 1986. What do genetics and ecology tell us about the design of nature reserves? *Biol. Conserv.* 35:19-40.

Soule, M. E., and B. A. Wilcox (editors). 1980. *Conservation biology: An evolutionary-ecological perspective*. Sinauer Assoc., Sunderland, MA, 395 p.

- Suchy, W. J., L. L. McDonald, M. D. Strickland, and S. H. Anderson. 1985. New estimates of minimum viable population size for grizzly bears of the Yellowstone ecosystem. *Wildl. Soc. Bull.* 13:223-228.
- Thibodeau, F. R. 1983. Endangered species: Deciding which species to save. *Env. Manage.* 7:101-107.
- Thomas, C. D. 1990. What do real population dynamics tell us about minimum viable population sizes? *Conserv. Biol.* 4:324-327.
- Tier, C., and F. B. Hanson. 1981. Persistence in density-dependent stochastic populations. *Math. Biosci.* 53:89-117.
- Tuckwell, H. C. 1974. A study of some diffusion models of population growth. *Theor. Pop. Biol.* 5:345-357.
- Tuljapurkar, S. D., and S. H. Orzack. 1980. Population dynamics in variable environments I. Long-run growth rates and extinction. *Theor. Pop. Biol.* 18:314-342.
- Turelli, M. 1977. Random environments and stochastic calculus. *Theor. Pop. Biol.* 12:140-178.
- U.S. Fish and Wildlife Service. 1985. Red-cockaded woodpecker recovery plan. Atlanta, GA.
- Waples, R. S. 1991. Definition of "species" under the Endangered Species Act: Application to Pacific salmon. NOAA Tech. Memo. NMFS F/NWC-194, 29 p.
- Waples, R. S. In press. Conservation genetics of Pacific salmon. II. Effective population size and the rate of loss of genetic variability. *J. Hered.* 81:000-000.
- Waples, R. S., and D. J. Teel. 1990. Conservation genetics of Pacific salmon. I. Temporal changes in allele frequency. *Cons. Biol.* 4:144-156.
- Watts, T., and W. Conley. 1981. Extinction probabilities in a remnant population of *Ovis canadensis mexicana*. *Acta Theriol.* 26:393-405.
- Wigner, E. P. 1960. The unreasonable effectiveness of mathematics in the natural sciences. *Commun. Pure Appl. Math.* 13:1-14.
- Wilcox, B. A. 1986. Extinction models and conservation. *Trends Ecol. Evol.* 1:46-48.
- Williams, M. 1991. Fishermen on the line. *Seattle Times*, April 1, Section A, page 1.

Wright, S. 1931. Evolution in Mendelian populations. *Genetics* 16:97-159.

Zimmerman, B. L., and R. O. Bierregaard. 1986. Relevance of the equilibrium theory of island biogeography and species-area relations to conservation with a case from Amazonia. *J. Biogeog.* 13:133-143.

APPENDIX A: EVALUATION OF NOMINAL AND EXPECTED UTILITIES FROM A MINIMUM VIABLE POPULATION

Given an initial size, a population's probability of persistence (p) can be plotted as a function of time (t). The probability of persistence for any self-reproducing population of positive initial size N declines from a value of $p=1$ at $t=0$, approaching $p=0$ as t becomes sufficiently large. Goodman (1987b) and Lande and Orzack (1988) have suggested that the plot of p against t may often be approximated by a negative exponential function. For any given value of t , p would presumably increase with N . The following equation may thus serve as an appropriate first approximation:

$$p = e^{-\alpha_1 t / N^{\alpha_2}}, \quad (\text{A1})$$

where α_1 is a positive constant and α_2 is a constant between 0 and 2 (the reason for the upper bound on α_2 will become apparent later). [Figure A1](#) shows an example corresponding to parameter values $\alpha_1=50.275625$ and $\alpha_2=1.6637656$ (values were chosen for illustrative purposes only).

Shaffer (1981) suggested defining the minimum viable population (MVP) as the value of N that results in a threshold p value at some given value of t . The values $p=0.95$ and $t=100$ are often used for this purpose. Those who employ this definition are generally quick to point out that although it is highly subjective, the need to select some (p,t) reference point is inescapable. One way of looking at the question of an appropriate reference point is from the perspective of a social utility function (e.g., Thibodeau 1983, Maguire 1986, Marcot 1986). That is to say, it can be argued that society would derive some amount of satisfaction, or utility, from realizing a given probability of persistence over a specified time horizon. A suitably general form for such a social utility function is the Cobb-Douglas production function:

$$U = \beta_1 p^{\beta_2} t^{\beta_3}, \quad (\text{A2})$$

where U represents utility, β_1 is a positive constant, and β_2 and β_3 are constants between 0 and 1 (the upper bound insures diminishing marginal utility). Because it simplifies the ensuing mathematics considerably, Equation (A2) will be restricted here by setting $\beta_3=0.5$ (since 0.5 is the midpoint of the logically possible range, it should also be a reasonably representative value).

Equation (A2) implies a set of indifference curves consisting of (p,t) loci along which U is constant. [Figure A2](#) shows an example corresponding to parameter

values $\beta_1=10.383474$ and $\beta_2=0.73363276$ (values were chosen for illustrative purposes only).

Thus, for any combination of p and t (such as $p=0.95$ and $t=100$), Equation (A2) defines a single value for the utility derived by society. For example, under the parameter values used to generate [Figure A2](#), the utility derived from the suggested criterion of $p=0.95$ and $t=100$ is 100 ([Figure A2](#)). However, this correspondence is deceptively simple, because deciding on an appropriate MVP results in not a single (p,t) pair but an entire locus of (p,t) pairs as described by Equation (A1). The possibility that the distribution of extinction times may not be adequately characterized by a single point is conjectured by Salwasser et al. (1986). This raises an important question: Is the utility that society can expect from a given value of N (the expected utility) equal to the utility associated with any arbitrary (p,t) pair that occurs along Equation (A1) (the "nominal" utility)?

The first step in deriving the expected utility for a given value of N is to convert Equation (A1) into a probability density function, giving

$$P(t) = \frac{\alpha_2 e^{-\alpha_1 t / N^{\alpha_2}}}{N^{\alpha_2}}, \quad (\text{A3})$$

where $P(t)$ is the probability of persistence rescaled so that the area under the curve equals 1.0.

The second step is to substitute Equation (A1) into Equation (A2), eliminating p as an explicit argument:

$$U(t) = \beta_1 \sqrt{t} e^{-\alpha_1 \beta_1 t / N^{\alpha_2}} \quad (\text{A4})$$

(U has been rewritten as $U(t)$ to emphasize the role of t in the equation).

The third step is to integrate the product of Equations (A3) and (A4) over t from zero to infinity, giving

$$E(U) = \int_0^{\text{infinity}} P(t)U(t) dt = \left(\frac{\beta_1}{2(1 + \beta_2)} \right) \sqrt{\frac{\pi N^{\alpha_2}}{\alpha_2(1 + \beta_2)}}, \quad (\text{A5})$$

where $E(U)$ is expected utility. Note that the upper bound of 2 placed on α_2 insures diminishing marginal expected utility. [Figure A3](#) gives an example corresponding to the same parameter values used to generate [Figures A1 and A2](#).

Although Equation (A5) describes $E(U)$ as a function of N , it can be rewritten in terms of p and t . To see this, first solve Equation (A1) for N as follows:

$$N = \left(\frac{\alpha t}{-\ln(p)} \right)^{1/\alpha_1}. \quad (\text{A6})$$

Equation (A6) can then be substituted into Equation (A5), yielding

$$E(U) = \left(\frac{\beta_1}{2(1 + \beta_2)} \right) \sqrt[3]{\frac{\pi t}{-\ln(p)(1 + \beta_2)}}. \quad (\text{A7})$$

The ratio between nominal utility and expected utility can be obtained by dividing Equation (A2) by Equation (A7), which eliminates t and β_1 . To find the locus of points along which nominal utility and expected utility are identical, Equations (A2) and (A7) can be equated, giving

$$\frac{-4(1 + \beta_2)^3 p^{2\beta_1} \ln(p)}{\pi} = 1. \quad (\text{A8})$$

Equation (A8) describes the curve shown in [Figure A4](#). For values of p below the curve, nominal utility will exceed expected utility, while for values of p above the curve, the reverse will hold.

As an example, [Figure A5](#) shows a case where an N value of 1,000 results in $p=0.95$ at $t=100$, which corresponds to a U value of 100 (parameter values used to generate this figure were the same as those used to generate [Figures A1 and A2](#)). Although the nominal utility is 100, the expected utility is about 178 ([Figure A3](#)). According to Equation (A8), the β_2 value used to generate [Figure A5](#) implies that any p greater than about 0.82 will result in expected utility exceeding nominal utility ([Figure A4](#)). Thus, the example shown in [Figure A5](#) tends to confirm the result given by Equation (A8).

To achieve an expected utility equal to the nominal utility of 100 attained at $p=0.95$ and $t=100$, N would have to be reduced considerably. The N value corresponding to a given level of $E(U)$ can be obtained by rearranging Equation (A5) as follows:

$$N = \left[\left(\frac{2(1 + \beta_2)E(U)}{\beta_1} \right)^2 \left(\frac{\alpha(1 + \beta_2)}{\pi} \right) \right]^{1/\alpha_1}. \quad (\text{A9})$$

For the example shown in [Figure A5](#), N would have to be reduced to a value of 500 in order to reduce $E(U)$ to the nominal level of 100 corresponding to $p=0.95$ and $t=100$. (At $t=100$, an N value of 500 corresponds to a p value of 0.85 and a nominal utility of about 92.)

[Figure A6](#) shows an example from the opposite side. Here it is assumed that the threshold values of p and t are 0.75 and 500, respectively. The other parameter values used are the same as those used to generate [Figure A5](#). In this example, an N value of about 933 is required to achieve the threshold p and t values. This corresponds to a nominal utility of about 188, but an expected utility of only about 168. To increase the expected utility up to the nominal level of 188, an N of about 1068 is required, corresponding to a new nominal utility of about 196 and a new threshold p of about 0.79 (at the same threshold value of t).

Because only the threshold (p,t) combination is usually reported when an MVP is being determined, society (or those making decisions for society) may incorrectly assume that the nominal utility associated with the threshold combination represents the expected utility of the corresponding MVP. If the threshold p is sufficiently high, such an assumption would always err on the safe side; that is, society would never overestimate its expected utility. According to Equation (A8), the breakeven value of p reaches a maximum of about 0.88 when $\beta_2=1$. At the other extreme ($\beta_2=0$), p values less than about 0.46 will always result in an overestimate of $E(U)$, while p values between 0.46 and 0.88 may result in overestimates or not, depending on the value of β_2 . Thus, the "safe" range of p values runs from about 0.88 to 1.0. Interestingly, the mid-point of this range is about 0.94, quite close to the threshold p value of 0.95 often suggested in the literature.

The central conclusion to be drawn from this analysis is that the threshold value of p should be relatively high, regardless of the threshold value of t or the value of any other parameter. For example, although $p=0.45$ and $t=300$ give virtually the same nominal utility as $p=0.95$ and $t=100$ in [Figure A2](#), these should not be used as threshold values, because the low p value guarantees that nominal utility will exceed expected utility.

APPENDIX B: ELASTICITY OF EXPECTED EXTINCTION TIME IN A SPECIAL CASE OF THE BIRTH-AND-DEATH PROCESS MODEL

Description of the Model

Leigh (1981) and Goodman (1987a, 1987b) have reparametrized the classic birth-and-death process model in terms of density-dependent rates of increase and their

variances. In the form used by Goodman, the model describes expected extinction time as follows:

$$E(T_N) = \sum_{i=1}^N \sum_{j=i}^{N_{\max}} \left[\left(\frac{2}{j [j \text{Var}(R_j) - E(R_j)]} \right) \prod_{k=i}^{j-1} \frac{h \text{Var}(R_k) + E(R_k)}{h \text{Var}(R_k) - E(R_k)} \right], \quad (\text{B1})$$

where N is initial population size, $E(T_N)$ is the expected extinction time when initial population size is N , N_{\max} is the maximum possible population size, R_j is the instantaneous rate of increase (a random variable) when the population is of size j , $E(R_j)$ is the expected value of R_j , and $\text{Var}(R_j)$ is the variance of R_j . (It should be noted that N_{\max} is not simply carrying capacity. While carrying capacity is an equilibrium that can be exceeded temporarily, N_{\max} is an absolute upper bound on population size that can never be exceeded.)

To simplify matters, let density dependence be eliminated by assuming that $E(R)$ and $\text{Var}(R)$ are both independent of population size. In a population managed for sustained yield, it might be reasonable to set the constant $E(R)$ value at zero. These two assumptions reduce the complexity of Equation (B1) considerably, giving

$$E(T_N) = \left(\frac{2}{\text{Var}(R)} \right) \sum_{i=1}^N \sum_{j=i}^{N_{\max}} \frac{1}{j^2}. \quad (\text{B2})$$

Although less awkward than Equation (B1), Equation (B2) still requires a number of computations that quickly becomes prohibitive as N or N_{\max} increase. This number can be reduced appreciably by rewriting Equation (B2) as

$$E(T_N) = \left(\frac{2}{\text{Var}(R)} \right) \left(N \sum_{i=1}^{N_{\max}} \frac{1}{i^2} - \sum_{i=2}^N \sum_{j=i}^{N_{\max}} \frac{1}{j^2} \right). \quad (\text{B3})$$

As N_{\max} becomes large, further changes in N_{\max} cause very little change in Equation (B3). Thus, for populations with high N_{\max} values, little accuracy is sacrificed by taking the limit of Equation (B3) as N_{\max} approaches infinity (this, in fact, was the original approach used by Leigh [1981]). In the case of Equation (B3), taking this limit involves computing the sum of reciprocal squares from 1 to infinity. This sum is Riemann's "zeta" function evaluated at 2, $\zeta(2)$, which converges to a value of 1.644934... (e.g., Abramowitz and Stegun 1965). Equation (B3) then becomes

$$E(T_N) = \left(\frac{2}{\text{Var}(R)} \right) \left(N \lambda^2 - \sum_{i=2}^N \sum_{j=i}^N \frac{1}{j^2} \right). \quad (\text{B4})$$

Elasticity

Salwasser et al. (1986) suggest that it is prudent to base conservation decisions not only on the protection that various conservation measures provide against extinction but on the incremental costs of those measures as well. In the context of the birth-and-death process model, this concept can be applied by examining how expected extinction time varies relative to incremental changes in N . A unit increment in N increases Equation (B4) as follows:

$$\begin{aligned} E(T_{N+1}) - E(T_N) &= \left(\frac{2}{\text{Var}(R)} \right) \left((N+1) \lambda^2 - \sum_{i=2}^N \sum_{j=i}^N \frac{1}{j^2} - \sum_{j=1}^N \frac{1}{j^2} \right) - \\ &\quad \left(\frac{2}{\text{Var}(R)} \right) \left(N \lambda^2 - \sum_{i=2}^N \sum_{j=i}^N \frac{1}{j^2} \right) \\ &= \left(\frac{2}{\text{Var}(R)} \right) \left(\lambda^2 - \sum_{i=1}^N \frac{1}{j^2} \right). \end{aligned} \quad (\text{B5})$$

Let the elasticity of $E(T_N)$, $\eta(T_N)$, be defined as

$$\eta(T_N) = N \left(\frac{E(T_{N+1}) - E(T_N)}{E(T_N)} \right) = \frac{\lambda^2 - \sum_{j=1}^N \frac{1}{j^2}}{\lambda^2 - \left(\frac{1}{N} \right) \sum_{i=2}^N \sum_{j=i}^N \frac{1}{j^2}}. \quad (\text{B6})$$

Equation (B6) describes the proportionate gain in expected extinction time relative to a small proportionate increase in initial population size, as shown in [Figure B1](#) for values of N up to 10,000. For example, at an initial population size of 1000, a unit increase in N would represent a relative change of 0.1%. This would correspond to a relative change in expected extinction time of about 0.0118%, for an elasticity of 0.118 (0.0118% divided by 0.1%). In [Figure B1](#), elasticity declines from a value of 0.392 at $N=1$ to a value of 0.092 at $N=10,000$. A value of 0.1 is obtained at $N=4,534$.

An important difference between $\eta(T_N)$ and $E(T_N)$ is that the former does not depend on $\text{Var}(R)$, whereas the latter is inversely proportionate to $\text{Var}(R)$ in the simplified model developed here. Thus, if one desired a relatively robust value of N to serve as a

default minimum viable population in cases where data are limited, it might be wise to select it on the basis of the corresponding elasticity of expected extinction time rather than the expected extinction time itself.

Although there is nothing "magic" about an elasticity of 10%, it is a round number to which people can easily relate. It should also be noted that choosing a pragmatic cutoff point is not without precedent in natural resource management. In fisheries management, for example, the harvest strategy known as $F_{0.1}$ is based on a similar pragmatic cutoff (when catch is plotted against the instantaneous rate of fishing mortality F , $F_{0.1}$ is the point at which the derivative of catch with respect to F is 10% of the derivative at the origin). The 10% criterion used to define $F_{0.1}$ was chosen not on the basis of compelling theoretical arguments, but simply because it resulted in a value that was useful. Thus, despite the purely pragmatic nature of its definition, $F_{0.1}$ enjoys considerable support among fisheries managers and scientists (e.g., Deriso 1987, Clark in press).

It is also interesting to note that the population size corresponding to an elasticity of 10% lies squarely within the range of minimum viable population sizes that have been suggested in the literature.

An Approximation

It has been suggested that expected extinction time should increase approximately with the logarithm of N (Leigh 1981, Ewens et al. 1987, Pimm et al. 1988). An approximation of Equation (B2) can serve to confirm this. Replacing the summations in Equation (B2) with integrals gives

$$E(T_N) \approx \left(\frac{2}{\text{Var}(R)} \right) \int_1^N \int_x^{N_{\max}} \frac{dy}{y^2} dz = \left(\frac{2}{\text{Var}(R)} \right) \left(\ln(N) - \frac{N-1}{N_{\max}} \right). \quad (\text{B7})$$

As N_{\max} approaches infinity, Equation (B7) increases exactly as the logarithm of N . For this special case, Equation (B7) tends to underestimate Equation (B4) by a fairly constant amount. At $N=1$, the difference is equal to $2\zeta(2)$, or 3.289868....

As N becomes large, the difference declines to a value of $2(1+\gamma)$, where γ is Euler's constant, 0.577216... (e.g., Abramowitz and Stegun 1965). Thus, a good approximation of Equation (B4) for large N (i.e., greater than about 10) is

$$E(T_N) \approx \left(\frac{2}{\text{Var}(R)} \right) [\ln(N) + 1 + \gamma]. \quad (\text{B8})$$

The elasticity implied by Equation (B8) is simply

$$\eta(T_N) \approx \left(\frac{N}{E(T_N)} \right) \left(\frac{dE(T_N)}{dN} \right) = \frac{l}{\ln(N) + l + \gamma}. \quad (\text{B9})$$

Equations (B8) and (B9) are obviously much less computationally intensive than their exact counterparts. For example, it is easy to see from Equation (B9) that $\eta(T_N)$ declines quite slowly at large N , not reaching a value of 0.05 until N exceeds 100,000,000. Thus, the elasticity of expected extinction time shares one of the characteristics common to all methods used to calculate minimum viable populations: there is no obvious point at which a population passes from being viable to being nonviable; instead, a judgement call must be made. As a fallback for use in data-poor situations, the population size corresponding to an elasticity of 10% (about 5,000 individuals) seems to be a reasonable candidate.

References Not Cited in Main Text

Abramowitz, M., and I. A. Stegun. 1965. Handbook of mathematical functions with formulas, graphs, and mathematical tables. National Bureau of Standards Applied Mathematics Series 55. U.S. Dep. Commer., Washington D.C., 1046 p.

Clark, W. G. In press. Choosing an exploitation rate on the basis of life history parameters. *Can. J. Fish. Aquat. Sci.*

Deriso, R. B. 1987. Optimal $F_{0.1}$ policies and their relationship to maximum sustainable yield. *Can. J. Fish. Aquat. Sci.* 44(Suppl. 2):339-348.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. *Am. Nat.* 132:757-785.