Ecological Applicationns. 2(1), 1992, pp. 3-17

INTEGRATING SCIENTIFIC METHODS WITH HABITAT CONSERVATION PLANNING: RESERVE DESIGN FOR NORTHERN SPOTTED OWLS[1]

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Abstract. To meet the requirements of Congressional legislation mandating the production of a "scientifically credible" conservation strategy for the threatened Northern Spotted Owl (*Strix occidentalis caurina*), the Interagency Spotted Owl Scientific Committee employed scientific methods to design a habitat reserve system. Information on the current and historical distributions of the owl and its habitats was reviewed in light of economic, political, and legal constraints; results were used to develop a preliminary reserve system of habitat "polygons." A map representing these polygons and their attendant properties served as a set of hypotheses that were tested. Statistical analyses of empirical data, predictions from ecological theory, predictions from population dynamics models, and inferences drawn from studies of related species were used to test properties of the preliminary map, including the number and sizes of habitat conservation areas (HCAs), their distribution, configuration, and spacing, and the nature of the landscape matrix between HCAs. Conclusions that failed to confirm specific map properties were used to refine the reserve system, a process that continued iteratively until all relevant data had been examined and all map properties had been tested. This conservation planning process has proven to be credible, repeatable, and scientifically defendable, and should serve as a model for wildlife management, endangered species recovery, and national forest planning.

Key words: habitat conservation planning; habitat fragmentatian; Northern Spotted Owl: old-growth forests; population models; scientific method.

INTRODUCTION

More than anv threatened or endangered species before it, the northern Spotted Owl (*Strix occidentalis caurina)* has become a cause célèbre in the struggle between groups representing disparate value svstems in a land of dwindling resources. The media portray the choice as simple - a choice between resource utilization, emplovment, and economic vitality on the one hand and rich, healthy ecosystems and security for the species and populations that they support on the other. The Northern Spotted Owl thus has become a symbol of the philosophical, moral, and social dilemma for our times. This dilemma, in the case of the owl, has provoked lawsuits, intense public and scientific disagreement, and rapidly diminishing options, and led the United States Congress to judge the situation a conflict to be resolved. In an amendment to an appropriations bill, Congress directed the United States Fish and Wildlife Service, United States Forest Service. National Park Service, and Bureau of Land Management to convene an Interagency Spotted Owl Scientific Committee (hereafter TSC) to "develop a scientifically credible conservation strategy for the Northern Spotted Owl."

Faced with this mandate, the Committee looked to emulate previous attempts at conservation planning under the federal Endangered Species Act of 1973. Section 10(a) of the Act, which authorizes the development of so-called "Habitat Conservation Plans" to "enhance the propagation or survival of the affected species" and "to the maximum extent practical, minimize and mitigate" the impacts of actions prohibited under the Act, provided little guidance. Indeed, no regulations, no standards, and no guidelines exist to direct the application of biological data to the design of reserves or reserve systems for imperiled species. While a number of studies have brought substantial quantitative information to conservation planning processes (see Gilpin 1989, Givnich et al. 1989, Soulé 1989, Menges et al. 1990, Murphy et al. 1990), none has offered a step-by-step application of biological data to the development of a reserve design.

Without a model appropriate to its complex task, the ISC struggled to develop a scientific protocol that would allow consideration of nonbiological factors in the development of a habitat conservation plan that would have the rigor of strong inference. Here we offer such a protocol, showing how the ISC incorporated hypothesis testing and iterative map revision in the development of a conservation strategy - a reserve design-for the Northern Spotted Owl. In this paper we

[1] Manuscript received 28 November 1990; revised 15 February 1991; accepted 25 February 199

attempt to generalize in order to enhance the value of this exercise as an example, and we hope that this presentation proves valuable in the development of conservation strategies for other species. However, we underscore that habitat conservation planning cannot be approached from a recipe: rather, each plan is a unique combination of an understanding of the target species and its habitats and of the scientific framework presented here.

PLANNING CONSIDERATIONS AND CONSTRAINTS

The Northern Spotted Owl, one of three subspecies of *Strix occidentalis,* ranges from southwestern British Columbia south through the Coast Ranges and Cascade Range of Oregon and Washington and into the Klamath Mountains Physiographic Province, which includes southwestern Oregon and the coastal mountains of northwestern California. In Oregon and Washington the species is found on both west and east slopes of the Cascade Mountains but is rarely found in mountains to the east.

While the species has been found to reside and breed in forests of diverse composition and structure and to show geographic variation in patterns of habitat use throughout its range, the Northern Spotted Owl is generally associated with extensive forest stands that provide forage, cover, and suitable nest sites. Nearly all observations of successful nesting, breeding, and fledging of young are from "old-growth" (i.e., mature or "ancient") forests, or from those younger forests that include the structural characteristics of old-growth forests (Thomas et al. 1990). Timber harvest, fire, and clearing for agricultural and urban land use have reduced these habitats, once widespread across southwestern Canada and northwestern United States, to < 10% of their original area. This broad regional decline in the extent of habitat and associated decline in Northern Spotted Owl numbers prompted a petition for federal intervention under the Endangered Species Act. After legal challenges and protracted review of biological information, the United States Fish and Wildlife Service announced conferral of threatened status to the subspecies (Federal Register 55[123]:26114-26194, 26 June 1990).

Demographic analyses of Northern Spotted Owl populations suggest that age-specific survival rates, and, in particular, variation in adult survival, strongly affect population dynamics (Lande 1988. Noon and Biles 1990). Reproductive success in the Northern Spotted Owl can vary greatly from year to year. In some years most pairs nest and produce offspring; in other years few pairs even attempt to nest. This variation may be related to fluctuations in abundance of the owl's primary prey, small mammals. For demographic analysis and conservation planning, three distinct life-history stages are recognized-juvenile (0 to 1 yr of age), subadult (1 to 2 yr of age, the period between dispersal and reproduction), and adult (>2 yr of age). A key aspect of the species' life history is that juvenile birds are forced to disperse from their natal area, sometimes over long distances, in search of suitable territories and mates (Forsman et al. 1984, Allen and Brewer 1985a, b, Gutiérrez 1985, Gutiérrez et al. 1985, Meslow 1985, Miller 1989). First reproduction usually occurs at 2 yr of age, but this is also variable (Franklin et al. 1990). The stage-structured simulation models employed in conservation planning for the Northern Spotted Owl were designed to parallel its three discrete life-history stages.

These demographic considerations and several crucial "sideboards" directed the structure of the habitat conservation planning process for the Northern Spotted Owl. First was the ISC's acknowledgment that more considerations were involved in the planning process than the biological factors that affect the fate of the owl. The very demand for conservation planning acknowledges conflicting interests and diverse values. The products of conservation planning, be they reserve designs, in situ management plans, or ex situ propagation activities, are prescriptions resulting from, or are adjuncts to, activities that place species at risk of extinction. At the outset of the process, planners must explicitly address competing interests or constraints. Nonbiological considerations that bear on the availability of habitat for reserve status- lands owned or managed by different jurisdictions, lands of varying monetary value, or lands having other distinguishing nonbiological qualities-must be integrated into the planning process *before* ecological data are used to produce the initial reserve design.

For the Northern Spotted Owl on public lands in the Pacific Northwest, a conservation strategy that would set aside all suitable habitat was viewed as biologically preferable, but not legally or politically viable. National Forest lands, for example, are managed under the 1976 National Forest Management Act, which requires that land management meet multiple-use objectives. Land management plans for national forests must "provide for diversity of plant and animal communities" and must "provide for outdoor recreation, range, timber, watershed, wildlife and fish." No available data supported the notion that lands subject to current standard modes of timber harvest could also support stable populations of Northern Spotted Owls. The ISC therefore acknowledged that significant amounts of public: land must be separately allocated both for commodity production and for owl habitat. Furthermore, the laws pertaining to the management of private timber lands were not considered to be conducive to comprehensive, biologically based habitat conservation planning. The ISC therefore made a crucial decision to exclude private lands from conservation planning considerations (a decision that. all else being equal, increased the required contribution of public lands to the ultimate conservation strategy).

Second, the application of biological information to conservation planning is a process that, like any pure or applied scientific endeavor, requires strict adherence to scientific methods (Murphy 1990). As Hairston (1989:2) has warned, ecologists (and, implicitly, their colleagues in wildlife biology and related fields) commonty appeal "to the complexity of nature, apparently in the hope of avoiding the rigorous thought that is required to formulate clear hypotheses, and to avoid devising proper tests to permit choices among competing hypotheses." Like the products of ecological experimentation, scientifically credible conservation strategies must be derived from procedures that yield strong inference (see Platt 1964). In the conservation planning process the ISC constructed alternative hypotheses related to reserve design, considered empirical data and theoretical models as tests to exclude hypotheses, and, using additional data and models, formulated and excluded further hypotheses. For purposes of habitat conservation planning hypotheses were represented on maps and included map properties that delineated management units. This provocative apiication of the scientific method to conservation planning added critical structure, repeatability, and credibility to the process and product as discussed below.

As a third consideration the ISC acknowledged that nonbiological constraints tend to drive conservation planners to the identification of as few "viable" popufations as are considered necessary to ensure species persistence. Toward the design of a reserve system adequate to the goal of species persistence, conservation planning must address two sources of threat to a target species. First, systematic pressures associated with human activities that act to threaten target species (including habitat destruction, overharvest of individuals, and toxic pollution) must be eliminated or controlled. The decision to exclude commercial timber harvest from areas allocated as habitat for the Northern Spotted Owl eliminated the most significant systematic threat to the species. Second, natural stochastic phenomena-that is, expected normal, random perturbations to populations and their habitats-also affect population persistence. Population viability analysis, as it has been described, is used to determine reserve design characteristics, such as the number of habitat patches, their sizes, and their geographic distribution, that would reduce the chances of population extinction from natural stochastic phenomena. These phenomena include: (1) loss of genetic diversity, including such factors as inbreeding depression and founder effects; (2) demographic stochasticity-chance events that affect reproduction or survival of individuals, such as biased age structures or skewed sex ratios; (3) environmental uncertainty, including temporal variation in habitat quality and the impacts of natural catastrophes; and (4) distribution phenomena, particularly disruption of landscape areas between habitat patches that mav affect dispersal and extinction-recolonization dynamics.

A conservation strategy that adequately mitigates the likelihood of species extinction due to these potential threats must state conservation goals in terms of Ievels of certainty of population persistence for specified periods of time. (Such a statement must recognize that the current state of the art in population viability theory and application does not allow a precise, quantitative evaluation of persistence likelihood for any species.) For any real population, it is currently impossible and certainly misleading to assign a numerical value to "high likelihood"; therefore, "high likelihood" is used qualitatively throughout this paper. For the Northern Spotted Owl the ISC's goal was to develop a conservation strategy that would provide a high likelihood of population stability and persistence throughout the species' range for ≈ 100 yr.

Two additional factors are important for conservation planning. First, stochastic phenomena differently impact populations of different sizes and distributions. While only the smallest demographic units are subject to the deleterious effects of genetic inbreeding, even large populations may be negatively impacted by catastrophic environmental events or by disruption of dispersal dynamics. Conservation planning, therefore, should first address stochastic phenomena that affect populations at their largest sizes - i.e., phenomena that are most inclusive in their impacts on species persistence. Planning should then sequentially address phenomena that act to reduce incrementally the likelihood of species persistence at diminishing population sizes. Distributional phenomena and environmental variation should be addressed first, followed by demographic stochasticity, and then deleterious genetic phenomena as required.

Second, stochastic perturbations that can put populations at risk can act synergistically to reduce the size of populations, thus reducing species persistence times. Gilpin and Soulé (1986) have described the interactions among stochastic phenomena as feedback loops between "extinction vortices" that determine population vulnerability. A population subject to multiyear drought, for example, may be reduced in size to a level at which stochastic demographic events may push it to extinction before favorable environmental conditions again prevail. Northern Spotted Owl populations, although demonstrably declining, are still relatively large and widespread; therefore the conservation strategy focused on distributional phenomena, likely environmental perturbations, and local demographic considerations. Because the loss of genetic diversity does not appear to be an immediate threat to this species, genetic considerations for long-term population survival were not central to conservation planning for the owl.

OVERVIEW OF THE PROCESS

The ultimate measure of success of a conservation strategy or habitat conservation plan is the long-term persistence of populations in natural habitats. Nonetheless, the immediate products of conservation planning normally are not populations of specific target sizes, but habitat reserves, conservation easements, or other set-aside lands that are designed to assure species persistence. These entities normally are represented on maps and by the information that maps convey, including political boundaries, topographic features, dominant vegetation? and elevation demarcations. The most basic information on the natural history and ecology of a target species is used to produce a preliminary map (or maps), the boundaries of which delineate the location, size, shape, and spacing of habitat patches planned for incIusion in a reserve or reserve system.

For the purposes of scientific planning, a preliminary reserve design map can be considered to have properties that serve as falsifiable hypotheses. In the conservation planning process a hypothesis can be defined as an assertion of a map property that is subject to tests with existing empirical information and theoretical predictions (from population viability analyses). Tests of these hvpotheses may be based on natural-history observations, analyses of empirical data, predictions from theoretical models, or predictions based on studies of related species. When test conclusions fail to confirm one or more properties of the preliminary reserve design, the proposed reserve system is adjusted. Successive map iterations are sequentially tested with available information. The final product, a conservation strategy or habitat conservation plan, is then portrayed as a map. A given map-based solution to a conservation challenge is not necessarily unique. It is, however, a solution that is fuIly supported by available empirical data and theoretical model predictions,

The conservation planning process is dependent upon spatially explicit information relevant to the species' ecology – particularly the distributions of populations, habitats, and resources. That information is best portrayed on independent map layers that, when overlaid to form a composite map, collectively provide the initial hypotheses for the conservation strategy. The first map layer should outline the current and historical geographic distribution of the target species. The scale of the first map layer is often dependent upon the extent of the target species' distribution, the scale at which the species responds to environmental variation, and the spatial extent of environmental disturbances that threaten the species. For example, Northern Spotted Owls have large annual home ranges (500-2000 ha), are widely distributed across Washington, Oregon, and northern California, and are threatened by extensive areas of habitat loss. The resolution provided by 1:250000 scale maps was sufficient for initial mapping of the owl's distributional range.

The second map layer should portray the current and historic distributions of suitable habitats, including disturbed areas with potential to recover to suitable habitat. The intersection of the species range (map layer 1) with currently and potentially suitable habitat (map layer 2) provides an initial outline of habitat conservation areas (HCAs), habitat "polygons" that are candidates for inclusion in the reserve network. For the Northern Spotted Owl the ISC had extensive information on habitat-use patterns from radio-tracking studies. Characterizing occupied habitats in terms of timber type categories used by the United States Forest Service and Bureau of Land Management allowed the use of maps from those agencies to plot the distribution of extant and potential habitat on public lands. The finer scale of resolution of habitat distribution provided by these maps (1:24000) allowed the detail essential to begin to delimit potential HCAs.

Available survey or census information from the range of the species provides the third map layer. Even limited information from highly localized habitat areas may be useful to identify known population centers, and, importantly, to determine quantifiable environmental correlates of habitat quality that may then be mapped. The association of survey data with specific habitat types allows projections of species occurrences from unsurveyed areas of similar habitat type. Density estimates of the target species from specific habitat types are particularly valuable, as they allow initial projections of potential population sizes for individual habitat polygons.

Extensive, but incomplete, survey data were available for the Northern Spotted Owl. Although most of those data did not allow reliable estimates of population density, the data did allow prediction of the presence of owls within similar habitat types and at specific locations. The survey data also proved particularly valuable in documenting extensive geographic variation in the owl's abundance. Density estimates were available from three intensive study areas (> 250 km^2 in size) located across the distribution of the Northern Spotted Owl. The restricted nature of density studies precluded any but very localized density estimates; however, the ISC was able to extrapolate these estimates to neighboring areas of similar habitat type and quality.

A fourth map layer depicts land ownership and use patterns? including areas currently set aside for the species and areas in permanent reserve status (such as wilderness areas, parks, etc.). At this initial stage of the process, lands available for conservation planning must be carefully distinguished from lands not available for planning. Significant subsequent changes in land availability would likely force a repeat of the entire planning process.

The combined intersection of the four map layers–the geographic range of the target species, the distribution of suitable and potentially suitabIe habitat, population density information, and land-use patterns–yields a first iteration of the conservation strategy (or reserve design), represented as a map. Polygons formed by the intersection of map data from each of the four map layers represent potential HCAs. The initial map of these polygons clearly indicated that the strategy for persistence of the Northern Spotted Owl would need to be evaluated in the context of a "metapopulation," or a population of populations (see Levins 1970, Shaffer 1985). The distribution of polygons was discontinuous across the landscape. HCAs were, for the most part, rather small (< 30 000 ha), irregular in shape, and geographically relatively widely separated (mean nearest-neighbor distance > 13 km). The landscape between HCAs (the landscape matrix) varied extensively in its suitability as habitat for the owl. The patchy distribution of HCAs reflected natural discontinuities in vegetation structure and composition, in topographical conditions, and in constraints resulting from human-induced habitat disturbance and land-ownership patterns. Additionally, substantial amounts of habitat that appeared suitable for the owl were treated as unavailable for conservation planning because of the decision to limit the initial reserve system to public lands.

Typically, few empirical data will have been used to construct the initial conservation map representing the proposed habitat-reserve system. That map represents the maximum size and number of HCAs available for planning purposes. Within the confines set by the initial map may be a large number of possible "solutions" that reflect different sets of constraints, each described by a unique set of reserve properties. It is at this point in the process that the initial map (and its attendant properties) is considered as a set of falsifiable hypotheses.

For the Northern Spotted Owl we used data from all pertinent biological studies and inferences drawn from those data to test the properties of the map-including the number and sizes of HCAs, their distribution, configuration, and spacing, and the nature of the landscape between the HCAs. Valid tests included statistical analyses of empirical data, predictions from ecological theory, predictions from population dynamics models, and inferences drawn from studies of related species. Not all hypotheses could be tested directly with empirical data and statistical models; however, all assertions were subjected to some sort of falsification procedure. If one or more properties of the map were falsified, conclusions drawn from tests that failed to confirm specific map properties were used to refine the map. The new map then became the new set of falsifiable hypotheses. This process continued iteratively until all relevant data had been examined and all map properties had been tested.

THE NORTHERN SPOTTED OWL EXAMPLE

A habitat conservation planning process is initiated on the presumption that a target species is declining-a presumption that often will not have been confirmed empirically. Appropriate confirmation entails tests, using relevant population data, of the null hypothesis that populations are stable or increasing. These tests necessitate accurate demographic information from as many locations as possible over as long a period as possible. Estimates of the finite rate of population change (λ) were available from three geographically distinct areas within the range of the Northern Spotted Owl, two of which, northern California and the Oregon Coast Ranges, had sequences of data longer than 3 yr. From both areas, detailed knowledge of the fates and reproductive status of banded owls provided estimates of survival and fecundity rates and, in turn, estimates of λ. If $\lambda > 1.0$, vital rates suggest that the population is increasing; if $\lambda = 1.0$, the population is stable; and if $\lambda < 1.0$, the population is declining. We tested the following null hypothesis:

H_0: The finite rate of population change (λ) is ≥ 1.0. (1)

The estimate of λ was < 1.0 at both sites, and the null hypothesis was rejected. (An estimate of λ from the Olympic Peninsula was < 1.0. The test, however, had low power since just 3 yr of data were available from this study area. Details of these and other tests of this hypothesis are found in Thomas et al. [1990: Appendix L].)

Given evidence of declining Northern Spotted Owl populations in two geographically separated portions of their range, and without clear evidence of other causal factors (e.g., hunting, interspecific competition, predation), a logical explanation was to attribute the decline to habitat loss. However, tests of a habitat-loss hypothesis required evidence of habitat selection by the owl as well as documentation that selected habitat(s) had become reduced in extent prior to owl population declines. A preliminary habitat-selection hypothesis was stated as:

H_0: Northern Spotted Owls do not differentiate among habitats on the basis of forest age or forest structure. (2)

All Northern Spotted Owl habitat studies rejected this null hypothesis and provided evidence in favor of habitat selection (these studies are too numerous to review here; a detailed summary is provided in Thomas et al. [1990: Appendix F]). In general, in Oregon and Washington, old-growth forest was the only habitat in which owls consistently nested and reproduced in greater numbers than would be expected from the proportional occurrence of that habitat type across the forested landscape. Only in the coastal redwood forests of northern California were Northern Spotted Owls also found to use younger forests disproportionately. At a relatively early stage (60-80 yr) these fast-growing forests exhibit stand characteristics similar to those of old-growth forests elsewhere.

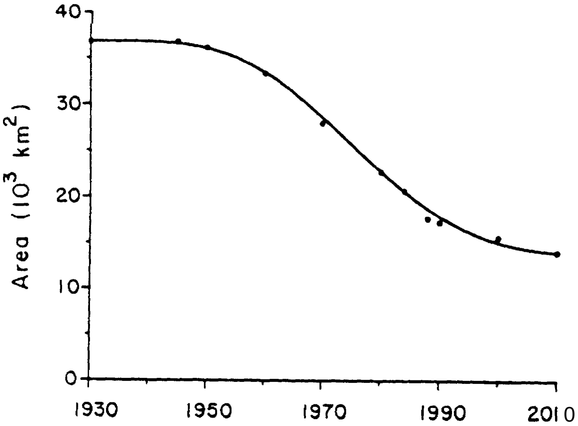

FIG. 1. Estimated trend in the areal extent of suitable Northern Spotted Owl habitat on NationaI Forest lands in Oregon and Washington for 1930-20 10. Estimates for 1990-20 10 are projections.

The rejection of hypothesis (2) allowed a test of a habitat-loss hypothesis, stated as:

H_0: No decline has occurred in the area1 extent of habitat types selected by Northern Spotted Owls for foraging, roosting, or nesting. (3)

The ISC explicitly tested this hypothesis based on data from National Forest lands in Oregon and Washington (national forests provide >70% of the remaining owl habitat). The analysis documented significant declines in the extent of suitable owl habitat, a trend that is projected to continue into the future (Fig. 1).

Given evidence of habitat specialization by the owl, declines in owl populations, and projected continuation of significant losses of suitable habitat, conservation planning for the species appeared justified- Rejection of hypotheses (1) - (3) provided the empirical support that contributed to the recommended listing of the Northern Spotted Owl as a threatened species under the Endangered Species Act (USDI 1990).

For the Northern Spotted Owl, the return to population stability is contingent upon first achieving a condition of no net loss of habitat and, second, providing sufficient habitat in a spatial configuration that allows for a balance between local extinction and recolonization events. The map resulting from the overlay process described above (see Overview of *the process)* portrayed the essential spatia1 information as HCA polygons with varying sizes, shapes, and spacing. The task was to test and refine that map until the arrangement of HCAs described a reserve system sufficient to allow the Northern Spotted Owl a high likelihood of persistence for 100 years. To do this, the ISC tested map-generated hypotheses in the context of five generally accepted concepts of reserve design (Diamond 1975, 1976, Den Boer I981).

The first reserve design concept was:

1) Species that are well distributed across their historical geographic ranges tend to be less prone to extinction than species confined to small portions of their historical geographic ranges.

A hypothesis that logically follows from this concept is:

H_0: The probability of species persistence is not related to the extent of its geographic distribution. (4)

Indeed, this concept is rather resistant to empirical testing for most species. Only a species that is essentially "extinction-proof' in portions of its range would provide data that might falsify this hypothesis. Because the frequency, intensity, and locations of catastrophic events that would eliminate entire owl populations are unknown, direct tests of this hypothesis with Northern Spotted Owl data were not possible. Instead we used an indirect test based on inductive arguments from extinction theory and studies of species whose extinction has been documented. For example, the mathematical model of Nisbet and Gurney (1982) suggests that time to metapopulation extinction increases exponentially with the number of local populations. As a consequence, a moderate degree of subdivision into local populations may increase overall persistence tielihood (Quinn and Hastings 1987). These arguments usually reference the concept of "risk spreading" (Den Boer 1981). Specifically, advantages are gained by species that are distributed widely across an extensive geographical area-the degree of environmental correlation among reserve areas is reduced, as is the likelihood of simultaneous extinction of populations. Several theoretical studies have demonstrated that correlation in the probabilities of experiencing major environmental perturbations among populations reduces the effective number of populations in a metapopulation (Goodman 1987, Harrison and Quinn 1989). In this context it is important to recognize that timber harvest throughout the range of the subspecies may act as a correlated environmental disturbance and may contribute to destabilization of the Northern Spotted Owl metapopulation.

Empirical studies of endangered species are few and rarely distinguish between the deleterious effects of reduced risk-spreading and the effects of reduced population size. One of the best examples is that of the heath hen (*Tympanuchus cupido),* a once rather widespread species that became confined to a single island off the coast of Massachusetts. The extinction of the species was, at least in a proximal sense, the result of successive local environmental perturbations that would have been unlikely to extirpate a more widely distributed species (Simberloff 1986; see also Thomas et al. 1990: Appendix N). Based on inferences from such empirical and theoretical studies, we rejected hypothesis 4. Implications of this rejection were straightforward. Constrained to a system of HCAs that would allow land management agencies to meet other legal obligations (e.g., the "viable populations" regulation in the 1976 National Forest Management Act), we chose at this juncture to distribute HCAs widely across the entirety of the Northern Spotted Owl distribution on public lands (rather than concentrate effort on a portion of that distribution). This decision had substantial impact on all further reserve design analysis.

The second basic reserve design concept was:

2) Large habitat patches that support large populations of a target species will tend to support that species for longer periods of time than will small patches that support fewer individuals.

Concept 2 suggests a relationship between habitat area and population size. For the Northern Spotted Owl, tests of hypotheses (1) - (3) indicate that the owl is limited by habitat area and predict some relationship between the size of an HCA and its carrying capacity. Estimates of carrying capacity were made independently for each habitat polygon, were adjusted for the current amount of suitable habitat, and were based on existing survey data and the expert opinion of field biologists familiar with individual polygons. A hypothesis then was stated in null form as:

H_0: No relationship exists between the size of an HCA and its carrying capacity for Northern Spotted Owls. (5)

The hypothesis was tested by regressing estimated carrying capacity on HCA size. A significant regression would lead to rejection of the null hypothesis. Since key aspects of the ecology of Northern Spotted Owls (e.g., population sizes, distributions, home range, prey selection, etc.) vary across the range of the subspecies, analyses were conducted separately by physiographic province (i.e., by widely recognized landscape units).

The ISC found that across provinces a significant relationship existed between HCA size and carrying capacity. Furthermore, habitat polygons of the same size on the Olympic Peninsula and in the Klamath Mountains in northern California differed in the number of owls they could support. The null hypothesis thus was rejected. Rejection of hypothesis (5) was not surprising; however, these tests provided additional support for habitat limitation, and allowed the incorporation of geographic variation in home-range size into population projections.

Additional confirmation of a relationship between habitat area and carrying capacity was provided by a number of landscape-level studies, all of which concluded that the removal of old-growth forests results in a decrease in the regional abundance of Northern Spotted Owls (reviewed in Thomas et al. [1990: Appendix H]). The size of HCAs appeared to be critical to habitat conservation planning for the Northern Spotted Owl.

Improvement of the regression models was needed to predict more precisely the sizes of populations that would occupy HCAs in a final reserve system. The ability to predict the carrying capacities of HCAs was important because many habitat polygons identified in the earliest map iteration were poorly surveyed. The regression models were used to identify HCAs that exhibited large differences between their predicted carrying capacities and observed population sizes (i.e., "outliers"). The ISC generated improved estimates of carrying capacities for these outliers by using province-specific estimates of pair home-range sizes, corrected for the observed overlap between adjacent pairs (Thomas et al. 1990: Appendix 1). Regression models were then recomputed, and the process continued until only anomalous observations remained as outliers. These HCAs deviated from the predicted size-population retationship due to, for example, unusual local vegetation patterns or topography, past disturbance history, or the condition of adjacent lands. The lack of fit for each unique HCA was formally justified by biologists familiar with the individual HCA and was documented in the conservation plan.

This procedure established a predictive relationship between HCA size and carrying capacity for Northern Spotted Owls. To address the goal of population persistence, however, required insights into the relationship between carrying capacity (thus HCA size) and local population stability. Specifically, the ISC asked how many owl pairs an individual HCA must support in order to have a high likelihood of local population stability in the face of demographic and mild environmental uncertainty. This question, stated as a null hypothesis, was:

H_0: No relationship exists between HCA size (or carrying capacity) and population stability (that is, the likelihood of population persistence). (6)

Initial information to reject this hypothesis was available from empirical studies of bird species occupying islands off the coast of Britain (e.g., Jones and Diamond 1976, Diamond and May 1977, Diamond 1984, and Pimm et al, 1988) and from population dynamics theory (e.g., Richter-Dyn and Goel 1972, Leigh 1981, Goodman 1987). Estimates of the relationships between population size and persistence time of large-bodied, nonmigrant birds from combined British island data provided valuable insights into minimum HCA sizes for Spotted Owls. Estimates indicated an average persistence time of 2 yr for populations with <2 pairs, ≈ 25 yr for populations of 10 pairs, and ≈ 50 yr for a single population of 20 pairs (Thomas et al. 1990:288-289). Further empirical support for an effect of population size on persistence is provided by census data from isolated populations of the Middle Spotted Woodpecker and Socorro Red-tailed Hawk (Pettersson 1985, Waiter 1991) For example, during the period of

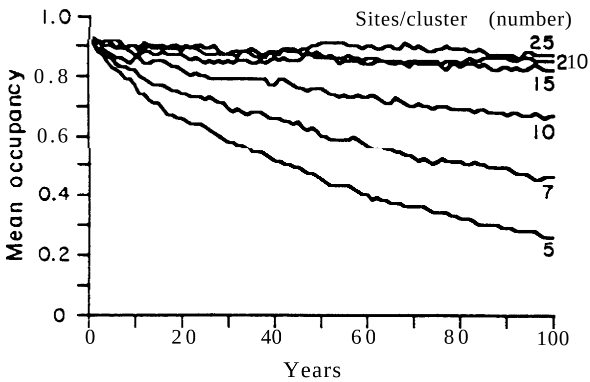

FIG. 2. Mean pair-occupancy proportion for the Northern Spotted Owl, plotted against time for a 100-yr simulation. Cluster size (number of pair-sites per nesting-site cluster) was varied from 5 to 25. All pair sites were assumed to be completely suitable habitat.

study (1967-1983) the woodpecker population reached a high of 25 individuals (≈ 8-10 pairs). By 1983, however, the population had gone extinct, presumably due to deleterious demographic or genetic effects associated with small population size.

Additionally, the ISC sought to test hypothesis (6) with a dynamic metapopulation model developed specifically for the Northern Spotted Owl. This model allowed the carrying capacity of simulated HCAs to be systematically varied in order to evaluate the effect of population size on population stability (Thomas et al. 1990: Appendix M, Lamberson et al., *in press).*

The basis of the dynamic metapopulation model was a continuous rectangular array of HCAs that collectively occupied 35% of the forested landscape. HCAs were assumed to be circular, and owl pair-territories within an HCA were assumed to be of equal size. The HCAs were assumed to be either totally or partially suitable habitat, and the landscape matrix between HCAs was assumed to be entirely unsuitable, except for purposes of dispersal. The carrying capacity of an HCA was equal to the number of suitable pair sites. The population size of an HCA was equal to the number of sites occupied by pairs. The model was an all-female, stage-projection model, with the stages being juveniles, subadults. and adults. This structure was similar to those previously presented by Boyce (1987) and Lande (1987, 1988). All juvenile owls were assumed to disperse from their natal territory in search of suitable, unoccupied sites- In the model the birds first search within the natal HCA; those that do not find suitable sites attempt to cross the matrix to search in adjacent HCAs. Demographic stochasticity was simulated by variation in survival rates and by variation associated with dispersal between HCAs. Low-intensity environmental variation (or uncertainty) was expressed by variation in fecundity to represent good and bad years for reproduction. Parameterization of this territory-cluster model was based primarily on the studies of Franklin et al. (1990).

The number of pair sites per HCA was systematically varied to simulate variation in HCA size. A simulated network of HCAs would persist where the average pair turnover rate at a site (due to mortality) and the average recolonization rate of unoccupied sites were in long-term balance. Persistence likelihood was estimated by plotting 100-yr trends in mean pair occupancy (number of occupied sites per HCA, averaged over all HCAs) for HCAs of different sizes. Two basic scenarios were simulated: the first assumed that all sites within an HCA were currently suitable, the second assumed that 60% of the sites within an HCA were currently suitable (the latter value was similar to forest conditions in the Pacific Northwest). Given the assumption of 100% suitability, we did not predict stabilization at high mean occupancy levels unless HCAs were sufficiently large to support at least 15 pairs of Northern Spotted Owls (Fig. 2). Based on the more realistic assumption of 60% suitability, mean occupancy did not stabilize at high levels until HCAs were large enough to support at least 20 pairs of owls (Fig. 3). Details on additional inferences drawn from the metapopulation model are found in Thomas et al. (1990: Appendix M).

Based on evidence from empirical studies and theory and the predictions of the metapopulation model, the null hypothesis of no relationship between HCA size (carrying capacity) and population stability (the likelihood of persistence) was rejected. The model results provided additional insights into a minimum target HCA size with a high likelihood of local population persistence, contingent upon some level of dispersal among HCAs. Model predictions, theory, and empirical studies were consistent, suggesting that, to be stable, a local population must consist of ≈ 15 or more pairs. However, for HCAs not composed of uniformly suitable habitat, population stability required ≥20 pairs of owls (Fig. 3). The ISC used 20 pairs as a minimum target population to select HCAs from available habitat polygons on the iterated map and to refine HCA boundaries.

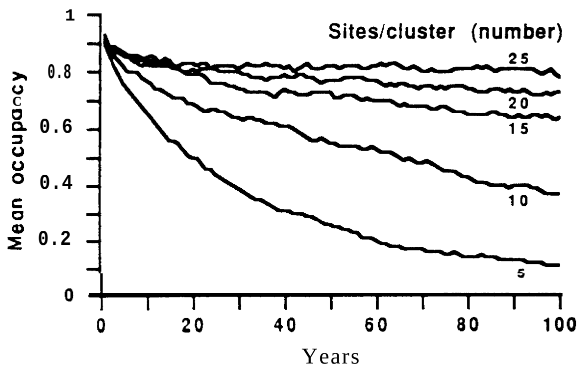

FIG. 3. Mean pair-occupancy proportion for the Northern Spotted Owl, plotted against time for a 100-yr simulation. Cluster size (number of pair-sites per nesting-site cluster) was varied from 5 to 25. Only 60% of the pair-sites were assumed to be suitable habitat.

The third reserve design concept invoked was:

3) Habitat patches that are continuous (less internally fragmented) in configuration tend to support species for longer periods than patches that are irregular in configuration (more fragmented).

An hypothesis that logically follows from this concept is:

H_0: Given a set of habitat patches that vary in their degree of fragmentation. no relationship exists between the extent of fragmentation within a patch and the persistence likelihood of species that occupy those patches. (7)

Little published information exists to document a relationship between population persistence likelihoods and degrees of fragmentation within individual habitat reserves. Pickett and Thompson (1978) discussed the dynamics of vegetation patches within habitat islands or reserves. They argue that patterns of vegetation disturbance and subsequent succession can profoundly affect extinction dynamics of animal populations within a reserve. Many proposed HCAs currently have abrupt edges created by clearcuts adjacent to old-growth forest. Disturbances at these edges, such as windthrow in forest patches, are likely to reduce the amount of suitable owl habitat. This effect, coupled with the observation that Northern Spotted Owls increase their home-range size in response to fragmentation (Forsman et al. 1984, Carey et al. 1990), suggests that fragmented HCAs will have lower carrying capacities for owls.

At the landscape scale, in contrast, there has been extensive discussion of fragmentation effects (e.g., Fahrig et al. 1983, Harris 1484, Fahrig and Merriam 1985, Burley 1989, Harris and Gallagher 1989) and an extensive literature based on a wide array of species. For example, studies of many forest-dwelling bird species have found that an increased ratio of forest edge to forest interior, the inevitable consequence of forest fragmentation, can have strong negative consequences (Whitcomb et al. 1976, Wilcove et al. 1986, Temple and Cary 1988, Yahner 1988). The species affected, mostly forest-interior songbirds, experienced increased levels of predation and brood parasitism (Whitcomb et al. 1981, Brittingham and Temple 1983, Wilcove 1935). Two indirect, but valuable, tests of this hypothesis at the geographic scale appropriate for Spotted Owl planning were available. Meyer et al. (1990) found that landscape samples centered on Spotted Owl nest sites contained a significantly higher percentage of old-growth forest and significantly larger average sizes of old-growth patches than similar areas at randomly selected sites. Bart and Forsman (1992) also found a significant relationship at a landscape scale between the amount of old-growth forest and the occurrence and productivity of Northern Spotted Owls.

Unfortunately, the specific effects of fragmentation within HCAs are difficult to separate from those of concomitant reduction in suitable habitat. To further test hypothesis (7), the dynamic metapopulation model was used. For these simulations all HCAs were assumed to be equal in size with potential carrying capacities of 25 pairs. Increasing fragmentation was simulated by varying the actual number of suitable sites within these HCAs from 25 down to 5. The fewer suitable sites within the HCA, the greater the likelihood that a dispersing juvenile owl would search unsuitable sites within its natal HCA. Given these assumptions, mean pair occupancy did not stabilize, over 100 yr, until $\approx 60\%$ (15 of 25) of the sites within HCAs were suitable. Based on the results from both modeling and empirical studies conducted at the landscape scale, null hypothesis (7) was rejected. The ISC concluded that populations in HCAs with contiguous suitable habitat exhibit a higher likelihood of persistence than those in HCAs in which habitat is more fragmented. At this point in the process, most HCA polygons that showed little potential to recover to contiguous blocks of suitable habitat even in the absence of timber harvest (that is, HCAs that had substantial natural irregularities, such as poor soils) were deleted from the reserve sys- tern. Exceptions were made to retain small HCAs in portions of the species' range where no large HCAs with the potential for contiguous habitat existed.

The fourth basic reserve design concept invoked was:

4) Habitat patches that are sufficiently close together to allow dispersal tend to support target populations for longer periods than habitat patches that are far apart.

This concept embraces the so-called "rescue effect" (Brown and Kodric-Brown 1977) that suggests that population stability in a habitat patch is contingent upon a balance between local population extinction and recolonization from neighboring populations. Considerable evidence from bird studies shows the importance of distance from mainland sources of migrants as a determinant of local species richness on continental shelf islands (Case 1975, Diamond 1975, Terborgh 1975, Soulé et al. 1979) and within recently isolated forest fragments (Burgess and Sharpe 1981, Whitcomb et al. 1981, Lynch and Whigham 1984; Wilcove et al. 1986). Particularly strong empirical support for concept 4 is provided by research on insular populations of pikas *(Ochotona princeps)* (Smith 1974, 1980). Smith demonstrated a dynamic equilibrium between extinction (inversely related to patch size) and recolonization (inversely related to inter-patch distance), as well as an increase in turnover rate with degree of isolation.

Consideration of (and empirical support for) the rescue effect argues that conservation planners should space HCAs to facilitate demographic interaction among them. The metapopulation model assumed that when

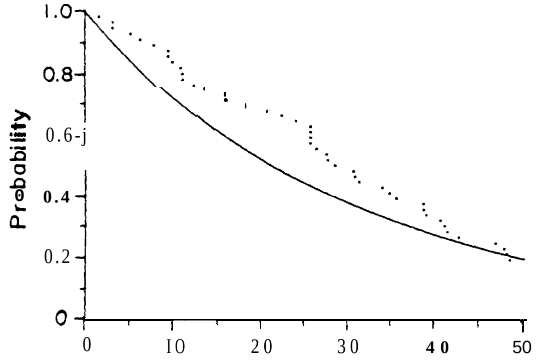

FIG. 4. Probability of successful dispersal by Northern Spotted Owls, plotted against distance. Figure is read as the probability of dispersing $\geq x$ kilometres.

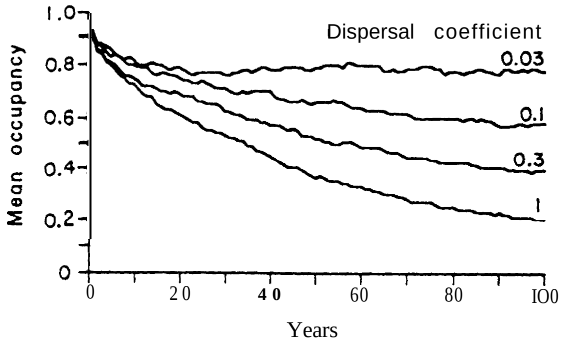

FIG. 5. Mean pair-occupancy by Northern Spotted Owls, plotted against time for a 100-yr simulation. The dispersal coefficient was varied from 1.0 (high environmental resistance to dispersal) to 0.03 (low resistance to dispersal). Cluster size was five pair-sites per cluster, all stocked with suitable habitat.

a juvenile owl failed to find a vacant suitable site and/or a mate within its natal HCA, it had some likelihood of successfully dispersing to a vacant site in a neighboring HCA. This assumption requires presence of HCAs within acceptable distances for dispersing owls. Without adequate dispersal routes, populations must be self-sustaining- an unlikely event in all but exceptionally large HCAs capable of sustaining very large populations. The putative importance of HCA spacing was addressed by testing two null hypotheses:

H_0: No relationship exists between the likelihood of a juvenile owl successfully dispersing and the distance dispersed. (8)

H_0: No relationship exists between the persistence likelihood of an HCA and the spacing among HCAs, (9)

To test the first of these hypotheses, dispersal was defined as the permanent movement of juvenile owls from one location to another. The distribution of dispersal distances from 56 radio-tracked juvenile birds was estimated, based on maximum dispersal distance computed as the greatest straight-line distance traveled by an individual from its natal site during the period of tracking, Only one bird was documented to have found a suitable nesting site and a mate. The remaining birds either died (68%), were subject to transmitter failure (27%), or simply disappeared (5%). Because of a possible relationship between dispersal distance and number of days of transmitter exposure, analyses were first conducted to determine if transmitters had any effect on maximum dispersal distance (Thomas et al. 1990:306). Given an apparent lack of a relationship between dispersal distance and the length of transmitter exposure, null hypothesis (8) was not rejected.

Based on the cumulative distribution of dispersal distances, the estimated probability of dispersing x kilometres, or farther, was regressed on distance (x). Lack of a significant regression would provide support for the null hypothesis. The data fit a negative exponential model ($R^2 = 0.97$ $P < .001$; Fig. 4), suggesting that dispersal capability declines with increasing distance from the natal area. Null hypothesis (8) thus was not supported by the data; hence, not only the sizes of HCAs but the distances between HCAs had to be viewed as critical elements in the reserve system design.

No data were available to test hypothesis (9) directly. The simulation model, however, allowed the systematic variation of risks associated with inter-HCA dispersal and estimates of its effects on mean pair occupancy of HCAs. The objective was to simulate the environmental resistance to dispersal that an owl could experience when traveling through the forest matrix, Two sources of mortality could result from dispersal between HCAs--(1) a juvenile could disperse in a direction that would not intercept an adjacent HCA, or (2) it could select an appropriate direction. The likelihood of successful dispersal between HCAs was modeled as a decaying exponential,

$$\Pr(\text{success}) = \exp[-k \cdot (\text{distance between HCAs})].$$

The effect of varying environmental resistance was evaluated by estimating the sensitivity of mean pair occupancy to variation in the dispersal coefficient k (preliminary estimates of k were provided by analysis of data on juvenile dispersal). For HCAs of size sufficient to hold five pairs, variation in the dispersal coefficient strongly affected mean occupancy (Fig. 5). The model assumed high resistance to dispersal across unsuitable habitat (the landscape matrix), and mean occupancy did not reach equilibrium. Simulated populations went to extinction. In contrast, the effects of varying the dispersal coefficient were much less pronounced in HCAs supporting at least 20 pairs (Fig. 6). All coefficients provided for long-term equilibrium; however, higher resistance provided by the landscape matrix resulted in significantly lower mean occupancy rates. Empirical and model-based results led to the rejection of hypothesis (9).

Collectively, the results of these two tests indicated that spacing between HCAs should be within the dispersal capabilities of juvenile owls. The ISC was unable, however, to bring empirical data directly to bear on the question of the exact spacing required among HCAs. After lengthy discussion following a Delphi approach (e.g., Soulé 1989), the ISC concluded that HCAs should be within the dispersal capability of approximately two-thirds of dispersing juveniles-about 20 km (12 miles). Comparison of the distributions of dispersal distances and nearest-neighbor distances among HCAs showed that nearly all HCAs described on previous map iterations were within the dispersal capabilities of two-thirds of radio-tracked juvenile owls (Thomas et al. 1990: Appendix P).

The final reserve concept invoked was:

5) Habitat patches that are connected by habitat corridors, or that are set in a landscape matrix of similar structure to the habitat patches, will allow a target species to disperse freely among patches and will tend to support a species for longer periods than habitats not so situated.

We were aware of few published accounts to confirm the corridor concept (for example, see Fahrig and Merriam 1985, Henderson et al. 1985). Preliminary results from Brazilian rainforests suggest that corridors may be effective in facilitating the recolonization of isolated forest fragments by ant birds (Lovejoy et al, 1986). Anecdotal evidence suggests that corridors may permit dispersal between patches for chaparral-requiring birds in California (Soule et al. 1988). However, no direct empirical tests of this concept were possible for Spotted Owls. Biological intuition, however, suggests that the presence of vegetation structure or other habitat features between HCAs that reduce the risk of mortality to dispersers should promote population stability. The results of modeling also suggest that factors that reduce the resistance to movement among HCAs will enhance population persistence (Fig. 6).

To address this concept in the conservation strategy, the ISC reviewed the character of landscapes through which radio-tagged owls had successfully dispersed. There was no evidence of directional movement along "corridors." Nearly all such landscapes, however, contained forested areas with canopy closure exceeding 40% and trees of moderate size. Therefore, standards and guidelines for forest management of the landscape matrix were proposed to ensure a high likelihood of movement of owls among HCAs. The conservation strategy specified that at least 50% of the forest landscape between HCAs consist of forest stands with a mean diameter at breast height ≥ 11 inches (28 cm) and canopy closure ≥40% (the 50-11-40 rule; Thomas et al. 1990:327). The adequacy of this management standard to provide for connectivity among HCAs can only be determined by future long-term monitoring of the HCAs.

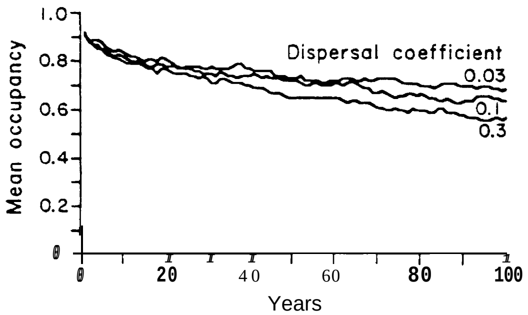

FIG. 6. Mean pair-occupancy proportion for Northern Spotted Owls, plotted against time for a 100-y simulation. The dispersal coefficient was varied from 0.3 (moderate en= vironmental resistance to dispersal) to 0.03 (low resistance to dispersal). Cluster size was 20 pair-sites per cluster, of which 50% were stocked with suitable habitat.

INTEGRATING THE RESULT'S OF HYPOTHESIS TESTS INTO THE MAP

As presented in the previous section, sequential tests of map properties, stated as null hypotheses, provided the guidelines for interim drafts of the conservation plan. For the Nor-them Spotted Owl, test results indicated a positive relationship between HCA size and carrying capacity, a positive relationship between HCA size and population stability (persistence likelihood), a negative relationship between juvenile dispersal capabilities and distance, and an inverse relationship between HCA spacing and population persistence. These reserve design guidelines, inferred from tests of explicit hypotheses, provided a basis for eliminating some HCAs from the conservation strategy, thereby offering opportunities for compromise involving legal considerations and economic concerns. Test results suggest that smaller HCAs. particularly those that are more isolated (all else being equal), would contribute less to the long-term conservation of the Northern Spotted Owl than larger, less isolated HCAs. As a result, a number of small, isolated HCAs, even those currently supporting owls, were removed from the reserve system and became candidate areas for timber harvest. This occurred. presumably, with acceptable cost to the likelihood of species persistence. In addition, the release of these potential HCAs represented a significant compromise and hopefully increases the likelihood of plan adoption.

The ISC thus used the results of hypothesis tests to edit the original map of HCA polygons into a, substantially smaller subset. One final task remained: to test the overall map for consistency between the projected number of owls per HCA, and HCA size and shape. A good relationship was expected since the projected carrying capacities of manv HCAs were adjusted bv location-specific home-range and densitv data. Some d;gree of deviation from a best-fit regression was expected because of geographic variation in key biological parameters (e.g., home-range size, habitat-use patterns,

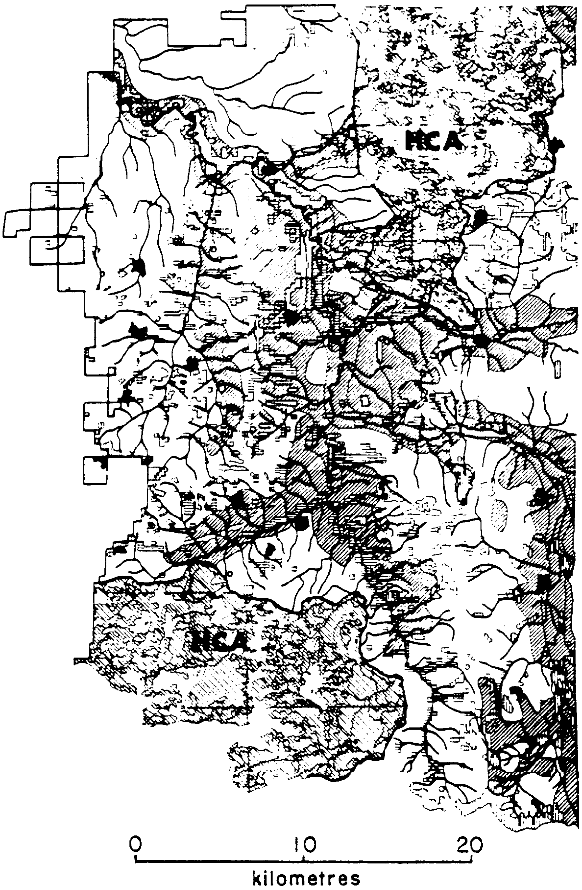

FIG. 7. Close-up of land allocations within a portion of the Mount Hood National Forest, Washington (state), USA. The map shows areas not appropriate for timber harvest (illustrated as hatching), demonstrating habitat connectivity along riparian and scenic corridors and between adjacent habitat conservation areas (HCAs) that facilitates Spotted Owl dispersal. Solid black areas represent 0.3-km^2 (80 acre) "retention areas," in which an active owl nest is located and timber harvest is not permitted.

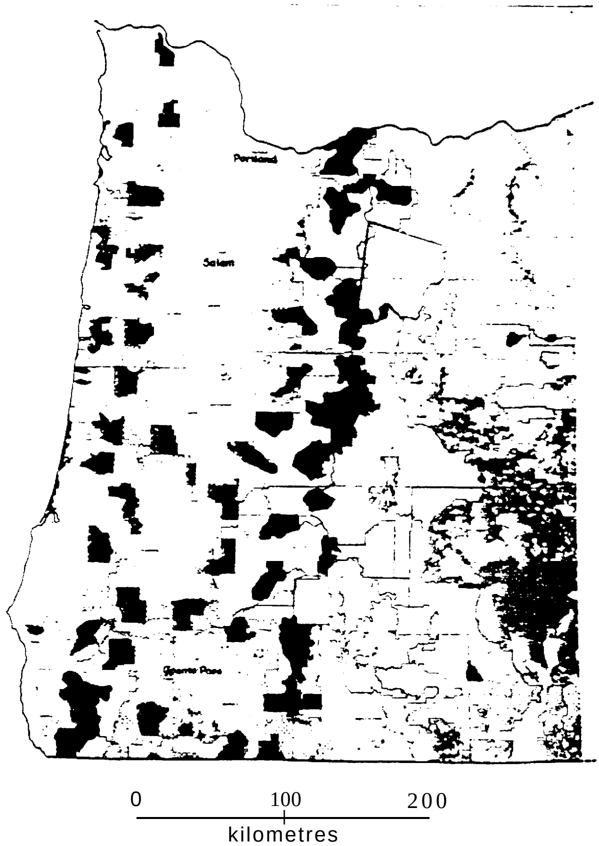

FIG. 8. Map showing the overall conservation strategy (distribution ofhabitat conservation areas, HCAs) for Oregon, USA. The darkest shaded areas are HCAs and Wilderness Areas; all light-shaded areas are other public lands.

etc.). For example, in the initial tests of hypotheses (5) and (7) a tendency for irregularly shaped HCAs to have projected populations smaller than predicted from area data alone was observed. Therefore, the ISC used as independent variables both the area and perimeter of each HCA to test the following null hypothesis:

H_0: No relationship exists between HCA size and configuration and HCA carrying capacity. (10)

Based on the penultimate conservation map of the entire range of the Northern Spotted Owl, a significant regression of carrying capacity on HCA area and perimeter (an edge effect) was found. The best-fit regression model had the form:

$$\ln(\text{projected population}) = b_0 + b_1 \ln(\text{HCA area}) + b_2 \ln(\text{HCA perimeter}).$$

Therefore, null hypothesis (10) was rejected and the ISC concluded that the conservation map was logically consistent. As before, regression diagnostics were used to identify "outlier HCAs," with final adjustments based on empirical data. The final product was a conservation strategy for the Northern Spotted Owl expressed in the form of maps of HCAs (Figs. 7 and 8).

DISCUSSION

An extensive literature addresses the philosophy, merits, and implications of the hypothetico-deductive process in scientific injury (e.g., Popper 1959, Platt 1964) and in wildlife biology in particular (Romesburg 1981). Fundamental issues that have generated the most controversy, such as the appropriate role of prior information in hypothesis formation, seem to call into question the very application of hypothesis testing in applied sciences. Suffice it to say, the process of hypothesis development and subsequent testing is predicated-even dependent- on some amount of prior information. Assumptions about the degree of threat to a population, species, or ecological community motivates the habitat conservation planning process. With that in mind, the values of the hypothetico-deductive method in habitat conservation planning are several.

First, although there is rarely a unique solution to a reserve design problem, the formation of demonstrably falsifiable hypotheses serves to exclude at least some potential conservation responses. Wiens (1984) suggested that field experiments in community ecology should emphasize "refutation of untenable hypotheses, rather than . . . vain verifications of favored hypotheses." Similarly, hypotheses that truly discriminate between empirically refutable reserve design alternatives should facilitate the dismissal of untenable habitat conservation plan options. Moreover, the falsification process assists in the development of alternative hypotheses, the subsequent testing of which focuses planning from conceptual issues to specific design options. For the Northern Spotted Owl, the process of testing the almost mundane null hypothesis-no relationship exists between HCA size and its carrying capacity-led to the recognition that the area necessary should vary across physiographic provinces.

Second, hypothesis testing in habitat conservation planning offers a useful framework for the timely consideration of extrinsic (nonbiological) constraints in the decision process. Since economic. legal, and social considerations motivate habitat conservation planning, many politicians and planners, not illogically, seek to resolve such issues with compelling biological data. However, biological data inevitably provide little helpful information that bears on the salient philosophical questions that drive habitat conservation planning- at what cost should species be protected and what level of certainty of population persistence is acceptable? Certainly biological data cannot resolve the hard practical decisions concerning the intrinsic worth of populations, species, and ecological communities. No exact population size of a certain species in a specific habitat can justify a single given land cost. In this arena, data and dollars simply do not equate. For that reason, we prescribe treatment of intransigent. extrinsic constraints as an initial step in the process. Extrinsic constraints thus define the available landscape for habitat conservation planning but are not otherwise involved in the application of biological data to the process.

Third, the framework that allows both biological and nonbiological contributions to the reserve design process logically orders that process so that it is easily repeatable. Since conservation strategies and habitat conservation plans are rarely unique solutions, and so much is virtually always at stake, the availability of a step-by-step schedule allows planners to document, justify, and defend their products. Conservation strategies and plans are commonly'subject to litigation upon completion, and the conservation biologists involved often experience extensive efforts to discredit their efforts (Murphy and Noon 1991). Antagonists normally exaggerate areas of uncertainty in the scientific process in an attempt to dismiss the importance of the habitats involved. In our opinion, the public has a pervasive misunderstanding of the scientific process. In general, the public fails to recognize that scientists conduct tests of hypotheses to disprove assertions about how the natural world functions. As a consequence, scientists cannot prove the truth of an assertion; rather, ultimately they fail to disprove hypotheses. This is the accepted norm to render conclusions "scientifically credible." An essential aspect of the habitat conservation planning process developed here is that the process of sequential map revision does not depend upon the ultimate truth of one or more specific empirical, model-based, or theoretical research results. Rather, the process follows inferences drawn from research results and hypotheses not falsified by specific tests. If one or more tests performed during the habitat conservation planning process are later shown to be flawed (for example, because of an error in a calculation or because of new information), the strategy is not undermined. On the contrary, the plan is appropriately viewed as having been exposed to one fewer valid test than planners had intended (see a full discussion in Murphy and Noon 1991).

A huge gap exists between the theory and empirical data that is available in biology and their application in efforts to conserve our wild. disturbed, and imperiled landscapes. The habitat conservation planning process is a credible vehicle for the resolution of conflicts that result from the intersection of a burgeoning human population, resource-hungry technologies, and a finite natural. world. The testing of map-based hypotheses is the fundamental means of applying data to, and acknowledging and addressing uncertainty in, the conservation planning process. The conservation planner, nonetheless, must remain aware that habitat conservation planning is driven by, and must be resolved to satisfy, diverse and often conflicting obligations.

Finally, we have emphasized five reserve design concepts that we perceive as universally crucial for consideration in species conservation efforts. Clearly, many species thrive in circumstances that do not meet the design criteria invoked here; however, such species-including edge-adapted, generalist, introduced, and/or weedy organisms-are rarely the targets of conservation efforts. But, for those species that are both adapted to early habitat successional stages and, in fact, are threatened or endangered, these reserve design concepts must be addressed with generous concomitant consideration ofhabitat management regimes to assure species persistence. In general, habitats set aside in the absence of intensive management may not be adequate to meet conservation goals over the long term. For those many species that are now solely restricted to remnant natural habitats (those species for which reserve design is a limited option), we suggest the application of the map-based scientific method presented here to the development of appropriate habitat management plans. Explicit, falsifiable hypotheses-and their rigorous testing with data from research and monitoring-can be as important to habitat management planning as the testing of such hypotheses has been to reserve design for the Northern Spotted Owl.

ACKNOWLEDGMENTS

We dedicate this paper to the dozens of field biologists whose extraordinary efforts provided the knowledge of distribution and habitat associations of Northern Spotted Owls that made this analysis possible. We greatly appreciate the efforts of our good friends and colleagues on the Interagency Spotted Owl Scientific Committee, in particular our fearless leader, Jack Ward Thomas. Jerry Vemer, David Wilcove, Reid Noss, Barry Mulder, Paul Ehr1ich, and Mike O'Connell savaged early drafts of this. much to the betterment of the final product. Kathy Switky in particular brought order and improved syntax to the endeavor. And, to our colleagues at the Center for Conservation Biology and the Redwood Sciences Laboratory, our special thanks. Grants from the William and FIora Hewlett Foundation, the New Land Foundation, and the National Science Foundation made this work possible.

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