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POPULATION VIABILITY ANALYSIS AND MANAGEMENT

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INTRODUCTION

With dramatic increases in awareness of management issues and programs that involve conservation of rare, threatened, and endangered organisms and ecosystems, the maintenance of species viability has become a focus of research efforts and management plans. Numerous examples of populations extirpated, species in decline, and ecological communities disrupted exist in nearly all taxonomic groups. Birds provide a telling example: nearly a thousand species, more than 11% of all existing bird species, are at some risk of global extinction (Collar and Andrew 1988). And certain particularly sensitive species groups are faring even worse; nearly a third of all parrots can be considered threatened or of concern (Collar and Andrew 1988).

The major contributing factor in this global crisis is the loss of natural habitats, particularly in tropical biomes. Only a small percentage of the world's remaining natural habitats have been protected in reserves or conserved for other purposes. In the Afrotropical realm, for example, as of 1986 only 42% of the original 8.22 million sq km of upland montane, woodland, and other dry forest types remained and only 15% of that remaining is protected. In the Indomalayan realm, the situation is even bleaker; as of 1986 only 28% of the original 3.41 million sq km of dry forest remained and just 11% of that remaining was protected (Harmon 1990). The status of other habitats, particularly wetlands, mangroves, and ancient forests, is worse yet.

Additional concerns for species viability have arisen from direct over-exploitation by humans for subsistence or sport hunting or from

secondary effects of increasing human urbanization with accompanying environmental pollution. The toll has been a burgeoning list of wildlife species at risk of local extirpation or global extinction. The USDI Fish and Wildlife Service has officially listed as endangered or threatened some 1,209 taxa (including species, subspecies, or distinct vertebrate populations) of plants, invertebrates, and vertebrates. As of now, however, only 311 of these taxa have approved recovery plans (Anonymous 1992). Also, in the U.S. there are 4-5 times as many candidate species that warrant listing but are not listed (Bean, this volume).

A need for procedures to identify, analyze, and plan for viable populations of wildlife thus is already apparent. This chapter draws from existing treatises that have discussed at length species extinctions (e.g., Hoage 1985, Pimm 1988) and population viability (e.g., Soul 1987), and presents a framework for analysis and management of viable wildlife populations. However, despite numerous case studies, linkage between biological data and conservation procedures remains opaque to land managers. The purpose of this chapter is to introduce basic concepts and to outline a procedure for population viability analysis (PVA) and management. First, we briefly describe population viability and its analysis. We then review some of the legal charges pertinent to managing for viable populations on public lands in the United States. Next, we outline the major ecological factors that affect the continued existence of populations, and provide a procedure to apply population viability information in a risk management framework. Finally, we consider the need for multiple-species, habitat-wide, and whole-ecosystem approaches to the successful conservation of viable populations.

DEFINITIONS OF POPULATION VIABILITY AND POPULATION VIABILITY ANALYSIS

Population viability refers to the probability of continued existence of geographically well-distributed populations over a specified time period. This probabilistic description demands clear definitions of several key terms (similarly see Murphy and Noon 1991). Probabilities can be estimated by various qualitative and quantitative means that can refer to: likelihoods of global or local extinction or target taxa; probabilities of population sizes dropping below low, but nonzero, thresholds (quasiextinction; Ginzburg et al. 1982); lengths of time to extinction; likely durations that populations can exist above quasiextinction levels; likelihoods that populations will remain spatially well-distributed; and numerous other measures that consider demographic and genetic bottlenecks, population recovery, and habitat occupancy rates (see Table 1). No one of these measures is alone sufficient to assess population viability; different suites of data and analyses are necessary to meet each conservation challenge that involves distinct sets of species and habitats.

Central to all planning efforts that involve population viability analysis is provision of well-distributed and interconnected habitats. Although some species are naturally patchily distributed, in general, the maintenance of distributions and connectivity is a key to sustaining geographically diverse and demographically healthy populations. In this paper, we describe a population or habitat as well-distributed if it is

maintained over the long term across at least its existing range of geographic, environmental, and ecological conditions. In some cases, the maintenance of a well-distributed population or habitat requires restoration of suitable conditions in portions of historic geographic ranges, particularly where needed to reconnect populations isolated by human activities.

Operational definitions of the term "well-distributed" have varied. For example, planning for viable wildlife populations on National Forests in the U.S. commonly pits competing interests for scarce resources -- such as with the commercial timber use of old forests of long-leaf pine (Pinus palustris) that also provide optimal habitat for the endangered red-cockaded woodpecker (Picoides borealis) in the southeast U.S.

Typically in such cases, much less than the full range of existing or historic conditions is targeted by conservation efforts due to competing economic interests. The appropriate definition then is a political decision that considered social welfare and other factors. The role of the biologist is to estimate and clearly articulate effects on species viability of a range of possible decisions.

The "specified period of time" over which a population is to be maintained also has been treated equivocally in past planning activities on public lands in the U.S. Planning time frames for management of public lands in the U.S. (and commonly elsewhere) typically are 1-10 years. Biologically, however, to ensure long-term genetic adaptability, phenotypic diversity, and high probabilities of population persistence, an appropriate planning time frame should be 10^0 to 10^2 that of the target species' generation time. Recommendations from conservation biology literature for

the appropriate time frame for planning for population viability have ranged from a century to a millennium (Soul and Wilcox 1980, Shaffer 1981, Frankel and Soul 1981). Such time frames are biologically desirable but seldom practical in both analysis and in setting management guidelines, particularly on public lands where revisions of management plans can occur every several years. Planning for long-term viability of species of ancient forests of the Midwest U.S., including restoration of forests lost to logging and urbanization, would likely entail rigorous management planning for time horizons of several centuries -- longer than the U.S. has been a nation. Thus, we recommend setting a timeframe of at least 10 generations of the target species for analyzing viability effects of proposed management plans; longer time periods should be considered if the species has a short generation time relative to planning horizons or frequencies of disturbance events. Longer time frames allow detecting population dynamic responses that may be masked over the short-term, although viability plans might apply for shorter time periods reflecting competing, non-biological constraints. This is a general guideline, however, and specific cases must be addressed individually. Indeed, there is professional disagreement on whether one time frame should be set for all PVA's for all purposes, or, as we offer here, if the time frame can be allowed to vary to account for differences in planning objectives, species ecologies, and disturbance dynamics.

Population viability analysis (PVA) is the procedure of estimating the likelihood of continued persistence of populations, metapopulations, or species, over specified time periods, given one or more management alternatives. PVA is neither a monolithic concept nor a cookbook

procedure. No single method for conducting a PVA exists. The host of factors potentially influencing the viability of a species and how those factors are analyzed and influenced by management activities are case-specific, although below we present a general assessment procedure.

Viability analysis for cheetahs (Acinonyx jubatus), for example, has focused on the genetic risks associated with population bottlenecks. O'Brien et al. (1985) have shown the cheetah to be monomorphic at essentially all gene loci investigated. Combined with low overall numbers and restricted geographic range, a high risk of inbreeding depression appears to exist. Whereas Barrowclough and Gutierrez (1990) have shown a similar lack of genetic variation in the northern spotted owl (Strix neotonalis caurina), its comparatively wide range and greater numbers have focused conservation planning on demographic factors that put the species at risk of local extirpation. In contrast, the threatened Bay checkerspot butterfly (Euphydryas editha bayensis) can be found in high population numbers, but is at risk to drought which can lead to dramatic population declines and disruption of metapopulations. Conservation planning for that species thus has focused on environmental perturbations and dispersal dynamics (Murphy et al. 1990).

Unfortunately for most species, reliable empirical data on historic population dynamic trends, the role of environmental conditions in regulating populations, and other crucial information simply do not exist. In such circumstances, only qualitative predictions can be made as to potential likelihoods of persistence and effects of management alternatives. In a very few cases, as with some especially well-studied threatened or endangered species, more is known and quantitative estimates

of extinction probabilities or other factors can be made through use of spatially-explicit simulation modeling of dynamic habitats and metapopulations (e.g., Harrison et al. 1988, Murphy et al. 1990, Harrison 1991, Murphy and Noon 1992) and use of demographic and genetic analyses of populations in situ (e.g., Eberhardt 1990, Haig and Norstrom 1991, Hedrick and Miller 1992). Yet, when data are lacking, proceeding with at least an interim, qualitative evaluation of viability status, despite a paucity of field data, may be required (Marcot and Salwasser 1991).

LEGAL CHARGES TO MANAGE FOR VIABLE POPULATIONS

Although much has been written on population viability and its analysis, few nations have laws or formal conservation policies that directly mandate analysis and management of viable populations. Most regulations that deal with conservation of sensitive, rare, threatened, or endangered species or their habitats only indirectly encourage population viability analysis and management. For example, India's 1988 National Forest Policy calls for widespread protection and restoration of forest habitats throughout the country, but does not directly mention definition, analysis, and management of viable fish and wildlife populations. Similarly, Great Britain's 1967 Forestry Act (as amended in 1985) mandates a balance between afforestation and "conservation and enhancement of natural beauty and ... flora [and] fauna," and their conservation guidelines emphasize habitat protection but not population viability explicitly (Forestry Commission 1990:2).

In the United States, the USDA Forest Service has an explicit mandate to address maintenance of viable populations of fish and wildlife on public lands. The National Forest Management Act (NFMA) of 1976 specified that the National Forest System be managed to provide for diversity of plant and animal communities to meet multiple-use objectives. Subsequent regulations for planning land and resource management (36 CFR 219), adopted in 1979 (refined in 1982 and undergoing current revision), augmented the diversity policy by requiring management of habitats to maintain viable populations of vertebrates. This requirement has been interpreted by the Secretary of Agriculture, upon the advice of a committee of scientists appointed to help implement the National Forest Management Act, to include the maintenance of viable populations of vertebrates (Committee of Scientists 1979; 36 CFR 9; see Salwasser et al. 1986). The regulations stipulate that "fish and wildlife habitat shall be managed to maintain viable populations of existing native and desired nonnative vertebrate species in the planning area" (36 CFR 219.19). The regulations also mandate that "all management prescriptions shall...provide for adequate fish and wildlife habitat to maintain viable populations of existing native vertebrate species" (36 CFR 219.27(a)(6)). The NFMA regulations define a viable population as "... one which has the estimated numbers and distribution of reproductive individuals to insure its continued existence is well distributed in the planning area."

Other Federal resource laws in the U.S. provide impetus for managing for viable wildlife populations on public lands. These other laws include the National Wilderness Preservation Act of 1964, the National Environmental Policy Act of 1969, and the Endangered Species Act of 1973

(as amended). Together, these laws reflect society's desire to maintain healthy and productive environments and biota.

FACTORS AFFECTING VIABILITY

Conditions that influence size and trend of wild populations can be categorized as demographic, genetic, and environmental (Shaffer 1981; see Table 2 which presents a universal list of major factors that should be explored in all PVA's). A thorough viability assessment should account for potential influences from each of these factors.

Demographic Factors

Demographic factors include variation in birth and death rates, which can cause a small isolated population to become extinct or to decline where other risk factors take effect (quasiextinction levels) (McGraw and Garbutt 1990, Pimm et al. 1988, Iwasa and Mochizuki). For example, Smith and McDougal (1991) found that variation in reproduction and first year survival in tigers (Panthera tigris) in Royal Chitwan National Park in Nepal were as important a set of factors affecting population stability as was quality of a female's territory. Demographic variation can reflect individual variation endogenous to the population, or effects of environmental noise on individual performance from exogenous factors.

Source and sink dynamics of local populations can form one kind of metapopulation structure, which can influence local and global likelihoods

of persistence (Harrison 1991, Pulliam 1988). A conservation strategy for the northern spotted owl in northwest U.S. was founded on metapopulation dynamics by sizing and spacing habitat conservation areas to ensure local demographic persistence and successful dispersal of owls among habitats and populations (Thomas et al. 1990).

Genetic Factors

Factors that affect population viability also include those that contribute to losses of genetic and allelic variation associated with population declines caused by habitat loss and geographic range reduction which, in turn, can lead to inbreeding depression and genetic drift (Owclough 1980). The likelihood of deleterious recessive alleles becoming fixed in a population is greater in species that are less vagile and that exist in small, isolated populations. Such likelihoods can be estimated with analytic models like those of Emigh and Pollak (1979).

Variation in the size of a reproductive population can depress the genetically effective population (or breeding) size (N_e), causing a given population to exhibit the characteristics of much smaller populations, or better, smaller genetic pools. For example, Smith and McDougal's (1991) study of tigers also showed that substantial lifetime variation in reproduction resulted in a lower effective population size ($N_e:N = 0.41$ and $N_e = 26$) and a higher risk of inbreeding, than if reproductive rates had been more constant through time. Variation in the reproductive output of individuals generally is much greater in smaller populations than in larger ones because fewer breeders are active each season.

Treatments of effective population size have varied. Hill (1979) and Lande and Barrowclough (1987) provided formulae for estimating N_e from life history parameters. In contrast, Pollak's (1983) method was based on changes in allele frequencies. Nei and Tajima (1981) linked genetic drift to declines in N_e . Whichever the method, the calculation of N_e , a central step in estimating potential effects of drift and inbreeding depression, is at best an inexact science. Harris and Allendorf (1989) underscored this observation in a report on the wide deviation in estimates of N_e from applying various published formulae on identical data on grizzly bear (Ursus arctos horribilis).

Environmental Factors

Environmental factors virtually always serve as the mediating forces that reduce population sizes to levels at which demographic variation and genetic threats put populations at risk. Environmental factors that affect population viability include systematic sources of threats including anthropogenically caused losses of habitat, interactions with alien species, overhunting, and impacts from pollutants and toxicants. Stochastic sources include normal environmental fluctuations (such as drought and deluge) and catastrophic events (such as wildfire). Studies of North American songbirds provide numerous examples of factors that contribute to population and species declines, including losses of forested wintering habitats relative to breeding habitats (Wilcove and Terborgh 1980), fragmentation of breeding forest habitats (Lehmkuhl and Ruggiero 1981, Lynch and Whigham 1984, Rosenberg and Raphael 1986), invasion by

competitors and nest parasites, particularly brown-headed cowbird (Molothrus ater) (Brittingham and Temple 1983), and other factors.

Few generic computer programs are available commercially (e.g., Ferson's [1988] RAMAS) or in the public domain (e.g., POPDYN, available from USDA Forest Service, Pacific Northwest Region) that can aid analyses of demographic, genetic, and/or environmental effects on population viability. This is probably because each species and circumstance is different and warrants unique models, and because the analytic science of population viability assessment is inchoate.

POPULATION VIABILITY RISK MANAGEMENT

In Situ Versus Ex Situ Management

The purpose of viability risk management is to implement planning guidelines to ensure long-term, in situ (in the field) conservation, productivity, and persistence of wildlife species. We emphasize in situ management for viable populations for several reasons. First, the most common cause of concerns over population viability is that of habitat loss. Successful in situ management demands conservation of adequate amounts and distributions of habitats to support target species. Second, ex situ (not in the field) conservation methods, such as captive propagation or zoo stock management, simply cannot replicate the diversity of natural conditions essential for long-term adaptation and evolution of genetic lineages. Third, most methods of translocations,

reintroductions, and captive propagation of small populations remain untested and have dubious value as long-term conservation strategies. For example, 100% of all reintroduced populations of bighorn sheep (Ovis canadensis) with fewer than 50 individuals have gone extinct within 50 years (Berger 1990). Likewise, captive breeding programs should be viewed as last-resort, high-cost, and high-risk manipulations of critically endangered species, such as of Puerto Rican parrot (Amazona vittata) (Wiley et al. 1992); alternatives to captive breeding are usually much less expensive. Finally, waiting until a population in decline reaches levels at which it becomes a legal or litigative concern, as with federal threatened species listings or court actions, hardly promotes conservation leadership. Population viability management is best used as a procedure to ensure the continued security in situ of species and taxa currently not threatened, as well to help plan the recovery of those that are threatened.

A 9-Step Process for Viability Risk Management

Specific guidelines and policies used to manage for viable populations will vary by species and with landowner goals. However, a general procedure to plan the management of population viability risk can be described as a 9-step process (after Marcot et al. 1986; Table 3).

Step 1. Screen for species at risk. In the first step, species are identified and screened for the immediacy of conservation concern. Species that should automatically be prioritized as viability concerns include those legally identified, as by USDI Fish and Wildlife Service or

equivalent agencies in other countries, as threatened or endangered (particularly if a recovery plan has not been developed and implemented). Useful screens also include "alert lists" such as The IGBP World Check-list of Threatened Birds (Collar and Andrew 1988), CITES (Council on International Trade of Endangered Species) appendices (although CITES addresses only international trade species), The Nature Conservancy's Natural Heritage Inventories, and the International Union for Conservation of Nature and Natural Resources' (IUCN) Red Data Books. IUCN in particular has categorized species as threatened, endangered, vulnerable, rare, indeterminate, and insufficiently known (e.g., Collar and Stuart 1985, King 1978-1979).

Schonewald-Cox (1983) presented a nine-class scale that depicts the degree of population security as a simple function of approximate effective population size. This approach proved helpful to identify the current level of viability concern for the northern spotted owl in the Pacific Northwest of the U.S. (USDA 1986). Other simple and useful screening tools follow rarity ratings like that of Rabinowitz et al. (1986), as modified by Marcot et al. (in prep.) to depict management priorities (Table 4). As an example, a species that has a restricted habitat specificity, narrow geographic distribution, and small population size throughout its range, such as Honey Creek cave blind salamander (Eurycea tridentifera) in Texas, U.S., would rank as having high viability concern and management priority. A species that similarly has restricted habitat specificity, but a wider geographic range and larger population size, such as the Oregon silverspot butterfly (Saxeria zerene hypolitta) would have a lower ranking. Other viability ranking criteria were developed by Lehmkuhl and Ruggiero (1991)

for old forest associated wildlife in Pacific Northwest U.S. Rankings were based on general life history traits, such as the vagility and habitat specificity of each species, and anticipated levels of vulnerability to forest management.

The depiction of current viability concerns can be aided by mapping habitats and species distributions. For example, Burke et al. (1991) depicted areas of viability concern by mapping habitat distribution of Stephen's kangaroo rat (Dipodomys stephensi).

A mapping procedure, used by one of us (BGM) to assess the viability status of spotted owls and other terrestrial species on National Forests of the U.S., can be useful with a wide variety of other species and habitats:

- (1) Map the current distribution of the target species.
- (2) Map the geographic range of suitable habitat. Use habitat suitability models to depict grades of habitat quality.
- (3) Delineate on map overlays the following distributional considerations of particular concern: population isolates, dispersal barriers, areas of low population crude density, and bottlenecks or critical links in habitat distribution.
- (4) Overlay locations of proposed activities that could compromise habitat quality, for each planning alternative considered. From this overlay, prioritize the areas of distributional concern for immediate conservation action.

Mapping can also be used to identify areas of high endemic species richness for conservation action. Examples include Collar and Juniper's (1992) range map of numbers of neotropical parrot species at risk of extinction, and Scott et al.'s (1988) range maps of the distribution of Hawaii's endangered native avifauna.

Step 2. Describe pertinent regulations and laws. The second step in the population viability management process is describing regulations and laws pertinent to conservation of wildlife species and habitats. This step includes defining the range of acceptable viability conditions that meet policy regulations or legal mandates, and identifying the key agencies or institutions responsible for carrying out viability management activities and coordinating those activities.

Step 3. Describe species' conditions and ecology. The third step is an in-depth status review of the species, including descriptions of the species life histories, ecologies, environmental relationships, trends, and reasons for viability concern or population decline. This step can entail basic field inventories of species and/or habitats and use of species-habitat relationships models.

Also useful -- some would argue essential -- in this step is use of demographic models and analyses. For example, Crouse et al. (1987) used a stage-based population model to assess population status and to aid conservation of loggerhead sea turtles (Caretta caretta). Kinnaird and O'Brien's (1991) use of demographic models suggested a high probability of extinction of a primate, the Tana River crested mangabey (Cercocebus

galeritus galeritus), over the next 50-100 years, and helped to identify population sizes that would better ensure long-term viability. Similarly, Knight and Eberhardt (1984) and Shaffer (1983) assessed future population sizes of the Yellowstone grizzly bear using stochastic demographic life table models. Many other examples are available from the literature. Such models are best used on species with adequate field data and to generate hypotheses for monitoring population trend and dynamics.

Simulation models are useful but not absolutely necessary for conducting a viability assessment. Perhaps it is useful to differentiate a quantitative PVA, which should make use of such models, from a qualitative population viability assessment, which can use a mix of professional judgment and empirical evidence to pose working hypotheses on population response to existing or proposed management actions. Examples of qualitative population viability assessments include the evaluations of the persistence of fungi, lichen, bryophyte, nonvascular and vascular plants, invertebrates, fish, and wildlife species and species groups (Thomas et al. 1993, FEMAT 1993). These evaluations relied on the judgment of panels of species and taxonomic group experts to qualitatively rank each species or species group according to their likelihoods of persisting well-distributed for a century or longer on National Forests (Thomas et al. 1993) or all federal lands (FEMAT 1993) in the Pacific Northwest U.S. Although distribution and amounts of late-successional forest habitats were projected over time, no population simulation models per se were used; thus, results should be treated as tentative working hypotheses on population response until additional monitoring and research studies can validate them.

Steps 4 and 5. Develop planning alternatives and evaluate viability effects. The next steps entail the development and evaluation of one or more management alternatives, assessing varying viability responses. A range of management alternatives can help display a spectrum of potential effects on population viability and other resources. Each alternative should be evaluated for its affect on population size, distribution, and persistence, as well as resource and economic tradeoffs and other non-biological considerations. Perceived and expected utilities of each planning alternative should be described in the context of agency mandates and public expectations (Nash 1991).

Murphy and Noon (1992) formalized a mapping process used to help op a habitat conservation strategy for northern spotted owls. The process includes mapping habitats and tentative conservation areas in a cycle of proposing and testing hypotheses of how well conservation strategies fit existing, real-world conditions.

Step 6. Array the alternatives by effect. The sixth step arrays alternatives according to anticipated effects, such as on benefits to population viability and availability of other resources. Indirect costs, opportunity costs, and forgone options should be clearly listed for each alternative. The range of acceptable alternatives that meet the decision criteria should thereby be identified and arrayed.

Steps 7, 8, and 9. Selection, implementation, and monitoring. The final steps entail selection of an alternative, implementation of the

alternative, and monitoring the results. Monitoring should be used to revisit all previous steps to adapt management as warranted by the data.

POPULATION VIABILITY RISK ANALYSIS

Objectives of Viability Risk Analysis

Population viability risk analysis evaluates potential effects on viability of populations from alternative courses of action. It is used to help craft conservation plans, inform the public, and aid decision-makers in differentiating among management alternatives. Specific objectives of a population viability risk analysis are to:

- o Estimate the overall likelihoods of success or failure of implementing possible management guidelines. What are possible outcomes? What is the overall range of possible outcomes, the set of more likely outcomes, and the most likely outcome? What are the probabilities of each outcome under distinct management guidelines?

- o Identify the key factors contributing to likelihoods of success or failure. What are the key biological parameters that most affect predictions of outcomes and their associated likelihoods? How do variations in the set of potential management guidelines influence success or failure of the strategies? Sensitivity tests of simulation models are useful for developing hypotheses of key factors to test through implementation and monitoring.

o Reveal the degree with which likelihoods of success or failure are accurately and precisely portrayed, and the sources and magnitudes of uncertainty in such predictions. How well are the parameters estimated that influence success or failure? Is the biological system understood adequately to make predictions of system response? How well are potential future short term and long term conditions predicted? How do various factors compound to affect success or failure?

o Evaluate the need for new information. How much would it cost to add to our knowledge to tighten confidence intervals of key parameters or gather further basic biological information? How would new knowledge help in refining predictions of outcomes and their associated likelihoods, or in devising new management strategies with lower social costs and equal (or

r) likelihoods of maintaining viable populations?

Use of Decision Theory for Analyzing Viability

In decision theory, risk analysis serves to qualitatively or quantitatively evaluate the likelihoods of different outcomes of potential management actions. In the ecological literature, population risk analyses have typically included evaluations of the likelihoods of extinction within specified time periods, estimated from results of stochastic models of population demography, although estimating likelihoods of other conditions and parameters is also tenable (see Table 1 which lists the variety of parameters idiosyncratically estimated by various PVA's).

Population viability risk analysis and management can be conducted in the context of decision analysis (Maguire 1986b, 1991). This approach requires the identification of key management decision sequences that

affect environments, habitats, and populations, and estimation of various responses of species and habitats to each management decision. Such data usually are not available; however, sometimes they can be estimated by extrapolating from available data or from using best professional guesses. More formal methods to derive professional judgments of potential outcomes include variations on the Delphi technique (Richey et al. 1985a, 1985b). Also, various forms of Bayesian statistics, such as use of sequential and empirical Bayes algorithms (Gazey and Staley 1986, Milne et al. 1989), can be used to initially select outcome probabilities and correct them over time from results of research and monitoring. Each of these approaches, however, has shortcomings that can add to prediction uncertainties, often in ways that are unknown or even not quantifiable. Many decision analysis methods, such as use of decision trees, are more useful for the risk management stage of conservation planning than for the initial and more clinical phase of risk analysis. In using decision analysis for viability risk management, clear decision criteria should be articulated along with the factors and value ranges used to rank and select alternatives.

Decision theory has been used for prioritizing conservation of fish and wildlife species in Florida (Millsap et al. 1990). It also has been used for viability assessments of Concho water snake Natrix harteri paucimaculata (Soul 1989), grizzly bear (Maguire 1986a), black-footed ferret Mustella nigripes (Maguire et al. 1988), tiger (Maguire and Lacy 1990), and Sumatran rhinoceros Dicerorhinus sumatrensis (Maguire et al. 1987).

Definition of Risk

The term risk has been used in literature on decision theory and in conservation biology in a wide variety of contexts and (mostly unarticulated) meanings (Marcot and Salwasser 1991). As examples, the term has been used to depict means and variances of projected future population sizes in probabilistic and deterministic modeling, to describe scientific uncertainties in available studies and data, and to depict the degree of conservatism in decision-making attitudes. In a conservation planning strategy designed to provide for viable populations, risk is the likelihood that implementing a particular strategy will not result in viable populations over time. Technically, viability risk can be estimated as the frequency of replicate runs of a stochastic demographic simulation that fail to remain above a particular population level over a specific simulation time.

Describing Uncertainties

Depicting uncertainties in scientific data and knowledge is one important aspect of evaluating risk. Risk analysis entails clearly displaying sources and degrees of uncertainty of the basic scientific information used to predict effects of implementing potential courses of action. Such uncertainties can include quantitative statistical estimates of the precision with which key parameters are known, such as estimating confidence intervals or standard errors of prediction of finite rate of change of population size. Also pertinent are describing both confidence

and power of statistical hypothesis tests, such as testing the null hypothesis that λ is greater than or equal to 1.

Uncertainties can also include qualitative statements of the degree of applicability of particular ecological concepts, theories, data sets, and models to the cases at hand. Concepts, theories, data, and models might be less directly applicable when environmental conditions have altered or if applied to an unknown or different ecological setting than the one in which the model was originally constructed.

In summary, predictions of potential effects of management alternatives on maintaining viable populations are influenced by: (1) degree of certainty of parameters and basic data used in projecting outcomes; (2) degree of applicability of concepts, theories, models, and data to the area of interest, including certainty of future conditions; (3) the (often unknown) propagation of errors caused by compounding parameters in multi-factor models; (4) sampling error in estimating central tendency and spread values (e.g., means and standard errors) of parameters; and (5) the degree of completeness and realism of the specific models used. As well, statistical properties of specific estimators, including bias, accuracy, and consistency, affect predictions of potential effects. Each of these potential influences should be discussed in a risk analysis of population viability.

TOWARD A MULTIPLE-SPECIES APPROACH

Conservation of species is a central facet of protecting biological diversity (Kelly and Harwell 1990). Species-specific analyses and management guidelines are most prudently applied in the context of providing for other species and habitats as well. Such a biodiversity- or ecosystem-centered approach might more economically and efficiently provide for multiple species' needs than would a species-by-species approach. It is critical, however, that attention be paid to threatened, endangered, sensitive, and rare species on species-specific level, as well.

Viability of populations indeed depends on the sustenance and vitality of whole ecological communities and ecosystems, ultimately including those of humans. This concept was highlighted by Clark et al. (1991) for managing resources in the Greater Yellowstone Ecosystem. Population viability analysis and management therefore are best integrated into more extensive resource management plans designed to provide for conservation of habitats and ecosystems as well.

One example of the need to integrate species-specific evaluations into a broader, coarse-filter approach to habitat management is the qualitative evaluation of species viability for planning management activities in late-successional and old-growth forests on National Forests of the Pacific Northwest U.S. (Thomas et al. 1993). Among other things, this evaluation was a test of how well management of old forests in the Northwest geared toward maintaining population viability of northern spotted owls would also suffice to ensure long-term viability of 667 other species closely associated with late-successional forests. Results suggested that habitat distribution and abundance for only about one-third of all such species would be provided to help ensure the species' viability. The other

two-thirds required more site- or substrate-specific management guidelines than the spotted owl management plan provided, or were so poorly known scientifically that a judgment could not be made. Thomas et al. (1993) thereby recommended additional management mitigations to provide for these other species, or suggested inventory and monitoring activities designed to provide basic empirical information on their habitat requirements. Thus, in this case, providing for the needs of northern spotted owls would not ensure viability of all other associated species.

Such approaches to multiple-species viability planning are just being developed elsewhere as well. For example, on Tongass National Forest, USDA Forest Service, in southeast Alaska, a viability analysis approach uses steps for screening species for viability concern, describing each species current viability status, and developing conservation strategies to meet multiple species needs (L. Suring, pers. comm.). This approach uses data on life history characteristics, notably home range area and dispersal capabilities, to craft size and spacing of old-forest habitat conservation areas. A different approach taken by Raphael (this volume) uses linear programming to describe the optimal combination of various vegetation successional stages needed to meet multiple species needs. Both approaches remain untested and more are sure to be developed. However, it is absolutely essential that species-specific analysis, planning, and management is retained in more holistic approaches to ecosystem management and biodiversity conservation.

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Table 1. Some expressions of the numerical viability of a population.

- o extinction likelihood -- the probability of a specific population becoming completely extinct (zero individuals remaining) within a specified geographic area over a specific duration of time (or at several points in time)

- o pseudoextinction likelihood -- the probability of a specific population declining to or below a specific population density or overall population size (typically nonzero) within a specified geographic area over a specific duration of time

- o time to extinction -- the duration of time from the present when the population is most likely to reach extinction or pseudoextinction levels (densities or population sizes)

- o duration of persistence of well-distributed population -- the duration of time that the population will likely continue to exist well distributed throughout at least its current range (well-distributed would be defined in terms of specific geographic locations or a range of ecological conditions); note that a population could fail to be well distributed but could be highly likely to continue to persist above extinction or pseudoextinction numbers or densities

- o probability of persistence of well-distributed population -- the likelihood that the population will continue to remain at or above a specific size or density; similar to pseudoextinction likelihood except that the level is not describing threatened status but rather one describing a minimally well-distributed pattern

- o degree of population bottleneck -- the expected size or density of populations passing through bottleneck periods, and associated anticipated effects

- o duration of population bottlenecks -- the duration of time through which the population would likely remain at small size or low density, daily affecting local or global extinction likelihoods or long-term adverse genetic effects

- o likelihood of recovery -- related to likelihoods of population bottlenecks are likelihoods that the population would recover from low densities or sizes over a specified geographic area and over a specified time period; such likelihoods might include consideration of recovery growth rates and qualities of habitats, and colonization rates of new habitats by dispersing organisms (founder rates)

- o rate of recovery -- the expected duration of time over which a population would expand in geographic range, density, or population size to specified levels

o occupancy rate of habitats -- the average proportion of potentially occupied sites that are predicted to be occupied over specific time intervals, or the proportion predicted to be occupied at a particular point in time; expressed also as proportion of habitat patches or reserves occupied by at least one individual or a breeding unit, the proportion of the landscape occupied by individuals or breeding units, the proportion of the landscape consisting of potentially occupied habitats or reserves, etc.

Table 2. Factors potentially affecting population viability. (After Marcot et al. 1986)

DEMOGRAPHIC

Variation in birth and death rates

Variation in size of reproductive population

Dynamics of source and sink populations

GENETIC

Inbreeding depression

Genetic drift

Loss of genic diversity through range subtraction

ENVIRONMENTAL

Loss of habitat

Chronic effects

Succession

Reduction of habitat quality or quantity by

human use

Shift of geographic locations of habitat

Climatic cycles

Catastrophic effects

Storms

Fires

Floods

Volcanoes

Insect or disease epidemics

Droughts

Human-caused acute alteration of habitat
conditions

Biological interactions

Predators

Competitors

Disease

Parasites

Reduction in prey abundance or availability

Pollutants, toxicants

Table 3. Component and steps in a population viability risk management (decision-making) process. (After Marcot et al. 1986)

1. Describe the species. Identify and screen for species at risk.
2. Describe pertinent regulations and laws. Define the range of acceptable conditions that meet policy regulations or law. Identify responsible agencies and institutions and coordinate their planning activities.
3. Describe species' conditions and ecology. Describe the species' environmental relationships and reasons for viability concern or population decline.
4. Develop planning alternatives. Develop a range of planning or management strategies. Describe risk attitudes of publics and responsible agencies and institutions. Describe perceived and expected utilities of planning alternatives. Identify factors and value ranges in decision criteria to be used to select among the alternatives.
5. Evaluate viability effects of the alternatives. Conduct a viability risk analysis. Analyze how the alternatives affect population size, distribution, and persistence, resource tradeoffs, and social concerns.

6. Array the alternatives according to anticipated effects. Assess the benefits to population viability, indirect costs, opportunity costs, and forgone options for each alternative. Identify and array the range of acceptable alternatives that meet decision criteria.
7. Select an alternative. Apply decision criteria to results and select a course of action.
8. Implement the alternative. Institutionalize management guidelines of the selected alternative. Develop budgets and track implementation.
9. Monitor results. Compile and interpret monitoring information; revisit s 1-8 as suggested by monitoring information and changing conditions.

Table 4. A method for prioritizing species for viability concern. Table entries depict priorities for viability concern. (Source: Marcot et al., in prep., after Rabinowitz et al. 1986).

Geographic				
distribution:	WIDE		NARROW	
<hr/>				
Habitat				
specificity:	BROAD	RESTRICTED	BROAD	RESTRICTED
<hr/>				
Local population size:				
<hr/>				
SOMEWHERE LARGE	very low	low	low	moderate
<hr/>				
EVERYWHERE SMALL	low	moderate	moderate	high
<hr/>				