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REPORT OF THE SCIENTIFIC ADVISORY PANEL ON THE SPOTTED OWL

William R. Dawson (Chair), J. David Ligon, Joseph R. Murphy, J. P. Myers, Daniel Simberloff, and Jared Verner

FOREWORD

The Cooper Ornithological Society is pleased to present the report of the Advisory Panel on the Spotted Owl to the ornithological community. This panel was asked to judge the present status and future probabilities of this owl's populations with increasing harvesting of old-growth forests in California, Oregon, and Washington. Further, the panel was to suggest research priorities to consolidate the information base on which timber management considerations will be made.

The importance of this issue is manifest in the report. Very probably fewer than 6000 of the two races *Strix occidentalis occidentalis* and *S.o. caurina* remain in Washington, Oregon, and California from Kern County northward, with an estimated 2000 breeding pairs in that area. The Mexican Spotted Owl (*S.o. lucida*) is even rarer. Some observers suggest that the owl is so closely tied to old-growth forests in the northern portion of its range that any further harvesting of these forests would reduce the species in proportion to the area harvested. Many millions of dollars of timber and related jobs hinge on the outcome of decisions made on harvesting of old-growth timber. Thus the biology of this owl is a sensitive issue, but one which deserves a complete and impartial hearing. I feel strongly that the issue received such a hearing from the panel.

A panel of experts was first suggested by the National Audubon Society which contacted the Cooper Society in mid-1985. To make the effort as broadly based as possible, the Society conferred with the President of the American Ornithologists' Union, Dr. Frances James. With Dr. James, we jointly appointed the panel and recommended to the Audubon Society that Dr. William R. Dawson be appointed chair. After his appointment, Dr. Dawson organized the panel, took testimony in the Pacific states, and carefully brought together the final product which you have below. The Audubon Society published a limited number of copies of the report (Audubon Conservation Rep. no. 7, 1986), but it is of such importance to the scientific community, and its history has been tied so directly to the Cooper Society, that we believe it is appropriate to publish it in *The Condor.*

As you will see, the report is extremely comprehensive and a model to all those who attempt such a task in the future. We have not included the appendices, which included a glossary, documents provided to the panel, the panel's agenda, and estimated costs of future research, as we felt that these were unnecessary to the scientific community's understanding of the problem.

The costs of the panel and of the publishing in *The Condor* were met by a private, anonymous donor. We are very grateful to this donor, and to each of the scientific panel members for their long hours of work, dedication to an excellent product, and their fairness in reaching their conclusions. Ornithology, and the Spotted Owl, will long be in their debt.

C. John Ralph
President

I. Introduction

A. Background

In recent years, the Spotted Owl (*Strix occidentalis*) has achieved a notoriety in the Pacific Northwest that contrasts sharply with its inconspicuous nature. This arises from the combination of (1) the close association of the owl with old-growth Douglas-fir forest from the western slope of the Cascades to the coast in Oregon and Washington and in the northwest coastal belt of California, with (2) indications of decline in the numbers of the species in this area as timber operations reduce the available old-growth habitat.

The principal remaining old-growth Douglas-fir forests in Oregon, Washington, and northwest California lie on federal lands, mainly those in the national forests. Cutting these forests without retention of adequate habitat for Spotted Owls could threaten the maintenance of viable populations. Formal concern for the species developed in the Pacific Northwest in the early 1970's. It initially focused on the Oregon population,

then came to include the birds in Washington State. First in response to recommendations of the Interagency Oregon Endangered Species Task Force and subsequently of the Spotted Owl Subcommittee of the Oregon-Washington Interagency Wildlife Committee, management directions for the Spotted Owl on national forests were developed, commencing in 1976. Revisions of these directions were necessary over the ensuing years, for knowledge of this bird in the Pacific Northwest was increasing (see Forsman et al. 1984).

The 1981 Draft Pacific Regional Plan was a benchmark in the management effort. It recommended numbers of Spotted Owl pairs and requirements on distribution to be evaluated in forest planning. This draft also included, in an appendix, the February, 1981, proposed revision of the Oregon Interagency Spotted Owl Management Plan. Issuance of the 1981 Draft Regional Plan was followed by the development of planning directions to the national forests for Spotted Owls and, in May, 1984, by publication of the Final Regional Guide and Final Environmental Impact Statement for the Pacific Northwest Region. A preferred alternative of maintaining 375 pairs of Spotted Owls on national forest lands in Oregon and Washington was specified. Sufficient old-growth habitat areas of 1000 acres (405 ha) each, based on the estimate contained in the 1981 revision of the Oregon Interagency Spotted Owl Management Plan, were to be provided to achieve this goal. Each of the national forests in the Pacific Northwest was assigned the portion of the 375 pairs of owls for which it would be responsible. As the land management plans of the forests developed, it was proposed that approximately 550 Spotted Owl habitat areas of 1000 acres (405 ha) each be maintained.

The appearance of the Final Regional Guide and Final Environmental Impact Statement was followed in October, 1984, by an appeal filed by the National Wildlife Federation, The Oregon Wildlife Federation, the Lane County Audubon Society, and the Oregon Natural Resources Council. This appeal characterized the management provisions for the Spotted Owl as inadequate for assuring long-term viability of the bird in the Pacific Northwest Region.

Representatives of the timber industry intervened in the appeal and claimed that the Forest Service was protecting more habitat than was required for a viable population of owls. The Secretary's Office of the Department of Agriculture reversed the Chief of the Forest Service's decision concerning the Final Regional Guide and Final Environmental Impact Statement, thereby necessitating the formulation of a Supplemental Environmental Impact Statement. This action has brought matters concerning the Spotted Owl in the Pacific Northwest into a new and critical phase that has intensified interest on the part of the timber industry, conservation groups, and various governmental agencies.

B. The Scientific Advisory Panel on the Spotted Owl: Background and Operations

As the controversy concerning the Northern Spotted Owl intensified, an anonymous donor provided the National Audubon Society with funds to allow formation of an Advisory Panel on the species. The composition of this panel was determined by the Presidents of the American Ornithologists' Union and the Cooper Ornithological Society. The Advisory Panel's members and professional affiliations are summarized in the list of authors of this report. The Panel includes both ecologists and ornithologists, none of whom had taken part in the controversy over the Spotted Owl among the various interests in the Pacific Northwest. The National Audubon Society asked the Panel to assess the status and prospects of the Spotted Owl insofar as current information allows, to specify priorities for future research, and to identify management strategies that would assure maintenance of a viable population over the long term. As we commenced our task in late fall, 1985, the appearance of the Supplemental Environmental Impact Statement was becoming imminent. We have been mindful of the likelihood that our deliberations and recommendations would be relevant to assessing the probable effectiveness of the management alternatives identified for the Spotted Owl in that document.

The Advisory Panel has approached its tasks with the realization that consideration of the Spotted Owl produces a special set of concerns. While the long-range viability of the species in the northwestern segment of its range is at risk if present harvest rates of the timber resources of old-growth Douglas-fir forests continue, prompt initiation of prudent management efforts affords a reasonable prospect of assuring the future of the bird in this segment. A major concern arises from the fact that the efforts that will prove

to be prudent are affected by both immediate and longer range considerations. They must not only benefit Spotted Owls in the near-term but also offer a sufficient range of options to respond to any needs for amending management plans that become apparent as information on the bird's population genetics, demography, and reproductive biology develops further.

The Advisory Panel has relied on a variety of sources in developing the information base used in preparing this report. We have solicited documents concerning the Spotted Owl from a broad spectrum of interested individuals and organizations. These documents include articles published in the open literature, reports, position statements, administrative directions, and memos (Appendix II). The Panel also conducted a series of hearings in Sacramento, California, and Vancouver, Washington, in December, 1985, in which researchers on the Spotted Owl and representatives of governmental agencies, the timber industry, and conservation groups, and private citizens presented statements and responded to questions. Participation in these hearings is summarized in Appendix III. The hearings were supplemented by a February, 1986, meeting in Boulder, Colorado, with representatives of the USDA Forest Services responsible for wildlife matters. Finally, the Panel has reviewed relevant parts of the general literature concerning population genetics, demography, and the biology of extinct, threatened, and endangered species to facilitate interpretation of the information available on the Spotted Owl.

In dealing with the Spotted Owl in Washington and Oregon, the Panel identified a general issue: the importance of this bird may well transcend its position as a single vertebrate member of a biological community. Its close linkage with old-growth Douglas-fir forests appears to make it a sensitive indicator of the condition and extent of this important plant assemblage. The importance of this assemblage in the Pacific Northwest is not confined to provision of timber, recreation, scenic values, habitat for an assortment of wildlife, and stable and productive watersheds. Such old-growth forest also supports an array of energy capture and nutrient cycling functions that are of fundamental and long-term importance to the ecology of the region (Maser and Trappe 1984). The Spotted Owl in the Northwest is thus a metaphor for a much broader set of environmental concerns.

As the Advisory Panel commenced its activities, it was deemed appropriate to extend attention to the populations of Spotted Owls in northwest California and in the Sierra Nevada (the taxonomy of these populations as it is currently understood is summarized in II.A). The former population resembles those in the Pacific Northwest in its close ties with old-growth forest. The latter, which occurs in the forests of the Sierra Nevada from the foothills up to approximately 8000 ft (2438 m) at the southern end of this mountain range, apparently differs from these other birds in not being so rigidly dependent on old-growth forest. We have not dealt with the Spotted Owls in Colorado, Utah, Arizona, New Mexico, or Texas. Of more immediate concern here, we have also omitted consideration of the birds in coastal central and southern California (i.e., in Monterey, San Luis Obispo, and Santa Barbara Counties south) owing to (1) a paucity of information on their habitat requirements, (2) lack of any data on demography, and (3) their probable isolation from more northern populations. G. I. Gould, Jr. (pers. comm.), estimates that this coastal central/southern Californian population contains only about 300 individuals. While not as threatened by timber harvesting as their more northern counterparts, these birds may be confronted by other human impacts. Their situation thus requires continuing surveillance.

In view of the above considerations, it is crucial for readers of this report to understand its major orientation. It speaks to prominent concerns and needs regarding the Spotted Owl over its range in Washington, Oregon, northwest California, and the Sierra Nevada, rather than dealing with the status of this bird only in a particular administrative jurisdiction of any single agency.

II. Present Knowledge of the Spotted Owl in the Pacific States

A. Distribution and Migratory Movements

The Spotted Owl was first described in 1860 by Xantus de Vesey on the basis of a specimen collected two years earlier at Fort Tejon, Kern County, California. Subsequent knowledge of the owl's range, occurrence, and morphological variation resulted in the recognition of three subspecies (Bent 1938; Peters 1940; Grinnell and Miller 1944):

Strix occidentalis occidentalis—California Spotted Owl. Range: southeastern Shasta County

south through the Sierra Nevada to Kern County; Coast Ranges from Monterey County to San Diego County; northern Baja California (Sierra San Pedro Martir).

S. o. caurina—Northern Spotted Owl (described by C. H. Merriam in 1898). Range: southwestern British Columbia; western Washington; western Oregon; northwestern California (south to Marin County and east to northeastern Shasta County).

S. o. lucida—Mexican Spotted Owl (described by E. W. Nelson in 1903). Range: southern Utah and central Colorado, south through mountainous regions of Arizona and New Mexico; Guadalupe Mountains of western Texas; mountains of northern and central Mexico south to Michoacan and Guanajuato.

Considerable doubt has always existed regarding the validity of the separation of northern and Californian subspecies. The presumed zones of separation involve a narrow belt extending through portions of Shasta County in northern California and a hiatus through the San Francisco Bay region on the coast. Intense speculation has also existed regarding possible geographic isolation of populations in the Pacific Northwest. In fact, the current position of the Washington Department of Game is that the owl is represented in the state by two discrete gene pools (Juelson 1985). The population occupying the Olympic Peninsula is considered to be reproductively isolated from owls in the Cascade Range by the non forested regions of the Puget Trough. The Department further hypothesizes that the Columbia River constitutes a barrier that genetically isolates the Cascades population in Washington from that in Oregon. Insufficient data exist at present to test these isolation hypotheses; this subject and its implication are dealt with in greater detail in other sections of this report (II.C, V.B).

The extent of movements of the species comprises another matter of uncertainty. Adult Spotted Owls were long regarded as sedentary, whereas juveniles were thought to follow a rather conventional owl pattern of post-natal dispersal. Several recent studies facilitated by radio-telemetric techniques support these views as they pertain to the owls of Oregon and northwest California (Forsman et al. 1984; Sisco 1984; Gutiérrez et al. 1985; Miller and Meslow 1985). B. G. Marcot, a member of the interdisciplinary team preparing the Supplemental Environmental Impact Statement to the Pacific Northwest Regional Guide, has recently summarized the combined results of the various juvenile disperal studies. Although 80% of the radio-tagged juveniles dispersed less than 12 mi (19.3 km), some 14% traveled 40 mi (64.4 km) or more, up to a maximum of 62 mi (99.8 km). The ability of some young owls to travel fairly great distances appears to cast further doubt on the effectiveness of the potential geographic barriers mentioned previously. However, much remains to be learned about dispersal distances and success through various types of landscape features and habitats.

A recent radiotelemetry study (Laymon 1985) in the central Sierra Nevada of California has revealed a hitherto undocumented pattern of seasonal migration by adult Spotted Owls. These birds began a downslope movement in late October, dispersing over distances as great as 19.9 mi (32 km), moving southwestward into distinctly different habitats (pine-oak woodland) where they remained until late winter. They returned to their nest sites in the mixed-conifer forest by mid-April. The downslope movement involved an average descent of 2297 ft (700 m; N = 4 birds), which allowed the owls to occupy winter ranges below the level of persistent snow. Laymon (1985) speculated that the behavioral differences (i.e., in habitat, prey utilization, and migration) between the owls of the Sierra Nevada and the populations of the Pacific Northwest may reflect genetic differences associated with subspecific differentiation (see II.A). However, L. W. Brewer and H. L. Allen (pers. comm.) reported that Spotted Owls in Washington also undertake movements between breeding and wintering ranges. Laymon (1985) correctly asserted that a different spectrum of management challenges is presented by downslope migration in the Sierra Nevada, which brings Spotted Owls into areas that are subject to increasing habitat alteration owing to various human impacts, a situation complicated by the multiple ownerships of the land involved.

B. Habitat Requirements and Prey Base

1. Habitat relations

Considerable effort has been expended in attempts to characterize definitively the habitat requirements of the Spotted Owl. A precise knowledge of the owl's habitat needs is of manifest importance to all parties in the controversy re-

garding the preservation of the species, as well as the larger issue of perpetuating significant segments of the old-growth Douglas-fir forest ecosystem. Prior to the 1970's, very little quantitative information had been acquired on the Spotted Owl's habitat use, local distribution, or abundance, and the bird was usually characterized in field guides and other literature as "rare," "uncommon," or "secretive."

The first published studies to address habitat requirements specifically were those of Gould (1974) in California and Forsman (1976) in Oregon. These have been followed by others seeking more precise definition of habitat needs. These research efforts have been sponsored and/or funded by federal and state agencies, universities, private conservation organizations, and private industry. Gutiérrez (1985) provided an overview of Spotted Owl research during the last decade, with particular attention to habitat studies and investigations of owl dependence on old-growth. Another useful summary of the owl's habitat requirements has been compiled by the interdisciplinary team in Chapter 3, Table 3-3a of the draft Supplemental Environmental Impact Statement (USDA Forest Service 1986). It should also be pointed out that habitat studies have not been confined to the breeding season; diligent attempts have been made to identify habitat needs during fall and winter (e.g., Sisco 1984; Laymon 1985).

The major findings of the various studies on habitat requirements of the Spotted Owl in Oregon, Washington and northwest California, can be summarized as follows:

(a) Most studies have revealed a close association of the Spotted Owl in the Pacific Northwest and northwest California with dense old-growth forest; researchers generally feel that this owl depends on such stands in these areas. A strong correlation appears to exist between age of forest stand and incidence of owl occupancy. Ninety-three percent of 1500 known owl sites in Oregon were in stands exceeding 100 years in age (Forsman et al. 1984). Similar patterns have been observed in Washington and northwest California. Conversely, very few occupied sites occur in stands with little or no old-growth (e.g., 10 out of 595 sites in Oregon, Forsman et al. 1984).

(b) Owls use all major coniferous forest types occurring at low and middle elevations (up to about 4000 ft [1219 m] in Washington) in the Pacific Northwest, with the exeption of certain pure stands with poor vertical foliage stratification (see Table 3-2 in USDA Forest Service 1986).

(c) Because labels such as "old-growth" and "mature" are imprecise and often ambiguous, researchers have characterized optimum Spotted Owl habitat as occurring in forests of uneven age having well-developed stratification (overstory, midstory, understory), with large trees having broken tops and cavities for nest sites, and with a considerable degree of "decadence," i.e., dead snags, many decaying logs, and much debris on the forest floor (see Carey 1985 for review). A detailed summary of specific habitat attributes combining results of all major studies to date is presented in Table 3-3a (in USDA Forest Service 1986, pp. 3–8, 3–9).

(d) The area of suitable habitat or home range required by Spotted Owls has received a good deal of attention. In Oregon, Forsman et al. (1984), using the convex polygon method, found a mean of 6600 acres (2672 ha) of total home range for six pairs of owls fitted with radio transmitters. The amount of old-growth in these home ranges averaged 2264 acres (917 ha). H. L. Allen and L. W. Brewer (pers. comm.) presented data on the home range requirements of Spotted Owls in Washington. The mean total home range area and area of old-growth forests in the home range of pairs amount to 7285 (N = 4 pairs) and 4202 (N = 3 pairs) acres (2949 and 1701 ha), respectively. The quantity of old-growth within the total home range appears to be the major determinant of home range size; where old-growth is broken up into patches or otherwise fragmented, home ranges are larger (Forsman et al. 1984). Size of home range as it relates to management guidelines will be treated in section III of this report.

(e) Like most species of owls, Spotted Owls do not build nests but use naturally occurring sites, which are readily available in the type of mature, decadent forests previously described. The great majority of nests in the Pacific Northwest have been found either in broken tree tops or in tree cavities resulting from heart rot; platform nests built by other species are also used if available. In the study by Forsman et al. (1984), 6 of the 47 nests found were in cavities, with platforms accounting for the remainder.

(f) Some attempts (e.g., Barrows 1980; Forsman et al. 1984) have been made to determine the preferred roosting habitat of the owls. Once again, a strong preference for old-growth forest

was indicated, with 90% of 645 day-roosting adult owls found in old-growth (Forsman et al. 1984) Weather conditions were observed to have a marked effect on perch position within the canopy. During warm weather, owls tended to roost on lower perches, generally in the understory. On the other hand, they roosted mainly in the overstory conifers during cold or rainy conditions.

(g) Several hypotheses have been advanced to account for the dependence of Spotted Owls on old-growth. Biologists who have studied the species extensively regard some five or six of these as being the most plausible; these have recently been evaluated by Carey (1985) and Gutiérrez (1985). In general, these hypotheses relate dependence on old-growth to: (1) availability of suitable nest sites; (2) provision of appropriate thermal cover, especially for avoidance of heat stress; (3) presence and availability of adequate prey, owing to the complex vegetational structure (treated as two separate hypotheses by Carey (1985); (4) protection from predation, especially by Great Horned Owls (*Bubo virginianus*) or Northern Goshawks (*Accipiter gentilis*), which presumably are hampered in foraging efficiency by the lack of open flight space under the closed canopy; (5) possible behavioral and physiological specialization owing to a long coevolutionary history of the owls with old-growth forests. Obviously, several of these hypotheses may each be partially responsible for the observed correlation of the owls with old-growth stands.

A potentially serious complication in the habitat relations of the Spotted Owl in northwest California, Oregon, and Washington arises from the recent appearance of the closely related Barred Owl (*Strix varia*) in the area. This new arrival displays a wider range of habitat preferences than its relative, but the possibility of competition between the two species exists (H. L. Allen pers. comm.; Allen and Brewer 1985). This could aggravate the problem of maintaining viable populations of Spotted Owls in the area with which this report deals.

The habitat relations of the Spotted Owl in areas outside of northwest California, Oregon, and Washington are not well known, although some data are available for the Sierra Nevada population (assigned to the subspecies *Strix o. occidentalis*; see II.A), specifically on distribution (Gould 1977, 1985), food habits (Barrows 1980; Laymon 1985), and general ecology and migration (Laymon 1985). Although noteworthy differences in behavior, migration, and food habits have been detected, the preferred nesting habitats in the Sierras resemble structurally those in the Pacific Northwest, in that the owls appear to require mature forests with understory development, good canopy closure, and some degree of decadence (Gould 1977). No detailed studies of the habitat relations of the owls resident in coastal areas of central California from Monterey County south and in the mountains of southern California (assigned to the same subspecies as the Sierran birds; see II.A) appear to be available, although Bent (1938) described several nests in canyon locations with well-developed riparian vegetation; some nests were in cavities or ledges on cliffs, whereas others were in trees.

As noted earlier, the Spotted Owls of Oregon, Washington, northwest California, and the Sierra Nevada are the primary object of this report. Nevertheless, for understanding the ecological range of the species, there is utility in mentioning some information on the natural history of the birds ascribed to the Mexican race (*Strix o. lucida*; see II.A). These birds, which inhabit the canyons and mountains of the southwest and Mexico, have not received intensive study in respect to habitat relations, but some general information is available. J. S. Ligon (1926) characterized the birds in the mountains of New Mexico as favoring "deep, narrow timbered canyons where there are always cool shady places." Six Spotted Owl localities in the Zion National Park region of southwestern Utah were in "very narrow, steep-walled canyons cut out of the Navajo Sandstone formation by intermittent streams at an elevation of approximately 5118 ft [1560 m]" (Kertell 1977). The narrow nature of the canyons used by the owls creates a temperature and moisture regime considerably more moderate than would otherwise be expected in this generally arid environment. Major plant species in the canyons include ponderosa pine, firs, and deciduous trees such as oaks and box elders. No sightings of owls have been recorded in Zion after September and they are assumed to migrate to lower, warmer elevations for the winter (L. Hayes pers. comm.).

2. Prey relations

The food habits and prey relations of Spotted Owls have been studied relative to the following:

(a) *Prey species consumed.*—Most of the key studies on the ecology of the owl in the Pacific

Northwest and the Sierra Nevada have included data on types of prey taken, with the result that we now have reliable information on the assortment of species used and their relative proportions in the diets of various populations. In Oregon, Forsman et al. (1984) analyzed over 4500 prey items, mainly from pellets, and found that 98% of the prey biomass consisted of vertebrates, with mammals accounting for 90% of the total. Mean body masses of prey ranged from 1.90–5.29 oz (54 to 150 g). Prey species composition varied with forest type; Northern Flying Squirrels (*Glaucomys sabrinus*) and Red Tree Voles (*Arborimys longicaudus*) were the dominant items in forests of Douglas-fir and western hemlock, while Dusky-footed Woodrats (*Neotoma fuscipes*) predominated in the diets of owls living in mixed-conifer forests. At higher elevations, Pocket Gophers (*Thomomys* sp.) and Red-backed Voles (*Clethrionomys* sp.) were the major items. Analyses of diets of Spotted Owls in the mixed-coniferous forest of northern California again show a preponderance of woodrats (Gutiérrez 1985), but Laymon (1985) found greater species diversity in the diet of the Sierran birds. His analysis of the contents of some 800 pellets shows approximately equal proportions of Northern Flying Squirrels, Dusky-footed Woodrats, and Western Gray Squirrels (*Sciurus griseus*). Dietary information on Spotted Owls in the southern mountain states and Mexico is scanty. Kertell (1977) identified remains of woodrats, pocket gophers, and beetles in pellets cast by Spotted Owls in Zion National Park.

(b) *Prey availability, abundance and seasonal variation.*—The available evidence points to greater frequency of Northern Flying Squirrels in the diets of owls in moist habitats, with woodrats predominating as food in drier situations. This is presumed to reflect differences in prey species abundance based on microhabitat and variations in general community structure. For example, Raphael and Barrett (1984) have shown a positive correlation between increasing age of old-growth stands and abundance (and presumably availability) of woodrats. Carey (1985, p. 106) suggested that the favored prey species may not be necessarily more abundant in old-growth than in younger stands, but that "the structure of old-growth forest is better matched to the Spotted Owl's size and method of foraging than the structure of younger forests and that this structure results in a greater availability of prey (more of what is there can be caught) than other environmental structures." In respect to seasonal variation in prey availability and diet, Forsman et al. (1984) found that Northern Flying Squirrels accounted for more than 60% of all prey taken during fall and winter months on one study area; this dropped to only 27% in mid-summer, when pocket gophers and other small mammals increased in frequency as they became more available and vulnerable to predation. Insects as prey were important only during late summer and early fall in this study.

(c) *Foraging behavior.*—Spotted Owls are largely "sit and wait" predators, scanning for potential prey then diving from an elevated perch; this tactic was used whether the intended prey item was on the ground or in the trees (Forsman et al. 1984). They have also been observed to pursue squirrels and other arboreal prey by hopping from limb to limb, and on one occasion to attempt to retrieve chipmunks hiding within a tree cavity by probing with the beak (Forsman et al. 1984). Gutiérrez et al. (1984) suggested that old-growth stands provide more potential foraging perches, and, combined with understory patchiness and gaps in the overstory, an optimum foraging environment for the owls. They further conjectured that Spotted Owls forage ineffectively in shrub-sapling communities and other densely vegetated habitats. Evidence from field studies (Solis 1983; Sisco and Gutiérrez 1984) suggests that different habitat types are used for foraging by males and females, with males hunting the denser forest stands. This difference may be related to greater maneuverability conferred on males by their smaller size (they average about 20.5 oz [582 g] body mass versus nearly 22.5 oz [637 g] for females, Earhart and Johnson 1970) and lighter wing loading. However, more observations are needed for proper evaluation of this possibility. Forsman et al. (1984) regularly observed caching (and later retrieval) of excess food by both wild and captive Spotted Owls.

(d) *Breeding success vis-a-vis fluctuations in diet.*—This subject has been explored by Barrows (1985) who provided data suggesting that an increase in the frequency of large prey (i.e., mammals weighing 3.53 oz [100 g] or more) taken by owls was accompanied by the birds' having improved reproductive success. This may reflect a correlation between owl breeding success and fluctuations of prey populations from year to year,

but direct evidence on dynamics of prey populations is not yet available. Nor are there adequate data on energetic requirements of successfully breeding pairs of Spotted Owls, although it can be assumed that birds could improve the energy cost-benefit relationship, especially in terms of reproductive energy, by taking as large prey items as feasible. Gutiérrez (1985) remarked that Barrow's selective predation hypothesis is supported by the relatively large size of the Spotted Owl's talons, in comparison with those of other species of its group. This would appear to be an adaptation for taking larger size classes of prey.

(e) *Sexual differences in prey selection.*—In addition to the findings on sexual differences in use of foraging habitat mentioned in II.B.2.c, the Oregon studies by Forsman et al. (1984) explored the possibility that male and female owls were partitioning food resources in a manner appropriate to the size dimorphism of the sexes; in other words, do males, which are smaller, take smaller prey than females? Results of the analysis revealed no significant differences in either composition of the diet or mean body mass of prey, and it was therefore concluded that no partitioning of food by the two sexes was occurring.

C. Population Estimates and Demography

1. Population estimates

Because the Spotted Owl is a secretive animal that inhabits relatively inaccessible sites, its precise number is not known. As concern over the owl's viability mounted and research efforts increased, previous estimates were found to be asymptotic and there is no reason to expect previously undetected owls to boost the current figure substantially. E. D. Forsman (pers. comm.) testified that there are approximately 1500 Spotted Owl sites in Oregon, of which about half currently are definitely occupied by pairs; of the remaining half, some fraction is occupied. L. W. Brewer and H. L. Allen (pers. comm.; USDA Forest Service 1986) estimated 500–600 pairs in Washington. G. I. Gould, Jr., testified that there are about 1460 known sites (where a pair of owls has been observed, young have been found between May and September, or a vocal defense of the area has been heard or solicited) of both subspecies in California (the majority of which are in the range of the Northern Spotted Owl), and that there might well be about 2100 such sites in total. By no means all of these are inhabited; for the known sites, pairs have been seen recently in 47%. The Ministry of Environment in British Columbia detected just four sites occupied by Northern Spotted Owls in 1984 (USDA Forest Service 1986). Thus, it is likely that there are between 4000 and 6000 individuals in the Pacific states.

2. Demography

All witnesses agreed that much more demographic information is required to assess both spatial and temporal variation in life history parameters. Heroic efforts have allowed estimates of some key parameters but for species such as the Spotted Owl, which are characterized by long potential lifespan, low reproduction under the best circumstances, and large geographic range, large sample sizes over long periods of time are required to estimate both means and variances. We cannot overstate the importance of reliable estimates for these means and variances. One of the main threats to the continued survival of small populations is "demographic stochasticity" (Shaffer 1981), chance variation in survival and reproduction. To say that mean adult survival probability is x%/year does not mean that exactly x% of the adults survive. Survival one year might be x/2% and another year it might be 3x/2%. Similarly, if the mean number of young produced per pair per year is 1, this does not mean that every year all pairs produce one offspring. By chance alone it could be that in one year very few pairs produce any offspring at all, whereas in another year many pairs might produce more than one offspring. Such random variation is inconsequential for large populations, but for small ones it could be catastrophic—a series of bad years could very quickly destroy a small population.

What is known about Spotted Owl demography in the Pacific Northwest and northwest California? Juvenile survival is particularly poorly known. Marcot (1985) suggested that the meager literature on first-year mortality of Spotted Owls (including predispersal fledgling mortality) indicates 39% death total during these stages. Mortality during dispersal was estimated as 80% so that total first-year survivorship is 12%. However, these estimates are based on only 136 and 33 birds, respectively (E. C. Meslow pers. comm.), and there is reason to think that many of the data were gathered during particularly bad years. Bar-

rowclough and Coats (1985) used the estimate of 19%, based on fewer data.

Yearly adult survival is also not well known. Barrowclough and Coats (1985), using data from only 26 birds tracked for 4 months to 3 years, and assuming an exponential distribution of adult lifespan, estimated yearly adult survival as 85%, a figure accepted by Marcot (1985) and Marcot (1986).

Although reports exist of 2-year-old females breeding (Gutiérrez 1985), Barrowclough and Coats (1985) assumed that first reproduction is normally at 3 years, a figure accepted by Marcot and Holthausen (1986). However, all birds at least three years old do not reproduce every year. An estimate of 0.50 juveniles per pair year was gleaned from 387 observed pairs (Marcot and Holthausen 1986); an earlier estimate of 0.67 (Barrowclough and Coats 1985) was based on only 119 pairs. The key missing demographic data are the age structure and sex ratio of the population. For their modelling effort, Marcot and Holthausen (1986) used 1985 data from banded, censused Humboldt County, California, birds (A. Franklin pers. comm.) to approximate the age structure as 0.35 juveniles: 0.12 subadults: 1.00 adults.

The observed demographic data alone give cause for great concern. If first-year survivorship were 0.12, if adults survived thereafter at the rate of 0.80/year, if breeding commenced in the third year, and if each pair produced 0.50 juveniles per year, then the replacement rate (R_0) of the population (the mean number of female offspring produced by a female during her lifetime) would be only 0.094. This would mean that, in every generation, the population would be multiplied by 0.094—a population of 3000 pairs would become extinct in four generations for demographic reasons alone, if one used these data in a model with non-overlapping generations that approximates the more complicated overlapping generation model. The generation length, given the estimated age structure and survival and reproduction rates, is about 5 years, so the demographic data, if taken at face value, would predict extinction in 20 years!

We hardly think the situation is this dire. After all, if these data on survival and reproduction did not vary from year to year, and if the above values were representative, we could project back just four generations (ca. 20 years) and expect to find over 38 million pairs of owls, an absurdity. Certain important possibilities have not been taken into account in our considerations thus far. One is that the demographic parameters were formerly more favorable, but recent drastic changes in survival and fecundity have occurred. This may be true to some extent, but this would not be a sufficient explanation of the dire prediction and absurd projection back in time.

To understand this point, we must return to the notion of demographic stochasticity, and the variation it introduces into the survival and reproduction parameters. Over the long-term, any species with essentially stable population size has an R_0 of 1.00: it exactly reproduces itself. However, in any year R_0 will not be exactly 1.00; some years it will be smaller, other years it will be greater. If we happened to look in a year when it was lower than 1.00, and used that lower rate, we would predict rather quick extinction, even if the value employed were only slightly less than 1.00. For example, suppose the estimated R_0 for the Spotted Owl had turned out to be 0.80 rather than 0.094. The same non overlapping generation model would still predict extinction in 36 generations. Moreover, if projected backwards, it would imply that 30 generations ago there were 2.4 million pairs of owls. When we take account of variability, we realize that an estimated R_0 of less than 1.00 could simply mean that the data were gathered during a series of bad years with abnormally high mortality and/or poor reproduction. Most of the expert witnesses who appeared before the Advisory Panel felt that, to some extent, the latter scenario is correct. However, 0.094 is an extraordinarily low estimated R_0 and, unless the normal variability of these parameters for this bird is very high, it is reasonable to argue that recent unfavorable changes in these parameters have contributed somewhat to the result. Only further data on variability of the parameters can clarify this matter.

Inclusion of variability to make more realistic models is a complicated matter mathematically and generally requires a computer simulation (e.g., Shaffer and Samson 1985). Statements such as the above, that the population will go extinct in four generations, are replaced by probabilistic statements: an x% probability exists that the population will go extinct in y years. We have not performed such a simulation, although the general result for small populations is that extinction is likely to be hastened if stochasticity is added so that the same parameters are now viewed as

means with a certain amount of variance (Shaffer 1981; Shaffer and Samson 1985). We emphasize that, if the mean parameters were anywhere near the values we describe above, the stochastic model would predict quick extinction for the owl, just as the deterministic one outlined above did.

Marcot and Holthausen (1986) attempted just such a simulation, including demographic stochasticity, and also a deterministic model similar to the one outlined above. Indeed, they found in both the deterministic model and all simulation runs that the population crashed quickly. To proceed at all, they chose to increase fecundity to 0.80 juveniles per pair per year and juvenile survivorship to 0.60, in order to approximate, in the deterministic model, the approximate recent population trends observed by E. D. Forsman and G. I. Gould, Jr., in Oregon and California, respectively. These values may be close to representative or they may be wildly optimistic. There are no data to tell us. Marcot and Holthausen (1986) also added stochastic variation to the survival and fecundity parameters, namely the degree of variation observed in several field studies conducted at different times by different investigators. As noted above, it is important to gather more data on such variability to firm up predictions generated by this sort of model; currently available data probably are too meager to allow a realistic estimate of variability. Thus, the Marcot and Holthausen simulation should be viewed as exactly the sort of approach that must be used to assess the likelihood of extinction from demographic stochasticity, *once data become available.* For now, the method cannot generate predictions in which we can place much confidence, although associated sensitivity analyses can pinpoint which parameters will have the most impact on predictions. This modelling effort must continue in order to give more precise estimates of the role of demographic stochasticity.

In sum, what we can say based on the available data is that the Spotted Owl is a species that, like the California Condor (*Gymnogyps californianus*), is characterized by low fecundity and high adult survivorship. Theory plus experience (see below) tell us that demographic stochasticity presents a real danger of extinction to such a species if average population size is low. Simulation models such as those of Shaffer and Samson (1985) and Marcot and Holthausen (1986) can say just how great the danger is from this source depending on exactly how low the population size is, but such models require more accurate estimates of the parameters and their variability than are currently available. The fact that a population of 3000 pairs could be predicted to face extinction in only four generations with observed parameter values, even without stochasticity, suggests that the population size is already "low" in this context. This may be especially so—the assumption has been that the rapid decrease in both deterministic and stochastic models with observed parameters is largely a result of a series of unfavorable years resulting in atypical parameter estimates. However, there is no direct evidence that such parameters are not representative, or nearly representative, of the owl in present conditions.

D. Longer-term Considerations

1. Preservation of heterozygosity

Small populations tend to lose genetic variability. There are two potential detrimental effects. First, it is possible that there will be insufficient genetic variation for the population to respond to subsequent environmental change. The population will decline for want of genotypes that can survive and reproduce well in the new environment. Second, small populations have an increasing fraction of homozygotes (for any genetic locus) for two reasons—genetic drift is greater in small populations, so alleles are lost (as noted above), and inbreeding is greater in small populations. In many (but not all) species, increasing homozygosity is accompanied by lowered fitness, apparently for two reasons. First, there is an increasing likelihood that an individual will be homozygous for lethal or severely deleterious alleles. Second, individuals that are heterozygous for more loci tend to be more fit, even if no single locus codes for a lethal or severely deleterious trait. The reason for this tendency is unknown, but the tendency is well established.

For both effects (insufficient genetic variation and increasing homozygosity), we wish to know how large the population must be if it is not to be threatened. However, the population sizes we must estimate are "effective population sizes" (N_e) rather than censused population sizes (N). The only circumstance under which the two population sizes are identical is if the sex ratio is 1:1, the numbers of individuals do not change, all individuals of either sex can potentially mate

with all individuals of the opposite sex, and all individuals contribute genes equally to the next generation. Any deviation from these conditions causes N_e to be lower than N. Examples would be some individuals producing more offspring than others, or a population so widely dispersed that individuals in one part of the range cannot mate with those in another part. For a specified censused population size and a particular deviation of conditions from the assumptions, equations are available that tell what the effective population size is. One can view the effective population size as the size of the population from the standpoint of genetic drift—a population with small N_e is one that loses alleles at a high rate, no matter what the censused population is. Without going into extensive mathematical details, we can state that an apparently small deviation from the stated conditions often produces a surprisingly large decrease in N_e.

There is no accepted view of how large a population must be to contain sufficient variation for evolution in the face of changing environments. Drift always causes variation to be lost while mutation introduces new variation and natural selection acts on this new variation. A widely cited estimate (Franklin 1980) that an N_e of 500 (which would frequently translate to a censused population of at least 1000) is required to preserve sufficient genetic variation cannot be supported on two grounds. First, it rests on only one trait (bristle number) in one species (a fruit fly); second, it is based on a model that assumes no natural selection. Lande, on whose paper (Lande 1976) Franklin based his analysis, says only that the number $N_e = 500$ is "about the right order of magnitude" [50–5000] and "subject to substantial scientific uncertainty" (Lande and Barrowclough 1986). For now, we can specify no minimum threshold number of individuals that would render the Spotted Owl immune to the problem of insufficient genetic variation. We *can* say that there is an increasing likelihood of a problem from this source the smaller the population is.

For the threat of increasing homozygosity, we can do substantially better, even though no direct evidence is currently available for the Spotted Owl documenting decreased fitness of very homozygous individuals. There is every reason to believe that adequate data on fecundity and longevity of individuals with different degrees of homozygosity would indicate the more homozygous ones to be less fit on average (Ralls and Ballou 1982a, 1982b, 1983). We cannot predict how severe this effect will be, as it is of different magnitudes in different species. But the effect is present in the vast majority of species that have been closely examined.

Because empirical data are available from animal breeders, there is a widely accepted rule of thumb that fitness will probably be adversely affected if the effective population size falls below 50 and will not likely be affected if it stays above this number. This is not a theoretical approach; it is simply an average gleaned from experience with several species. The census number that allows an N_e of 50 depends on the degree to which the species violates the conditions outlined above, but it can be much greater than 50.

How does the present Spotted Owl population stand with respect to effective population size, and what would be the effect of a management plan that substantially reduced the current census number? Barrowclough and Coats (1985) have attempted to deal with this question. Based on the very incomplete demographic information discussed above, they concluded that currently the Spotted Owl population is equivalent to a metapopulation divided into several demes, each with an effective population size of about 220. If the censused population were reduced to about 1800 adults, they find the effective population size for the demes would fall to about 87. If this were so, in turn, it would still leave N_e above the critical number of 50, but not by much.

We find two potential problems with this analysis, both of which would tend to lower N_e. First, Barrowclough and Coats specifically assumed that the demographic traits of the birds, including mortality and reproductive rates, would not be affected by increasing patchiness of the environment if the population were reduced through habitat alteration. There are many ways in which this assumption could be violated. As just two examples, we suggest that survivorship would be reduced as young owls disperse, because they would have to go farther, and that reproduction might be lower because there would be fewer prospective mates. Second, Barrowclough and Coats used the equation of Wright (1969) for populations continuous over an area. The Spotted Owl population is *not* continuous over its range; many regions are uninhabited because the present habitat is not suitable. Wright also derived an equation for the situation where a

population is dispersed only in a narrow strip: 1-dimensional rather than 2-dimensional. For similar demographic parameters, N_e for the 1-dimensional equation is much less than for the 2-dimensional equation. It appears to us that the Spotted Owl falls somewhere between these two extremes. The outline of the proposed network in the management plan suggests that owls certainly cannot successfully disperse in all directions from most proposed sites. Rather, at best they will have sites accessible in three of four directions and in many cases the proposed sites are in lines, as in Wright's 1-dimensional model, though the lines will be relatively close together relative to observed owl dispersal distances. Without more knowledge of the owl's dispersal behavior we cannot say more than this, but we believe the effective population sizes may have been somewhat overestimated by Barrowclough and Coats on this account.

In sum, there is no reason for complacency about such small effective population sizes. They seem to be right around a point that has been found insufficient in several other species (Frankel and Soulé 1981), although there is so much uncertainty about the data that current estimates must be viewed as preliminary. Nevertheless, at least until we learn more about the effect of homozygosity on Spotted Owls, it appears to us that the threat from demographic stochasticity is greater, certainly in the short-term, than that from increasing homozygosity.

2. Extrinsic forces

A small population can be gravely threatened by fluctuations in the biotic and abiotic environment. Epizootic diseases, an extraordinary number of predators, a temporary decline in the prey base, adverse weather—all these irregularly occurring events impinge on any population and, through their effects on survival and reproduction, can produce major population declines. They exacerbate the "normal" contribution of demographic stochasticity. Because small populations are much closer to zero to begin with, a greater probability exists that such events can cause extinction. As one example, if an unusual mortality source were density-independent and increased each individual's probability of death to D, the probability that the entire population would go extinct would be D^N, which is a rapidly decreasing function of the population size, N. Probably for any unusual threat one could produce more or less complicated mathematical models, but they would all be idiosyncratic and it would be difficult if not impossible to generalize about how large a population must be to attain immunity to threats of this nature. For some sorts of threats, such as diseases, a certain amount of fragmentation of the metapopulation into partially isolated demes is likely to help mitigate the effect (Simberloff and Abele 1982). All we can say is that stochastic events of this kind are much more likely to impinge heavily on a species with few individuals, such as the Spotted Owl.

E. Extinction: Historical Lessons for Management of Spotted Owls

1. Overview

To put these threats to the Spotted Owl in perspective it is useful to talk generally about the difficulties that small populations have in persisting and then about empirical observations. Extinction can be viewed as a two-stage process. Tabulations of historical extinctions of vertebrates show that the overwhelming majority were ultimately anthropogenous–human activity such as habitat destruction and hunting initiated a trajectory that inevitably led to extinction of the particular species (references in Simberloff 1986). However, in many instances these activities ceased well before extinction occurred. What seems to have happened is that reduction of a population from many thousands down to very few thousands or hundreds entrained certain biological processes that ensured extinction even without the persistence of the initial anthropogenous stress. So even though the ultimate cause of recent extinctions can almost always be ascribed to human activity, the proximate causes—the reasons why reduced populations do not usually stabilize at low numbers—are functions of population biology and are currently under intense study (Soulé 1983).

Broadly speaking, there are four reasons why very small populations are not likely to persist: (1) demographic stochasticity; (2) genetic deterioration; (3) extrinsic forces; (4) social dysfunction. We have defined and discussed (1)–(3) above with respect to the Spotted Owl. Social dysfunction arises in two ways. First, certain species have characteristic social behavior that renders them especially vulnerable to extinction—for example, group mating displays (Soulé 1983). Second, once

a population is very small there may be too few individuals to stimulate or consummate some critical behavior, such as some sort of group stimulation of mating behavior. For the Spotted Owl no such behavior has been described.

2. Historical extinctions

We know very little about the death throes of species that have become extinct in historic times, but all four of these factors are implicated in some of them (Simberloff 1986). A good example is the Heath Hen (*Tympanuchus cupido cupido*). Most conservation books state that habitat alteration and hunting eliminated it from the eastern United States in 1932. However, these activities stopped well before 1932 and the extinction of the Heath Hen is a complicated matter (Bent 1932). The species was originally found from Maine to Virginia and was common in sandy scrub-oak plains. Because Heath Hens were easily killed they were quickly exterminated from accessible areas and disappeared from Connecticut and mainland Massachusetts soon after 1840. A few persisted in New York (Long Island), New Jersey, and Pennsylvania but by 1870 the last individuals were restricted to Martha's Vineyard, Massachusetts. There were 200 birds left by 1890, and fewer than 100 by 1896.

Extinction would certainly have followed quickly except for the establishment in 1908 of a 1600-acre (648-ha) refuge for the last 50 birds. The refuge habitat was systematically improved and by 1915 Heath Hens could be found all over the island: 300 or more birds could easily be flushed from the planted corn and clover, and the population was estimated at 2000. Then began a concatenation of disasters that ended in extinction. In spite of unusual precautions to prevent fires from spreading, a conflagration during a gale in 1916 swept through the breeding area destroying birds, nests, eggs, cover, and food. A hard winter followed, and an unprecedented flight of Northern Goshawks (*Accipiter gentilis*) in its midst reduced the population of Heath Hens to fewer than 150 birds, mostly males. A slight rally in the next few years was insufficient and extensive inbreeding, declining sexual vigor, and the excess of males brought the birds to the brink of extinction. Worst of all, in 1920 the poultry disease blackhead, brought to the island with domestic turkeys, killed many Heath Hens. Only 13 birds remained by 1927, 11 of which were males. In 1928 there were only 2 birds, and after December 8 of that year, only one survived—it was last sighted on March 11, 1932.

We see in this tale that at least three factors—demographic stochasticity, genetic deterioration, and extrinsic forces—played a role in the demise of the Heath Hen, and that this trajectory or some version of it was inevitable even after direct human destruction had stopped. The population, even when it reached 2000, was sufficiently small that there was high likelihood that one or more of these factors would reduce it greatly and, ultimately, take it to extinction.

The travail of the Heath Hen is the best studied extinction process for a bird. However, various of the factors enumerated above can be strongly implicated in other species such as the Ivory-billed Woodpecker (*Campephilus principalis*) and the Carolina Parakeet (*Conuropsis carolinensis*). Two related threads run through many avian (and other) extinctions: numerical decline and habitat specialization. As numbers decline, the four forces already discussed become ever more likely to lead to extinction. Species with narrow habitat requirements are often subjected to a double threat. As their habitats become reduced and progressively more patchily distributed, not only are numbers reduced but formerly continuous populations are depleted. This depletion fragments these formerly single populations into a series of small populations having very limited interactions. At this point the threat is much greater for two reasons. First, each small population is much more likely to undergo extinction than is a single large population, simply because its numbers are smaller. Second, once a small population is eliminated by any means (environmental catastrophe, demographic stochasticity, etc.), the site is much less likely to be recolonized than would be a piece of suitable habitat embedded in a large, continuously inhabited range.

The Ivory-billed woodpecker, which inhabited virgin hardwood forests of the southeastern United States, is the classic example of the vulnerability of a species tied to old-growth habitat. The major logging activity leading to the extirpation of these woodpeckers took place between 1885 and 1910–15 (Tanner 1942), and the disappearance of the birds in a particular area coincided closely with timber cutting. The last record of breeding ivory bills was in 1939 in a remnant tract of virgin forest, only about 15 years after the major logging activity in the region. The fate of Ivory-billed Woodpecker illustrates that

once the habitat of a specialized species, even one with a large geographic range, is largely destroyed, extinction can occur very rapidly.

3. Endangered species

Many extinct and endangered species, such as the Heath Hen and Whooping Crane (*Grus americana*), became or have become concentrated in a single geographic area. Such a circumstance leads to an increased probability that one or a few chance events will eventually lead to extinction. Recognition of this fact led the U.S. Fish and Wildlife Service to initiate a program designed to develop a second free-living population of Whooping Cranes (USFWS 1978a, 1978b), in addition to a captive population. To date, no reproduction has occurred in the second population (currently consisting of 28–32 birds) and the sole reproducing population remains extremely vulnerable to just such a scenario (e.g., a hurricane on the Texas coast during the time the cranes are present).

The Red-cockaded Woodpecker (*Picoides borealis*) of the southeastern United States has been designated an endangered species. Like the Spotted Owl, it is a habitat specialist dependent on old-growth forest, and thus, like the owl, a topic of intense controversy. Although this species has a large geographic range extending from the southern Atlantic coast to Oklahoma and Texas, its habitat has been greatly reduced (USFWS 1985) by timber harvesting. Currently it occurs only in fragmented pockets of suitable habitat. Loss of habitat continues and we can expect, in the absence of prompt and effective management, that the woodpeckers eventually will be restricted to a few widely separated populations at best (USFWS 1985; Ligon et al. 1986).

The Black-footed Ferret (*Mustela nigripes*) is perhaps the most dramatic example of the inherent vulnerability of species with highly restricted geographic ranges. The excitement generated by the rediscovery of this animal near Meeteetse, Wyoming, in 1981 has been dampened by the subsequent decline in the population from over 100 individuals in 1984 to 15–31 in 1985 (Weinberg 1986). The precipitous decline was apparently caused by the introduction of a contagious disease, canine distemper, into this sole remaining population.

In many respects, the Kirtland's Warbler is the best studied rare and endangered species of bird in North America. Breeding Kirtland's Warblers are restricted to jack pine (*Pinus banksiana*) barrens in a few countries in the Lower Peninsula of Michigan, and within jack pine forest the ecological requirements of this bird are highly specific (Mayfield 1960). Although there is no evidence suggesting that the birds were ever widespread or common within historic times, they probably were most numerous in the 1880's and 1890's (Mayfield 1960). The first complete census, undertaken in 1951, indicated about 500 breeding pairs, as did the second census a decade later. However, the third census, in 1971, documented a population decline to about 200 breeding pairs (Mayfield 1978). This decline was attributed primarily to the effects of Brown-headed Cowbirds (*Molothrus ater*) on the nesting success of the warblers. Emergency measures were initiated to control cowbirds in the breeding areas and to manage large tracts of national and state forest lands exclusively for the warblers. These strong measures stemmed the decline in numbers of breeding birds, but over the past decade they have not led to an increase. However, without human intervention the species would probably be extinct today (Mayfield 1978).

One might argue that species composed of few individuals can persist over time and that several hundred pairs of Spotted Owls should be sufficient to preserve the species in the area dealt with in this report: Oregon, Washington, northwest California, and the Sierra Nevada. The Whooping Crane, Snail Kite, and, possibly, Kirtland's Warbler (Table III) might be regarded as cases supporting this viewpoint. However, such a conclusion would be spurious. Although numbers of cranes and kites have increased dramatically on a percentage basis over the past few years, their ranges remain so restricted and/or their habits so specialized that a single catastrophic event could exterminate them. Similarly, the Kirtland's Warbler continues to be extremely susceptible to an unpredictable event, either on its breeding or wintering grounds. Despite concentrated major efforts on its behalf, this species has not increased in numbers over the past 15 years. In short, the increased or stabilized numbers of these three populations probably should be viewed as no more than minor interludes on a time-numbers chart; the birds are almost as vulnerable to environmental perturbation as when their respective numbers were at their lowest.

TABLE III. Some endangered species or subspecies of American birds and current estimates of their numbers in the wild.[1]

Species	Number of birds[2]
Wood Stork (*Mycteria americana*)	2400
California Condor (*Gymnogyps californianus*)	5–7
Snail Kite (*Rostrhamus sociabilis plumbeus*)	600
Bald Eagle (*Haliaeetus leucocephalus*)	3300
Peregrine Falcon (*Falco peregrinus*)	300
Attwater's Prairie Chicken (*Tympanuchus cupido attwateri*)	900
Masked Bobwhite (*Colinus virginianus ridgwayi*)	300
Yuma Clapper Rail (*Rallus longirostris yumanensis*)	2000
Whooping Crane (*Grus americana*)	96 (natural population)
Inland Piping Plover (*Charadrius melodus circumcinctus*)	1600
Eskimo Curlew (*Numenius borealis*)	A few dozen at most
Red-cockaded Woodpecker (*Picoides borealis*)	4500–10,000
Kirtland's Warbler (*Dendroica kirtlandii*)	400
Dusky Seaside Sparrow (*Ammodramus maratimus nigrescens*)	0

[1] Estimates provided by S. W. Hoffman, USFWS.
[2] Estimates based on various census procedures and assumptions (e.g., for the monogamous Kirtland's Warbler, a singing male is taken to represent a pair of birds). For the Snail Kite, Bald Eagle and the Peregrine Falcon, the population sizes specified pertain to the birds in (a) Florida, (b) the contiguous 48 states, and (c) in the U.S. Rocky Mountains, respectively.

4. General lessons

What general lessons do species such as the Ivory-billed Woodpecker and/or Kirtland's Warbler provide? (1) Species with specialized habitat requirements often are incapable of altering this behavior. (2) Habitat loss thus leads inevitably to decreased numbers. (3) The decreased numbers are likely to be accompanied by fragmentation into small populations. Once the small populations start being extinguished, recolonization of their sites is so infrequent that geographic range contracts. (4) Restriction of geographic range to one or a few sites leaves a species particularly vulnerable to extinction from environmental stochasticity. (5) Thus, once a severe decline in numbers owing to habitat loss begins, it can accelerate and quickly lead to extinction. (6) Low numbers of specialized individuals are highly vulnerable to new ecological factors, and such factors are often unpredictable. Who would have thought the Brown-headed Cowbird eventually would threaten the Kirtland's Warbler with extinction, or that the Barred Owl would expand its range sufficiently to overlap that of the Spotted Owl? (7) Once a species is reduced in numbers to some low point, its continued existence becomes increasingly precarious and large scale human intervention, often expensive, is required to prevent extinction (e.g., Kirtland's Warbler, Whooping Crane). Even so, such programs may be unsuccessful (e.g., Heath Hen, California Condor).

Although all of the species' scenarios we have discussed above have points in common with and points in which they differ from the case of the Spotted Owl, the two species that stand out as the most instructive are the Ivory-billed and Red-cockaded Woodpeckers. In each case the bird has (or had) a broad geographic range but is (or was) restricted to old-growth forest. Such forest was originally widespread throughout the bird's range, but was reduced in extent, becoming increasingly patchy. The Ivory-billed Woodpecker was eventually reduced to just one restricted population and the elimination of that population constituted extinction. The Red-cockaded Woodpecker is in the process of being reduced to small and increasingly isolated populations. Little imagination is required to see either the Red-cockaded Woodpecker or the Spotted Owl's following a tragic trajectory similar to that of the Ivory-billed Woodpecker. Because this owl seems so highly dependent on old-growth forest in most of the area with which this report is concerned, because its reproductive rates are so low and variable, and because established adults are extremely sedentary, the possibility of its extinction as its habitat is further reduced must be taken seriously. The range of the Spotted Owl is still large, a circumstance making it appear that this bird is immune to the sort of catastrophe that ultimately befell the Heath Hen. But the Heath Hen, and, more analogously, the Ivory-billed Woodpecker once had large, continuous

ranges and each of these was eventually eroded to a point where only a single, narrowly distributed population remained.

With these concerns founded on the fates of several North American bird species in mind, we urge conservatism and additional research (see V.B) in development of management schemes for the Spotted Owl. The key point to be gained by review of the fates of other specialized North American bird species is that a conservative approach is essential. Currently available options must not be foreclosed. In particular, if the number of owls is reduced below some as yet undetermined minimum, extinction might ensue so quickly that no action could stop it.

III. Alternatives Presented by the USDA Forest Service for Management of Spotted Owls in the Pacific Northwest Region

Much of the information that the Advisory Panel has received pertains to the status and prospects of the Spotted Owl on national forests of the Forest Service's Pacific Northwest Region. We have tried to maintain a broader orientation than this, extending our concern to populations in northwestern California and the Sierra Nevada, which we believe are linked with their more northerly counterparts via suitable habitat in the national forests of Northern California and southern Oregon. We are convinced that our orientation toward developing recommendations for maintenance of viable populations of Spotted Owls over a broad geographical area in the Pacific states is more sound biologically than confining our attention to one regional jurisdiction of the Forest Service. Moreover, it calls attention to the vital role that other agencies—federal, state—as well as private interests should play in: (1) maintaining suitable habitat for Spotted Owls where it presently exists in land under their respective jurisdictions; and (2) restoring key parts of the historic range of these birds (e.g., coastal portions of southern Washington and northern and central Oregon).

Our recommendations speak to the numbers of Spotted Owls needed to assure maintenance of a viable population for Oregon, Washington, northwest California, and the Sierra Nevada, but we cannot ignore the management alternatives that are likely to be included in the Supplemental Environmental Impact Statement under consideration for the bird by the Pacific Northwest Region of the Forest Service. The national forests administered by this unit contain most of the old-growth Douglas-fir forest available to this bird in Oregon and Washington. The management alternatives receiving detailed evaluation in the course of preparing the Supplemental Environmental Impact Statement (USDA Forest Service 1986) are listed below.

(a) *Provide no formal measures to protect the Northern Spotted Owl.*

(b) *Provide habitat areas for owls located in areas not suitable for timber production and provide dispersal habitats in a stepping-stone fashion to link these areas.*

(c) *Provide 417 habitat areas for Northern Spotted Owls with each habitat at least 300 acres (121 ha) in size.*

(d) *Provide 551 habitat areas at 1000 acres (405 ha) each.*

(e) *Provide 810 habitat areas at 1000 acres (405 ha) each.*

(f) *Provide 784 habitat areas in clusters of three areas each. Each cluster of three habitats will be 6600 acres (2672 ha).*

(g) *Provide 1000 habitat areas averaging 2200 acres (891 ha) each.*

(h) *Provide for no further reduction in Spotted Owl habitat and, in addition select areas capable of growing into suitable habitat condition.*

(i) *Provide 551 habitat areas averaging 2200 acres (891 ha) each.*

(j) *Provide 620 habitat areas averaging 2200 acres (891 ha) each in Oregon and 4200 acres (1700 ha) in Washington.*

(k) *Provide 1000 habitat areas averaging 2900 acres (1174 ha) each.*

The two considerations we wish to comment on in this section of our report are spatial in nature. The first of these concerns the size of the habitat areas to be managed. Recent findings suggest that the area of old-growth required in the home ranges of Spotted Owls increases between northwest California-Oregon and Washington. The area of old-growth forest contained in the home ranges of pairs averages approximately 2000 acres (810 ha) in northwestern California (ca. 1900 acres or 769 ha) and Oregon (ca. 2300 acres or 931 ha), but is 4200 acres (1700 ha) in Washington (H. L. Allen and L. W. Brewer pers. comm.). We are thus drawn to the alternative (j) that takes this difference into account. The situation is complicated by the fact that the figure for the Sierran population appears to differ from

the figures cited thus far. Preliminary information based on movements of radio-tagged individuals indicates that the average old-growth in the home ranges of pairs is 1200 acres (486 ha) (S. A. Laymon pers. comm.).

As we have discussed previously (II.B), the home ranges of Spotted Owls vary considerably, presumably in relation to quality and structure of habitat (including degree of fragmentation). Thus use of average figures for management standards will fall short of meeting the needs of the above-average segment of the population. Most of the management alternatives under review by the Forest Service reflect a concern for maintenance of heterozygosity through prevention of excessive inbreeding. Habitat areas are to be no more than 12 mi (19.3 km) apart when arranged in clusters of three. With single habitat areas, the distance is not to exceed 6 mi (9.7 km). The concern with establishment of a network of Spotted Owl habitats is well taken. The network is critical not only from a genetic standpoint but also for facilitating repopulation of areas lacking one or both members of an owl pair as a result of predation or other stochastic event. With our interest in treating the needs of the Spotted Owl in northwest California and the Sierra Nevada, as well as in Oregon and Washington, certain linkages appear especially important. These include the connections between: (a) habitat areas in coastal Oregon and in the Oregon Cascades; and (b) such areas in the Sierra Nevada and those in northwestern California and southern Oregon. Bureau of Land Management holdings (the so-called "O and C Lands") represent the key to (a). In the case of (b), the portions of the Shasta and Lassen National Forests in Shasta County, California, as well as adjacent private lands are involved.

IV. Implementation and Monitoring of Management Efforts

A. Implementation

Any management plan developed to assure long-term maintenance of Spotted Owls can achieve that objective only with effective implementation. We have learned of several cases where implementation of current Forest Service direction for Spotted Owls has fallen short of the stated standards and guidelines. Elements essential for effective implementation of any plan include (1) a clear understanding by decision makers of the problem and of the public's concerns; (2) a sincere desire to take action in line with legal mandates and the public's wishes; (3) development of rigorous and clear standards and criteria for on-site implementation of the selected planning alternative; (4) conscientious execution of the final management plan and implementation standards; (5) unambiguous accountability for item (4); (6) periodic evaluation (monitoring) to assure that the plan is working; (7) research on major unknowns; and (8) adaptation of the management plan to new knowledge.

The significance of the problem (item 1 above) is indicated by the many published studies and analyses summarized in previous sections of this report; by laws such as the National Environment Policy Act, the Endangered Species Act, and the National Forest Management Act; and by public pressures expressed in court actions. Because we believe that most decision makers sincerely want to manage resources in accordance with the public's wishes (item 2), we address here only items (4), (5), and (6). Items (7) and (8) are discussed in V.

B. Executing the Management Plan

If the plan is clearly written, its execution should largely follow as from a cookbook. However, such a plan should contain some provision for flexibility consistent with final goals, to deal with unforeseen contingencies and new information. For example, certain objectives may not be immediately attainable because required conditions are unavailable. In such cases, a manager should select the alternative most likely to assure early attainment of these objectives. In this connection, implementation of present Forest Service standards and guidelines for Spotted Owls sometimes has resulted in the selection of habitat areas later found to be devoid of owls. Some of these areas even fail to meet the minimum management requirements. Instead, they were selected to fulfill network criteria, thus satisfying another requirement of the guidelines and assuring, through management for eventual old-growth conditions, that a fully functional network will eventually become established. Nevertheless, because the network has been developed to assure long-term maintenance of the population, it must also provide immediately for a sufficient number of breeding pairs, lest irreversible deleterious effects ensue. Given present uncertainties about

what that exact number is, we should not risk foreclosing future options for attaining various levels of population viability by reducing the actual number of breeding pairs below a level currently viewed as "safe" (see V.B.1). Consequently, for each habitat area in the network that cannot be shown (by repeated on-the-ground surveys) to have a breeding pair of owls, an interim home range with a known breeding pair should be added to the network. We define "interim" here as the period extending until such a time as the network site is confirmed to have use/occupancy by a breeding pair of Spotted Owls.

C. Identifying Accountability

Accountability should fall to those who make decisions. Apparently this process can founder in the Forest Service as well as in other agencies and organizations, because of a high turnover rate among line officers. The person who made the key decisions not infrequently has been transferred by the time a problem is discovered. We have no easy remedy for this situation, although longer tours of duty for line officers would help.

More effective use of the current performance evaluation system would also be valuable. For example, a sample of performance standards for Forest Supervisors and District Rangers contained only one direct mention of Spotted Owls. Management attainment items typically were identified only by reference to sections of the Forest Service Manual, making it difficult for the uninformed to understand what these attainments really should be and how they might relate to Spotted Owls or other resources. In contrast, this was not true of attainments associated with timber outputs and forest regeneration. These were usually identified specifically in the standards, in addition to being referenced to sections of the Manual. Some would construe this as evidence that multiple-use management in the Forest Service really means timber first and other resources second.

We suggest that accountability for wise stewardship of all resources in our national forests would be better accomplished with a different approach to the yearly writing of performance standards, especially those of Forest Supervisor and District Rangers. Specifically, targets, at least for the major attainments in each resource category (e.g., timber, wildlife and fisheries, range, watershed, soil, recreation, and cultural) should be spelled out clearly and specifically in the performance standards, as is now done only for timber targets. For brevity, some of the minor attainments might still be itemized by reference to the Manual.

D. Periodic Evaluation (Monitoring)

An effective monitoring system is needed to determine (1) occupancy rate of habitat areas in the network by breeding pairs of Spotted Owls, (2) population level and structure, and (3) reproductive rate. The data provided by this system are crucial to determination of whether management directions are being met and whether these directions are adequate for maintenance of viable population levels. Details of any proposed monitoring system should be subjected to review by specialists outside the lead agency for the area involved. In addition, because a viable population of Spotted Owls requires an area vastly larger than that of any national forest, the implementation, execution, and administration of a monitoring program should be the direct responsibility of the state or regional line officers in the agencies dealing with that area. Performance standards of those officers should be clear and explicit on this matter. Current arrangements concerning monitoring and accountability for it impress the Advisory Panel as inadequate to accomplish the objectives. Additional funding or redirection of existing funding undoubtedly will be required, if improved arrangements for accountability and monitoring are to be fully effective.

V. Future Research

A. Introduction

The many uncertainties regarding the ecology of the Spotted Owl and translation of ecological data into an effective management plan help to identify several topics about which additional information is needed. We hope that procurement of this information will ultimately allow relaxation of some of the guidelines recommended in this report, especially those relating to the number of breeding pairs required for maintaining a viable population and the area of old-growth forest needed to support each of those pairs.

It is vital that periodic consultation and coordination (at least annually) occur among the various principal investigators undertaking this research. These efforts will assure (1) that duplication of effort occurs only when needed for replication of key studies or to understand the nature

of geographic variation in various parameters of Spotted Owl ecology and behavior, and (2) that comparable methods will be used when necessary and appropriate.

It is also important to remember that the purpose of the research undertaken is to increase the effectiveness of the management effort. Provision must be made for translating new information from research, following collation and rigorous analysis, into improvements in the management plan. Just as the results from monitoring and the management plan form one feedback loop, research and this plan form another.

B. Research Topics

At least seven major areas of Spotted Owl biology require further study. Where appropriate, we have identified subcategories within those areas, with a brief explanation of why the information is needed and, occasionally, some opinions regarding appropriate methods. Finally, we have assigned priority rankings (on a scale of 1 to 5, with 1 the highest priority) based both on the urgency of the requirement for the information and on how accurate we believe existing data to be. We supplement the comments provided in this section with Appendix III, which contains estimates of the costs of the research program proposed.

1. Demography

a. *Survivorship of juvenile and second-year birds* (Priority 1)
b. *Mean age at first reproduction* (Priority 1)
c. *Age-specific reproductive rate* (Priority 1)
d. *Adult survivorship* (Priority 3)
e. *Voice identification of individual Spotted Owls* (Priority 2)

Research on the above items will provide badly needed information on the structure of Spotted Owl populations. These items need study over an extensive geographic area in relation to habitat characteristics and home range size, especially in old-growth areas. We recommend against the use of radio-transmitters on juvenile Spotted Owls because of uncertainty about the effects of these devices on juvenile survivorship. Radiotelemetry is a standard and highly successful technique for adult raptors. The Advisory Panel's concern relates to the possible encumbrance a transmitter represents for a young bird during the period in which it is perfecting its hunting and flying skills. This demographic research would be aided significantly by technology permitting identification of individual Spotted Owls by voice. Prompt efforts to secure this technology, forms of which appear to exist now, should be undertaken.

2. Dispersal of Spotted Owls

a. *Possible barriers* (Priority 1)

The Puget Trough and the Columbia River might be significant barriers to dispersal of Spotted Owls to and from the Olympic Peninsula and between Washington and Oregon, respectively. Knowledge of these barriers substantially affects the decision on the number of breeding pairs needed to maintain a viable population, so an early resolution is critical. Banding of predispersal young, analysis of mitochondrial DNA and allozymes in owls from both sides of these potential barriers, and assessment of homing by territorial adults displaced across the barriers could facilitate resolution of this question. We recommend against use of radiotelemetry not only for the reason specified in V.B.1, but also because the effort would require an inordinate number of transmitter-equipped birds.

b. *Juvenile dispersal* (Priority 3)

Little information is available about the mean dispersal distance for birds that survived and reproduced. Thus, further studies of this topic are needed. Records of banding returns available from the U.S. Fish and Wildlife Service should be searched, if this has not been done already. In addition, an extensive program of banding predispersal young should be implemented, followed by intensive searches to relocate as many of those birds as possible. As above, we recommend against further use of radio-transmitters for this purpose.

3. Reproductive success

a. *In relation to disturbance such as timber harvesting* (Priority 2)
b. *In relation to habitat characteristics* (Priority 2)

Appropriate features include total size of home range, area of old-growth forest, amount and nature of habitat fragmentation, composition of the vegetation, vegetational structure (number of tree layers, decadence of standing trees, amount of shrub cover, amount of dead-and-downed woody material), and past and present human disturbance (e.g., roads, habitations, recreation areas).

c. *In relation to prey base* (Priority 3)

4. Geographic variation in ecology and behavior

a. *Home range size* (Priority 2)

Information on latitudinal variation in home range size (and included old-growth forest), in particular, may ultimately allow relaxation of the guidelines we have proposed on this issue, especially in the southern part of the range with which we are concerned (i.e., northwestern California and the Sierra Nevada). In addition, altitudinal variation and variation between east and west sides of the Cascades should be explored. Radiotelemetry with adult birds is probably the most feasible approach.

b. *Habitat characteristics* (Priority 2)

c. *Food supply and foraging behavior* (Priority 3)

d. *Migration* (Priority 3)

Migration by birds in Washington between apparently equivalent breeding and winter home ranges needs further study. Furthermore, altitudinal migration by birds in the Sierra Nevada needs further consideration. What, if anything, can be done to assure protection of those Spotted Owls on the winter range, especially in the face of continued residential development in this range?

e. *Geographic variation in risks of predation* (Priority 4)

5. Vulnerability to predation

a. *Vulnerability in relation to habitat characteristics* (Priority 3)

We are particularly concerned with the possibility that increasing habitat fragmentation may subject Spotted Owls to greater risks of predation in connection with their having to travel in relatively open places to reach various segments of their habitat area.

b. *Major species of predators on Spotted Owls* (Priority 4)

6. Displacement of Spotted Owls by Barred Owls (Priority 4)

Although this is potentially a critical issue, management agencies can do little about it at this time other than minimizing habitat disturbance and reduction in size of habitat areas. Its ecological significance, however, makes it a likely topic for funding from other sources, such as the National Science Foundation. Comparison of survival rates between radiotagged and otherwise marked juvenile Barred Owls could allow some assessment of whether our concerns about using radiotelemetry with juvenile Spotted Owls have any basis.

7. Taxonomy (Priority 5)

Uncertainty exists as to whether separation of the Spotted Owl into two subspecies in the Pacific states will stand the test of modern systematic analysis. Whatever the case, some gene flow does appear to occur through Shasta County, California between segments of the population in the Sierra Nevada and those adjoining them in northern California. However, this may be confined to periods coinciding with or immediately following environmental conditions favoring higher than normal reproductive success (G. I. Gould, Jr. pers. comm.). We suspect that for all practical purposes the Sierran birds should be viewed as a southern extension of the population in Oregon and northern California.

The research needs enumerated in V.B 1–7 entail a major effort in terms of both time (at least 15 years for certain items) and money. But the uncertainties in management plans advanced to date for the Spotted Owl will remain until answers are available for most of the above topics. Meanwhile, the only prudent course is conservative management of Spotted Owls to ensure that no essential, future option is foreclosed.

VI. Recommendations

A. Introduction

Most of the remaining habitat suitable for Spotted Owls in Oregon, Washington, northwest California, and the Sierra Nevada is on public land administered by several agencies, primarily the Forest Service. The management plan being developed by this agency will inevitably involve a reduction in habitat available for these owls as timber harvesting proceeds. The specialized habitat requirements of the Spotted Owl, which extensively involve old-growth Douglas-fir in northwest California and the Pacific Northwest, will undoubtedly make a decline in the population of this bird a prominent consequence of this reduction. Depending on the management alternative adopted, this could involve over half of the Spotted Owls currently living in this area. Such a conscious decision for population reduction to a critical level in a non pest species must

surely be unique in the history of wildlife management. The current population of Spotted Owls in California, Oregon, and Washington already is as low or lower than some of the species or subspecies considered by the USFWS to be endangered. Historically, population declines and/or extinctions of North American birds precipitated by human actions have been based on ignorance of one sort or another. However, in this case a considered judgment of a federal agency could begin or accelerate an irreversible decline in the Spotted Owl in northern California, Oregon, and Washington. We caution that more may be involved here than the maintenance of a viable population of a single species of vertebrate. The role of the Spotted Owl as an indicator of the condition and extent of old-growth Douglas-fir forest inevitably links its status with that of some basic relationships concerning energy capture and nutrient recycling within old-growth that are probably of inestimable functional importance to the overall ecology of the Pacific Northwest.

The Advisory Panel has attempted to be as risk-averse as possible in the development of its recommendations for Spotted Owls over the area of Washington, Oregon, northwest California, and the Sierra Nevada. While no recommendations can be risk-free, we do believe that ours give a reasonable chance of protecting the birds in the near term, as well as avoiding the foreclosure of options that may be needed as further information is obtained. The best prospect is the maintenance of a sufficient number of Spotted Owls over a broad enough area and it is this combination our recommendations are designed to provide.

The crucial parts of our recommendations, of course, deal with the number *and* distribution of Spotted Owls that we judge to provide a reasonable prospect for maintaining a viable population in Oregon, Washington, northwest California, and the Sierra Nevada. Nonetheless, it is vital that we also offer guidelines concerning implementation of any management plan and the research needed to put management of the owls on the firmest basis possible. We therefore put forward our recommendations organized into three categories reflecting these considerations.

B. Recommendations Concerning Numbers, Home Ranges, and Distribution of Spotted Owls

(1) *The management program for Spotted Owls in Oregon, Washington, northwest California, and the Sierra Nevada should be directed to maintenance of a minimum total of 1500 pairs of these birds* (see II.C–E). This number is based on recent surveys indicating a *confirmed* population for this overall area of approximately 2000 pairs of Spotted Owls. The Advisory Panel believes that 1500 pairs is an absolute minimum for providing any prospect for long-term survival of the Spotted Owl in northwest California, the Sierra Nevada, and the Pacific Northwest. We are marginally comfortable with this number (which is similar to those characterizing several of the birds listed in Table III) only because the Spotted Owl has a widespread and relatively uniform distribution over this area, in contrast to the restricted distributions characterizing most birds currently regarded as endangered. Our numerical recommendation is thus predicated on the maintenance of this broad distribution. To put the minimum number of 1500 pairs in perspective, we must point out that it represents a decline of 25% from the presently confirmed level of 2000 pairs for the area to which our recommendation pertains. We believe that management proposals involving any smaller numbers of Spotted Owls are unrealistic and incapable of ensuring viability, especially in the absence of firm data concerning important aspects of the owl's population dynamics.

Regarding implementation of this recommendation, we assume that responsibility for maintenance and monitoring of the local populations of Spotted Owls must involve a broad spectrum of federal, state, and private organizations. The Forest Service manifestly will have to assume the lead role in these activities, by virtue of the extensive areas of habitat contained in the national forests. However, the Bureau of Land Management will also have a particularly vital role to play. Indeed, the completion of the habitat network critical to sustaining a proper distribution of the owls is heavily dependent on BLM lands in Oregon.

(2) *Current geographic distribution of the Spotted Owls in Oregon, Washington, northwest California, and the Sierra Nevada should be maintained through a habitat network system like that under development by the Forest Service and cooperating agencies* (see II.D–E, III., IV.B, IV.D). As noted above, this recommendation is inseparable from that specifying the number of pairs of owls. All habitat management areas targeted for the network must have specific map locations that are readily identifiable by the pub-

lic. The need is to provide *immediately* for a sufficient number of breeding pairs of owls. Because the present network system includes many habitat areas that are unoccupied by Spotted Owls, an equal number of "interim" home ranges with known breeding pairs should be added to the network until the areas originally included in the network plan are shown to contain breeding pairs. These interim home ranges should be compatible with the dispersal guidelines used to develop the network. To assure that the network is fully integrated, it is especially important that the segment of it on lands administered by the Bureau of Land Management between the Coast Range and the Cascades in Oregon be included. It is equally critical that all existing home ranges in the Shasta County, California, portions of the Shasta and Lassen National Forests be protected to sustain the linkage across State Highway 299 between the Sierran and northwest Californian segments of the Spotted Owl population with which we are concerned. Acquisition of private land containing active home ranges in this area could significantly contribute to maintenance of this linkage.

(3) *The view that an effective breeding population of 500 always suffices to maintain sufficient genetic variability for subsequent evolution in a changing environment should be discarded from management formulations* (see II.D). As we note in this report (II.D.1), the value of 500 for effective population size (N_e) rests on a poor model applied to one trait in fruit flies. No particular value of N_e can guarantee adequate genetic variability against all environmental contingencies. Moreover, one cannot specify the probability that sufficient genes will exist in a population of particular size without defining the magnitude and nature of the changes confronting it. Unfortunately, these changes cannot be forecast. Therefore all one can say is that the species may be endangered by insufficient genetic variability and that there are fewer alleles, other things being equal, in small populations than in large ones. The Advisory Panel believes that adverse developments for the Spotted Owl arising from demographic and environmental stochasticity are more immediate concerns than loss of heterozygosity and possible inbreeding depression.

(4) *Habitat areas that include 4500 acres (1823 ha) of old-growth forest should be retained for pairs of Spotted Owls in the Washington portion of the network. Habitat areas for accommodating pairs in Oregon and northwest California should provide 2500 acres (1013 ha) of old-growth. On the basis of preliminary information, we recommend that the figure for old-growth in the home ranges of pairs of Spotted Owls in the Sierra Nevada be 1400 acres (567 ha).* (See III) Because certain home ranges with less than the prescribed area of old-growth forest are known to support breeding pairs of Spotted Owls, deviations from the prescription may be allowed, contingent on adequate documentation and approval of a standing committee of experts, the majority of which is drawn from neither the agency involved nor industry. Relaxation of these prescriptions concerning habitat areas should be permitted only if research establishes unquestionably the safety of such an action.

C. Recommendations Concerning Accountability for and Implementation of Management Plans

(1) *Current procedures for guaranteeing accountability of agency personnel responsible for assuring maintenance of viable populations of Spotted Owls should be improved* (see IV.C). This recommendation is directed toward the Forest Service because of its primary role in the management effort, but it should have benefit for other agencies as well. Performance standards should include explicit targets for wildlife and fisheries, range, watershed, soil, recreation, and scenic and cultural values, in addition to timber. Attainment of targets in the various categories should receive equal emphasis.

(2) *A well-designed monitoring system should be implemented on a sample basis* (see IV.D). This system must give reliable estimates of (a) the proportion of network home ranges supporting breeding pairs of Spotted Owls and (b) reproductive rates in relation to population maintenance. The results this system provides should be subject to ongoing review, to determine whether adjustment of the management effort is required. These results should be subject to periodic review by the public.

D. Recommendation for Research

(1) *A well-designed program of intensive and extensive research should be undertaken as soon as possible* (see V.B). Uncertainty about several critical features of the population biology of the Spotted Owl preclude development of a "fail-safe" management plan at this time. These are reflected in the priorities accorded our various

research recommendations. General guidelines for appropriate studies, accompanied by preliminary estimates of costs, are provided in Appendix IV. It is important that management plans be responsive to new information arising from research efforts, following its collation and thorough analysis.

VII. Summary and Synopsis of Recommendation

The Scientific Advisory Panel on the Spotted Owl has developed a set of recommendations concerning the maintenance of the viability of this bird in an area that includes Oregon, Washington, northwest California, and the Sierra Nevada. Some of these deal with the number of birds required, their distribution, and area of their home ranges. The remainder concern implementation and monitoring of management plans, and research needed to increase the precision of the management effort. Our approach differs from that used by the agencies, notably the USDA Forest Service, for it emphasizes number of birds rather than number of habitat areas, and it deals with a natural segment of the Spotted Owl's distribution in the Pacific states rather than a single administrative jurisdiction of a particular agency. Our orientation has been prompted by two considerations: biological reality and the need to involve in the management effort the whole series of agencies administering land containing suitable habitat for these owls in the Pacific Northwest, northwest California, and the Sierra Nevada.

Our recommendations consist of the following:

(1) *The management program for Spotted Owls in Oregon, Washington, northwest California, and the Sierra Nevada should be directed to maintenance of a minimum total of 1500 pairs of these birds.*

(2) *Current geographic distribution of the Spotted Owls in Oregon, Washington, northwest California, and the Sierra Nevada should be maintained through a habitat network system like that under development by the Forest Service in cooperation with other agencies.*

(3) *The view that an effective breeding population of 500 always suffices to maintain sufficient genetic variability for subsequent evolution in a changing environment should be discarded from management formulations.*

(4) *Habitat areas that include 4500 acres (1823 ha) of old-growth forest should be retained for pairs of Spotted Owls in the Washington portion of the network. Habitat areas for accommodating pairs in Oregon and northwest California should provide 2500 acres (1013 ha) of old-growth. On the basis of preliminary information, we recommend that the figure for old-growth in the home ranges of pairs of Spotted Owls in the Sierra Nevada be 1400 acres (567 ha).*

(5) *Current procedures for guaranteeing accountability of agency personnel responsible for maintenance of viable populations of Spotted Owls should be improved.*

(6) *A well-designed monitoring system should be implemented on a sample basis.*

(7) *A well-designed program of intensive and extensive research should be undertaken as soon as possible.*

We believe these measures provide a reasonable chance of maintaining a viable population of Spotted Owls in Oregon, Washington, northwest California, and the Sierra Nevada over the near-term and of retaining options that may be needed as research provides a basis for a more precise standard of management. In the judgment of the Advisory Panel, the case of the Spotted Owl in northwest California and the Pacific Northwest involves more than the welfare of a single vertebrate species. The value of this bird as an indicator of the condition and extent of old-growth Douglas-fir forest may well facilitate protection of some basic functional relationships of this plant assemblage that are vital to the overall ecology of the Pacific Northwest.

VIII. Literature Cited

ALLEN, H., AND L. W. BREWER. 1985. Range overlap of the Spotted Owl (*Strix occidentalis caurina*) and the Barred Owl (*Strix varia*) in Washington and implications for the future. Unpublished abstract of presentation made at Session 11 (Symposium on the Biology, Status, and Management of Owls) of Raptor Research Foundation Symposium on the Management of Birds of Prey. International Meeting, 9–10 November, 1985, Sacramento, California.

BARROWCLOUGH, G. F., AND S. L. COATS. 1985. The demography and population genetics of owls, with special reference to the conservation of the Spotted Owl (*Strix occidentalis*). In: R. J. Gutierrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service, Gen. Tech. Rep. PNW 185:74–85.

BARROWS, C. W. 1980. Feeding ecology of the Spotted Owl in California. Raptor Research 14:73–78.

BARROWS, C. W. 1985. Breeding success relative to fluctuations in diet of Spotted Owls in California. In: R. J. Gutiérrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service, Gen. Tech. Rep. PNW 185:50–54.

BENT, A. C. 1932. Life histories of North American gallinaceous birds. U.S. Nat., Mus. Bull, 162, xi + 490 pp.

BENT, A. C. 1938. Life histories of North American birds of prey (Part 2). U.S. Nat. Mus. Bull, 170, viii + 482 pp.

CAREY, A. B. 1985. A summary of the scientific basis for Spotted Owl management. In: R. J. Gutiérrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service, Gen. Tech. Rep. PNW 185:100–114.

EARHART, M., AND N. K. JOHNSON. 1970. Size dimorphism and food habits of North American owls. Condor 72:251–265.

FORSMAN, E. D. 1976. A preliminary investigation of the Spotted Owl in Oregon. M.S. Thesis, Oregon St. Univ., Corvallis. 127 pp.

FORSMAN, E. D., E. C. MESLOW, AND H. M. WIGHT. 1984. Distribution and biology of the Spotted Owl in Oregon. Wildlife Monogr. 87:1–64.

FRANKEL, O. H., AND M. E. SOULÉ. 1981. Conservation and evolution. Cambridge University Press, Cambridge.

FRANKLIN, I. A. 1980. Evolutionary change in small populations. In: M. E. Soulé and B. A. Wilcox, eds., Conservation biology: an evolutionary-ecological perspective, pp. 135–149. Sinauer Associates, Sunderland, Mass.

GOULD, G. I., JR. 1974. The status of the Spotted Owl in California. Calif. Dept. Fish and Game, Non-game Wildlife Investigations. 56 pp.

GOULD, G. I., JR. 1977. Distribution of the Spotted Owl in California. Western Birds 8:131–146.

GOULD, G. I., JR. 1985. Management of Spotted Owls by the California Department of Fish and Game. In: R. J. Gutiérrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service, Gen. Tech, Rep. PNW 185:21–26.

GRINNELL, J., AND A. H. MILLER. 1944. The distribution of the birds of California. Pacific Coast Avifauna 27, 608 pp.

GUTIÉRREZ, R. J. 1985. An overview of recent research on the Spotted Owl. In: R. J. Gutiérrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service Gen. Tech. Rep. PNW 185:39–49.

GUTIÉRREZ, R. J., D. M. SOLIS, AND C. SISCO. 1984. Habitat ecology of the Spotted Owl in northwestern California: implications for management. Proc. Soc. Am. Foresters, 1983:368–373.

GUTIÉRREZ, R. J., A. B. FRANKLIN, W. LAHAYE, V. J. MERETSKY, AND J. P. WARD. 1985. Juvenile Spotted Owl dispersal in northwestern California: preliminary results. In: R. J. Gutiérrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service, Gen. Tech. Rep. PNW 185:60–65.

JUELSON, T. 1985. Managing Northern Spotted Owls in Washington: the position of the Washington Department of Game. In: R. J. Gutiérrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service, Gen. Tech. Rep. PNW 185:31–33.

KERTELL, K. 1977. The Spotted Owl at Zion National Park. Western Birds 8:147–150.

LANDE, R. 1976. The maintenance of genetic variability by mutation in a polygenic character with linked loci. Genetical Res. 26:221–235.

LANDE, R., AND G. F. BARROWCLOUGH. 1986. Effective population size, genetic variation, and their use in population management. In: M. E. Soulé, ed., Viable populations, pp. 87–123. Cambridge University Press, Cambridge.

LAYMON, S. A. 1985. General habits and movements of Spotted Owls in the Sierra Nevada. In: R. J. Gutiérrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service, Gen. Tech. Rep. PNW 185:66–68.

LIGON, J. D., P. B. STACEY, R. N. CONNER, C. E. BOCK, AND C. S. ADKISSON. 1986. Report of The American Ornithologists' Union Committee for the conservation of the Red-cockaded Woodpecker. Auk 103:848–855.

LIGON, J. S. 1926. Habits of the Spotted Owl (*Syrnium occidentale*). Auk 43:421–429.

MARCOT, B. G. 1985. Summary of statistics of Northern Spotted Owls for Audubon Advisory Panel. Unpublished ms, 14 pp., Dec. 5, 1985.

MARCOT, B. G., AND R. HOLTHAUSEN. 1986. Spotted Owl viability analysis—Process documentation for the Regional Guide Supplement. Pacific Northwest Region, U.S. Forest Service. Unpublished ms, Feb. 19, 1986.

MASER, C., AND J. M. TRAPPE (tech. eds.). 1984. The seen and unseen world of the fallen tree. Gen. Tech. Rep. PNW-164, 56 pp. U.S. Forest Service, Pacific Northwest Forest and Range Experiment Station (in cooperation with USDI Bureau of Land Management), Portland, Oregon.

MAYFIELD, H. 1960. The Kirtland's Warbler. Cranbrook Institute of Science, Bloomfield Hills, MI, Bull. 40, xi + 242 pp.

MAYFIELD, H. F. 1978. Brood parasitism: reducing interactions between Kirtland's Warblers and Brown-headed Cowbirds. In: S. A. Temple, ed., Endangered Birds. Management techniques for preserving threatened species, pp. 85–91. Univ. Wisconsin Press, Madison.

MILLER, G. S., AND E. C. MESLOW. 1985. Dispersal data for juvenile Spotted Owls: the problem of small sample size. In: R. J. Gutiérrez and A. B. Carey, eds., Ecology and management of the Spotted Owl in the Pacific Northwest. U.S. Forest Service, Gen. Tech. Rep. PNW 185:69–73.

PETERS, J. L. 1940. Check-list of birds of the World, Vol. IV. Harvard Univ. Press.

RALLS, K., AND J. BALLOU. 1982a. Effects of inbreeding on infant mortality in captive primates. Internat. J. Primatol. 3:491–505.

RALLS, K., AND J. BALLOU. 1982b. Effects of inbreeding on juvenile mortality in some small mammal species. Lab. Anim. 16:159–166.

RALLS, K., AND J. BALLOU. 1983. Extinction: lessons

from zoos. In: Schonewald-Cox, C. M., S. M. Chambers, B. MacBryde, and L. Thomas, eds., Genetics and conservation, pp. 164–184. Benjamin/Cummings, Menlo Park, California.

RAPHAEL, M. G., AND R. H. BARRETT. 1984. Diversity and abundance of wildlife in late successional Douglas-fir forests. Proc. Soc. Amer. Foresters, 1983:352–360.

SHAFFER, M. L. 1981. Minimum population size for species conservation. Bioscience 31:131–134.

SHAFFER, M. L., AND F. B. SAMSON. 1985. Population size and extinction: a note on determining critical population sizes. Am. Naturalist 125:144–152.

SIMBERLOFF, D. 1986. The proximate causes of extinction. In: D. M. Raup and D. Jablonski, eds., Patterns and processes in the history of life, pp. 259–276. Springer-Verlag, Berlin.

SIMBERLOFF, D., AND L. G. ABELE. 1982. Refuge design and island biogeographic theory: effects of fragmentation. Am. Naturalist 20:40–51.

SISCO, C., AND R. J. GUTIÉRREZ. 1984. Winter ecology of radio-tagged Spotted Owls on the Six Rivers National Forest, Humboldt Co., CA. Final Report. U.S. Forest Service, Six Rivers National Forest. Eureka, CA. 140 pp.

SOLIS, D. M., JR. 1983. Summer habitat ecology of Spotted Owls in northwestern California. M.S. thesis, Humboldt St. Univ., Arcata, CA. 168 pp.

SOULÉ, M. E. 1983. What do we really know about extinction? In: Schonewald-Cox, C. M., S. M. Chambers, B. MacBryde, and L. Thomas, eds., Genetics and conservation, pp. 111–125. Benjamin/Cummings. Menlo Park, California.

TANNER, J. T. 1942. The Ivory-billed Woodpecker. Res. Rep. no. 1. National Audubon Society, xii + 111 pp.

USDA FOREST SERVICE. 1986. Chapters 1–6 of working draft of Supplement to Final Environmental Impact Statement for the Pacific Northwest Regional Guide. Unpublished ms.

USFWS. 1978a. The way of the Whooping Crane. USFWS, Denver, Colorado, 3 pp.

USFWS. 1978b. The transplant experiment. USFWS, Albuquerque, New Mexico, 3 pp.

USFWS. 1985. Red-cockaded Woodpecker recovery plan. USFWS, Atlanta, GA, 88 pp.

WEINBERG, D. 1986. Decline and fall of the Black-footed Ferret. Natural History 95 (2):62–68.

WRIGHT, S. 1969. Evolution and the genetics of populations, vol. 2: The theory of gene frequencies. University of Chicago Press, Chicago.

Reprint requests should be directed to William R. Dawson, Museum of Zoology, The University of Michigan, Ann Arbor, MI 48109.

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