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VIABILITY CONSIDERATIONS FOR MANAGING SPOTTED OWLS IN SOUTHERN CALIFORNIA MOUNTAINS

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ABSTRACT

Concern for viability of spotted owl populations throughout the western U.S. has prompted specific habitat management guidelines on federal lands, public debate on efficacy of such guidelines, and a series of technical writings on the nature and assessment of population viability. A viable population is defined as one with adequate numbers, well distributed throughout its range, that has an estimated likelihood of persisting for a specified period of time. A 95 percent likelihood for at least a century has been one definition proposed in the scientific literature. Viability of spotted owls in southern California mountains might be affected by variation in reproductive and survival rates among individuals and over time; loss of genetic variation from inbreeding depression, genetic drift, founder effects, and genetic bottlenecks; systematic and catastrophic loss of habitat, including effects of habitat fragmentation and isolation, changes in climate and environmental quality, and fires; and interactions with competitors, predators, disease, and parasites. A population viability assessment procedure entails four main steps: (1) identifying current and future extent of suitable habitat, (2) relating the extent and variation of habitat to capability for supporting spotted owl populations, (3) identifying and analyzing potential effects from viability risk factors, and (4) summarizing the viability factors in a risk analysis framework. An integrated program of research and monitoring can be used to reduce areas of uncertainty and test the hypotheses of management guidelines in an adaptive management framework.

Specific evaluation criteria should be developed for assessing results of research and monitoring.

INTRODUCTION

Concern for the long-term viability of populations of northern spotted owls (Strix occidentalis caurina) in western Washington and Oregon and northwestern California has led to the recent federal designation of the subspecies as threatened, and to the development of an interagency scientific strategy for its conservation (Thomas et al. 1990). USDA Forest Service identifies the species as an indicator of the condition and management of old growth conifer forests in western Washington and Oregon, which provide unique habitats for a wide variety of vertebrates. Decline in spotted owl populations and concern for the security of their old growth habitats and attendant species has led to the development of a series of management plans for spotted owl habitat, for both the northern and the California race (S. o. occidentalis) on federal lands. The key factor threatening the fate of many spotted owl populations has been identified as decline in the absolute amount of habitat and a change in its spatial distribution, i.e., the severing of habitat linkages across the landscape. Thus, concern for the fate of old forest habitats, spotted owls per se, and other species associated with old forests has been expressed for federal, state, and even industry and other private forest lands throughout the west.

Spotted owls in southern California inhabit a type and array of habitats unique within the species' range in the three Pacific states. These have been described as relatively narrow canyons and drainages of both conifer and hardwood trees, set among mountain ranges separated from one another and from larger, more contiguous spotted owl populations in the southern Sierra Nevada (Gould et al. 1987, Gutiérrez and Pritchard 1989, 1990). Questions have been raised as to the viability of such small, seemingly isolated populations in the southern California Transverse and Peninsular Ranges. This paper summarizes the concerns for viability of spotted owl populations in these locations -- particularly on National Forest lands -- and presents a framework for assessing and planning for their long-term persistence.

POPULATION VIABILITY CONCEPTS FOR MANAGEMENT

What constitutes a viable population? In the early to mid-1980's, the concept of "minimum viable population" was thought to be useful for describing a density above which vitality and safety of a wildlife population are ensured and below which extinction is inevitable (Lacava and Hughes 1984, Reed et al. 1986). Such a simple threshold was initially identified for avoiding genetic erosion of a single, isolated population, and later for avoiding demographic declines (Samson et al. 1985, Shaffer 1983, Shaffer and Samson 1985). However, as other factors complicating future viability began to be explicitly considered (Table 1), the concept of an easily identifiable minimum population size became problematic (Conner 1988).

More recently, a viable population has been defined in terms of probability of persistence. A population is viable when it is capable of being self-sustaining and having a very high likelihood (such as 95 percent or greater) of avoiding a multitude of risks of extinction over the long term, such as 100, or even 1000, years (Shaffer 1981). Population sizes and distributions necessary to meet these criteria likely vary among species and circumstances, such as seen with viability analyses for grizzly bear (Ursus arctos horribilis) (Eberhardt et al. 1986, Knight and Eberhardt 1985) and concho water snake (Natrix harteri paucimaculata) (Soulé 1989).

From the perspective of managing viable populations on National Forest land, the Regulations (36 CFR 219.19) implementing the National Forest Management Act of 1976 mandated that viable populations of all native and desired non-native vertebrates be maintained. The Regulations stipulated that, on National Forest lands, minimum specific management requirements shall be crafted such 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 Regulations defined 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." The planning area typically consists of a National Forest. The Regulations make clear that (1) managing for reproductive individuals is crucial, (2) both numbers and distribution of those individuals are important to viability, (3) continued existence is the goal, not merely presence, and (4) distribution must allow for interaction of individuals in the population. The question of "insuring" continued existence relates to providing habitat such that the estimated likelihood that a population can endure risks over a specified period of time is high (Salwasser et al. 1986). As well, to manage for viability of a population that spills beyond the boundaries of the planning area -- a national forest -- it is necessary to also consider the current state and future condition of habitat occurring on other lands as they contribute to the size and trend of the overall biological population.

VIABILITY RISKS FOR SPOTTED OWLS IN SOUTHERN CALIFORNIA

Forest Service plans for managing northern spotted owl habitat have used a risk analysis approach for considering the degree of threat to spotted owl populations under various management scenarios (USDA Forest Service 1988a, Marcot and Holthausen 1987, Marcot 1986, Thomas et al. 1990; after Shaffer 1981; also see Shaffer 1990). Such an approach might prove useful for assessing viability effects of management of spotted owl habitat in southern California. Of special concern in southern California is the isolation of relatively small populations numbering perhaps in the low to mid hundreds. Although spotted owls have apparently persisted as isolation populations on Mt. San Jacinto and Palomar Mountain in southern California for nearly 100 years (Gutiérrez and Pritchard 1990), such populations are susceptible to a variety of risks. The following section describes those risk factors and concepts of viability risk assessment that might prove useful in evaluating persistence of southern California spotted owls and efficacy of existing or proposed management guidelines.

Factors Causing Viability to be at Risk

Risk factors that can endanger the future vitality of a population can be categorized into three main headings: demographic, genetic, and environmental (Table 1). In general, risks are greater when populations are small and isolated.

Demographic risks. -- The term demographic risks refers to the probability of a population declining to moribund levels or to local extinction because of variations in age-specific or age-class specific birth and death rates ("vital rates") (Goodman 1987). Two kinds of variations can contribute to fluctuations and declines in populations. The first, **environmental (population) stochasticity,** is caused by factors extrinsic to the population and refers to the variation in annual values of vital rates averaged over all members of the population. Mean values of population-wide vital rates can fluctuate over time because of variations of environmental conditions affecting the population more or less as a whole, such as seasonal or annual variations in prey availability or weather conditions. By incurring a few chance years or breeding pulses with low fecundity and survival rates, resultant population declines can increase risks of local extinction (Iwasa and Mochizuki 1988, Berger 1990, Thomas et al. 1990).

For example, in the assessment of northern spotted owl populations (USDA Forest Service 1988a) the average annual fecundity rate calculated from several studies was 0.49 owlets of both sexes born per adult female per year. This population average was calculated by combining estimates among studies conducted during different years and at different geographic locations. The mean value was allowed to vary randomly among years in a demographic life table model, simulating annual changes in effects of stochastic environmental conditions affecting this particular vital rate. The bounds of the variations were derived from calculating population standard deviations of the values among the studies, assuming these bounds represented a typical range of values expected to be encountered in the field. The validity of this assumption is unknown. A similar assessment was done for age-class specific survival rates.

A second kind of variation, **demographic (individual) stochasticity,** is intrinsic to the population. This refers to variation in vital rates among individuals within a population at a given point in time (Hatch 1988). For example, the average fecundity rate of 0.49 owlets born per adult female per year is in turn an average among adult females that individually vary from 0 to some upper limit. Demographic stochasticity is a property of all finite populations that experience random variations in population growth. It influences persistence probabilities when populations are small, and tends to average out in large populations (approximately >100 individuals). Demographic uncertainty is easy to represent in dynamic computer simulations, such as with binomial sampling for survival probabilities (B. Noon, pers. comm.).

The greater the variance in demographic vital rates, including fecundity as well as survivorship, the greater the variation in occupancy rates of habitats over time. Moreover, the finite rate of population change (lambda) is sensitive to each vital rate parameter in varying degrees (Noon and Biles 1990). For example, with untruncated stable stage-class projection matrices, which represent lack of senescence in fecundity rates, lambda is much more sensitive to variation in adult survivorship than to variation in other vital rate parameters. Thus, one can expect that effects of demographic stochasticity on the finite rate of population change would vary considerably according to such individual and population parameters as longevity, reproductive senescence, and stage- or age-specific fecundity and survival rates.

Environmental and demographic stochasticity are usually viewed as independent events. Changes in the expected value of a vital rate (environmental change) does not necessarily change the shape (variance) of its distribution. The magnitude of demographic uncertainty is strongly density-dependent; the environmentally induced component of demographic uncertainty is only moderately density-dependent. This changes to only a slight density-dependence in a geographically structured population, not to be expected in the small population isolates of spotted owls in southern California.

The mean and variances of vital rates to represent environmental and demographic stochasticity are poorly known for spotted owl populations. Nor is it well understood, either specifically or for spotted owls or in general, how the two sources of variation interact to affect risks to short- or long-term persistence of wildlife populations. The subjacent mechanisms and major causes of environmental (population) and demographic (individual) variations also are not well understood.

Genetic risks. -- Another source of viability risk is genetic risks. This refers to adverse effects on population vital rates from loss of genetic variation within the population (Barrowclough 1980, Shaffer 1985, Emigh and Pollak 1979, Lande 1988b). Specifically, loss of allelic diversity means that deleterious, recessive alleles can be expressed in greater proportion in homozygous conditions. Loss of allelic diversity can arise from several kinds of population dynamics.

Inbreeding depression occurs in small, isolated populations where related individuals interbreed. Related individuals share a higher proportion of genes than do unrelated individuals. Conversely, unrelated individuals better represent the diversity of genes available in the general gene pool of the population. Inbreeding causes the loss of some alleles and fixation in homozygous genotypes of other, deleterious, recessive alleles. This results in (1) the deleterious, recessive alleles to be expressed phenotypically in homozygous conditions, and (2) overall decreases in genetic diversity of the population. It is generally assumed that loss of genetic diversity as from accumulated inbreeding results in lower survival, reproductive rates, and overall fitness of individuals.

Genetic drift causes increases in the proportion of homozygosity in a population. It is related in one sense to inbreeding depression, as it occurs in small, isolated populations. Genetic drift is the random loss of alleles (and their associated genes) among generations in populations from a "sampling effect." In small populations, not every type of gene will be passed on to the next generation. Some vanish as chance recombinations fail to "select" the gene in the next generation.

Loss of genetic variation is a concern because it renders the population unable to respond, with different phenotypes or behaviors, to changes in environmental conditions (Caswell 1983). Overall, genetic effects become greater concerns with smaller population sizes. As populations get very small (low 100 to tens of breeding individuals), the probability of inbreeding or genetic drift increases nonlinearly. That is, a linear decline in population size might trigger an exponential decline in genetic diversity, leading to a rapid erosion (simplification) of the genome, an increase in expression of deleterious genotypes, and a significant decline in reproductive fitness of individuals and their offspring.

Another source of genetic simplification of a population is the **founder effect.** This refers to the colonization of an area by a small number of individuals that represent only a small proportion of the overall genetic diversity of the source population. If the colonizers interbreed and remain reproductively isolated from their source, the gene pool of their new population is markedly simpler and, in short order, may contain a disproportionately high frequency of homozygosity, especially of deleterious alleles. Founders might incur problems of inbreeding or genetic drift if the population remains small.

Related to the founder effect is that of **genetic bottlenecks.** This occurs when an isolated population declines in numbers to a point where inbreeding or drift can operate to further simplify the genome. Factors affecting the severity of genetic bottlenecks include the original genetic diversity of the population, the size and demographic characteristics of the population, the type of social structure and mating systems as affecting rate of interchange of alleles, and particularly the duration of the bottleneck period. Some species, such as whooping crane (Grus americana), have rebounded with surprising vigor after serious founder or bottleneck effects, whereas others, such as Puerto Rican parrot (Amazona vittata) and Florida panther (Felis concolor coryi), might be unable to recover from genetic bottlenecks and might be suffering irrevocable losses of genetic variation. Still others, such as black-footed ferret (Mustela nigripes) and California condor (Gymnogyps californianus), have suffered severe bottlenecks and minute population sizes, but have been captive-reared and are about to be re-released into the wild. Their fate is as yet unknown.

Although theoretically present in some small, isolated populations, inbreeding depression, genetic drift, founder effects, and bottlenecks have yet to be empirically demonstrated in spotted owl populations. In spotted owls, as with most other species, genetic events have not been empirically related to changes in vital rates and, ultimately, to population size, trend, and persistence.

Environmental risks. -- The third major category of viability risk factors is environmental risks, which can affect population viability through loss of habitat, biological interactions with other species, and direct threats to individuals from pollutants and toxicants. **Loss of habitat** and changes in habitat distribution are perhaps the greatest short-term threats to spotted owl populations. Habitat can be lost from systematic, chronic events, including vegetation succession, habitat fragmentation, and climatic changes. Vegetation succession is not per se a threat to spotted owl habitat, except in cases where natural development of old forest conditions -- specifically closed and diverse forest canopies for roosts, large trees as nesting substrates, and large down wood for prey habitat -- has been curtailed by forest management, so that prevalence of secondary succession of young forests becomes the threat.

Habitat fragmentation is probably one of the most insidious causes of declines in habitat suitability for spotted owls, although there is little direct evidence of its effects on population size and trends. Suitable spotted owl habitat can become fragmented -- divided into small, scattered patches -- by a number of causes, including road building, timber harvesting, recreational and urban development, and fire. Fragmentation severs a contiguous population into partially or fully isolated subpopulations (i.e., a metapopulation, sensu Shaffer 1985). The subpopulations then suffer greater threats from other risk factors, such as loss of genetic variation and demographic and environmental stochasticity (Fahrig and Paloheimo 1988, Hastings 1990, Hastings and Wolin 1989, Pulliam 1988, Quinn and Hastings 1987, Wilcove 1987). Interactions of habitat fragmentation on population isolation, successful recolonization of vacant habitats, and demographic stability are poorly understood in general and specifically for spotted owls, but potentially can greatly affect population regulation (Hughes 1990). (See Morrison et al., in press, for recommendations for managing habitat of metapopulations to provide for viability.)

Habitat fragmentation increases the amount of forest edge in a landscape. Edge habitats provide introduction routes for predators and competitors (Wilcove 1987) and can adversely change temperature and moisture regimes in forest interiors. Spotted owls in southern California seem to select habitats providing cooler, moister conditions, much as found with both the northern and Mexican (S. o. lucida) races (e.g., Ganey 1988). However, it is unknown to what degree edge effects from habitat fragmentation would adversely influence microclimates in southern California mountain habitats.

Habitat suitability can also decline from slow changes in climatic conditions (Graham 1988). Climate changes in southern California are potentially a very real threat to habitat conditions. Increases in acid precipitation, decreases in air quality from smog and air-borne particulates, and changes in temperature means and variations from increasing urbanization, all can contribute to increased physiological stress of vegetation (Layser 1980) and capability of habitats to continue to produce resources necessary for maintaining prey populations and associated species (e.g., see Kricher 1975, Meslow and Keith 1971, Stinson 1980, Botsford et al. 1988). Such effects on spotted owl populations and habitats in southern California are unquantified. Some have speculated that longer-term changes in climate, as from global warming, may cause vegetation to shift upward in elevation. If so, land should remain available at higher elevations to provide for such locational shifts over the long run.

Habitat can also be lost from catastrophic, acute events, including storms, fires, floods, volcanoes and other geologic activities, outbreaks of forest insects and disease, droughts, and short-term, human-caused changes in habitat availability or conditions. Because of their stochastic nature, it is particularly difficult to predict likelihoods and effects of catastrophic events. Ideally, the following parameters should be statistically evaluated to estimate probabilities of habitat loss from catastrophes: location, frequency, extent, duration, type of catastrophic event, and the specific effect on habitat conditions from each event type. Such data are seldom available. Habitat variability over time, as from catastrophes and longer-term changes, can greatly influence likelihoods of population extinction (Lande and Orzack 1988, Leigh 1981). Also, there might be lag effects on populations from catastrophes (Knopf and Sedgwick 1987).

Wildfires often drastically change habitat conditions, and wildlife have been documented to shift behaviors and distributions accordingly (Apfelbaum and Haney 1981, Balda and Overturf 1977, Emlen 1970, Soulé et al. 1988). Fire has always been a natural part of the spotted owl forest ecosystem in conifer forests of the Pacific Northwest (Agee 1989, Swanson and Morrison 1988) and southern California woodlands and chaparral (Keeley et al. 1981). Large fires in northern California and southern Oregon during summer 1987 caused losses of some spotted owl habitat areas. However, the fires also burned some forests in a rather patchy pattern. As forests regrow in these areas, large trees and down wood (residual old growth components) might contribute to the suitability of the young-growth forest for spotted owls substantially sooner than if such elements were not present. This hypothesis needs observational and experimental verification. However, some evidence for such effects can be seen in other locations and forest types where residual old growth forest components apparently have been key factors contributing to occurrence of spotted owls and spotted owl pairs. But evidence also suggests that young-growth forests with scattered, old growth components are likely not as suitable as true, extensive old growth forests. Old growth forest provides a far superior habitat for more consistently maintaining breeding pairs.

Another risk to viability of spotted owl populations is from **biological interactions.** Starvation and predation potentially can affect population size (McNamara and Houston 1987). Further north, it is known that great horned owls (Bubo virginianus) and northern goshawk (Accipiter gentilis) are two major predators of spotted owls. It is not clear, however, that they directly depress sizes or trends of local spotted owl populations, nor that these predator species respond to changes in forest conditions in a way that would put spotted owl populations at risk. Ongoing studies are assessing effects of forest fragmentation on great horned owls (Johnson and Meslow 1989) and spotted owls (Meyer et al. 1990) in western Oregon and comparative physiology between great horned and spotted owls in the southwest U.S. (Ganey and Balda 1989).

Barred owls (Strix varia) are increasing their range west and southward in the Pacific Northwest (Allen 1985, Hamer 1985, Taylor and Forsman 1976), although they have not yet reached southern California. The long-term effect of the barred owl's range expansion on sizes and trends of northern spotted owl populations are not known. It is speculated that barred owls might competitively exclude northern spotted owls from their habitats, as a number of anecdotal observations suggest (Hamer 1988, Hamer et al. 1987). Barred owls seem to have a more catholic set of habitat requirements and a greater capability for successful dispersal than do spotted owls. Three spotted-barred owl hybrids ("sparred owls," <u>Strix</u> <u>occidentalis</u> x <u>varia</u>) have been discovered in Oregon and Washington (E. Forsman, pers. comm.), and one hybrid male has successfully back-crossed with a barred owl female. However, it is unknown if hybrids of both sexes are fertile and could produce viable offspring, nor if hybridization will be more common than competitive exclusion between the species. At present, great horned owls, goshawk, and barred owls do not seem to be a significant concern for affecting viability of spotted owls in southern California. However, much more remains to be learned of the role of predators and competitors there. The effect of disease and parasites on viability of spotted owl populations is little known. Some empirical observations (Gutiérrez 1989b, Hoberg et al. 1989) and theoretical population models (May 1988, Scott 1988) suggest they might be an important factor for consideration (also see Hunter et al. 1987, Thorne and Williams 1988). Also, at present, pollutants or toxicants do not seem to be directly threatening any of the spotted owl races. However, several northern spotted owls died in northern California during the 1987 fires, not from direct loss of their habitat but possibly from increased concentration of air-borne particulates. Also, a disproportionate number of females died than did males in this incident (B. Noon, pers. comm.). As noted above, indirect effects of air pollution in southern California mountains may play a major role in changes in health of the forest habitats over time, but this needs study.

Modeling Population Viability

Population viability assessment procedure. -- The general procedure for assessing population viability of northern spotted owls (USDA Forest Service 1988a) entailed four main steps. First, suitable spotted owl habitat was defined and its extent and distribution was quantified over time for each planning alternative being tested. Defining suitable habitat is not as simple as merely listing stand structural components. Recent studies have highlighted the importance of secondary habitat for unpaired, floating members of spotted owl populations. Also, juxtaposition of old forest stands with younger stands has been seen to affect the degree of suitability. However, no field studies have yet reported specific forest stand composition and structures that represent primary and secondary habitat conditions for spotted owls in southern California, although such studies are in progress (Noon, pers. comm.).

Second, capability of habitat to provide for spotted owl populations was estimated over time for each planning alternative. Estimates of habitat capability should account for how various degrees of habitat suitability and habitat distribution, notably fragmentation, provide for the needs of reproductive pairs. Also, occurrence and distribution of habitat providing for dispersing individual spotted owls, especially juveniles, should be accounted for in capability estimates.

Third, effects of viability risk factors on population persistence are identified and estimated qualitatively or quantitatively. Finally, the separate influences on population persistence from each risk factor are combined in a risk analysis framework. Modeling risk factors and evaluating their composite effects on population viability constitutes a major part of a population viability analysis and is discussed next.

Assessing demographic risks. -- Factors affecting demographic stability of a population include those that contribute to both environmental and individual variability in fecundity and survivorship rates. The most commonly used tools for assessing environmental variation are stage-based population models and stochastic life tables (e.g., Crouse et al. 1987, Eberhardt 1987,1988). Persistence time of northern spotted owl populations has been estimated by use of static and stochastic life tables (Franklin et al. 1990, Barrowclough and Coats 1985, Marcot and Gutiérrez 1987, USDA Forest Service 1988a). Static population trend, typically measured by calculating a mean and confidence interval of the finite rate of population change (lambda), with eigenanalysis of population projection matrices, is another modeling tool that has been used (Lande 1988a, Noon and Biles 1990, Thomas et al. 1990 Appendix L). Lande (1988a) used partial differentiation and Noon and Biles (1990) used simulations to assess sensitivity effects on lambda and on population persistence time from varying vital rates, particularly age of first reproduction, reproductive senescence and longevity, and stage class-specific survivorship and fecundity rates.

Some have argued that demographic models should account for various kinds of dynamics. These include density dependent facilitation of vital rates (Boyce 1987; e.g., Ginzburg et al. 1990), habitat fragmentation effects (Doak 1989, Lande 1988a), reproductive contribution by extremely old individuals (the problem of truncation of the life table; Lande 1988a, Noon and Biles 1990; also see Krementz et al. 1989), variability in habitat suitability, and other factors. Unfortunately, empirical data to drive such assessments for spotted owls -- both northern and California subspecies -- have been mostly lacking. One exception is the crude assessment of effects of habitat fragmentation on pair persistence included in the Forest Service's (1988a) analysis.

Spatially explicit models of habitat fragmentation and occupancy by spotted owls are a promising facet of viability analysis (Bovet and Benhamou 1988, Fahrig and Paloheimo 1988, Hastings 1990, Horton et al. 1989, Laymon and Barrett 1986, Laymon and Reid 1986, Marcot 1987, Patton and Ganey 1988). Such models can be used to simulate use of vegetation patches by individuals and owl pairs in a home range area. Lamberson et al. (1989) devised a patch colonization model to assess population persistence of black-footed ferrets. Folse et al. (1990) created a prototype computer system that joins models of (1) foraging and movement behavior of mountain lions (*Felis concolor*), (2) suitability of mountain lion habitat, and (3) a geographic information system, to predict effects of habitat patch patterns on persistence of mountain lion family units in a landscape. Doak (1989) and Lande (1988a) produced simpler, analytic models of occupancy of habitats by northern spotted owls; their models, like those of USDA Forest Service (1988a), underscored that habitat fragmentation, population demography, and dispersal and search characteristics of individual owls can greatly influence population persistence.

Simulations of northern spotted owls by Thomas et al. (1990 Appendix M) included individual-territory models and territory-cluster models. The simulations were used to assess effects of the owl's dispersal capability and search efficiency, as well as landscape dynamics, secondary habitat types, and variations in cluster size.

In modeling persistence time of spotted owl populations based on demographic trends and parameter variations, one constraint is the need for unbiased, accurate estimates of population structures and vital rates (Burgman et al. 1988, Chao 1988, Eberhardt and Simmons 1987). Direct observation and counts of eggs or nestlings in the nest *per se* are not feasible methods with spotted owls. Thus, counting owlets shortly after they have left the nest but prior to dispersal in the fall is one of the best ways to empirically estimate fecundity rates of known pairs. Use of a field protocol (USDA Forest Service 1988b) for detecting and observing spotted owls solves many problems of observer variability. It also helps standardize timing and techniques of detecting and counting young near the nest site, so that results gathered across locations, years, and observers are comparable. In addition, a rigorous statistical basis for establishing a sampling frame for such monitoring studies (Max et al. 1990, Azuma et al. in press) is necessary for sound estimates.

Accurate estimation of age-class specific survivorship rates is also a problem in spotted owl studies, as the owls are typically long-lived and must be reobserved annually over a long period of time. Banding individuals, with a concerted reobservation effort, can help provide such estimates (Bown and Lint 1989). Banding can help yield reliable survivorship estimates except for the first two years of life when dispersal outside an intensive reobservation area can result in underestimates of sub-adult survival rates (Franklin et al. 1990).

Assessing genetic risks. -- Little empirical work has been done on assessing degree of genetic variability of spotted owls. Gutiérrez (1989a) found little genetic variation in specimens of northern and California races. Further studies are in progress to collect and analyze blood serum samples from northern race specimens. The degree of homozygosity in southern California populations might be an important factor affecting future adaptability.

Assessments to date of how loss of genetic variation can affect population persistence have generally applied basic theory on the rate of loss of genetic variation in small, isolated populations. Barrowclough and Coats (1985) estimated the size of effective population (N_e) by a formula designed to account for fluctuations in overall population size, dispersal distance of juveniles, density of adult pairs, and other factors. They then related population size to potential degree of inbreeding, and assumed that cumulative inbreeding rates represented declines in reproductive fitness of individuals. The approach was also used in the viability analysis conducted by USDA Forest Service (1988a; see also Marcot and Holthausen 1987, Salwasser et al. 1984). However, there are no standards for, and there is much controversy over, the correct formula for estimating N_e and procedures for estimating its components. Also, nothing is known empirically about how inbreeding depression affects fitness of spotted owls. Until studies are conducted, mathematical analyses of loss of genetic variation from inbreeding and other factors should be treated as hypotheses.

Other genetic considerations include genetic drift, founder effects, and effects of genetic bottlenecks. Lacy (1987) addressed the general problem of assessing loss of genetic variation in a managed population by accounting for genetic drift, mutation, immigration, selection, and isolation. Each of these mechanisms could be operating in the isolated mountain populations in southern

California, although at this time this is speculation.

Assessing environmental risks. -- A number of environmental factors have been included in viability assessments of spotted owls. However, thus far, only USDA Forest Service (1988a) modeled actual amounts and rates of expected loss of suitable habitat over time, under various forest planning alternatives, and across all land ownerships throughout the range of the northern race. Their assessment included short-term loss of habitat from harvesting timber and long-term gain of habitat from forest regrowth. They also related the proportion of suitable habitat remaining on a national forest to the degree of habitat fragmentation and usability by (occupancy rate of) spotted owls within home ranges.

Effects of climatic change on habitat suitability have not been quantified in any analysis of any spotted owl population. Also, no analysis has quantified likelihoods and degree of expected loss of spotted owl habitat from catastrophes. Fire simulation models (e.g., Keane et al. 1990, Potter and Kessell 1980; D. Roberts, Utah State University, pers. comm.) might prove useful if the base empirical data on frequency, extent, location, and effect of fires can be parametrized. Fire effects on habitat suitability might prove especially pertinent in the southern California mountains. Similar models predicting likelihood of catastrophic habitat loss from storms, floods, droughts, other natural catastrophes, as well as human activities, might add realism to prognostications of persistence times of California spotted owl populations. As well, further studies of biological interactions and effects of air pollutants on habitat quality in southern California mountains are needed.

Viability risk analysis. -- It is not understood how the various factors affecting viability (Table 1) interplay. Gilpin and Soulé (1986) hypothesized that various components of population phenotype, environment, and population structure and fitness interact in complex feedback loops to intensify likelihoods of population decline. Most others have addressed viability components of spotted owl populations singly.

There is virtually no empirical understanding of how separate viability risk factors interact for spotted owls. Thus, USDA Forest Service (1988a) assumed they operated, and assessed them, independently, and then combined results into a single, qualitative statement of composite risk (Table 2). Degree of viability risk was expressed on an ordinal scale with five categories (Table 2) ranging from very low to very high likelihood of continued existence of well-distributed spotted owl populations. The five rank-order categories were specifically defined to relate to each major risk factor that could be quantified (see definitions in footnote a of Table 4). Table 3 shows how this rank order scale was used to denote levels of viability for the isolated, northern spotted owl population inhabiting the Olympic Peninsula in Washington, under one management alternative. Also, additional risk factors that could not be quantified, particularly influence of competitor species and catastrophic loss of habitat, were considered qualitatively and were used to adjust a specific viability ranking up or down accord to professional judgment of likelihood of effects. Similar decision theory approaches to viability risk analysis (Marcot 1986) have also been used for assessing population conditions and persistence of grizzly bears (Maguire 1986), zoo populations of tigers (*Panthera tigris*; Maguire and Lacy 1990), concho water snake (Soulé 1989), and other species.

Managing for Viable Spotted Owl Populations in Southern California

In developing a best strategy for managing for viable spotted owl populations in southern California, each of the viability risk factors discussed in this paper should be evaluated at least qualitatively. To begin, evaluations need not demand quantitative analyses of field data or use of complicated statistics and simulation models. Much can be learned, however, from a rigorous approach, and nothing replaces basic knowledge gained from field ecology studies of populations and habitats.

Under the multiple use mandate on National Forest land, the best management practices must consider both the needs for maintaining long-term population viability, and any considerations for competing, alternative use of the resources. The best practices might be those that furnish fully adequate amounts and distributions of spotted owl habitats -- providing for interacting spotted owl pairs, densities of prey populations, and habitat conditions for owls, prey, and other species associated with such habitat conditions, following the indicator species approach -- in a landscape that is also used for other resources.

Federal land management agencies, in particular USDA Forest Service and USDI Bureau of Land Management, are under charge to manage the public's land under multiple-use scenarios. In this context, providing for spotted owl habitat, with its high perceived opportunity value as a timber or recreational resource, has historically led to management decisions that attempt to balance competing interests in the land base and that, by design, compromise future viability of the species. In southern California, spotted owl habitat is not as directly threatened by conversion of old growth forests to young growth forests from timber harvesting, as it is in the range of the northern subspecies. However, devising habitat management guidelines in southern California entails understanding impacts from concomitant use of the land for other interests. In particular, effects of, and consideration for, urban recreationists must be included in the assessments and planning guidelines. A risk analysis framework that rigorously arrays and assesses impacts on population viability would likely prove most helpful for crafting forest management guidelines that maintain viability. Such an assessment would identify forest management activities that affect demographic, genetic, and environmental factors that in turn put viability at risk.

RESEARCH AND MONITORING NEEDS

Spotted owl populations occurring on southern California mountains are likely isolated demographically from one another and from other subpopulations. Further, each population numbers at best in the low hundreds. Such conditions should raise an alarm for long-term viability, especially considering the greatly increasing use of the national forest lands by urban recreationists, and the life history of the species, particularly its high site tenacity, long life span, and low reproductive rate.

The obvious and best short-term tactic for conserving the owl is to protect all known spotted owl habitat sites and conduct thorough inventories for more. Additionally, studies should continue on owl population dynamics, movement patterns of spotted owls through various mountain and intermountain landscapes, and stand-specific vegetation structure and composition. Additional empirical understanding of effects of competitors, predators, disease, and catastrophic events such as fires and windstorms, would add to reliability of viability assessments. Models of habitat suitability and capability to support spotted owl populations should account for fragmentation, catastrophic events, regrowth of vegetation, and cumulative effects of human use.

As developed by the USDA Forest Service's Spotted Owl Research, Development, and Application Program, monitoring population responses should be an integral part of habitat management guidelines. Specifically, the extent and quality of suitable spotted owl habitat in southern California should be tracked over time. As well, key behavioral attributes of individuals and population parameters should be monitored. These might include turnover rates of individuals on territories, frequency of divorces, and declines in reproductive rates of adults and survival rates of adults and juveniles. Such parameters constitute an "early warning system" to signal an impending population decline much sooner than simply monitoring habitat occupancy.

However, we need to understand how such early warning signals can be influenced by declines in available habitat. For example, occupancy rates of habitats by spotted owls, as well as turnover rates and rates of juvenile mortality during dispersal, can be artificially inflated by short-term packing of individuals displaced from disturbed habitats. If the rate of disturbance (from timber harvest, fires, urbanization, etc.) of suitable habitat slows, turnover, occupancy, and juvenile mortality rates might relax to lower, equilibrial values. However, questions remaining to be answered include, is there any guarantee that the declining turnover will not be followed by a continuation of decline in occupancy, and ultimately by local extinction? Are there thresholds of habitat distribution below which the population cannot equilibrate? Even if turnover rates and other parameters theoretically can be used as an early warning system, do we actually know enough to interpret them? Turnover rates should be tracked in a monitoring program, but interpreted in light of other parameters. It may be obscured by short-term effects, just as occupancy rate is. Additional studies focused on movement dynamics in changing landscapes, and spatial models of habitat occupancy that incorporate realistic changes in habitat amount and distribution (Lamberson, Noon, and McKelvey, in prep.), will be vital tools for helping gauge presence and degree of such effects, and thus in helping us correctly interpret early warning signals.

Also, in a monitoring program, specific criteria for triggering reevaluation of management guidelines should be defined, such as those presented in Table 4. These criteria can change over time as we learn more about population ecology of the species, but they are essential for testing the hypotheses of management guidelines, that is, for closing the loop in the process of adapting management direction to new information.

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Table 1. Factors that can cause population declines or extinction (modified from Salwasser et al. 1986).

DEMOGRAPHIC

- Environmental stochasticity: random variations in annual population means of birth and death rates
- Demographic stochasticity: random variations of bird and death rates among individuals at a given point in time

GENETIC

- Inbreeding depression
- Genetic drift
- Founder effect
- Genetic bottlenecks

ENVIRONMENTAL

- Loss of habitat
  - Systematic processes
    - Vegetation succession
    - Habitat fragmentation
    - Climatic changes
  - Catastrophic processes
    - Storms
    - Fires
    - Floods
    - Geologic events (e.g., volcanoes)

Droughts

Human-caused acute alterations of habitat conditions

Biological interactions

Predators

Competitors

Disease

Parasites

Forest insect and disease outbreaks

Reduction in prey abundance or availability

Pollutants, toxicants

Table 2. Rule set for estimating probability of persistence of a population, as used with the viability assessment of northern spotted owls in Oregon and Washington (USDA Forest Service 1988a).

	DEMOGRAPHIC AND GENETIC STABILITY		HABITAT SIZE	HABITAT DISTRIBUTION
Probab. level[a]	Demographic effect (prob. of N > min)[b]	Genetic effect (inbreed. coeffic.)	HSI value[c]	Nearest-neighbor distances (mi)[d]
VERY HIGH	>0.95	≤0.05	>0.95	<2
HIGH	0.80-0.95	0.06-0.20	0.80-0.95	2-6
MODERATE	0.60-0.79	0.21-0.35	0.60-0.79	7-15
LOW	0.40-0.59	0.36-0.50	0.40-0.59	16-21
VERY LOW	<0.40	>0.50	<0.40	>21

[a]Probabilities of persistence classes are defined as follows:

VERY HIGH (VH): Continued existence of a well-distributed population on the planning area at the future date is virtually assured. This is likely even if major catastrophic events occur within the population, research finds that the species is less flexible in its habitat relationships, or if demographic or genetic factors are more significant than assumed in this analysis.

HIGH (H): There is a high likelihood of continued existence of a well-distributed population in the planning area. There is limited latitude for catastrophic events affecting the population or for biological findings that the population is more susceptible to demographic or genetic factors than was assumed in the analysis.

MODERATE (M): There is moderate likelihood of continued existence of a well-distributed population in the planning area at the future date. There is no latitude for catastrophic events affecting the population or for biological findings that the population is more susceptible to demographic, genetic, or habitat distribution factors than was assumed in the analysis.

LOW (L): There is a low likelihood of continued existence of a well-distributed population in the planning area at the future date. Catastrophic, demographic, genetic, or habitat distribution factors are likely to cause elimination of the species from parts or all of its geographic range during the period assessed.

VERY LOW (VL): There is a very low likelihood of continued existence of a well-distributed population in the planning area. Catastrophic, demographic, or genetic factors are highly likely to cause elimination of the species from parts or all of its geographic range during the period assessed.

[b]Probability that a population, with stochastic birth and death rates, will exceed a population size representing a well-distributed population, within a

specified period of time. These probabilities were estimated as the proportion of stochastic Leslie-matrix life table runs using fluctuating reproductive and juvenile survival rates that remained above specific population levels. Well-distributed population sizes were defined for each population modeled as the theoretical density that would result from a distribution of breeding pairs spaced no further apart than the median dispersal distance of juveniles (23 miles).

[c]Habitat Suitability Index values are the probability that a designated spotted owl habitat area of given amount would actually support a breeding pair. (See USDA Forest Service 1988a for model used for quantifying this relationship.)

[d]Habitat distribution as compared to dispersal distances of juvenile spotted owls. (See USDA Forest Service 1988a.)

Table 3. Examples of describing 4 management alternatives for providing spotted owl habitat on USDA Forest Service lands in the Pacific Northwest, showing probabilities of persistence afforded to each population (Table 2), as used with the viability assessment of northern spotted owls in Oregon and Washington (USDA Forest Service 1988a).

Description of alternative	Area	Probability of persistence[a] to year: 15	50	100	150
1. DO NOT SPECIFICALLY MANAGE FOR SPOTTED OWL HABITAT -- habitat would therefore be provided by default in wilderness or other reserved areas.	OLPE[b]	M	L	VL	VL
	WACA	M	L	L	VL
	ORCA	VH	M	L	L
	CORA	c	M	L	L
2. PROVIDE A NETWORK DISTRIBUTION OF HABITAT AREAS RANGING FROM 1000 TO 2700 ACRES OF SUITABLE HABITAT FOR EACH AREA	OLPE	M	M	M	L
	WACA	M	M	L	L
	ORCA	VH	H	M	L

3. MAINTAIN ALL CURRENTLY SUITABLE HABITAT -- no additional harvesting or reduction of habitat would be allowed on National Forest lands.	OLPE	H	H	M	M
	WACA	H	H	M	M
	ORCA	VH	H	H	H

[a]Probability of persistence as defined in Table 2. VH = very high, H = high, M = moderate, L = low, VL = very low.

[b]Levels of protection are shown for each population, denoted by Physiographic Provinces: OLPE = Olympic Penninsula, WACA = Washington Cascades, ORCA = Oregon Cascades and Klamath Mountains, CORA = Oregon Coast Range. CORA is isolated only under Alternative 1 and is part of the ORCA population under Alternatives 2 and 3.

[c]Oregon Coast Range not isolated at this time period.

Table 4. Examples of "early warning" parameters and reevaluation criteria ("trigger points") for use in a spotted owl monitoring program. These are not currently implemented, but are presented here to illustrate the concept. (Modified after a draft list from R. Holthausen, pers. comm.)

Habitat amount and distribution

- o Finding that total inventory of suitable habitat in any province deviates by more than 20% from figures used in assessments.
- o Catastrophic or chronic loss of designated habitat at a rate greater than 10% in a single year; or any combination of rates and years that yield a mean projected loss greater than 10% per decade.
- o Finding that cumulative harvest of undesignated suitable habitat in any province exceeds rate projected in planning assessments by more than 10% over a five-year period.
- o Catastrophic loss of more than 20% of suitable habitat over any time period in reserved areas without demonstrated replacement.

Capability of Habitat to Support Spotted Owls

- o Finding that capability to support spotted owls in designated and reserved habitat deviates up or down by more than 20% from predicted figures.
- o Failure of designated habitat on other ownerships to support at least 80% of the number of projected pairs, or decision on these lands to change habitat protection plans by more than 20%.

Habitat Requirements

- o Finding that more than 20% of the breeding pairs in any province occupy annual ranges containing less than 500 acres of habitat considered suitable for spotted owls.
- o Peer reviewed research that demonstrates an average breeding pair habitat requirement that deviates by more than 20% from figures cited and used in assessments.

Occupancy rates

- o Failure to establish a habitat area network with 80% occupancy by breeding (or potentially breeding) pairs within 3 years from issuance of a habitat management decision. (Note - the occupancy figure used could vary depending on the target habitat area size).
- o Occupancy decline of 10% or more in any province in a single year, or 20% or more in a 5-year period, within designated and reserved spotted owl habitats.

Population Trend and Demography

- o Persistence of a lambda value of < 1.0 for five years in any province.
- o Finding that the net or ecological density of pairs in any province deviates by more than 20% from figures used in assessments.
- o Observation of a net reproductive rate in any province that exceeds the maximum rate used in assessments.
- o Turnover rates of individuals or pairs on territories, or divorce

rates of pairs, significantly higher than that observed or expected in contiguous blocks of highly suitable habitat.

- High and prolonged rates of reproductive failures within one or more populations, or unsuccessful dispersal of juvenile cohorts, persisting for two or more years.

<u>Federal Listing</u>

- Federal listing of the spotted owl as threatened or endangered in any province, or failure to delist the species after federal listing.

<u>Monitoring and Research</u>

- Failure to implement or continue the monitoring and research programs needed to establish any of the above, or failure to disclose information coming from these programs.