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MANAGEMENT OF THE SPOTTED OWL: A Case History in Conservation Biology

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ABSTRACT

Official conservation efforts for the northern spotted owl began in the United States in 1975 when it was declared "threatened" in the state of Oregon; efforts continued in a sporadic and unsystematic way through the 1980s. In 1989 the Interagency Scientific Committee (ISC) was established by Congress and charged with the development of a scientifically defensible conservation strategy covering the entire range of the northern spotted owl, which includes parts of the states of Oregon, Washington, and California. The ISC collated all spotted owl research and approached questions concerning the need for a conservation strategy and the efficacy of potential reserve designs as testable hypotheses. Because the hypothesis tests were based on incomplete data and highly stylized population models, uncertainty concerning the conclusions of the ISC remained. Subsequent research focused on answering those uncertainties, and here we revisit the ISC's conclusions, asking which if any of them have been invalidated. The ISC's major conclusions have remained robust: The population of spotted owls is declining due to reductions in old growth habitat. Subsequent trend-analyses confirmed the levels of population decline calculated by the ISC and in addition concluded that the rate of decline was accelerating. The ISC's response to these conclusions was to recommend the establishment of an extensive network of large reserves. Subsequent research and more detailed computer modeling have confirmed the conceptual validity of this conservation plan but suggest that optimistic assumptions led the ISC to propose a minimal reserve structure. Current federal management plans in the Pacific Northwest propose more habitat than the ISC envisioned, providing a greater likelihood of persistence.

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INTRODUCTION

The conservation saga of the northern spotted owl ***(Strix occidentalis caurina)*** is long and controversial (63, 85). Even today, despite the subspecies' listing as threatened under the Endangered Species Act (ESA), controversy continues, and some observers continue to assert that the owl's population is not in jeopardy, (e.g. 17). Numerous field studies indicate that the fate of the northern spotted owl is inextricably linked to the fate of large, old (> 150 years) trees. By 1950 almost all old forest on private lands in western Washington and Oregon and northwestern California had been harvested. The remaining 10-15% of the original old forest was found almost exclusively on public lands administered by the Forest Service (FS) and Bureau of Land Management (BLM). After World War II, old forests on these lands began to be cut at the rate of 28,000-40,000 ha per year (85). Given the combined effects of forest fragmentation and habitat loss, listing the subspecies under the ESA was inevitable.

The vulnerability of the owl to continuing habitat loss was officially noted as early as 1975 when the state of Oregon designated the subspecies as "threatened." Thereafter, a series of public responses chronicled an increasing concern for its fate: In 1981 the Fish and Wildlife Service (FWS) recognized the threats to the owl but concluded that the subspecies did not yet warrant listing under the ESA (92). In 1983 the Forest Service (FS) designated the owl an "indicator species" of the integrity of old-growth forest ecosystems in the Pacific Northwest (PNW) (88), and in 1984 special management action was proposed in Oregon (habitat was protected around 375 owl pairs). In 1985 a team of scientists designated by the National Audubon Society concluded that the subspecies was headed toward listing and that immediate management intervention was justified (23). In 1987 the FWS conducted a second status review but again concluded that listing was not warranted. This decision was appealed, and the Federal District Court ruled that the decision not to list was "arbitrary and capricious," triggering the initiation of a third status review. In 1988 the FS adopted a special management plan for the owl but acknowledged that the species had a "poor" long-term chance of success. The plan was appealed by environmental groups, on the basis of failure to comply with existing environmental laws, and by the timber industry claiming unjustified economic hardship.

Against this increasingly hostile and polarized background, in 1989 Congress intervened and proposed an interim solution. By attaching a rider to the 1990 Interior Appropriations Bill (Section 318), Congress specified additional protection for the northern spotted owl, established a harvest-level acceptable to the timber industry, and exempted federal agencies (FS and BLM) from legal appeals. (Timber sales contracted under the Section 318 provision are still being disputed in 1996 as a consequence of the Recission Bill signed by

President Clinton.) A key provision of Section 318 was the establishment of an Interagency Scientific Committee (ISC) charged with the development of a long-term conservation strategy for the northern spotted owl on public lands. Jack Ward Thomas was selected as leader of that committee.

The ISC delivered its report to four agency heads (FS, BLM, National Park Service, and FWS) and Congress in April, 1990 (84). The conservation strategy called for the designation of approximately 2.4 million ha of federal lands, in addition to suitable habitat already in wilderness areas and national parks, to be arranged in a network of habitat conservation areas (HCAs), widely distributed throughout the range of the northern spotted owl.

Individuals active in the domains of economics, public policy, and politics were unnerved by the magnitude of the proposed conservation "solution." Ultimately, however, the most significant impact of the northern spotted owl conservation plan has been the increased scope of planning efforts for management of FS and BLM lands in the Pacific Northwest. The original focus on conservation of the northern spotted owl has expanded markedly to include viability concerns of other species, including aquatic organisms, invertebrates, plants (86), and indeed, the maintenance of the entire forest ecosystem (90). This most ambitious effort began in April 1993, when President Clinton established the Forest Ecosystem Management Assessment Team (FEMAT) to develop management options for Pacific Northwest forests within the range of the northern spotted owl. Despite a much broader focus, conservation planning for the northern spotted owl remains central to these additional planning efforts.

Since 1990, research on the northern spotted owl has continued and, in some cases, accelerated. The new information has increased our understanding of the ecology and life history of the owl, including new insights into its demography, distribution, habitat relations, behavior, and associations with prey. Significant advances have also taken place in conservation biology in general, and specifically in the principles of reserve design and the dynamics of spatially structured populations in the context of real landscapes (29, 54, 65, 66).

In this review, we do not attempt to discuss all facets of northern spotted owl biology and the challenge to conserve this subspecies. First, comprehensive reviews of new sources of information on northern spotted owl biology have recently been published (37, 86). Second, the scope of the conservation issue, in terms of its many economic, social, and legal ramifications is simply too broad. Instead we focus on the scientific foundation of the recommendations of the ISC and subsequent conservation strategies. We review the methods, data, and logic brought to bear to find a scientifically credible solution to the challenge of northern spotted owl conservation. Our approach is to revisit three fundamental hypotheses tested by the ISC (58, 84) and to re-evaluate the decisions based on those hypotheses in the context of more recent information and continuing advances in our understandings of the dynamics of wild populations. Similarly, we revisit the five basic principles of reserve design invoked by the ISC (58, 84, 97) and reassess their relevance to current understandings of conservation planning and reserve design.

FUNDAMENTAL HYPOTHESES TESTED BY THE ISC

To develop a scientifically credible conservation strategy, the ISC used the hypothetico-deductive methods of hypothesis testing (57, 58, 74, 75). Three hypotheses are generally applicable to species whose populations are threatened by the loss and fragmentation of their habitat. These hypotheses, framed in the context of the northern spotted owl conservation plan, were:

1. H_0: The finite rate of change ($\lambda \propto N_{t+1}/N_t$) of the northern spotted owl population is ≥ 1.0.
2. H_0: Northern spotted owls do not differentiate among habitats on the basis of forest age, structure, or composition.
3. H_0: No decline has occurred in the areal extent of habitat types selected by northern spotted owls for foraging, roosting, or nesting.

Null Hypothesis 1: Declining Populations

Estimates of λ are based on the eigenanalysis of stage projection matrices (22), parameterized from extensive field studies using capture-recapture and other standardized methods (35). The first null hypothesis was originally rejected based on the observation that λ was significantly less than 1.0 at two long-term demographic study sites (84). More rigorous tests of this hypothesis are now possible, based on data from several additional study sites widely spaced across the owl's range, and additional years of data from the original sites (32). A recent reanalysis of the demographic data from 11 study sites resulted in the overwhelming rejection of this hypothesis (16). Current estimates of λ, adjusted for bias (see below), indicate that populations of resident, territorial females have declined at an estimated rate of 4.5% per year from 1985 through 1993. Currently, only one study area reports a λ-estimate that suggests a stable population (41).

Greater availability of banding data and advances in the methods of analysis (e.g. 14, 48) have allowed more insight into a possible time dependency in the survival rates. Importantly, adult females show a significant, negative time-trend in annual survival rate over the period 1985–1993 (15), the parameter that most influences the value of λ (47, 60). Thus, as the USFWS Recovery Team

(93) and Burnham et al (15, 16) concluded, the rate of population decline has probably accelerated since the ISC's original analyses.

Based on statistical criteria and data availability, the analysis of Burnham et al (15, 16) was more rigorous than that by the ISC; Burnham et al used more study sites, years, capture histories, and sophisticated modeling techniques. Recently, however, concerns have been raised that these analyses may be based on negatively biased parameter estimates that lead to underestimates of λ (7). As discussed below, parameter estimates were adjusted for bias (15, 16), but Bart (7) argues that additional biases exist, increasing the likelihood of type I errors when testing hypothesis 1.

BIASES IN THE ESTIMATES OF λ Reliable estimates of rates of population change (h) require accurate and precise estimates of the age- or stage-specific birth and death rates (22). It is important, therefore, to examine thoroughly possible sources of bias in the parameter estimates and to adjust for those biases whenever possible. For the northern spotted owl, concern over possible biased estimates has focused on birth and first-year survival rates.

Bias *in the estimation of birth rate (b)* *The* two possible sources of bias in the estimation of *b,* one positive and one negative, both arise from limitations in sampling efficiency. If breeding pairs are more readily detected than nonbreeding pairs, they would be overrepresented in the sample, introducing a positive bias to *b.* On the other hand, death of some newborns prior to detection would lead to an underestimate of productivity and a negative bias in *b*. The consensus among owl biologists is that these sources of bias are minimal, and no bias-adjustment has been developed.

Bias in the estimation of juvenile survival rate (s_0) Owl biologists have been most concerned about a negative bias in the estimation of s_0. Bias may arise because juvenile birds emigrate from the study area, survive at least one year, and are never reobserved. The consequence is that λ is underestimated. To adjust for this source of bias, an estimate of juvenile emigration rate (E) is needed. Assuming that emigrating juveniles survive at the same rate as nonemigrants, data derived from the radio-tracking of juvenile owls allowed Burnham et al (15, 16) to estimate E and adjust the Jolly-Seber (40, 80) estimate of s_0. The upward adjustment of s_0 increased the estimate of λ, but the null hypothesis of a stable or growing population was still consistently rejected *(16).*

Limits to inference from estimates of λ Estimates of λ pertain to rates of change over the period of study only for the population of territorial owls, not the floaters (see 7 for a counter opinion). Moreover, it is indefensible to use these estimates to compute past population sizes or future trends. To do so, one must assume constant birth and death rates, an untenable assumption for northern spotted owls (16). For example, fecundity varies annually, possibly because of winter/early spring weather patterns (99).

Additional variation in the parameters can arise due to sampling errors. Sampling variation arises from the fact that relatively few individuals in a population produce most of the offspring (34, 94), a pattern observed in virtually all extensive studies of lifetime reproductive success among birds (59). An additional limitation may arise as an artifact of sampling. When λ is estimated from a heterogeneous population consisting of a mixture of source and sink territories (64), inferences about population trend are uncertain. The overall A-estimate from a heterogeneous population is a weighted average-with weights determined by the abundance of the two types of territories in the sample. Weighted A-estimates < 1 .O could arise even though the population as a whole were stable or growing.

Given these understandings, estimates of persistence likelihood for a population based on a heterogeneous sample must incorporate other relevant factors-for example, the smallest source population needed for local stability. Source populations are determined by the constraints of demographic and environmental stochasticity and the spatial distribution of breeding pairs (e.g. 45). For more global considerations, overall persistence of a metapopulation is determined by the number and spatial distribution of locally stable source populations. Rare, catastrophic events require that local populations be widely dispersed so that adverse effects are not experienced simultaneously by all local populations (24).

Vigorous debate over the shortcomings of demographic studies (70), complexities of the sampling process, limitations of the capture/recapture models (e.g. 48), and difficulties in the direct interpretation of h-estimates (7) have led to more cautious interpretations of rates of population change. Despite these cautions, however, the weight of evidence still leads to a rejection of hypothesis 1 (16,32).

Null Hypothesis 2: Habitat Specialization

All studies of northern spotted owl habitat use reviewed by the ISC led to rejection of the second null hypothesis and concluded that owls select old forests, or younger forests that have retained characteristics of old forests (84). An apparent exception occurred in the coastal redwood forests of northern California, where owls were also found in younger stands (30, 81). At an early age, redwood forests (representing < 7% of the owl's range) exhibit stand characteristics similar to those of old-growth forests elsewhere. However, even in these forests, owls nest in stands with a residual, large-diameter, old tree component (30). Owls may persist in these highly managed landscapes because of abundant prey, such as dusky-footed woodrats, which thrive in early seral habitats (18, 78, 84).

Studies published since Thomas et al (84) have provided additional falsification of hypothesis 2 (i.e. 5, 9, 12, 18, 20, 39, 49, 69, 83). Most studies of habitat selection relating to tests of hypothesis 2 have recently been reviewed (4, 86).

The accumulated knowledge from habitat studies allows a discussion of habitat use and the validity of hypothesis 2 at several spatial scales, including within and among forest stands, and home range and landscape scales. In the Oregon Coast Range (19), the Klamath Province in California (83), and the eastern slopes of the Washington Cascades (12), further study has confirmed selection for conifer-dominated stands characterized by large, old-tree components and closed canopies. However, patterns can vary geographically, with selection for old-growth forest at the stand level more pronounced west of the Cascade Mountain crest (43) than to the east (13). A stronger geographic contrast in habitat use occurs in northwestern California and southwestern Oregon where selected nest sites often had a well-developed hardwood understory (9, 42, 73, 83), a vegetation type absent from sites used elsewhere in the owl's range. Nest tree selection and nest substrate, however, showed even greater geographic variability- in the eastern Washington Cascades (12) nests were in clumps of mistletoe ***(Arceuthobium douglassi),*** and nest trees were generally smaller and younger than in Oregon (31) and California (43), where nests were in stick platforms or side cavities in large trees.

Most habitat-use information is provided by studies in which the owls are fitted with radio transmitters. The study by Blakesley et al (9), based on a sample from a contiguously distributed, local population in northwestern California, is an exception. Site selection within this local geographic distribution was significantly nonrandom, with daytime use concentrated in mature and old-growth forest. The selection of stands with old-growth components was most pronounced for nest sites.

At a landscape scale, the most extensive work is Carey et al (20). Based on data collected from owls fitted with transmitters in southwestern Oregon and the Olympic Peninsula, Carey et al (20) found significant landscape-level effects on home-range size and overlap, adult behavior, and the age composition of breeding pairs. Specifically, home-range size and overlap increased significantly in heavily fragmented landscapes, an effect that was more pronounced in mixed-conifer than in Douglas-fir forest. In general, twice as much old-growth forest was included within pair home ranges in landscapes dominated by Douglas-fir than in landscapes dominated by mixed-conifer forest. Particularly relevant to hypothesis 2, Carey et al (20) found selection for old forest to be significant at three spatial scales- landscape, annual home range of pairs, and foraging and roosting site selection by individuals within home ranges.

A number of studies have investigated habitat selection at multiple spatial scales (42, 49, 56, 72, 73). The general conclusion from these studies is that northern spotted owls select nest and roost sites in mature and old growth forest in areas that are less fragmented than the surrounding landscape. The spatial scale of selection around nest and roost sites (territory size) varies geographically from approximately 450 ha in northwestern California (42) to > 1800 ha in Oregon (73) and >3200 ha in Washington (49).

In summary, northern spotted owls show extensive geographic variation in patterns of habitat use, but consistent associations between owl nesting and roosting locations and old-growth forest components have been found in all studies throughout the range of the owl. The weight of evidence, therefore, leads to a rejection of hypothesis 2 from a local to landscape scale. In general, the removal of old forest and its components results in reduced owl habitat.

CURRENT UNDERSTANDING OF HABITAT SELECTION Recent habitat studies have been less descriptive and more explanatory. Geographic variation in habitat use and area requirements has been most readily explained by variation in the abundance and composition of the prey base (18, 20, 98). For example, most studies continue to demonstrate strong selection of old forest stands by foraging owls; use of younger forests seems to be related to both the presence of hardwoods and the abundance of dusky-footed and bushy-tailed woodrats [***Neotoma fuscipes*** and ***N. cinera,*** respectively; (98), (20), (18)]. In northwestern California and southwestern Oregon, conifer-dominated forests below 1250 m often have hardwood understories, and dusky-footed wood rats are the major prey species (2, 31, 82, 95, 98). In contrast, at higher elevations, and throughout the rest of the owl's range, flying squirrels ***(Glaucomys sabrinus)*** are the primary prey (18, 20, 31, 84). Woodrats respond positively to forest harvest and fragmentation- they reach their highest densities in young, regenerating clear-cut with abundant brush (67, 68, 78, 84). Though most woodrats live in stands too dense for foraging owls (78), woodrats regularly move from these stands into adjacent old forest (79). Flying squirrels are generally found in their highest densities in mature and old-growth forest, and they decrease in density in logged areas (20, 96; but see 76).

Variation in home-range size also seems related to prey base. Home range size decreases with increased abundance of medium-sized prey (18), and with increased abundance of woodrats in the diet (98). In areas where flying squirrels are the primary prey, home-range size decreases as the amount of old forest within the home-range increases (19, 20).

Though the prey abundance hypothesis currently has the most support, other factors such as differences in stand structure and microclimate may contribute to the selection of old forest (77). For example, northern spotted owls have a narrow thermoneutral zone (36), and selection for older forests may facilitate thermoregulation (3).

Null Hypothesis 3: Habitat Trends

The rejection of hypothesis 2 led the ISC to test hypothesis 3. Based on data from National Forest lands in Oregon and Washington (which provide >70% of all remaining owl habitat), the ISC found significant declines since 1940 in the extent of owl habitat, a trend projected to be continued into the future (58). Additional evidence since the ISC Report provides data for California (53), and more regionally specific estimates of habitat loss are found in the draft Recovery Plan (93). Figure 1 (93) is indicative of the magnitude and uniformity of habitat loss throughout the range of the northern spotted owl.

The most recent estimates of rates of habitat loss were made as part of the FEMAT process (86). Analysis of logging records on public lands within the demography study areas found that owl habitat was declining at a rate of 0.9 to 1.5% per year on FS study areas and 1.3 to 3.1% per year in study areas managed by the BLM. Analyses of habitat loss on three study areas using LANDSAT imagery, including both public and private lands, was 1.1 to 5.4% per year (86). The highest rate of habitat loss was on BLM's Medford District, in Oregon, which also recorded the highest rate of decline in the owl population (16).

In general, the relationship between the amount of habitat and population trend is poorly understood. A specific test, at the landscape scale, of the

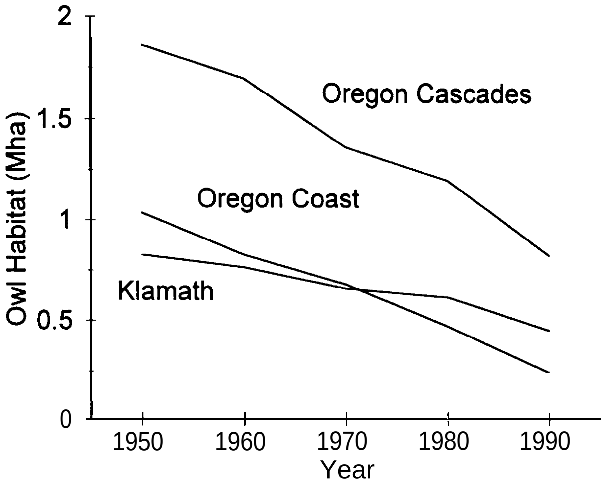


Figure 1 Trends in northern spotted owl habitat for three regions in the Pacific Northwest. Acreage trends include all ownerships. Data from Reference 93.

hypothesis that demography (survival, fecundity, and growth rate) was independent of the amount and pattern of habitat was not rejected (70). The absence of significant relationships is surprising given the extensive empirical evidence of selection for mature and old-growth forests. In the data used for this analysis (70), the amount of old forest surrounding pairs of owls was significantly greater than in the surrounding landscape for 10 of the 11 demographic studies (32). The most parsimonious explanation for the lack of pattern concerns spatial scale. Relationships between demography and habitat are more pronounced at the within-population scale with individual reproductive pairs the unit of analysis, rather than entire subpopulations (70). In support of this assertion, significant linear relationships between the proportion of suitable habitat within the home range and fecundity (5, 8, 73) and adult survival rate (5, 8) have been reported.

Conclusion

Based on studies reported since the ISC Report, decisions on the three null hypotheses remain the same. The observation that the resident, territorial population of northern spotted owls is in decline is most parsimoniously explained by the past and ongoing decline in the owl's habitat-mature and old-growth forest in the Pacific Northwest.

This downward trend in habitat is particularly relevant to territorial species with obligate juvenile dispersal, such as the spotted owl. Based on predictions from theoretical models, sharp thresholds to persistence are approached as habitat is lost and fragmented (44-46, 84). One extinction threshold arises directly from the loss of habitat: if the amount of suitable habitat is reduced to some small fraction of the landscape, the difficulty of an owl's finding a suitable territory leads to extinction (Figure 2). The second is due to an Allee effect (1)-if population numbers fall too low, the probability of finding a mate drops below the level required to maintain reproductive rates required for population stability.

THE RESERVE DESIGN PROCESS

Rejection of the three fundamental hypotheses justified management intervention to arrest the decline in the northern spotted owl population. Towards this goal, the ISC adopted a map-based planning approach that focused on the location, size, shape, spacing, and context of habitat patches planned for inclusion in a reserve system. The goal of this planning exercise was to propose a reserve design that would establish local, stable populations of owls, widely distributed throughout their historic range. Even though suitable habitat was projected to continue to decline outside of reserves for at least the next 50 years (89), habitat loss within reserves would stop and the process of renewal begin.

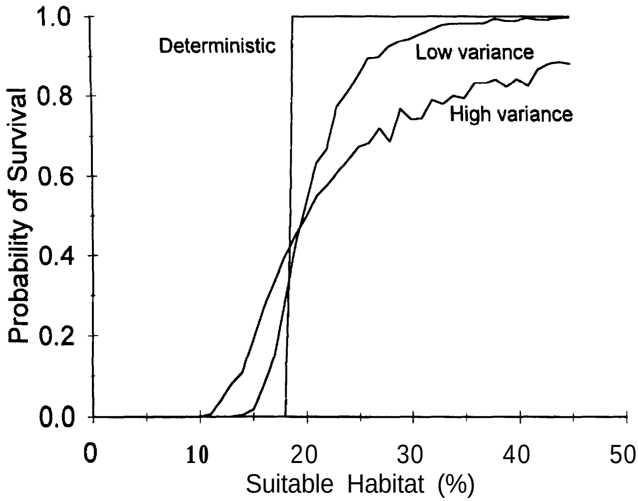


Figure 2 250 year survival probability as function of the proportion of the landscape suitable for nesting. Probability functions were generated using a stochastic model in which owls are forced to search the landscape in order to find both mates and suitable habitat (84, Appendix M; 44).

To provide scientific rigor, the reserve design was portrayed as a map with quantifiable properties that served as falsifiable hypotheses. That is, assertions of map properties were subject to testing with empirical data or theoretical predictions (58). The ISC used information from four map layers (current and historic northern spotted owl distributions; current and historic habitat distributions; known owl locations; land ownership) that, when overlaid, collectively provided the preliminary outline of a reserve system. The initial map represented the maximum size and number of habitat conservation areas (HCAs) available for planning purposes.

The distribution of HCAs was discontinuous (58, 84), suggesting that a feasible reserve design would result in a metapopulation-spatially distinct local populations "connected" by dispersal (38, 50, 51). In the Pacific Northwest, habitat discontinuities result from many factors including diverse topography and natural variation in vegetation structure and composition, and from clear-cut timber harvest and permanent land conversion reflecting patterns of private ownership.

Working within the constraints of available habitat and land ownership, the system of HCAs had to provide sufficient habitat to assure a balance between local extinction and recolonization events. The best biological solution for the northern spotted owl was to designate all potential HCAs as part of the reserve system. This solution was not, however, politically, socially, or economically acceptable (85). Therefore, a process was needed to select a subset that would meet the conservation objective. Towards that goal, the ISC tested map-generated hypotheses in the context of five widely accepted concepts of optimal reserve design.

MAJOR RESERVE DESIGN PRINCIPLES INVOKED

Drawing from the fields of population viability analysis (10) and island biogeography (52), the ISC constructed its strategy around five principles that, in various forms, are central to conservation biology (24-26, 97):

1. Species that are well distributed across their range are less prone to extinction than species confined to small portions of their range.
2. Large blocks of habitat supporting many individuals are more likely to sustain those populations than are small blocks of habitat with only a few individuals.
3. Habitat blocks in close proximity facilitate dispersal and recolonization and are preferable to widely dispersed blocks.
4. Contiguous, unfragmented blocks of habitat are superior to highly fragmented blocks of habitat.
5. Habitat between protected areas is more easily traversed by dispersing individuals the more closely it resembles suitable habitat.

Subsequent refinement of the conservation strategy was based on the results of map-based tests of these five principles stated as falsifiable hypotheses (58, 84). To the extent possible, hypothesis tests were direct, based on empirical data collected from studies of the northern spotted owl. When this was not possible, indirect tests were based on ecological theory, data from similar species, or the predictions of simulation models (84). In an iterative fashion, test results were used to reject or retain various map-based elements of alternative reserve designs (58).

One area of scientific uncertainty relevant to reserve design for the northern spotted owl was the minimum size and spacing of HCAs for local population stability. Only general design rules were available from the conservation literature and existing biogeographic principles were too broad for specific application to the northern spotted owl problem. To refine the design rules, fundamental aspects of spatial structure and discontinuous habitat were incorporated into simple simulation models. These models extended the work of Lande (46) and further investigated the effects of habitat loss and fragmentation on territorial species. Based on information from field studies, these models were structured and parameterized specifically in terms of northern spotted owl life history. Using occupancy rate of home range-sized units of suitable habitat as the dependent variable, model simulations investigated the effects of reducing habitat amount and fragmentation, and the benefits of clustering habitat into blocks (HCAs) of various sizes (28, 44, 45, 84).

THE ROLE OF COMPUTER MODELS IN THE CONSERVATION STRATEGY

These initial models became the focus of considerable debate, both in Congressional hearings and in legal challenges to the ISC Report (63, 85). By changing model assumptions or parameter estimates, it was possible to suggest, for example, that the proposed reserve design was inadequate for the owl's persistence, or that the strategy set aside more habitat than was needed. These arguments, however, overly stressed the role of the models and downplayed the fundamental role of owl biology. For the most part, the ISC reserve design (HCA size, spacing, and number) was a logical consequence of the basic biology and life history of the northern spotted owl. The simple combination, for example, of home-range area requirements, habitat use patterns, and minimum population sizes for persistence (7 1) required the designation of large acreages of suitable habitat (mature and old-growth forests) dispersed throughout the owl's range.

A general finding was that arranging suitable habitat into large blocks asymptotically increased the mean occupancy rate of suitable sites (21, 28, 45; Figure 3). Higher levels of pair occupancy, in turn, translated into an increased likelihood of persistence. ISC model results were based on four critical assumptions that could not be directly tested: 35% of the forested landscape was within HCAs; on average, 60% of the area with an HCA would be suitable habitat in the future; each HCA was "connected" to adjacent HCAs by way of dispersal; and females had no problem in finding mates. Given these assumptions, model results suggested a minimum HCA size sufficient to provide 20 pair sites (territories/HCA) spaced not more than 19 km apart sufficed to provide for stable populations (Figure 3; 44, 45, 61, 84). Importantly, given a target equilibrium population size, arranging suitable habitat into blocks required less total area to be set aside than if habitat were randomly arranged as single-pair sites (45).

In summary, the ISC's conservation strategy, portrayed as a map, was described by the number, size, and distribution of its HCAs, and prescribed minimum habitat criteria between HCAs. In retrospect, it is clear that these rules were generated based on optimistic assumptions. Depensatory density-

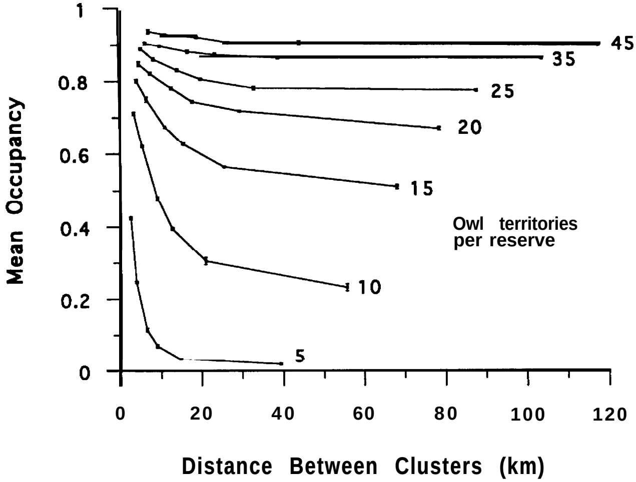


Figure **3** Average proportion of sites occupied by reproductive pairs as a function of reserve spacing and size. Occupancy levels were generated using a stochastic model which simulated habitat search within and between reserves (45, 61, 84).

dependent effects due to difficulties in finding mates at low densities (1, 22) and environmental stochasticity were not modeled. Reserve shape and spacing were also optimal, and potential losses from source populations in the reserves to the exterior sink areas were probably underestimated. In addition, the habitat in many of the proposed reserves was < 60%, and in these areas habitat recovery was likely to be slow.

UNDERSTANDING GAINED THROUGH ADDITIONAL COMPUTER MODELING

Much of the modeling since the ISC report has addressed the consequences of these simplifying assumptions. The initial models were useful for demonstrating the interactions of populations with hypothetical landscape geometries, but they were unable to incorporate the complexities of real landscapes. One of the most influential recent themes in conservation biology is that the distribution of populations and their habitats- their geometry within the larger landscape context-strongly influence population trends and extinction likelihoods (29, 54, 65, 66, 87). For managers to benefit from this new understanding (6) and for the incorporation of the necessary level of detail, spatially explicit models interfaced with real landscape patterns would be required.

Effects of Reserve Shape

A circular HCA of a given size has the minimum perimeter to area ratio. Early owl models assumed circular reserves and did not explore the effects of HCA shape on population stabi1ity. Recent models allowing habitat to be clustered into different arrangements (45, 61), and a "stepping stone" model in which irregular habitat clusters could be directly represented (54), suggest that edge effects can be significant. The best shape for a reserve is round, the poorest are long and narrow or irregular. Irregularly shaped clusters have much higher losses to edge effects and lower occupancy rates than the round clusters assumed by the ISC (54). The potential losses associated with edges suggest that the high occupancy rate for clusters of 20-25 pair-sites (Figure 3) was an artifact of the ISC's model assumption of circular clusters; HCAs that were irregular in shape would need to support >25 pairs for comparable levels of occupancy.

Northern Spotted Owl Modeling and the Evolution of Land Management Plans

Even though the model results, in conjunction with empirical data from dispersal measurements and biogeographic theory, provided a basis for a reasonable set of rules controlling size and spacing of the reserves, the actual map was highly constrained by geography and land-ownership. Further, up-to-date vegetation maps for the National Forests and BLM lands were not available, so the habitat conditions of both the HCAs and the intervening landscape were approximations. These limitations, in combination with the uncertainty about current habitat conditions, precluded direct tests of the efficacy of the reserve design. During the latter stages of the ISC process, work began on a new owl model designed to directly incorporate vegetation maps, through a GIS (Geographic Information System) interface, into a habitat-based popu1ation dynamics mode1 (54). Better habitat maps became available as need increased-a consequence of demand by the Spotted Owl Recovery Team (93) and President Clinton's charge to solve the "timber crisis" and avoid future "train wrecks" in the Pacific Northwest (see FEMAT introduction).

The first attempt to model the impacts of the conservation strategy on public lands was made by the BLM in conjunction with the FWS Recovery Team in 1992 (93). For timber harvest scheduling, specific forest stand data derived from GIS were stratified into productivity classifications, constrained by alternative management strategies, and evaluated to determine the pattern of harvest that maximized wood fiber production (27). A 1000 ha (approximate territory size for owls in this area of Oregon) hexagonal grid was placed over these simulated Iandscapes, and based on the fraction of older forest within the cell, the relative quality of each cell was evaluated. This process was repeated at

10-year intervals for each of six proposed management alternatives, creating dynamic landscape projections 100 years into the future (27).

Linking Vegetation to Demographics

To implement the process, habitat attributes were associated with birth and survival rates through a series of regression equations (5, 8, 39, 93). The attribute that best explained variation in survival, fecundity, and nest density was the amount of mature (> 120 years old) forest within a home range-sized area surrounding an owl nest site (5, 8, 39, 73). Based on these data, functions relating survival, fecundity, and the probability of nesting to the amount of mature and old forest in a home-range-sized hexagon were estimated. These functions provided initial estimates of the vital rates associated with different amounts of mature forest. Finally, BLM biologists assessed the time required for stands to recover to owl habitat after a variety of silvicultural treatments (clear-cut, various partial cuts). The combination of rules controlling spatially explicit harvest scheduling, post-harvest recovery rates, and habitat quality provided the information needed for model parameterization and allowed comparison of land management plans.

Modeling FEMAT Alternatives

As the FEMAT team expanded its mandate to consider all species associated with old-growth forests, the draft BLM plan was subsumed into this larger effort. The proposed FWS Recovery Plan (93)-virtually identical to the ISC's strategy-was retained as one of 10 land management options for public lands [Option 7; (90)]. Because all other options in FEMAT addressed concerns for numerous species other than the northern spotted owl, Option 7 had the smallest reserve acreage and the least stream protection of the 10 options proposed. Option 1 was the most restrictive, with the preferred option (Option 9) fitting approximately midway between 1 and 7. A decision was made in late 1993 to model owl dynamics across the range of the northern spotted owl using methods developed to evaluate BLM management alternatives (27, 69) and a spatially explicit owl model (54, 55). The task was to compare the conservation benefits of options 1, 7, and 9, plus an option that retained all currently suitable owl habitat (69).

Given identical rules concerning vegetation quality and the owl’s behavior, and assuming no regrowth of suitable habitat, the plans diverged greatly in terms of both the expected number of owls and their distribution over the landscape (Figures 4*a-d*). Option 9 was similar to Option 1 in both Washington and California but projected a smaller and more disjunct owl population for Oregon (cf Figures 4*b* and 46). Option 9, however, retained large blocks of habitat within the Cascades, and the demographic stability of these blocks was expected to be high (Figure 4*d*). Option 7 (Figure 4*c*), on the other hand, provided significantly less protection for all areas with the exception of the Olympic Peninsula (where virtually all federal land is reserved under all options). Under rules that predict large, stable populations given current habitat conditions (Figure 4*a*), Option 7 produced few, widely spaced areas with stable populations (cf. Figures 4a and 4*c*).

Reanalysis of Owl Populations on the Olympic Peninsula

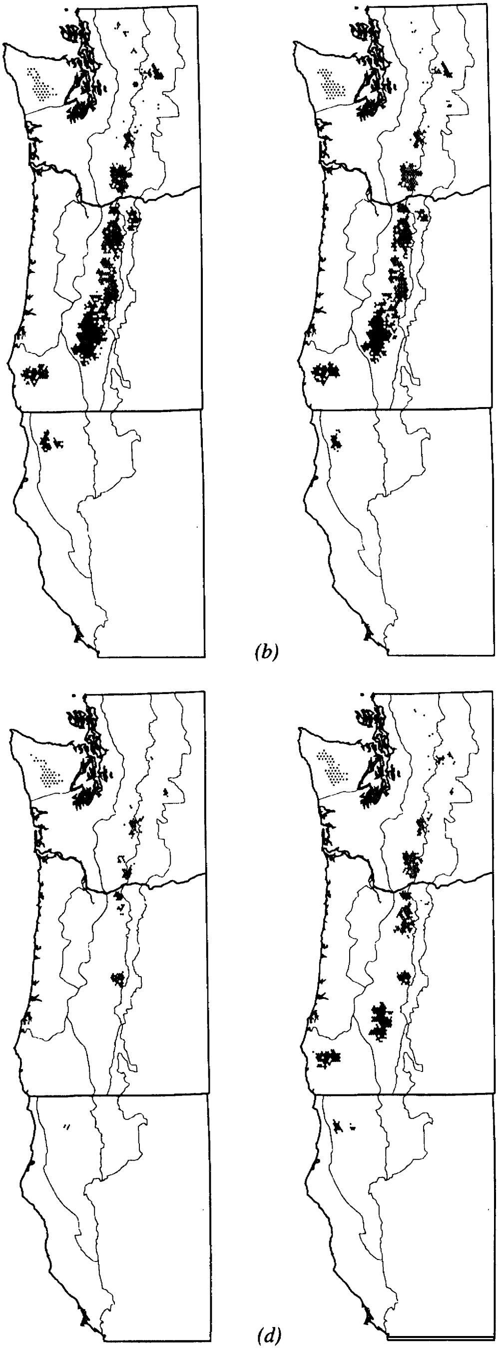
The most comprehensive attempt to update the ISC analysis of population stability occurred in 1994 when a team of modelers and owl biologists was formed to analyze the stability and degree of isolation of owl populations on the Olympic Peninsula in Washington (39). In its analyses, the team used the most current parameter estimates (33), explored owl population dynamics in the context of a spatially explicit model (54, 55), and forecast future population sizes and distributions on the basis of empirical relationships between demographics and habitat quality (5, 8, 93).

Habitat-demography relationships were estimated by regressing habitat condition (amount of old forest) on estimates of survival and fecundity (8, 39). Initial population estimates were derived from survey-based estimates of owl numbers within Olympic National Park (62). Territory size and the elevational range of northern spotted owls was determined from radiotelemetry studies (84). Survival rate estimates were based on the recent advances in capture/recapture modeling (48), and juvenile survival rate estimates were adjusted for emigration based on extensive data from radio-tagged juvenile owls (E Forsman, unpublished data).

Accurate maps of current owl habitat on public, state, and private lands were available, allowing reserve size and shape to be directly modeled (Figure 5). These maps also allowed the testing of assumed habitat demography relationships relative to the current distribution of owls. Assumed demographic rules produced sink habitat in areas with < 30% suitable habitat, source habitat in areas with > 40% habitat, and $\lambda \simeq 1.0$ for habitat classes with 30–40% suitable habitat (8, 39)-model results that conformed well to habitat distributions around known owl sites on the Olympic Peninsula.

TRANSITION DYNAMICS AND EQUILIBRIUM ANALYSIS

Given full implementation of their strategy, Thomas et al (84) argued that the northern spotted owl population should reach a positive equilibrium size sometime within the next 100 years. In making this argument they assumed three conditions: the amount and distribution of habitat would become fixed and sufficient to support a stable population, and the population would quickly



(a) (b) (c) (d)

converge to its habitat-based carrying capacity. These understandings were theoretically formalized (46, 44, 84). If the combination of critical habitat amount and territory occupancy rate fell below a critical landscape threshold (labeled G* in Figure 6), the population would follow a trajectory to extinction. Once on this trajectory, even large increases in habitat proportion are unlikely to stabilize the population unless juvenile search ability is very high (Figure 6). For these reasons, and because habitat was far below modeled levels in many areas (particularly on BLM lands in Oregon), transition dynamics were particularly important to any assumptions of long-term stability of the reserve system.

Analysis of Transient Dynamics in the ISC

The existence of threshold points, arising from habitat loss and distribution, has been demonstrated in a number of the owl models (44, 46, 84). If these models forecast reality, the success of the conservation strategy depended on reaching a condition of no-net-loss in suitable habitat before the population encountered an extinction threshold. The ISC concluded (84), "Our knowledge of the model structure and of spotted owl dispersal and search capabilities is incomplete, however, and we cannot accurately predict the population size, suitable habitat, or amount of habitat fragmentation thresholds that, once crossed, would lead to a population crash." Since that time no further insights have arisen relative to the locus of the thresholds.

Despite the possible existence of thresholds, the ISC was confident its strategy would eventually arrest the population decline and stabilize its dynamics. That this equilibrium would probably be far below the current population levels was fully understood by the ISC: "In the worst case scenario, we estimate that the strategy could result in a 50 to 60% reduction in current owl numbers. This figure assumes that all pair sites outside of the HCAs will eventually be lost through habitat removal or become permanently vacant because of demographic factors resulting from increasing isolation" (84).

The ISC assumed that habitat within the HCAs would recover to the extent specified and subsequently would retain nearly full occupancy by owls. For the reserve in total, this was an optimistic scenario. In fact, little likelihood existed

Figure 4 Modeled pair occupancy (dots represent locations occupied at a rate ≥ 70% during simulation runs of 100 years) if all current habitat were retained (4*a*), and assuming implementation of FEMAT (90) Options 1, 7, and 9 (4*b*, c, and *d* respectively). Mapped areas include western Washington, Oregon, and northwestern California and assumed no habitat regrowth for 100 years into the future (69).

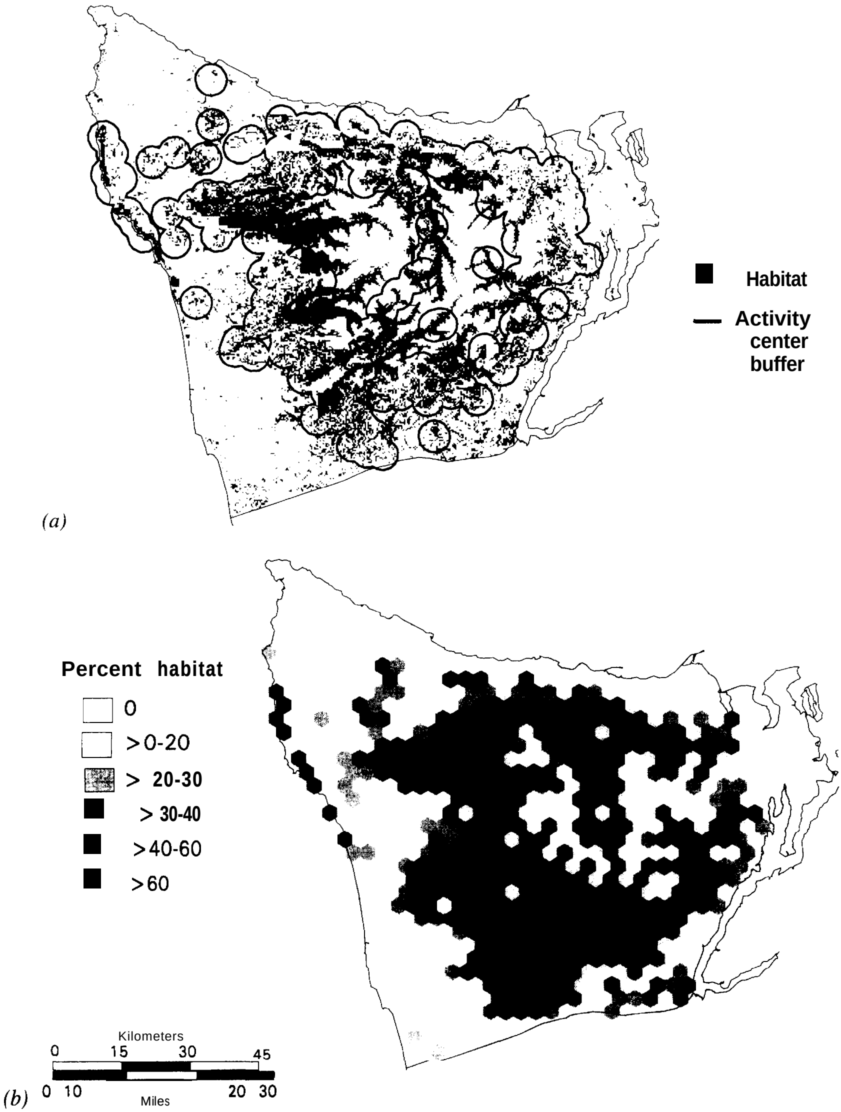


Figure 5 Owl habitat on the Olympic Peninsula (a) and derived 1500 ha hexagonal cells (b) used for model simulation (39). Known owl activity centers are circled on map ***a***. Shading (b) indicates the percentage of habitat within hexagonal cells.

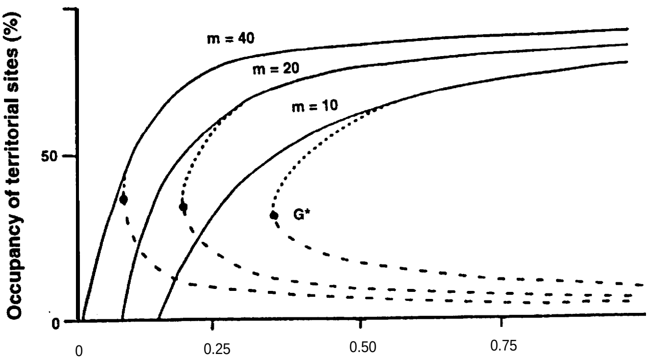


Figure 6 Model output showing the locations of stable and unstable equilibria based on both habitat occupancy and proportion of the landscape in suitable habitat. The solid lines represent no mate search, hence no Allee effect. The dotted and dashed curves show a stable and unstable Allee effect, respectively. The three M values represent different search efficiencies, with 40 the most vagile. If occupancy is too low, the population will follow the unstable ***(dashed)*** equilibrium. G* is the minimum proportion of suitable habitat for which stable positive equilibria can be achieved. If habitat proportions fall below G*, the population will go extinct regardless of initial occupancy (44).

that many of the HCAs would recover to their potential. Upon reexamination of HCAs on BLM lands in Oregon, reserve acres were fewer than originally estimated. This area of the owl's range is characterized by a "checkerboard" of ownerships with little likelihood of achieving > 50% owl habitat without mandating contributions from private property. Recent modeling that explicitly looked at harvest and regrowth in the next 50 years forecast the ISC's worst-case scenario. Assuming optimistic modeling rules that allow a stable or increasing population given current habitat levels, the models projected 50-60% declines in owl populations in Oregon and California if the ISC strategy (renamed Option 7 in FEMAT) was implemented (69; cf Figures 4a and 4c). Thus, the combination of continued harvest of old forest and the slow renewal rate of owl habitat suggested a substantial population decline before a new equilibrium was reached (69).

Population Stability Due to Regional Variability

Given the wide geographic distribution of the northern spotted owl, and natural variation in both forest condition and the owls' response to disturbance, it is unlikely that a global extinction threshold occurs at a specific point. Rather, a range of suitable habitat proportions likely exists in which the population trajectory becomes strongly negative (Figure 2). Further, the range of habitat proportions that defines this region varies in both space and time. Temporal and spatial variations in the threshold region arise from the inherent stochastic nature of the environment and the geographic variation in the species' ecological relations (for example, geographic variation in the owl's habitat associations and prey relationships).

It is therefore unlikely that the entire northern spotted owl population would simultaneously move past an extinction threshold. For example, we suspect that northern spotted owls in the Coast Range of Oregon may occupy habitats within or below the threshold region, but those in the Klamath Mountains in California probably do not (Figures 1 and 4). Both the amount and distribution of suitable habitat (86) and the population trend (15, 16, 32) vary geographically throughout the species' range.

Geographical variability will provide some degree of collective stability during the transition period. For example, crossing a habitat threshold in one part of the species' range may have little or no effect on the species' population dynamics in other parts of its range. Thus, assuming the existence of self-sustaining populations in parts of the species' range, growth of suitable habitat where the owl population has collapsed should lead eventually to recolonization of the collapsed areas by immigration from other populations (11). Both these assumptions were critical to the overall success of the strategy, and well within accepted ecological theory and empirical observations from a variety of species.

Habitat recovery will take longer in some parts of the owl's range than in others (69; Figure 4). Thus the transient behavior of local owl populations will vary depending on local rates of habitat renewal. Populations currently in precipitous decline and occupying areas deficient in habitat may continue to decline at least until a condition of no-net-loss of habitat occurs. During the interim, it is possible that some populations may collapse.

VARIABILITY IN DEMOGRAPHIC RATES Although the available demographic data indicate that the northern spotted owl's population is declining (15, 16), interpretation of these trends, relative to proximity to a threshold point, is unclear. Based on a meta-analysis, there is universal evidence for accelerating rates of decline in adult female survivorship, but individual study areas vary in the degree to which they show this trend (15, 16, 32). Given geographic variation in the location of threshold regions, the proximity of local owl populations to such regions, and potential confounding effects of increased intraspecific competition among owls as a result of packing by displaced birds, no general inference to threshold points can yet be drawn. Nevertheless, the demographic results are troubling and suggest some prudent modifications to the original conservation strategy.

IS THE CURRENT CONSERVATION STRATEGY ADEQUATE?

Since 1990, insights provided by the study of habitat relations and demography have confirmed the fundamental premises of the KC-the owl requires large areas of late seral forest within its home range, and the loss and fragmentation of suitable habitat leads to population declines. Because the basic biological understandings have not changed, the ISC's reserve design has remained conceptually robust. Large reserves, widely distributed across the landscape, are needed to retain the owl's current range.

Will Owl Populations Reach a New Equilibrium?

Although supporting examples were drawn from empirical studies (mostly island studies), model results played an important part in the ISC's assumption of a future, stable equilibrium. Retrospectively, it is noteworthy that the questions of long-term stability within the modeling context were never rigorously pursued by the ISC. Although Thomas et al (84) noted that short-term patterns in population persistence could lead to very different results in the long term, the model used to test potential reserve designs was not extended beyond 100 years. The decision to truncate the models runs was based on the pragmatic argument that decision makers could not plan beyond this time horizon.

Subsequent modeling suggests that reserves with a carrying capacity of 20 pairs are stable only if juvenile search efficiency is high and edge effects are minimal (54, 55). To achieve local stability within the constraints of real landscapes, more recent modeling suggests that carrying capacities of perhaps 30-40 pairs per HCA are needed. In addition, a few large reserves (> 100 pairs) significantly safeguard against population extinction. For these reasons, the original reserve design proposed by the ISC represents a minimum system, with greater risks to persistence then initially envisioned.

More recent, multispecies plans have also viewed the ISC as minimally acceptable. For example, in alternative plans for management of northwestern forests within the range of the northern spotted owl, the ISC's strategy [Option 7, (90)] provided the smallest acreage in reserves. All other options started with the ISC's reserve design and added additional reserve acreage. The adopted alternative (91), Option 9, added > 800,000 ha to the reserve system in areas adjacent to HCAs and of similar habitat quality. Some of these additions resulted in large reserve areas capable of supporting local populations of 40 to > 170 owl pairs (39, 69). Simulation results suggest that these large reserves should support stable populations under a wide variety of demographic assumptions

(69; Figure 4d). While range reductions are possible, global extinction appears to be much less likely under Option 9.

The long-term dynamics of owls in the smaller HCAs and the matrix lands between HCAs are less clear. Here too, however, Option 9 provides a variety of restrictions on land use that exceed those proposed by the ISC. The ISC strategy assumed no suitable nesting habitat in the forest matrix-rather, it stipulated a minimal habitat structure to facilitate dispersal between HCAs [50% of the land with tree diameter > 28 cm and with canopy closure > 40% (84)]. Option 9 provides for 40 ha reserves around known owl sites in the matrix, and for 46-91 m riparian buffers along all streams (approximately 40% of the matrix lands lie within these “riparian reserves”). In addition, 15% of the trees must be retained within each cutting unit, preferably in groups, and these trees will be exempted from future cutting (91). These are significant restrictions, and greatly increase the likelihood that owls will nest within matrix areas as well. Thus, given full implementation of the management standards in guidelines of Option 9 (91), we believe the prognosis for the long-term (> 100 years) persistence of the northern spotted owl appears to be very favorable.

In conclusion, the process used by the ISC to develop a scientifically credible reserve design-the hypothesis-testing framework, and the generation of maps with testable properties- is tenable. The scientific methods that evolved and were advanced during the northern spotted owl research program provide an exemplary model of how to acquire a defensible foundation for conservation planning. In the context of the contentious arena in which they have sought solutions to complex problems, we believe the northern spotted owl researchers and their colleagues have made significant contributions to the conservation sciences.

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