Advanced Interagency Consultation Training

Study Guide for Measures of Risk

Objectives of this Module

1. Identify the terms that are used to describe measure species' risk of extinction
2. Discuss the interpretations of the various ways of measuring species' risk of extinction
3. Discuss the strengths and weaknesses of the various methods of measuring species' risk of extinction

Introduction

Section 7 of the Endangered Species Act of 1973, as amended, requires federal agencies to insure that any action they authorize, fund, or carry out is not likely to jeopardize the continued existence of threatened species or endangered species or destroy or adversely modify critical habitat that has been designated for these species. The section 7 regulations define *jeopardize the continued existence of* as "to engage in an action that reasonably would be expected, directly or indirectly, to reduce appreciably the likelihood of both the survival and recovery of a listed species in the wild by reducing the reproduction, numbers, or distribution of that species." The section 7 regulations further defined *destruction or adverse modification* as a direct or indirect alteration that appreciably diminishes the value of critical habitat for both the survival and recovery of a listed species," although that regulatory definition has since been invalidated by Court.

These two regulatory definitions have been the subject of extensive debate and discussion for many years. In particular, the Services and many others have debated the meaning of the term "reduce appreciably the likelihood of both the survival and recovery" in the definition of jeopardy. This module will not revisit or recapitulate those debates. Instead, this module will focus on the units that are used to measure (a) a species' risk of extinction or persistence and (b) the value of habitat for species. Better knowledge of the units that are used to measure a species' risk of extinction will help make future discussions of the proper interpretation and application of the jeopardy definition more productive.

The Measures of Risk Facing Species

The literature of population biology and conservation biology uses six general ways of measuring a species' likelihood of becoming extinct in the wild: (1) estimated time to extinction; (2) mean time to extinction; (3) median time to extinction; (4) modal time to extinction; (5) probability of extinction in an interval of time; and (6) probability of extinction over any interval of time (see Beissinger and Westphal 1998, Boyce 1992, Burgman et al. 1993, Caswell 2001, Morris and Doak 2002 for further discussion of these terms and concepts). In many instances, these same units to measure a species' risk of extinction are easily converted into a species' likelihood of persisting in the wild by subtracting the extinction risk from 1 (or likelihood of persistence = 1 – risk of extinction).

It is important to remember that all of these measures are estimates the rely on probabilities. None of these measures, by themselves, assert that a species' risk of extinction is certain. Until the moment that the last member of the last population actually dies, there is always a chance of preventing the species from becoming extinct.

In addition, three measures of population growth can also function as measures of a population's or species' risk of extinction: continuous rate of increase (r), finite rate of increase (λ), net reproductive rate (R_0), and the Dennis statistics (μ and σ^2). These measures of a population growth often form the foundation for the measures of extinction risk that were outlined earlier and that are discussed in greater detail below. When they are combined with estimates of their variance and changes in their mean and variance over time, these measures of a population's growth can serve as robust measures of a population's extinction risk or, alternatively, the population's chances of persisting over time.

Rates of Increase

The *continuous rate of increase* (also called intrinsic rate of natural increase, rate of natural increase, or instantaneous growth rate) or *r* is the *per capita* growth rate, while the *finite rate of increase* (also called population multiplication rate) or lambda (λ) is the rate at which a population grows *per unit time*. The two rates of increase are related to one another by the equations $r = \ln(\lambda)$ and $\lambda = e^r$.

A population is stable when its continuous rate of increase is 0.0; a population is declining when its continuous rate of increase is negative (< 0.0) and growing when its continuous rate of increase is positive (>0.0). A population is stable when its finite rate of increase is 1.0; a population is declining when its finite rate of increase is less than 1.0 and growing when its finite rate of increase is greater than 1.0.

Population growth rates are usually estimated using either census data over time or from demographic data (fecundity and survival). To estimate population growth rates with census data, the data are analyzed using the linear regression of the natural logarithm of abundance over time. To estimate population growth rates with demographic data, the data are analyzed using the Euler-Lotka equation or population projection matrices. Although these two methods produce similar results, the two methods are affected by population density: the census method has greater statistical power to detect a population decline with high-density populations while the demographic method has greater statistical power with low-density populations.

The two statistics (μ and σ^2) proposed by Dennis et al. (1991) provide an alternative way of capturing a population's growth rate that combines an estimate of a population's trend (μ) with an estimate of the variance in that trend (σ^2). Like the other two measures of population growth, the Dennis statistics are estimated with census data (there is no demographic method for estimating these statistics) using the linear regression of the natural logarithm of abundance over time.

Net Reproductive Rate

The *net reproductive rate* normally represents the number of daughters an average, adult female can be expected to produce in her lifetime and is interpreted as the population's rate of increase *per generation*. For most species, a net reproductive rate of 1.0 (in which a female replaces herself during her lifetime) means a population that is not growing, a net reproductive rate less than 1.0 signifies a population that is declining per generation, and a rate that is greater than 1.0 signifies a population that is growing per generation.

Estimated Time to Extinction

The *estimated time to extinction* estimates the number of years it would take for a population or a species to decline to zero individuals. The correct interpretation of the estimated time to extinction is "Based on current population trends, the species can be expected to become extinct by 2020" or "Based on current population trends, the species has about 20 years before extinction." This measure of risk also appears in the published literature as "The species is estimated to have n years before extinction" or "The species is expected to become extinct by 2020" although these interpretations misrepresent the accuracy and precision of this measure of risk.

The estimated time to extinction is the simplest way to measure a species' risk of extinction, but it is also the least rigorous or robust of the various estimates. In particular, this measure of risk ignores the effect of population variance on extinction risk (the greater the variance, the greater the risk), ignores the effect of population structure or composition on the population's extinction risk (it does not distinguish between the number of adults in a population), and generally does not produce a confidence interval that can be used to assess the reliability of the estimate. Although this measure may underestimate a large population's risk of extinction (populations > 500 individuals), it can produce reliable estimates for small populations (<100 individuals). The estimated time to extinction has been applied to the endangered white abalone (Davis *et al*. 1998), Snake River spring and summer chinook salmon (Mundy 1999), 355 populations of 100 species of British birds (Pimm *et al*. 1988), and Peary caribou (Caughley and Gunn 1994).

There are several methods of estimating time to extinction that vary in complexity (Goodman 1987, Leigh 1981, Pimm *et al*. 1988); the most common of these methods relies on a linear regression based on abundance information collected over time (Caughley and Gunn 1994). There are two general variations of this regression method: one using unconverted population sizes and a second converting population sizes to their natural logarithm; the latter generally produces more reliable estimates.

It is fairly easy to estimate a population's or species' time to extinction using the trend function available in most spreadsheet software. Build a table with one column containing the years, accompanied by a second column containing the population estimates for a particular year. Then display the data in a chart (either scatter plot or line chart) and use the "trend" function (linear trend) to create an estimate of the time to extinction (for example, in Excel you would select Chart from the menu and select the command "Add Trendline").

Mean Time to Extinction

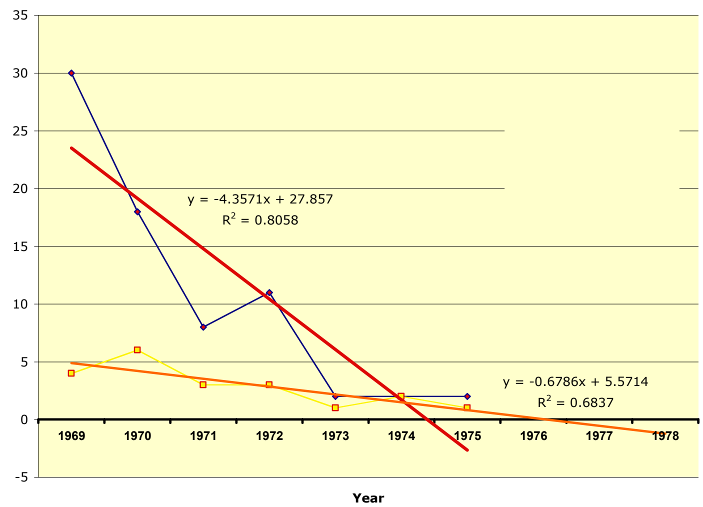
The *mean time to extinction* estimates the average number of years it would take for a population or a species to decline to zero individuals. The correct interpretation of the mean time to extinction is "Based on current population trends, on average the species could be expected to become extinct by 2020" or "Based on current population trends, on average the species has about 20 years before extinction." This measure of risk also appears in the published literature as "The species is estimated to have an average of n years before extinction" or "The species had an average risk of becoming extinct by 2020" although these interpretations misrepresent the accuracy and precision of this measure of extinction risk. Our interpretations should specify whether simulations were deterministic (that is, they did not allow variables to vary over time) or stochastic (that is, they allowed one or more variable to vary over time).

The mean time to extinction is the most common way of measuring a species' risk of extinction, although it will tend to underestimate a species' extinction risk compared with other measures of risk (see figure 4). Depending on the method used to calculate this measure, the mean time to extinction might ignore the effect of population variance on extinction risk, ignore the effect of population structure or composition on a population's or species' extinction risk, and might not produce a confidence interval that can be used to assess the reliability of the estimate. Some of these methods are easy to compute using spreadsheet software like Excel or more advanced analytical packages like *Matlab* or *Mathematica* have commands that will automatically compute the mode of a distribution of values (for example, you can compute the mean of any distribution using the *Descriptive Statistics* of the Excel *Data Analysis* add-in).

Median Time to Extinction

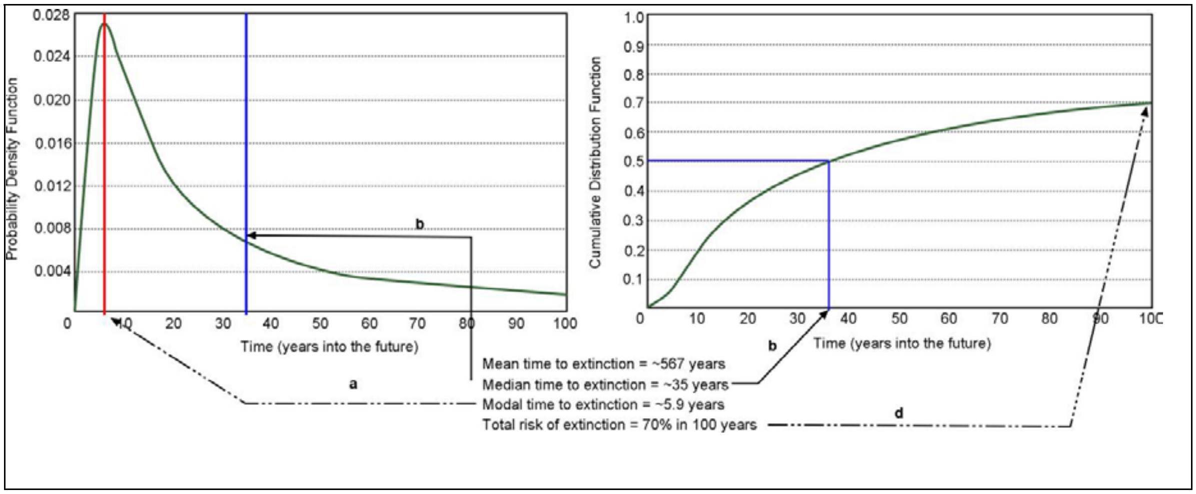
The *median time to extinction* is the time at which half of all simulations estimate it would take for a population or a species to decline to a threshold (this measure usually estimates time to quasi-extinction — or a pre-set, lower population threshold — rather than absolute extinction). The correct interpretation of the

Figures 2 and 3. Estimated time to extinction for the Dusky seaside sparrow population on Merritt Island, Florida, using unconverted population numbers. The year the regression line crosses the x-axis provides the estimated time to extinction. This illustrates different estimates that would be produced using males versus females. The regression coefficients (R^2 = 0.8058 for males and 0.6837 for females) provides a coarse measure of the reliability of the estimate. Compare the estimates from the unconverted population numbers with the estimates using data that have been converted to their natural logarithm before building a trend line (lower panel). In this case, converting the population numbers of their natural logarithm improved the estimates using male, but did not improve the estimates using females. From data contained in Sykes, Jr. (1980)



median time to extinction is "Based on simulations using the species' current population patterns, the species' median time to extinction is *n*-years." Our interpretations should specify whether simulations were deterministic (that is, they did not allow variables to vary over time) or stochastic (that is, they allowed one or more variable to vary over time). See Line B, Figure 4, for an illustration of median time to extinction.

Figure 4. Different measures of risk illustrated using data from the California clapper rail. The left chart shows a probability distribution function (PDF) for the amount of time required for the population to decline to 5 individuals; the right chart shows the same information as a cumulative distribution function (CDF). The mean time to extinction (line not shown) had been estimated as 567 years; the median time to extinction (which is easily read off of the CDF, line b) is ~35 years; the modal time to extinction (which is easily read off of the PDF, line a) is ~ 5.9 years. The total risk of extinction (line d) is 70% in 100 years. See text for discussion. Figure adapted from Morris and Doak (2002).



Dennis et al. (1991) and Morris and Doak (2002) argue that the median time to extinction is one of the best ways to measure a species' risk of extinction and have offered several ways of calculating this risk using census data, life tables, or projections of population matrices. Depending on how it is computed, this measure of risk can include the effect of population variance on extinction risk (the greater the variance, the greater the risk), the effect of population structure or composition on the population's extinction risk, and will produce confidence intervals that can be used to assess the reliability of the estimate. The estimated time to extinction has been applied to Bay checkerspot butterflies (Morris and Doak 2002), desert tortoise (Morris et al. 1999), whooping cranes (Dennis et al. 1991), Palila (Dennis et al. 1991), Puerto Rican parrots (Dennis et al. 1991), red-cockaded woodpecker (Dennis et al. 1991, Morris et al. 1999), and grizzly bears (Morris et al. 1999, Morris and Doak 2002), among others.

The methods used to compute the median time to extinction are more complex than those used to compute the estimated time to extinction, but some of the more commonly-used methods only require census information (see Dennis et al. 1991; Morris et al. 1999; and Morris and Doak 2002). Spreadsheet software like Excel or more advanced analytical packages like *Matlab* or *Mathematica* have commands that will automatically compute the mode of a distribution of values (for example, you can compute the median of any distribution using the *Descriptive Statistics* of the Excel *Data Analysis* add-in).

Modal Time to Extinction

The *modal time to extinction* is the time at which the greatest number of all simulations estimate it would take for a population or a species to decline to a threshold (like median time to extinction, this measure usually estimates time to quasi-extinction — or a pre-set, lower population threshold — rather than absolute extinction). The correct interpretation of the median time to extinction is "Based on simulations using the species' current population patterns, the species' most common time to extinction is *n*-years." Our interpretations should specify whether simulations were deterministic (that is, they did not allow variables to vary over time) or stochastic (that is, they allowed one or more variable to vary over time). See Line A, Figure 4, for an illustration of modal time to extinction.

As you can see from Line A, Figure 4 (preceding page), the modal time to extinction will often over-estimate a species' risk of extinction compared to other measures (that is, it will predict the lowest times to extinction). This is primarily because most distributions of a species' time to extinction are right skewed (see the left chart in Figure 4, the risk of extinction is higher in the short-term, then tapers to the right). Depending on how it is computed, the modal time to extinction can include the effect of population variance on extinction risk (the greater the variance, the greater the risk), the effect of population structure or composition on the population's extinction risk, and will produce confidence intervals that can be used to assess the reliability of the estimate.

The methods used to compute the modal time to extinction can be fairly simple: spreadsheet software like Excel or more advanced analytical packages like *Matlab* or *Mathematica* have commands that will automatically compute the mode of a distribution of values (for example, you can compute the mode of any distribution using the *Descriptive Statistics* of the Excel *Data Analysis* add-in).

Probability of Extinction in an Interval of Time

The *probability of extinction in an interval of time* is the a population's or species' probability of declining to a lower population threshold (like several of the earlier measures, this measure of extinction usually estimates time to quasi-extinction — or a pre-set, lower population threshold — rather than absolute extinction). This measure of risk is usually represented as $P(e)_x$ where x is the interval of time.

This measure of extinction risk most commonly appears as "the probability of extinction (or quasi-`extinction) in 100 years" or $P(e)_{100}$ (for example, Gaona *et al*. 1998, Morita and Yokota 2002, Shephard *et al*. 1997). For example, see Line D, Figure 4 (preceding page) which illustrate the California clapper rail's probability of extinction in a 100 years. However, it is important to remember that there is nothing magical about a 100-year forecast; in fact, the further into the future we forecast, the more variance we add to the forecast and the more unrealistic those forecasts can become (Feiberg and Ellner 2000, Morris and Doak 2002). To correct for this problem, estimates of extinction risk should report probability of extinction over a shorter series of time intervals that can include long-term projections (for example, probability of extinction over 10, 25, 50, and 100 years). Because of this problem, we should not use this measure of risk to forecast far into the future (forecasts further than 100 years). Any estimate of a species' probability of extinction over an interval of time should specify whether simulations were deterministic (that is, they did not allow variables to vary over time) or stochastic (that is, they allowed one or more variable to vary over time). To convert the probability of extinction in an interval of time into probability of persistence over that same interval of time, subtract P(e) from 1 (probability of persistence in an interval of time = $1 – P(e)_x$)

The probability of extinction in an interval of time is one of the most common measures of extinction risk in the literature. It has been applied to grizzly bears (Morris et al. 1999, Morris and Doak 2002), Iberian lynx (Gaona *et al*. 1998), white-spotted char (Morita and Yokota 2002), and Westslope cutthroat trout (Shephard *et al*. 1997), any of extinction simulations conducted using VORTEX software (for example, Florida panther, key deer, Karner blue butterfly, or Kirtland's warbler), or simulations conducted for the International Union for the Conservation of Nature Specialist Survival Groups (for example, Ethiopian wolf and African rhinoceros), which also use VORTEX software.

The methods used to compute the probability of extinction in a particular interval of time cover the range of complexity and can rely on census information, life tables, and matrix population models. The methods can be deterministic or stochastic; the latter will often rely on software developed specifically for population projection (for example, VORTEX and Poptools, which have been included on the compact disk distributed in this class).

Probability of Extinction

The *probability of extinction*, also called the *probability of ultimate extinction*, is the probability of extinction at any time in the future. For a variety of reasons, this measure of risk is not as common as the other measures discussed in this study guide. In essence, the probability of extinction is a long-term forecast of a species' extinction risk and, as a result, is very sensitive to any assumptions used to produce the estimate. In addition, most species can be expected to become extinct over geological time intervals, so this measure of risk tends to incorporate some of that certainty.

The probability of extinction is also a measure of risk commonly applied to metapopulations, multi-site populations, or regional populations (Caughley and Gunn 1994, Gotelli 2001, Morris and Doak 2002). As a result, this measure of risk can be useful when you are dealing with multiple populations or subpopulations and want to estimate how increasing or decreasing the extinction risk to one or more of these populations (or subpopulations) changes the extinction risk of the metapopulation or regional population (see Gotelli 2001, pages 83 – 96 for methods and examples).

Concluding Remarks

In the scientific literature, a species' risk of extinction is captured by a small number of measures: time to extinction, mean time to extinction, modal time to extinction, median time to extinction, probability of extinction in a particular time interval, and probability of extinction. These measures of a species' risk of extinction provide a common set of terms and common units of measure that are essential to interagency consultation, if for no other reason than they unit our discussions with those of the larger scientific community.

Because of the strengths and weaknesses of the methods used to compute these measures of risk, you should use more than one measure of risk in any consultation instead of a single measure. That will allow you to use one measure to verify estimates produced by the second measure. Different authors recommend different measures, but generally

1. Median time to extinction provides the most unbiased estimate of a species' extinction risk.
2. Mean time to extinction will tend to underestimate a species' extinction risk.
3. Modal time to extinction will tend to overestimate a species' extinction risk.
4. Probability of extinction in a particular interval of time is more robust when we do not forecast too far into the future (ideally 10, 25, or 50 years instead of 100 years). The more variance associated with our estimates, the more unrealistic our long-term forecasts become.
5. Several authors have recommended using *median time to extinction* AND *probability of extinction* in a particular interval of time as the most reliable measures of the extinction risk facing species or populations (Beissinger and Westphal 1998, Burgman et al. 1993, Morris and Doak 2002).

Whenever you encounter or use these measures of risk, insist on receiving and providing a confidence interval for your estimate (which the illustrations in this study guide did not provide to make it easier to focus on the actual measures of risk).

Literature Cited

Beissinger, S. R., and M. I. Westphal. 1998. On the use of demographic models of population viability in endangered species management. Journal of Wildlife Management 62:821-841.

Boyce, M. S. 1992. Population viability analysis. Annual Review of Ecology and Systematics 23:481-506.

Burgman, M. A., S. Ferson, and H. R. Akcakaya. 1993. Risk assessment in conservation biology. Chapman & Hall, New York, New York.

Caswell, H. 2001. Matrix population models, Second Edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Caughley, G., and A. Gunn. 1996. Conservation biology in theory and practice. Blackwell Science, Inc., Cambridge, Massachusetts.

Davis, G. E., P. L. Haaker, and D. V. Richards. 1996. The perilous condition of white abalone *Haliotis sorenseni*, Bartsch, 1940. Journal of Shellfish Research 17:871-875.

Dennis, B., P. L. Mulholland, and J. M. Scott. 1991. Estimation of growth and extinction parameters for endangered species. Ecological Monographs 61:115-143.

Fieberg, J., and S. P. Ellner. 2000. When is it meaningful to estimate an extinction probability? Ecology 81:2040-2047.

Gaona, P., P. Ferreras, and M. Delibes. 1998. Dynamics and viability of a metapopulation of the endangered Iberian lynx (*Lynx pardinus*). Ecological Monographs 68:349-370.

Gotelli, N.J. 2001. A primer of ecology. Third Edition. Sinauer Associates, Inc., Sunderland, Massachusetts.

Morita, K., and A. Yokota. 2002. Population viability of stream-resident salmonids after habitat fragmentation: a case study with white-spotted charr (*Salvelinus leucomaenis*) by an individual based model. Ecological modelling 155:85-94.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Theory and practice of population viability analysis. Sinauer Associates, Inc. Publishers, Sunderland, Massachusetts.

Morris, W. F., D. F. Doak, M. Groom, P. Kareiva, J. Feiberg, L. R. Gerber, P. Murphy, and D. Thomson. 1999. A practical handbook for population viability analysis. The Nature Conservancy, Arlington, Virginia.

Pimm, S. L., H. L. Jones, and J. Diamond. 1988. On the risk of extinction. The American naturalist 132:757-785.

Shepard, B. B., B. Sanborn, L. Ulmer, and D. C. Lee. 1997. Status and risk of extinction for westslope cutthroat trout in the Upper Missouri River Basin, Montana. North American Journal of Fisheries Management 17:1158-1172.

Sykes, P. W., Jr. 1980. Decline and disappearance of the Dusky seaside sparrow from Merritt Island, Florida. BioScience 34:728-737.

Further Reading

Akçakaya, H. R., and J. L. Atwood. 1997. A habitat-based metapopulation model of the California gnatcatcher. Conservation Biology **11**:422-434.

Akçakaya, H. R., M. A. Burgman, and L. R. Ginzberg. 1999. Applied population ecology. Principles and computer exercises., Second Edition. Sinauer Associates , Inc., Sunderland, Massachusetts.

Akçakaya, H. R., M. A. McCarthy, and J. L. Pearce. 1995. Linking landscape data with population viability analysis: management options for the helmeted honeyeater *Lichenostomus melanops cassidix*. Biological Conservation **73**:169.

Anthony, L. L., and D. T. Blumstein. 2000. Integrating behaviour into wildlife conservation: The multiple ways that behaviour can reduce Ne. Biological Conservation **95**:303-315.

Armbruster, P., P. Fernando, and R. Lande. 1999. Time frames for population viability analysis of species with long generations: an example with Asian elephants. Animal Conservation **2**:5.

Armbruster, P., and R. Lande. 1993. A population viability analysis for African elephant (*Loxodonta africana*): how big should reserves be? Conservation Biology **7**:602-610.

Armstrong, D. P., and J. G. Ewen. 2001. Estimating impacts of poison operations using mark-recapture analysis and population viability analysis: an example with New Zealand robins (*Petroica australis*) of Acaena (Rosaceae) species in New Zealand. New Zealand journal of ecology **25**:29-38.

Armstrong, D. P., and J. G. Ewen. 2002. Dynamics and viability of a New Zealand Robin population reintroduced to regenerating fragmented habitat. Conservation Biology **16**:1074-1085.

Asquith, N. M. 2001. Misdirections in conservation biology. Conservation Biology **15**:345-352.

Baguette, M., S. Petit, and F. Queva. 2000. Population spatial structure and migration of three butterfly species within the same habitat network: Consequences for conservation. Journal of Applied Ecology **37**:100-108.

Beissinger, S. R. 1995. Modeling extinction in periodic environments: Everglades water levels and Snail Kite population viability. Ecological Applications **5**:618.

Beissinger, S. R., D. R. McCullough, and R. Frankham. 2002. Population viability analysis. Nature **419**:1.

Botsford, L. W., and J. G. Brittnacher. 1998. Viability of Sacramento River winter-run chinook salmon. Conservation Biology **12**:65-79.

Bradstock, R. A., M. Bedward, J. Scott, and D. A. Keith. 1996. Simulation of the effect of spatial and temporal variation in fire regimes on the population viability of a *Banksia* species. Conservation Biology **10**:776-784.

Bro, E., F. Sarrazin, J. Clobert, and F. Reitz. 2000. Demography and the decline of the grey partridge *Perdix perdix* in France. Journal of Applied Ecology **37**:432-448.

Brook, B. W. 2000. Pessimistic and optimistic bias in population viability analysis. Conservation Biology **14**:3.

Brook, B. W., J. R. Cannon, R. C. Lacy, C. Mirande, and R. Frankham. 1999. Comparison of the population viability analysis packages GAPPS, INMAT, RAMAS and VORTEX for the whooping crane (*Grus americana*). Animal Conservation **2**:9.

Brook, B. W., and J. Kikkawa. 1998. Examining threats faced by island birds: A population viability analysis on the Capricorn silvereye using long-term data. Journal of Applied Ecology **35**:491-503.

Brook, B. W., and J. Kikkawa. 1998. Examining threats faced by island birds: A population viability analysis on the Capricorn silvereye using long-term data. Journal of Applied Ecology **35**:13.

Brook, B. W., L. Lim, R. Harden, and R. Frankham. 1997. Does population viability analysis software predict the behaviour of real populations? A retrospective study on the Lord Howe Island Woodhen (*Tricholimnas sylvestris* (Sclater). Biological Conservation **82**:119-128.

Brook, B. W., J. J. O'Grady, A. P. Chapman, M. A. Burgman, H. R. Akcakaya, and R. Frankham. 2000. Predictive accuracy of population viability analysis in conservation biology. Nature **404**:385-387.

Burgman, M. A. 2001. Population viability analysis for bird conservation: Prediction, Heuristics, Monitoring and Psychology. Emu **100**:347.

Bustamante, J. 1996. Population viability analysis of captive and released bearded vulture populations. Conservation Biology **10**:822-831.

Chapman, A. P., B. W. Brook, T. H. Clutton-Brock, B. T. Grenfell, and R. Frankham. 2001. Population viability analyses on a cycling population: A cautionary tale. Biological Conservation **97**:61-69.

Coulson, T., G. M. Mace, E. Hudson, and H. Possingham. 2001. The use and abuse of population viability analysis. Trends in Ecology & Evolution **16**:219-221.

Crone, E. E., and J. L. Gehring. 1998. Population viability of *Rorippa columbiae*: Multiple models and spatial trend data. Conservation Biology **12**:1054-1065.

Cuthbert, R. 2003. Population viability analysis. Biological Conservation **114**:153.

Dinnâetz, P., and T. Nilsson. 2002. Population viability analysis of *Saxifraga cotyledon*, a perennial plant with semelparous rosettes. Plant Ecology **159**:11.

Doak, D., P. Kareiva, and B. Klepetka. 1994. Modeling population viability for the desert tortoise in the Western Mojave desert. Ecological Applications **4**:446.

Doak, D. F., and L. S. Mills. 1994. A useful role for theory in conservation. Ecology **75**:615-626.

Elliott, G. P. 1996. Mohua and stoats: a population viability analysis. New Zealand journal of zoology **23**:239.

Ellner, S. P., J. Fieberg, D. Ludwig, and C. Wilcox. 2002. Precision of population viability analysis. Conservation Biology **16**:4.

Emlen, J. M. 1995. Population viability of the Snake River chinook salmon (*Oncorhynchus tshawytscha*). Canadian Journal of Fisheries and Aquatic Sciences **52**:1442-1448.

Evans, K., M. A. Hindell, and D. Thiele. 2003. Body fat and condition in sperm whales, *Physeter macrocephalus*, from southern Australian waters. Comparative Biochemistry and Physiology Part A Molecular & Integrative Physiology **134A**:847-862.

Evans, M. E., E. S. Menges, and D. R. Gordon. 2003. Reproductive biology of three sympatric endangered plants endemic to Florida scrub. Biological Conservation **111**:235-246.

Evans, M. E. K., R. W. Dolan, E. S. Menges, and D. R. Gordon. 2000. Genetic diversity and reproductive biology in *Warea carteri* (Brassicaceae), a narrowly endemic Florida scrub annual. American Journal of Botany **87**:372-381.

Ferreras, P., P. Gaona, F. Palomares, and M. Delibes. 2001. Restore habitat or reduce mortality? Implications from a population viability analysis of the Iberian lynx. Animal Conservation **4**:10.

Forys, E. A., and S. R. Humphrey. 1999. Use of population viability analysis to evaluate management options for the endangered lower keys marsh rabbit. Journal of Wildlife Management **63**:251-260.

Fowler, C. W., and J. D. Baker. 1991. A review of animal population dynamics at extremely reduced population levels. Report of the International Whaling Commission **41**:545-554.

Fu, Y.-B., G. Namkoong, and J. E. Carlson. 1998. Comparison of breeding strategies for purging inbreeding depression via simulation. Conservation Biology **12**:856-864.

Gardenfors, U. 2000. Population viability analysis in the classification of threatened species: Problems and potentials. Ecological bulletins:10.

Gilpin, M. 1996. Forty-eight parrots and the origins of population viability analysis. Conservation Biology **10**:3.

Goldstein, P. Z., R. DeSalle, G. Amato, and A. P. Vogler. 2000. Conservation genetics at the species boundary. Conservation Biology **14**:120-131.

Grant, A., and T. G. Benton. 2000. Elasticity analysis for density-dependent populations in stochastic environments. Ecology **81**:680-693.

Griffiths, R. A., and C. Williams. 2000. Modeling population dynamics of great crested newts (*Triturus cristatus*): a population viability analysis. The Herpetological Journal **10**:157-164.

Guo, Chen, and Hu. 2002. Population viability analysis of giant pandas in the Yele Nature Reserve. Journal for Nature Conservation **10**:35-40.

Haig, S. M., J. R. Belthoff, and D. H. Allen. 1993. Population viability analysis for a small population of red-cockaded woodpeckers and an evaluation of enhancement strategies. Conservation Biology **7**:289-301.

Harcourt, A. H. 1995. Population viability estimates: Theory and practice for a wild gorilla population. Conservation Biology **9**:134-142.

Haydon, D. T., M. K. Laurenson, and C. Sillero-Zubiri. 2002. Integrating epidemiology into population viability analysis: Managing the risk posed by rabies and canine distemper to the Ethiopian Wolf. Conservation Biology **16**:1372-1385.

Hegland, S. J., M. Van Leeuwen, and J. G. B. Oostermeijer. 2001. Population structure of *Salvia pratensis* in relation to vegetation and management of Dutch dry floodplain grasslands. Journal of Applied Ecology **38**:1277-1289.

Heppell, S. S., H. Caswell, and L. B. Crowder. 2000. Life histories and elasticity patterns: Perturbation analysis for species with minimal demographic data. Ecology **81**:654-665.

Holmes, E. E., and W. F. Fagan. 2002. Validating population viability analysis for corrupted data sets. Ecology **83**:8.

Hosack, D. A., P. S. Miller, J. J. Hervert, and R. C. Lacy. 2002. A population viability analysis for the endangered Sonoran pronghorn, *Antilocapra americana sonoriensis*. Mammalia **66**:24.

Kenney, J. S., J. L. D. Smith, A. M. Starfield, and C. W. McDougal. 1995. The long-term effects of tiger poaching on population viability. Conservation Biology **9**:1127-1133.

La Montagne, J. M., R. L. Irvine, and E. E. Crone. 2002. Spatial patterns of population regulation in sage grouse (*Centrocercus* spp) population viability analysis. Journal of Animal Ecology **71**:672-682.

Lacy, R. C. 2000. Structure of the VORTEX simulation model for population viability analysis. Ecological bulletins:191.

Lafferty, K. D., and L. R. Gerber. 2002. Good medicine for conservation biology: The intersection of epidemiology and conservation theory. Conservation Biology **16**:593-604.

Larson, M. A., M. R. Ryan, and R. K. Murphy. 2002. Population viability of piping plovers: Effects of predator exclusion. Journal of Wildlife Management **66**:361-371.

Leaper, R., G. Massei, M. L. Gorman, and R. Aspinall. 1999. The feasibility of reintroducing Wild Boar (*Sus scrofa*) to Scotland. Mammal Review **29**:239-259.

Leberg, P. 1998. Influence of complex sex determination on demographic stochasticity and population viability. Conservation Biology **12**:456-459.

Lennartsson, T., and J. G. B. Oostermeijer. 2001. Demographic variation and population viability in *Gentianella campestris*: Effects of grassland management and environmental stochasticity. Journal of Ecology **89**:451-463.

Lepage, C., and P. Cury. 1997. Population viability and spatial fish reproductive strategies in constant and changing environments: An individual-based modeling approach. Canadian Journal of Fisheries and Aquatic Sciences **54**:2235-2246.

Li, D., and Z. Jiang. 2002. Population viability analysis for the Przewalski's gazelle. Russian Journal of Ecology **33**:6.

Li, X., and D. Li. 1998. Current state and the future of the crested ibis *Nipponia nippon*): A case study by population viability analysis. Ecological Research **13**:323.

Lindenmayer, D. B., I. Ball, H. P. Possingham, M. A. McCarthy, and M. L. Pope. 2001. A landscape-scale test of the predictive ability of a spatially explicit model for population viability analysis. Journal of Applied Ecology **38**:36-48.

Lindenmayer, D. B., T. W. Clark, R. C. Lacy, and V. C. Thomas. 1993. Population viability analysis as a tool in wildlife conservation policy: with reference to Australia. Environmental Management **17**:745-758.

Lindenmayer, D. B., and R. C. Lacy. 1995. Metapopulation viability of arboreal marsupials in fragmented old-growth forests: comparison among species. Ecological Applications **5**:183.

Lindenmayer, D. B., and R. C. Lacy. 1995. Metapopulation viability of Leadbeater's possum, *Gymnobelideus leadbeateri*, in fragmented old-growth forests. Ecological Applications **5**:164.

Lindenmayer, D. B., R. C. Lacy, and M. L. Pope. 2000. Testing a simulation model for population viability analysis. Ecological Applications **10**:580.

Lindenmayer, D. B., M. A. McCarthy, H. P. Possingham, and S. Legge. 2001. A simple landscape-scale test of a spatially explicit population model: Patch occupancy in fragmented south-eastern Australian forests. Oikos **92**:445-458.

Lindenmayer, D. B., and H. P. Possingham. 1996. Applications of population viability analysis in conservation biology in Australia. GeoJournal library **35**:102.

Lindenmayer, D. B., and H. P. Possingham. 1996. Ranking conservation and timber management options for Leadbeater's possum in southeastern Australia using population viability analysis. Conservation Biology **10**:235-251.

Loison, A., O. Strand, and J. D. C. Linnell. 2001. Effect of temporal variation in reproduction on models of population viability: A case study for remnant arctic fox (*Alopex lagopus*) populations in Scandinavia. Biological Conservation **97**:347-359.

Lubow, B. C. 1996. Optimal translocation strategies for enhancing stochastic metapopulation viability. Ecological Applications **6**:1268.

Maguire, L. A., G. F. Wilhere, and Q. Dong. 1995. Population viability analysis for red-cockaded woodpeckers in the Georgia piedmont. The Journal of wildlife management **59**:10.

Mangel, M., and C. Tier. 1994. Four facts every conservation biologist should know about persistence. Ecology **75**:607-614.

Mann, C. C., and M. L. Plummer. 1999. A species' fate, by the numbers. Science **284**:36-37.

Marmontel, M., S. R. Humphrey, and T. J. O'Shea. 1997. Population viability analysis of the Florida manatee (*Trichechus manatus latirostris*), 1976-1991. Conservation Biology **11**:467-481.

Maschinski, J., R. Frye, and S. Rutman. 1997. Demography and population viability of an endangered plant species before and after protection from trampling. Conservation Biology **11**:990-999.

McCarthy, M. A., S. J. Andelman, and H. P. Possingham. 2003. Reliability of relative predictions in population viability analysis. Conservation Biology **17**:982-989.

McCarthy, M. A., and L. S. Broome. 2000. A method for validating stochastic models of population viability: a case study of the mountain pygmy-possum (*Burramys parvus*). Journal of Animal Ecology **69**:599-607.

McCarthy, M. A., and D. B. Lindenmayer. 2000. Spatially-correlated extinction in a metapopulation model of Leadbeater's Possum. Biodiversity and Conservation **9**:47-63.

McCarthy, M. A., D. B. Lindenmayer, and H. P. Possingham. 2000. Testing spatial PVA models of Australian treecreepers (Aves: Climacteridae) in fragmented forest. Ecological Applications **10**:1722.

McCarthy, M. A., D. B. Lindenmayer, and H. P. Possingham. 2001. Assessing spatial PVA models of arboreal marsupials using significance tests and Bayesian statistics. Biological Conservation **98**:191-200.

McCarthy, M. A., H. P. Possingham, J. R. Day, and A. J. Tyre. 2001. Testing the accuracy of population viability analysis. Conservation Biology **15**:1030-1038.

McCullough, B., and C. I. Bocetti. 2003. Population viability analysis. Ecology **84**:536.

McGee, B. L., D. J. Fisher, L. T. Yonkos, G. P. Ziegler, and S. Turley. 1999. Assessment of sediment contamination, acute toxicity, and population viability of the estuarine amphipod *Leptocheirus plumulosus* in Baltimore Harbor, Maryland, USA. Environmental Toxicology and Chemistry **18**:2151.

McGraw, J. B. 2001. Evidence for decline in stature of American ginseng plants from herbarium specimens. Biological Conservation **98**:25-32.

Menges, E. S. 1990. Population viability analysis for an endangered plant. Conservation Biology **4**:52.

Menges, E. S. 2000. Population viability analyses in plants: Challenges and opportunities. Trends in Ecology & Evolution **15**:51-56.

Morris, W. F., P. L. Bloch, B. R. Hudgens, L. C. Moyle, and J. R. Stinchcombe. 2002. Population viability analysis in endangered species recovery plans: Past use and future improvements. Ecological Applications **12**:5.

Murphy, D. D., K. E. Freas, and S. B. Weiss. 1990. An environment-metapopulation approach to population viability analysis for a threatened invertebrate. Conservation Biology **4**:41.

Nantel, P., D. Gagnon, and A. Nault. 1996. Population viability analysis of American ginseng and wild leek harvested in stochastic environments. Conservation Biology **10**:608-621.

Nickelson, T. E., and P. W. Lawson. 1998. Population viability of coho salmon, *Oncorhynchus kisutch*, in Oregon coastal basins: Application of a habitat-based life cycle model. Canadian Journal of Fisheries and Aquatic Sciences **55**:2383-2392.

Parysow, P., and D. J. Tazik. 2002. Assessing the effect of estimation error on population viability analysis: an example using the black-capped vireo. Ecological Modeling **155**:14.

Paulsen, C. M., and R. A. Hinrichsen. 2002. Experimental management for Snake River spring-summer chinook (*Oncorhynchus tshawytscha*): Trade-offs between conservation and learning for a threatened species. Canadian Journal of Fisheries and Aquatic Sciences **59**:717-725.

Penn, A. M., W. B. Sherwin, G. Gordon, D. Lunney, A. Melzer, and R. C. Lacy. 2000. Demographic forecasting in koala conservation. Conservation Biology **14**:629-638.

Pergams, O. R. W., R. C. Lacy, and M. V. Ashley. 2000. Conservation and management of Anacapa Island deer mice. Conservation Biology **14**:819-832.

Pfab, M. F., and E. T. F. Witkowski. 2000. A simple population viability analysis of the critically endangered *Euphorbia clivicola* R.A. Dyer under four management scenarios. Biological Conservation **96**:263-270.

Plissner, J. H., and S. M. Haig. 2000. Viability of piping plover *Charadrius melodus* metapopulations. Biological Conservation **92**:163-173.

Poschlod, P., S. Fischer, and S. Kiefer. 1996. A coenotical approach of plant population viability analysis on successional and afforested calcareous grassland sites - Towards an ecological flora data base. GeoJournal library **35**:219.

Quintana-Ascencio, P. F., E. S. Menges, and C. W. Weekley. 2003. A fire-explicit population viability analysis of *Hypericum cumulicola* in Florida Rosemary Scrub. Conservation Biology **17**:433-449.

Rae, J. G., and T. A. Ebert. 2002. Demography of the endangered fragrant prickly apple cactus, *Harrisia fragrans*. International Journal of Plant Sciences **163**:631-640.

Ratner, S., R. Lande, and B. B. Roper. 1997. Population viability analysis of spring chinook salmon in the South Umpqua River, Oregon. Conservation Biology **11**:879-889.

Reed, J. M. 2003. Population viability analysis. The Auk **120**:237-239.

Reed, J. M., C. S. Elphick, and L. W. Oring. 1998. Life-history and viability analysis of the endangered Hawaiian stilt. Biological Conservation **84**:35-45.

Reed, J. M., L. S. Mills, J. B. Dunning, E. S. Menges, K. S. McKelvey, R. Frye, S. R. Beissinger, M.-C. Anstett, and P. Miller. 2002. Emerging issues in population viability analysis. Conservation Biology **16**:7-19.

Reed, J. M., D. D. Murphy, and P. F. Brussard. 1998. Efficacy of population viability analysis. Wildlife Society Bulletin **26**:244-251.

Ruggiero, L. F., G. D. Hayward, and J. R. Squires. 1994. Viability analysis in biological evaluations: concepts of population viability analysis, biological population, and ecological scale. Conservation Biology **8**:364-372.

Saether, B.-E., S. Engen, R. Lande, P. Arcese, and J. N. M. Smith. 2000. Estimating the time to extinction in an island population of song sparrows. Proceedings of the Royal Society of London, Series B: Biological Sciences **267**:621-626.

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

Shaffer, M. L. 1990. Population viability analysis. Conservation Biology **4**:39.

Sjögren-Gulve, P., and T. Ebenhard, editors. 2000. The use of population viability analyses in conservation planning. Wallin and Dalholm, Lund, Sweden.

Song, Y.-L. 1996. Population viability analysis for two isolated populations of Haianan Eld's deer. Conservation Biology **10**:1467-1472.

Southwood, T. R. E., R. M. May, M. P. Hassell, and G. R. Conway. 1974. Ecological strategies and population parameters. American Naturalist **108**:791-804.

Taylor, B. L. 1995. The reliability of using population viability analysis of risk classification of species. Conservation Biology **9**:551-558.

Taylor, R. J., T. Regan, H. Regan, M. Burgman, and K. Bonham. 2003. Impacts of plantation development, harvesting schedules and rotation lengths on the rare snail *Tasmaphena lamproides* in northwest Tasmania: a population viability analysis. Forest Ecology and Management **175**:12.

Thomas, C. D., R. J. Wilson, and O. T. Lewis. 2002. Short-term studies underestimate 30-generation changes in a butterfly metapopulation. Proceedings of the Royal Society Biological Sciences Series B **269**:563-569.

Thompson, P. M., B. Wilson, K. Grellier, and P. S. Hammond. 2000. Combining power analysis and population viability analysis to compare traditional and precautionary approaches to conservation of coastal cetaceans. Conservation Biology **14**:1253-1263.

Todd, C. R., S. Jenkins, and A. R. Bearlin. 2002. Lessons about extinction and translocation: Models for eastern barred bandicoots (*Perameles gunnii*) at Woodlands Historic Park, Victoria, Australia. Biological Conservation **106**:211-223.

Vandermeer, J. H., and D. E. Goldberg. 2003. Population ecology. First principles. Princeton University Press, Princeton, New Jersey.

Verboom, J., R. Foppen, P. Chardon, P. Opdam, and P. Luttikhuizen. 2001. Introducing the key patch approach for habitat networks with persistent populations: An example for marshland birds. Biological Conservation **100**:89-101.

Vucetich, J. A., and T. A. Waite. 1998. On the interpretation and application of mean times to extinction. Biodiversity and Conservation **7**:1539-1547.

Walters, J. R., L. B. Crowder, and J. A. Priddy. 2002. Population viability analysis for red-cockaded woodpeckers using an individual-based model. Ecological Applications **12**:249.

Wemmer, L. C., U. Ozesmi, and F. J. Cuthbert. 2001. A habitat-based population model for the Great Lakes population of the piping plover (*Charadrius melodus*). Biological Conservation **99**:169-181.

Zhou, Z., and W. Pan. 1997. Analysis of the viability of a giant panda population. Journal of Applied Ecology **34**:363-374.