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Analyzing Population Viability of the Spotted Owl in the Pacific Northwest

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Introduction

> *In conservation it is not a question of blueprints for the future. All that is attempted is to provide conditions, based on our best scientific insight and subject to the present-day social and economic restraints, which will make it possible for an evolutionary succession of organisms to continue, inevitably subject to the social consent of future generations.*
>
> Frankel and Soulé (1981:7)

Planning for the type, distribution and amount of habitat for wildlife species on national forests has become one of the focal issues in implementing the National Forest Management Act of 1976 and pursuant regulations (36 CRF 219). The regulations call for maintaining well-distributed populations and for sustaining viability of all native and desired non-native species. (The regulations have often been cited erroneously as mandating the planning and management for *minimum* viable populations, whereas, in fact, the phrase "minimum viable population" does not appear.) Two central problems that are emerging are (1) how to provide habitat for widely distributed but scarce species whose habitat has high economic value and (2) how to assess population viability. These problems have been preeminent in planning habitat for the spotted owl (*Strix occidentalis*) in the Pacific Northwest Region (primarily Washington and Oregon) of USDA Forest Service.

In this paper, we first outline the history of the spotted owl controversy, then discuss the process by which, in developing a habitat plan, we analyzed the viability of spotted owl populations throughout the Pacific Northwest. We conclude by comparing our approach to others' for the spotted owl and other species, and we pose several unanswered questions regarding the planning for species viability on national forest land.

History of the Viability Analysis

The spotted owl is widely distributed throughout western Washington and Oregon and several other western states. The owl appears to prefer mature and old-growth coniferous forest, which often also has high economic value for timber production. Originally, in 1979, the Pacific Northwest Region of USDA Forest Service adopted a management plan proposed by the Oregon Interagency Wildlife Committee. The plan called for providing 290 habitat areas for spotted owls in Oregon on National Forest land (400 total habitat areas in Oregon over all lands). In 1981, using data provided by Forsman's (1980) research on home range sizes, the Committee recommended an increase in acreage of suitable habitat per pair (old-growth coniferous forest) from 300 acres (121 ha) to 1,000 acres (405 ha). The Region adopted this proposal, along with criteria for spacing the habitat areas throughout the existing range of spotted owls on national forest land.

The increase to 1,000 acres (405 ha) brought considerable criticism from groups concerned with the continued commercial harvest of timber, who asserted that too much habitat was being provided, and from conservation groups who asserted that too little was being provided to ensure viability of the species in the Northwest. In 1984, a group of environmental organizations appealed the spotted owl portion of the regional plan in the Pacific Northwest Region on several grounds. The appeal asked that the area of suitable habitat provided per pair be increased from 1,000 acres (405 ha) (the smallest amount of suitable habitat observed within the home range of a spotted owl pair) to 2,200 acres (890 ha) (the average amount). Eventually, the appeal reached the Office of the Deputy Assistant Secretary of Agriculture. As a result, the Pacific Northwest Region was instructed to develop a Supplemental EIS (SEIS) to the regional plan and analyze an array of alternatives for planning spotted owl habitat. The analyses in the SEIS were to assess potential risks to viability of the species and impacts on other resources, primarily the timber economy of the region. What follows is a description of the portion of the Draft SEIS dealing with the analysis of population viability of the spotted owl.

Analysis of Population Viability

Approaches to assessing population viability have traditionally centered on the problem of genetics, especially the effects of inbreeding depression on realized fitness in small and genetically isolated populations (Frankel and Soulé 1981, Schonewald-Cox et al. 1983). A viable population has often been defined in the literature in terms of a minimum population size below which the population faces imminent extinction, as from inbreeding depression, and at or above which the population is in some sense secure (e.g., Shaffer 1983, Samson et al. 1985, Reed et al. 1986, Wilcox 1986).

The work by Soulé and Wilcox (e.g., Soulé and Wilcox 1980, Soulé 1986) and Shaffer (1983) has helped focus the questions associated with population viability by guiding attention to the complex of factors that make a population susceptible to extinction. Recent approaches have focused attention on a suite of factors, including life history traits (Wu and Botkin 1980, Hubbell and Werner 1979), the dynamics of habitat patches and habitat fragmentation (Chesson 1981, Lynch and Whigham 1984, Usher 1985), and other aspects of genetics (Allendorf and Leary 1986, Ralls et al. 1986). As a means for developing and assessing management plans, population viability has been viewed as a probabilistic phenomenon, and approaches to modeling viability have taken the form of a risk analysis (Salwasser et al. 1984, Marcot 1986).

We assessed population viability of the spotted owl as a risk analysis and attempted to quantify several main factors that may cause populations to be at risk. We defined viability as the likelihood that a well-distributed population would persist to specified future times. Our approach synthesized current theory on population viability and considered genetics, demographics, environmental variability, habitat change, and habitat distribution and spacing as potential risks to continued existence of a population. Specifically, the viability analysis required: (1) assessing empirical information on the biological and ecological attributes of spotted owls; (2) assessing the probability that several key factors would cause local or global extinction—these factors included habitat fragmentation and isolation of populations, inbreeding, variability in birth and death rates, environmental catastrophe, and interspecific interaction; and (3) summarizing these results in terms of the probability of continued existence of spotted owl populations under a number of alternative habitat management plans. First, we describe the biology of the northern spotted owl, and then discuss the viability assessment.

Biology of the Spotted Owl in the Pacific Northwest

Habitat. Spotted owls are found throughout a variety of low- to mid-elevation conifer and mixed conifer-hardwood vegetation types in the Pacific Northwest. Studies have consistently reported spotted owls using mature and especially old-growth forest stages for foraging, roosting and nesting (Forsman et al. 1977, 1984, Brewer 1985, Solis 1984, Sisco and Gutiérrez 1984, Marcot and Gardetto 1980, Gould 1979, Garcia 1979). Studies of habitat preference have been used to infer that spotted owls require older-age forest stages, although this has been challenged by some biologists.

Breeding biology. Spotted owls are generally monogamous. Adults seem to have a high site fidelity and usually inhabit territory areas year-round. Eggs are laid in March to April and hatch during April to May. Owlets leave the nest by May to June, although the young do not fully fledge until sometime in June or July. Parental care continues until September, when the young disperse from the natal roost area.

Demography. Demographic attributes of spotted owls are poorly known. The reproductive rate averages 0.48 young per pair per year (standard deviation over eight studies is 0.43 young per pair per year) (Table 1); this estimate includes breeding as well as nonbreeding pairs, and is an index to mean reproduction over time and space. Reproductive effort and success seem to vary considerably among years and locations. Spotted owls probably do not breed until the third year of life, although two-year-old birds have occasionally been observed nesting (Barrows 1985, Miller et al. 1985). Average life span is unknown, but Delmee et al. (1978, 1980) reported that the tawny owl (*Strix aluco*), a related species in Europe, may live to at least 15 years.

Table 1. Reproduction rate of spotted owls.[a]

Number of juveniles observed	Number of pairs observed	Year(s) observed	Source
64	111	1983–85	Franklin et al. (1986)
75	158	1982–85	Miller and Meslow (1985)
11	16	1984–85	Meslow et al. (1986)
1	1	1984	Miller et al. (1985)
63	96	1972–74	Forsman (1976) Forsman et al. (1984)
0	56	1984–85	Allen and Brewer (1986)
N=214	N=438		

[a]Mean fledging rate $= \frac{214}{438} = 0.49$ juvenile per pair.

Little is known of survivorship rates of spotted owls. There are no reported data on or estimates of mortality rates of spotted owl eggs, hatchlings or nestlings. Observations of fledged or nearly fledged young near the nest site suggest a predispersal mortality rate of 40 percent per year (standard deviation over four studies was 0.18 percent per year) (Table 2). Radio telemetry data on dispersing juveniles suggest that dispersal mortality may average 82 percent (Table 3). Thus, overall first-year survivorship may be estimated as $(1 - 0.40)(1 - 0.82) = 0.11$. However, as with reproductive rates, mortality rates may vary between years and areas according to habitat availability, weather and food. Franklin et al. (1986) estimated survivorship of 26 banded adults as 96 percent.

A life table based on the above values of demographic attributes (Table 4) suggests that the rate of change of spotted owl populations is 0.84 per year, indicating that, on average, populations are undergoing a marked decline. In contrast, Forsman et al. (1984) estimated that spotted owl populations in Oregon have been declining more on the order of about 1 percent per year over the last decade. Their reported decline is probably related more to habitat loss than to intrinsic demographic conditions.

It is undetermined whether our summary of demographic attributes represent long-term averages and, thus, if our estimate of marked population decline is accurate. The estimate of the rate of change is most sensitive to changes in juvenile survivorship. It is unknown whether predispersal mortality of juveniles was estimated accurately or if survival was affected by the radio transmitters and harnesses used to determine dispersal mortality.

Dispersing young owls use a wider variety of habitat structures than do adult owls (Gutiérrez et al. 1985, Miller and Meslow 1985). However, patterns of dispersal distance, directions and rates, and orientations of juvenile spotted owls to habitat and physiographic features appear variable and are poorly understood. Maximum dispersal distances (defined as the straight-line distance from the natal area to the farthest radio point observed) of 58 radio-tracked juveniles averaged 27 miles (43 km) (median 23 miles [37 km]) (Forsman 1980, Miller and Meslow 1985, Gutiérrez et al. 1985). Ninety-five percent of all dispersing juveniles traveled at least 2 miles (3 km), 85 percent traveled at least 6 miles (10 km), 65 percent traveled at least 15 miles (24 km) and 40 percent traveled at least 21 miles (34 km). This frequency distribution was used later to indicate the effects of habitat spacing on the probable distribution of owls.

Table 2. Predispersal mortality rate of juvenile spotted owls.[a]

Number of juveniles observed	Number of juveniles died	Year(s) observed	Source
32	11	1972, 1975	Forsman et al. (1984)
59	28	1982–1985	Miller and Meslow (1985)
33	8	1983–1984	Gutiérrez et al. (1985)
11	7	1985	Laymon (1985)
N=135	N=54		

[a]Mean predispersal mortality rate $= \frac{54}{135} = 0.40$.

Table 3. Dispersal mortality rate of juvenile spotted owls, first year of life.[a]

Fate	Number of juveniles	Source
Alive (A)	7	Meslow and Miller (1986), Miller (personal communication)
Dead (D)	2	Forsman (1980)
	22	Meslow and Miller (1986)
	12	Gutiérrez et al. (1985)
Transmitter failure during dispersal (T)	4	Meslow and Miller (1986)
	9	Gutiérrez et al. (1985)
Settled, then transmitter failure (S)	1	Gutiérrez et al. (1985)
Unknown (U)	1	Meslow and Miller (1986)

[a]Overall dispersal mortality $= \dfrac{\mathrm{D}}{\mathrm{A+D+S}} = \dfrac{36}{7+36+1} = 0.82.$

Table 4. Female spotted owl life table and calculations of rate of population change.[a]

Age class (x)	Birth rate (m_x)	Death rate (q_x)	Survival rate (p_x)	(d_x)	(l_x)	(l_xm_x)	(xl_xm_x)
0	0	0.89	0.11	0.890	0.997	0	0
1	0	0.04	0.96	0.004	0.107	0	0
2	0.24	0.04	0.96	0.004	0.103	0.025	0.049
3	0.24	0.04	0.96	0.004	0.098	0.024	0.071
4	0.24	0.04	0.96	0.004	0.094	0.023	0.091
5	0.24	0.04	0.96	0.004	0.091	0.022	0.109
6	0.24	0.04	0.96	0.004	0.087	0.021	0.125
7	0.24	0.04	0.96	0.003	0.083	0.020	0.140
8	0.24	0.04	0.96	0.003	0.080	0.019	0.153
9	0.24	0.04	0.96	0.003	0.076	0.018	0.165
10	0.24	0.04	0.96	0.003	0.073	0.018	0.176
11	0.24	0.04	0.96	0.003	0.070	0.017	0.185
12	0.24	0.04	0.96	0.003	0.067	0.016	0.194
13	0.24	0.04	0.96	0.003	0.065	0.016	0.202
14	0.24	0.04	0.96	0.002	0.062	0.015	0.209
15	0.24	0.04	0.96	0.060	0.060	0.014	0.215
						0.266 $= R_0$, net reproductive rate	2.083

[a]Estimate of r, observed instantaneous rate of change:

$$r \approx \frac{\Sigma(l_xm_x)\ \ln[\Sigma(l_xm_x)]}{\Sigma(xl_xm_x)} = -0.17$$

Estimate of lambda, finite rate of change:

$$\text{lambda} \approx \exp(r) = \exp(-0.17) = 0.84$$

Home range size. Home range sizes of adult spotted owls in Washington and Oregon have been studied by using radio telemetry (Table 5). Home ranges of individual birds average 5,178 acres (2,096 ha) and composite home ranges of pairs average 6,733 acres (2,725 ha). The area of suitable habitat (mature or old-growth conifer forest) within annual pair home ranges averages 3,456 acres (1,399 ha) and ranges from 1,008–5,959 acres (408–2,412 ha). It has been assumed that these estimates of areas of suitable habitat represent what the birds prefer and require, although some biologists have challenged this assumption.

Viability Analysis

The analysis of viability of spotted owl populations encompassed Washington, Oregon, northwestern California and the Sierra Nevadas. Populations of spotted owls throughout the planning area were delineated by physiographic province (Table 6). The process involved four main steps (Table 7).

Step 1: Estimate the amount and distribution of habitat. An inventory was collected on the current amount and distribution of suitable spotted owl habitat on all lands. This took the form of map overlays outlining suitable habitats on national forest lands and total acreage summaries from other land bases by physiographic province. Suitable spotted owl habitat was defined based on literature descriptions. We used a linear programming model (FORPLAN) of timber harvest and stand growth rates to estimate the amount of suitable habitat on national forest land that would occur in future years under each planning alternative. We also assumed that habitat in reserved land, such as USDA Forest Service wildernesses, Research Natural Areas and National Parks, is in a more-or-less dynamic equilibrium, although no specific data were available on rates of catastrophic loss and regrowth.

Step 2. Estimate capability to support breeding pairs. We gauged the capability of habitat to support breeding pairs under each alternative by a process that accounted for (i) current and future fragmentation of habitat, (ii) the probability of a spotted owl pair occupying a site of given area of suitable habitat, and (iii) isolation of populations. First, we developed an index of habitat fragmentation by measuring from maps the spatial dispersion of suitable habitat on national forest land. Areas of

Table 5. Home range sizes and amount of suitable habitat within home ranges of spotted owls in Washington and Oregon.

State	Mean annual home range (ac)	Mean suitable habitat within annual home range (ac)	Source
Washington	7,268 (N=4)	4,203 (N=3)	Allen and Brewer (1986), Brewer (1985)
Oregon	6,020 (N=3)	2,709 (N=3)	Forsman et al. (1984), Forsman and Meslow (1985)
Overall mean	6,733	3,456	

Table 6. Populations of spotted owls in the Pacific Northwest considered in the viability analysis.

Physiographic province[a]	Population[b]					
	1	2	3	4	5	6
Olympic Peninsula	x					x
Washington Cascades		x				x
Oregon Cascades			x	x		x
Klamath Mountains[c]			x	x		x
Oregon Coast Range			x		x	x
Sierra Nevadas						x

[a]After Franklin and Dyrness (1973).
[b]Populations 1–3 assume that the Puget Trough (Washington), Columbia River Gorge (separating Washington and Oregon), and the junction zone of the northern race (*Strix occidentalis caurina*) and the California race (*S. o. occidentalis*) in northern California are barriers to dispersal. Populations 4 and 5 additionally assume that the Willamette Valley (Oregon) will act as a dispersal barrier after 15 years under planning alternatives that designate little spotted owl habitat. Population 6 assumes no dispersal barriers throughout the range from southern Sierra Nevadas to northern Washington. It is unclear which, if any, of the physiographic barriers may be inhibiting dispersal.
[c]Klamath Mountains physiographic province includes southwestern Oregon and northwestern California.

suitable habitat were counted as usable by spotted owls only if the habitat occurred in at least 300 acres (121 ha) within sample circles representing potential home range areas of spotted owl pairs. Because of fragmentation effects, the fraction of suitable habitat that would be usable by spotted owl pairs ranged from 85–100 percent, depending on national forest and time period.

Second, the probability of a spotted owl pair occupying a site of given area of suitable habitat, $P(O|S)$ was gauged by measuring the area of suitable habitat at random and at known occupied sites. These data were used in the following Bayesian formula:

$$P(O|S) = \frac{P(S|O)\ P(O)}{P(S)} \qquad \text{(Eq. 1)}$$

where $P(S|O)$ is the conditional probability of a site having a particular amount (acreage) of suitable habitat, given that it is known to be occupied by breeding pairs of spotted owls, $P(O)$ is the unconditional probability that any randomly chosen habitat area would be occupied by a breeding pair of spotted owls, and $P(S)$ is the

Table 7. Outline of the procedure for assessing viability of spotted owl populations.

1. Estimate the current and future amount and distribution of spotted owl habitat.
2. Estimate the capability of habitat to support spotted owl pairs.
3. Investigate the probability of local or global extinction from the following factors:
   a. effects of random birth and death rates;
   b. effects of inbreeding;
   c. effects of environmental catastrophes; and
   d. effects of interspecific interactions, mainly competition and predation.
4. Estimate the overall probability of continued existence to specified times in the future.

unconditional probability that any randomly chosen habitat area would have S amount of suitable habitat within a spotted owl annual pair home range area. The result of applying the formula was an area suitability index that suggested that the capability of sites to support a pair of spotted owls with a given area of suitable habitat is lower in the physiographic provinces in Washington than such areas in Oregon.

Third, the total amounts of current and future suitable habitat estimated in Step 1 were corrected for fragmentation and for probability of use as a function of area of suitable habitat (Eq. 1). This resulted in an estimate of habitat capability expressed as the potential number of spotted owl pairs. Such an estimate should not be confused with and is likely to be weaker than an actual population census and empirical information on population trends. Unfortunately, no such censuses or empirical studies of population trend had been conducted on spotted owls.

Finally, in estimating capability to support spotted owl pairs, we considered the degree to which populations may be isolated among physiographic provinces. We inferred population isolation by comparing the distances among suitable habitats to dispersal distances of juvenile spotted owls, and by considering the type of land between population areas. For purposes of analysis, we assumed: that the Olympic Peninsula population was isolated; that the Columbia River Gorge may be a barrier to dispersal, thereby separating the populations in the Washington and Oregon Cascades; that, under some future conditions, the Oregon Coast Range population may be isolated; and that the population in the Klamath Mountains may be isolated from that in the Sierra Nevadas. We also estimated overall capability and analyzed viability for all physiographic provinces combined, which assumed that there are no dispersal barriers throughout the planning area.

Step 3. Assess risks to continued existence. The next step was to analyze the risks to continued existence under each alternative for each population and time period.

A. *Effects of random birth and death rates.* Demographic risk to continued existence is a measure of the likelihood that a population would not be able to endure periods of low birth rates and high death rates and would not be well-distributed at specified points in time. Shaffer (1983) and Knight and Eberhardt (1985) used life tables to model demographic risk of grizzly bear (*Ursus arctos horribilis*) populations. Likewise, we used a time-dynamic, stochastic Leslie matrix life table to determine demographic risks. We used empirically derived average values of demographic parameters (reviewed above) to assess general population trends. Standard deviations of fledging rates and predispersal mortality rates of juveniles were used to model variations in birth and death rates, that is, the stochastic component of demographic effects.

We defined a well-distributed population as one whose density is greater than a theoretical density of breeding pairs being distributed at the median dispersal distance of juvenile spotted owls. The proportion of life table runs in which population sizes fell to or below these densities was the measure of demographic risk, i.e., the probability that a population of the beginning size would not continue to exist at well-distributed densities.

Results of the demographic modeling suggested that the likelihood of a population maintaining itself at well-distributed densities decreased over time. Also, small isolated populations (e.g., the Olympic Peninsula population) incurred a higher risk than large, widely distributed populations (e.g., the Oregon Cascades and Klamath

Mountains populations). Specific likelihoods of risk were estimated for each expected population size.

B. *Effects of inbreeding*. A second risk to continued existence is loss of genetic heterogeneity through inbreeding. At high rates of inbreeding, natural selection is unable to offset the fixation of deleterious recessive alleles in the population. The result is that the population suffers depressed reproductive success and may not be able to maintain itself. We estimated the probability of populations incurring excessive loss of genetic heterogeneity by using the formula for estimating the degree of inbreeding, as shown in Hartl (1980) and presented by Salwasser et al. (1984). The calculation accounted for the effective population size (number of interbreeding animals effectively contributing genetic material to successive generations) and the number of generations over which inbreeding would occur. We calculated inbreeding effects for each spotted owl population.

When the degree of inbreeding was less than 0.20, we gauged the probability of continued existence as high or very high; when the degree of inbreeding was greater than 0.35 the probability of continued existence was low to very low. Results suggested that few populations were small enough and would be isolated long enough (out to 150 years in our assessments) to incur serious problems from inbreeding. In addition, results suggested that populations would be more likely to incur risks to continued existence from demographic effects (random birth and death rates) than from genetic (inbreeding) effects.

C. *Effects of environmental catastrophes*. Another factor that may influence continued existence of a population is the occurrence of environmental catastrophes, such as fire, storms, insects, disease and volcanoes. Ideally, assessing the probability of habitat loss and population reduction or extinction resulting from these factors would entail applying field data on location, frequency and area affected by catastrophes. Unfortunately, such data were unavailable or nonexistent. Thus, we had to treat the effects of catastrophes in an *ad hoc* fashion, such as by assuming that small and isolated habitat areas may incur a greater risk to windthrow than would larger and less-isolated habitats.

D. *Effects of interspecific interactions*. A final component in assessing risks to continued existence is interspecific interactions, especially competition and predation. Specifically, spotted owls seem susceptible to competitive exclusion of habitats by barred owls (*Strix varia*), which have been expanding into the northern range of the spotted owl (Hamer et al. 1987). Spotted owls are also preyed on by great horned owls (*Bubo virginiana*) and goshawk (*Accipiter gentilis*) (Forsman 1980). Barred owls and great horned owls seem to respond favorably to cutover or fragmented landscapes, such as would be produced under intensive forest management suggested by most of the planning alternatives. Ideally, the effects on viability of spotted owls would best be predicted by using data on the distribution, habitat use and rate of spread of these three other species. Unfortunately, as with environmental catastrophes, except for anecdotal reports, such data were nonexistent. We considered the possible effects of both catastrophes and interspecific interactions subjectively in the next step of the process.

Step 4. Estimate the overall probability of continued existence. Four main risk factors assessed in Steps 2 and 3 were then combined into a rank order scale (Table 8). The risk factors focused on abundance and distribution. Abundance of spotted owls

Table 8. Factors used to assess probability of continued existence of spotted owl populations.

Probability of continued existence of a well-distributed population	Demographic and genetic effect		Habitat	
	Demographic effect (Prob. of N > min)[a]	Genetic effect (Inbreeding coefficient)	Size (area suitability index value)[b]	Distribution (nearest-neighbor distance, mi)[c]
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]Proportion of stochastic Leslie matrix life table runs using fluctuating reproductive and juvenile survival rates that remained above a population size representing a well-distributed population. Well-distributed population sizes were defined for each population modeled as the theoretical density that would result from a distribution of breeding pairs no further apart than the median dispersal distance of juvenile spotted owls (23 miles: 37 km).
[b]Probability that a designated spotted owl habitat area of given amount of suitable habitat would actually support a breeding pair. See text for description.
[c]Habitat distribution as compared with dispersal distances of juvenile spotted owls.

determined the degree to which demographic and genetic factors may put a population at risk. Distribution of spotted owls and spotted owl habitat determined the spacing between habitat areas and the probability of sites being occupied by pairs based on the amount of available suitable habitat.

Discussion

Viability as Risk

The rank order scale expressed the overall probability of continued existence of each population under each planning alternative to future points in time, and ranged from very high to very low. In this way, the results were expressed in the form of a risk analysis. Importantly, no single population size was denoted as a "minimum viable population"; rather, viability was expressed in terms of the probability that a well-distributed population was likely to persist up to a particular year. In this risk framework, it then became the onus of the decision maker to select (and explain) a minimally acceptable probability level and duration of time by weighing biological, social, political and economic factors, as well as implications of scientific uncertainty under each alternative.

The assessment of risk to population viability has come a long way since the seminal paper on the topic by Salwasser et al. (1984). Their framework considered principally genetic risk, which, at that time, was thought to be the primary factor that may imperil a vertebrate population. Theoretical and practical work since then has shifted focus to demographic risk and, as with this study, to a complex of intrinsic and extrinsic factors.

Viability and Other Species

An assessment of population viability as thorough as that conducted for the spotted owl has been pursued on only a few species, including the grizzly bear in Yellowstone

National Park (Shaffer 1983, Knight and Eberhardt 1984), red-cockaded woodpeckers (*Picoides borealis*) in the southeastern United States (Ligon et al. 1986) and the Mount Graham red squirrel (*Tamiasciurus hudsonicus grahamensis*) in Arizona (R. Wadley, personal communication). Pettersson's (1985) assessment of the extinction of the middle spotted woodpecker (*Dendrocopos medius*) in Sweden also considered factors similar to those we explored. As there are yet no standards for assessing population viability, each of these studies focused on a different set of factors that may influence population viability.

However, all authors seemed to agree that factors affecting viability do not occur as deterministic, independent and isolated causes. Rather, factors are often compounding. For example, habitat fragmentation may serve to isolate populations, which may make them more susceptible to inbreeding depression. This, in turn, may decrease overall reproductive rates and fitness, and increase susceptibility to poor environmental conditions, resulting in local extinctions from low juvenile survival rates. Although some authors modeled effects of demographic and environmental variability, none quantified how these and other factors interplay. How such ingredients interact is poorly known, even in theory (although Gilpin and Soulé 1986 have attempted a recent integration). In our analysis of spotted owls, we likewise assessed the various extinction factors independently from one another for two reasons: there was no available, accepted theoretical construct by which we could quantify interaction among the various factors; and we distrusted an assessment of viability based on what would be only a single and complex simulation model.

Other Assessments of Spotted Owl Viability

Since we began the viability assessment, two other scientific appraisals of spotted owl viability have appeared. The first was by Lande (1985), who took a much simpler approach to assessing risk. Lande used a static, analytical model of how suitable habitat would be occupied by spotted owls, given its relative scarcity across the landscape. Lande's assessment portended that, in the future, suitable habitat would be highly fragmented and incur very low occupancy by spotted owls. Based on his model results, Lande called for widespread preservation of suitable habitat in the Pacific Northwest.

The second viability assessment was by an Audubon Advisory Panel (Dawson et al. 1986). The Panel used a case study approach by appraising population sizes and life history characteristics of other avian species that have gone extinct, such as the heath hen (*Tympanuchus cupido cupido*), or are now moribund, such as the red-cockaded woodpecker. By inspecting other species, the Panel recommended that no less than 1,500 pairs of spotted owls be maintained throughout Washington, Oregon and California (in the north Coast Range and the Sierra Nevadas).

The merits to these two approaches—static analysis and case study—are that they were relatively simple and required only a modest investment of time and effort. They did not attempt to differentiate quantitatively among various factors that may cause a population to be in peril. As with our study, both approaches used a fair dose of professional judgment, although neither established explicit guidelines for considering how and when a population was determined to be at risk. Still, there is much to be said for using subjective assessments and professional judgments for evaluating population viability, as the basic quantitative tools are still being hewn.

While these assessments used widely differing approaches, their similarities are significant and should be noted. All three assessments concluded that spotted owl numbers are low enough to cause concern, and that risk to the population is increasing over time. They also agreed that the most serious immediate risk to the population is demographic rather than genetic. Demographic risks include both the risk created by variations in birth and death rates and risk associated with failures to recolonize habitat patches over time. The Audubon Panel study and our analysis identified demographic stochasticity as producing the most immediate threat, while the Lande study concentrated on failure to occupy habitat. In fact, these risks are strongly interrelated. Finally, despite some differences in details, all three studies concluded that maintenance of the owl population will require the establishment of a well-distributed landscape of habitat areas.

The value of our analysis must ultimately be judged against the following three criteria: (1) biological value—the light it shed on the current and likely future condition of spotted owl populations; (2) management value—the identification of the most sensitive areas for population monitoring and research; and (3) legal value—the foundation provided for agency decision making in a situation where legal challenges are likely. Judged against criterion 1, our assessment has done an adequate job. However, projections of population viability will always be theoretical, and our assessment has no stronger claim on the truth than do the Audubon Panel or Lande assessments. Judged against criterion 2, our assessment was relatively successful in identifying the most sensitive gaps in our knowledge of the spotted owl's status and life history. Further, our research recommendations differed only slightly from those of the Audubon Panel's report, so we must conclude that both approaches provided valuable information on research and monitoring needs. Finally, judged against the third criterion, our assessment provided a well-structured and well-documented basis for management decisions that must be made by USDA Forest Service. Where professional judgment was used in the analysis, it was always placed in the context of well-documented model assumptions and ranking systems. A major difference between the agency context of our effort and the organizational and academic contexts of the Audubon Panel and Lande assessments is that we were legally required to document all phases of the viability analysis, including those using objective, subjective and professional judgments. Such documentation made the analysis very accessible for criticism. We believe that this accessibility will also help judge whether we made reasonable interpretations of the information available on spotted owls.

In addition to these technical assessments of spotted owl viability, a number of academicians, public resource agencies and biologists critiqued the draft management plan (environmental impact statement) in which our viability analysis appeared. Some of the comments defined acceptable levels of population viability, generally being an assurance of at least a high probability of continued existence out to 100 or 150 years in the future. To our knowledge, this is the first time that population viability has been expressed in terms of risk and specific probabilities of continued existence, in which public response explicitly defined what was acceptable in terms of levels of risk and time periods over which that risk should be considered.

Questions Raised

Finally, because of the explicit manner in which viability risks were addressed in this study, several as-yet-unanswered questions have arisen. These may direct future development of viability assessments.

What is a reasonable planning horizon for considering viability? We assessed potential effects out to 150 years and considered even longer-term effects. However, the habitat planning alternatives would be instituted only for some 10–15 years before a reevaluation may occur.

Should there be a blanket decision on the acceptable level of certainty of continued existence of all vertebrate species on public lands, or should acceptable levels be determined on a case-by-case basis by weighing resource trade-offs under each circumstance? As similar viability issues are raised with other species, this issue will likely emerge.

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