United States
Department of
Agriculture

Forest Service

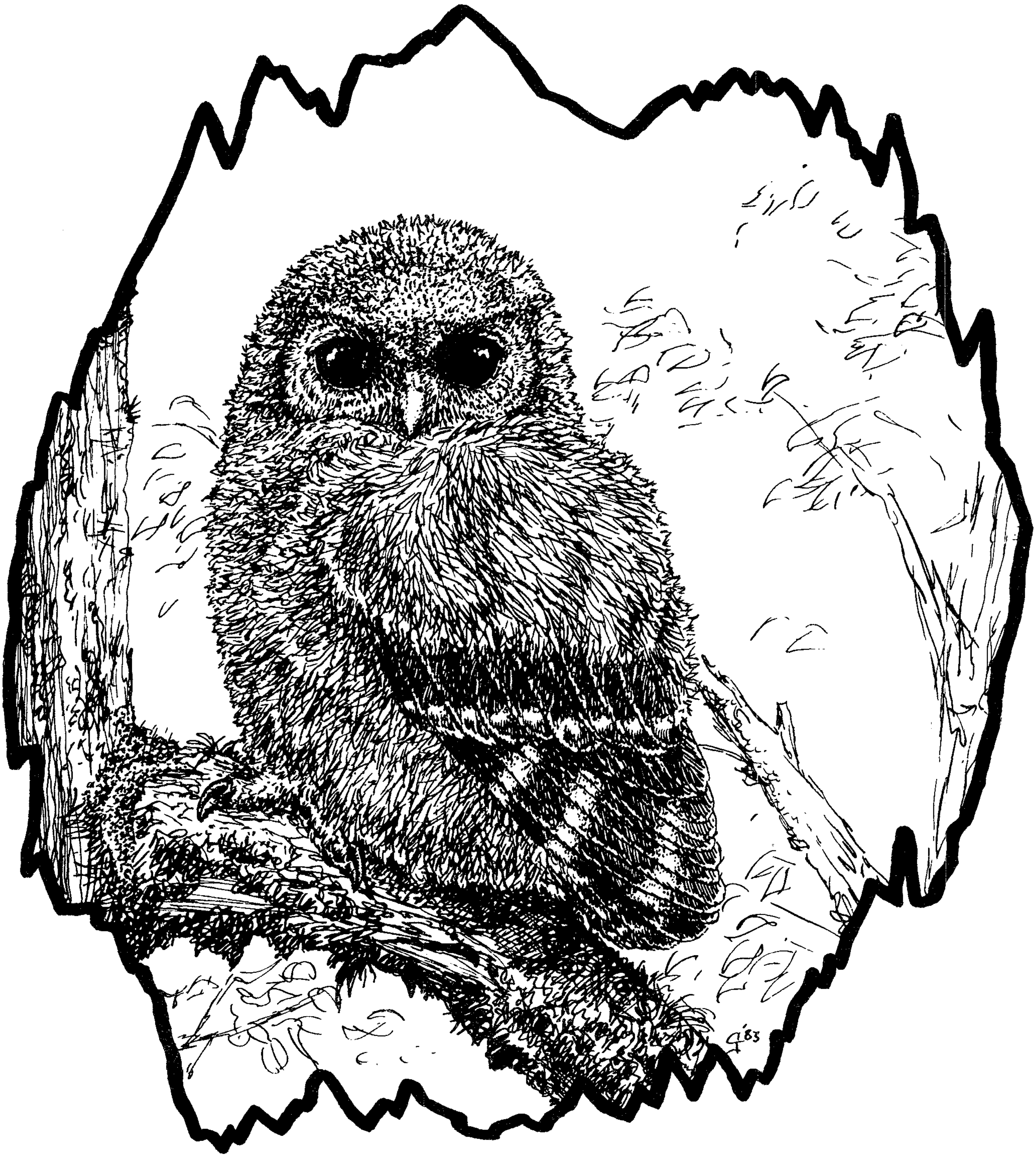
Pacific Northwest
Forest and Range
Experiment Station

General Technical

PNW-185

September 1985

Ecology and Management of the Spotted Owl in the Pacific Northwest



Cover art courtesy Cynthie Johnson, Department of Wildlife, Humboldt State University, Arcata, California.

Ecology and Management of the Spotted Owl in the Pacific Northwest

Arcata, California
June 19-23, 1984

Ralph J. Gutierrez and Andrew B. Carey
Technical Editors

Sponsored by:
Cooper Ornithological Society
Humboldt State University
USDA Forest Service, Pacific Southwest Forest and Range Experiment Station
USDA Forest Service, Pacific Northwest Forest and Range Experiment Station

Published by:
U.S. Department of Agriculture, Forest Service
Pacific Northwest Forest and Range Experiment Station
Portland, Oregon
General Technical Report PNW-185
September 1985

CONTENTS

F

5

INTRODUCTION

RALPH J. GUTIIERRZ AND ANDREW B. CARRY

The spotted owl, Strix occidentalis, has become a species of concern to ornithologists, wildlife biologists, foresters, and environmentalists because of its apparent need for old-growth coniferous forest in the Pacific Northwest. Because of the concern about spotted owls, a symposium was convened by the Cooper Ornitholoical Society during its annual meeting in 1984. [1]/ The society wished to bring concerns about spotted owls before public, scientific scrutiny. Gutiérrez was asked to arrange the symposium, and Carey was invited to cochair the symposium. Together, we expanded the objectives of the symposium and planned this publication.

The symposium was organized into three sections: management, research, and theory. We felt that an understanding of the laws and regulations governing Federal land management, the state of spotted owl management, the biology of spotted owls, and the predictions of ecological theory were all essential for planning and evaluating future research and management for the spotted owl. We wished to bring this information together in an arena of unconstrained discussion and exposition of ideas. Thus we invited both managers and researchers dealing with spotted owls and theoretical biologists who did not have experience with the spotted owl. Because we had limited time for presentations, not all papers published here were presented at the symposium. We have included the unpresented papers to ensure a published report that would be a complete treatment of spotted owl research and management in the Pacific Northwest.

[1]/ The 54th Annual Meeting of the Cooper Ornithological Society, 1984 June 19-23, Arcata, CA.

PLANNING AND MANAGING FOR THE SPOTTED OWL IN THE NATIONAL FORESTS, PACIFIC SOUTHWEST REGION

W. Dean Carrier

ABSTRACT: The spotted owl (Strix occidentalis caurina) has been listed as a sensitive species by the Pacific Southwest Region USDA Forest Service. Past and present-studies-and surveys have led to the development of a region-wide network of owl territories to comply with the maintenance of viable populations as required by the National Forest Management Act. A brief explanation of the network is included.

HISTORY

In 1973 and 1974, the California Department of Fish and Game and the USDA Forest Service funded an inventory of spotted owls to better understand the status of this species in California. This work was carried out by Gould (1977) and resulted in a state-wide population estimate of 192 pairs in five major population concentrations.

During this period individual Forests also began to assess owl populations and habitats and to consider owls in Forest multiresource management activities. Fairly intensive surveys of suspected owl habitats were carried out in at least four National Forests.

W. DEAN CARRIER is the threatened and endangered species biologist for the Pacific Southwest Region of the USDA Forest Service, San Francisco, Calif.

Following the passage of the National Forest Management Act of 1976 (NFMA) and the issuance of the regulations implementing it, the Forest Service began to assess many wildlife and fish species to ensure that viable populations were being maintained, as the Act requires. The spotted owl, because of its purported need of old-growth coniferous habitats, became the focal point of this requirement.

In 1978 the Oregon Interagency Task Force developed a habitat management plan and population requirements for spotted owls on public lands in Oregon. The Pacific Southwest Region followed this lead and began to assimilate data on spotted owl populations and habitat use in National Forests in California. Between 1975 and the present (1984) the Region has initiated, funded, or assisted in no less than 10 individual research projects or status evaluations of spotted owls.

Because the Pacific Southwest Region chose to treat both subspecies of spotted owl (Strix occidentalis caurina and S. o. occidentalis) identically, the system used-is based on the Oregon-Washington Interagency Wildlife Committee's plan with one major exception. This exception is that the actual assessment and allocation of numbers of territories is relegated to the individual Forests.

PLANNING STRATEGY

Using known habitat requirements, as taken from available research data, the task of identifying the numbers and networks of territories to be maintained was assigned to each Forest. To determine these population goals, the Regional plan established guidelines for developing an interacting network of spotted owl territories that would be distributed throughout the geographic range of the species in California north of the Tehachapi Mountains. The criteria provide for grouping, spacing, and specific characteristics of spotted owl territories. The criteria were based on data collected in Oregon and in the numerous local studies that had been conducted in the National Forests of northern California, and on the west slope of the Sierra Nevada range. Habitat requirements were based heavily on the studies by David Solis in the Six Rivers National Forest and by Steve Laymon in the central Sierra Nevada.

It must be stressed that the development of a Regional network, based on a predetermined set of habitat conditions necessary to provide for spotted owl occupancy, was mainly an exercise in modeling National Forest management activities as they relate to and interact with other resource and land uses. In other words, on-the-ground maintenance of individual territories may differ under the standards developed for Land Management Planning. As with most species, local habitat conditions and long-term adaption to specific situations may well be important factors in the success of individual pairs. Broad standards and guidelines cannot encompass all these factors; thus, local adjustments are necessary when actively applying these guidelines to specific areas of land. The modeling assesses the overall costs in terms of other forest resources of maintenance of spotted owl habitat, and on-the-ground application provides for the actual needs of the individual pairs making up this network.

The system for spotted owl habitat maintenance in the Pacific Southwest Region was based on the best information available. This is not to say that we have all the answers; however, our methods were designed to provide for the currently documented needs of this species. Research in the Pacific Northwest and California was reviewed and used in the development of our criteria. The pioneering work of the Oregon Interagency Spotted Owl Task Force and the subsequent development of the guidelines for maintaining viable populations of spotted owls in that State were major factors used in the development of the Pacific Southwest Region's system.

SPOTTED OWL TERRITORIES

The first level of the network is the territory. Territories are areas suitable for maintaining one breeding pair of owls. The ecological characteristics of territories have been determined through research and then translated into vegetative components. For the most part, a territory is comprised of a core area within which the nest site, or probable nest site, is located. This area is to contain 300 acres of suitable habitat. If this amount is not available, the existing stand is maintained. In addition to this core area, an additional 700 acres of habitat within l-1/2 miles of the nest site will be maintained in no more than three parcels, one of which must suffice as an alternate core area.

GROUPED TERRITORIES

The second level of this system is the grouped territories (formerly called Spotted Owl Management Areas or "SOMAS"). These are normally comprised of three individual territories spaced within l-1/2 miles of each other. Some overlap is allowed in providing acreage requirements for the three territories.

FOREST NETWORK

The third level of the system is the Forest network. This provides for a system of interacting groups of territories spaced throughout the known geographic range of the spotted owl in that Forest. The network provides for spacing of these groups between 6 and 12 miles apart although single territories can be no further than 6 miles from adjacent ones.

INTERACTING NETWORKS

The fourth level is the interacting network between National Forests and other public and private land areas maintaining spotted owl habitat. Forests are required to coordinate with adjacent land managers and their networks are reviewed and approved by the Regional Forester.

CURRENT STATUS

Territories for spotted owls have now been delineated in all National Forests, with the exception of the five southern Forests where all known territories will be protected. Using currently accepted survey techniques, territories are presently being verified and boundaries further refined.

The network for National Forest lands in California will provide for approximately 500 pairs. This is exclusive of those pairs that are not a part of the network, but are protected by other land management constraints (e.g., wilderness) and those owls in the five southern Forests. Other resource management agencies and private lands will provide additional territories to add to the overall maintenance of spotted owls in California.

DISCUSSION

The managing of lands to provide for the needs of late vegetative successional species is a new and inexact art, at best. For years, we have had the ability to set back succession for the enhancement of deer, quail, and pheasants; to modify habitat for turkeys, grouse, and elk; or to protect habitats for many other species. There is, however, little evidence of purposeful management to speed up or manage for vegetative succession to provide for those habitats that are developed at the climax end of succession.

In implementing this system we are assuming that the spotted owl will maintain viable populations over time. But, how will we know if the system is working? What additional research is needed to assure this? Are known changes caused by land management activities or a natural sequence of events? These are but a few of the many questions that are asked of us as we try to measure the exactitudes, demanded by the scientific community, with experimental land management schemes based on state-of-the-art information. It is doubtful that there will ever be "enough" information. As natural and human-caused changes occur in these ecosystems, wildlife population will fluctuate accordingly, but probably not altogether predictably. Who will be the one to decide whether global climatic changes, as predicted by some hydrologists, or artifical habitat changes are responsible for population fluctuations in species.

LITERATURE CITED

Gould, Gordon I., Jr. Distribution of the spotted owl in California. Western Birds. 8: 131-146; 1977.

HISTORY AND CURRENT STATUS OF SPOTTED OWL (*STRIX OCCIDETALIS*) HABITAT MANAGEMENT IN THE PACIFIC NORTHWEST REGION, USDA, FOREST SERVICE

Philip L. Lee

ABSTRACT : As information has become available on the status of the spotted owl and its habitat needs, the emphasis on managing for the owls has increased on National Forests. Management of old-growth forests has evolved from rapid conversion of the stands to young timber to the acceptance of the need to retain this special habitat for species such as the spotted owl. Detailed direction for the assessment and development of spotted owl habitat during Forest Planning has been given to National Forest Supervisors by the Regional Forester.

INTRODUCTION

Prior to 1970 little was known about the spotted owl (*Strix occidentalis*) or its habitat in the forests and it was not given any priority in management of National Forests. What little data existed on the owl indicated it was rare and that few sightings had been made. During the early 1970's, as work progressed on legislation for the management and protection of threatened and endangered species, the spotted owl was proposed as "threatened" by the USDI Fish and Wildlife Service (U.S. Department of Interior, Fish and Wildlife Service 1973).

As more people began to look for the owl, and particularly as it became the object of graduate studies, enough was learned about it to question the need for a Federal listing. As a result the owl was not listed at the Federal level but was classified in Oregon as threatened and in Washington as a sensitive species. The spotted owl was given the designation "sensitive" by the Regional Forester, Pacific Northwest Region of the Forest Service (Region 61, and thus was afforded special consideration by management.

Following passage of the National Forest Management Act in 1976 regulations were written for implementation of the Act. These regulations gave special emphasis to the spotted owl because it met many of the criteria for a "management indicator species". Those criteria (Code of Federal Regulations, 36 CFR 219.19(l)) were: (1) that decreases in spotted owl populations indicated potential negative effects of planned management programs; (2) the owl was on the threatened species list in Oregon; (3) the owl was a species of special interest; and (4) the owl represented other species that were dependent upon a major biological community, the old-growth forest.

PHILIP L. LEE is Range, Watershed, Fish and Wildlife staff officer, Siuslaw National Forest, Pacific Northwest Region, USDA Forest Service, Corvallis, OR.

In the short time that the spotted owl has been of special interest a lot of information concerning its life history and habitat requirements has been collected. New information has required a continual change in management direction by Federal land managers. This change is evident in the numerous memoranda and letters between the various agencies and interest groups and in direction being developed for Forest Planning, which I review in this paper.

EARLY PLANNING AND MANAGEMENT STRATEGIES

It is not my intent to go into the details of the early planning efforts regarding numbers of owls or habitat requirements. It is important to note, however, the evolution of acceptance of biological Information and the development of direction for management of National Forest lands for spotted owls.

An interagency committee made up of biologists from the Forest Service, Bureau of Land Management, Fish and Wildlife Service, Oregon Department of Fish and Wildlife, and Oregon State University was formed in 1973 to prepare the first Spotted Owl Management Plan. Objectives of the plan were to determine the number and distribution of spotted owls in Oregon and to recommend habitat management practices. The recommendations coming from this first effort were so controversial that on August 16, 1973, the Regional Forester (Region 6) and the State Director of the BLM in Oregon issued a joint statement that it was undesirable to retain 300 acres of old-growth timber around every known spotted owl nest site. Reasons given were: "(1) rigidly cast prescriptions tend to become the accepted practice...; (2) it appears reasonable to assume that the present old-growth stands located within acceptable elevation limits, contain spotted owl populations...; (3) we are confident that further analysis will verify that sufficient old-growth timber stands exist to provide interim. . .protection.... (4) determination of the desired State-wide production level...should be resolved before total protection of all sighting areas...is undertaken...and; (5) the management by individual animal location philosophy, when applied to all species... presents a land management spectre of considerable magnitude." Management of old-growth timber is a sensitive issue, and there was a desire by some to liquidate the old growth and replace it with young forests. Agency managers were cautious in making decisions that set aside large acreages of old-growth forest until more evidence supported the need.

During the next 3 years evidence continued to come from research and in 1976 the Regional Forester issued direction that "Known nesting sites will be protected until BUMP'S (Biological Unit Management Plans) were developed..." (memorandum from Region 6 Director of Fish and Wildlife Management November 24, 1976). At this same time the BLM suggested that several enclaves where birds were concentrated should be set aside and not harvested for 10 years, during which time investigation would continue.

Management recommendations and a statewide goal of 400 pairs of nesting spotted owls were established from the first Oregon Spotted Owl Management Plan. In January 1977 the Oregon Endangered Species Task Force recommended to the Regional Forester a proposal for interim spotted owl guidelines. These guidelines, supplementing the 1976 long-range goal of 400 pairs of spotted owls in Oregon were: (1) for one year--1977--protect all nests and areas where the owls had been sighted; and (2) during that year the task force would develop objectives and management prescriptions to meet the goal and also identify the number and distribution of habitats needed to maintain a viable population in Oregon.

In May 1977 the Regional Forester responded to the task force that the National Forests would protect spotted owl habitat as recommended except where timber sales already existed or were planned for sale in 1977. The task force was able to keep its commitment and issued a review copy of the "Spotted Owl Management Plan" on November 3, 1977. The intent was to continue to obtain data and update the plan as needed. The next update occured in May 1979. Biologists from the State of Washington also joined in the planning process and there is now an Oregon-Washington Interagency Wildlife Committee that considers matters pertaining to the spotted owl, along with other concerns.

Region 6 Spotted Owl Management Guidelines as based on the management plan, were appealed by the Oregon Wilderness Coalition on the assumption that spotted owl habitat would not be adequately protected. As a result of this appeal, a new effort was made to insure that minimum viable populations would be protected while Forest Planning was in process. The details for this action were described by memoranda in 1980 from the Regional Forester to Forest Supervisors. In March 1981 the Interagency Committee recommended that the guidelines be revised to include the option of providing 1,000 acres of old-growth timber per pair until research more clearly defines the habitat needs of the owl.

In May 1981 a "Draft Pacific Northwest Region Plan" was issued by the Regional Forester. This plan included the proposed revision of the Oregon Interagency Spotted Owl Management Plan. This document set recommendations on size and distribution of habitat and populations by ownership and described spotted owl habitat. In May 1984 the draft became the "Regional Guide for the Pacific Northwest Region." [1] Direction for spotted owl habitat management planning is included in that document and is discussed later in this paper.

CURRENT NATIONAL DIRECTION

Recent U.S. Department of Agriculture direction that affects the spotted owl is Departmental Regulation Number 9500-4 dated August 22, 1983. The following excerpts show how this regulation emphasizes the requirements of management and planning under the National Forest Management Act.

"It is the policy of the Department to assure that the values of fish and wildlife are recognized, and that their habitats...are recognized and enhanced, where possible...

"A goal of the Department is to improve, where needed, diverse, native...populations of wildlife... while fully considering other department missions...

"Habitats for all existing native...species... will be managed to maintain at least viable populations of such species...habitat must be provided for the number and distribution of reproductive individuals to ensure the continued existence of a species throughout its geographic range.

"Habitat goals... will be established and implemented. This will be accomplished through the Forest planning process...Habitat goals will be coordinated with State Comprehensive Plans developed cooperatively."

The Secretary established a Fisheries and Wildlife Issues Working Group to monitor implementation of the regulation and to coordinate management with other Federal and State agencies. This direction was incorporated in Forest Service Manual 2603 in June 1984 and the policy for "Wildlife, Fish and Sensitive Plant Habitat Management" was updated.

CURRENT FOREST PLANNING DIRECTION IN REGION 6

In the draft regional plan each Forest was assigned a number of pairs of owls to be used in development of the Forest plans. These numbers were to be tested in the planning process to determine their validity. A total of 375 pairs were assigned to the Forests, 263 in Oregon and 112 in Washington (the 400 pairs for Oregon mentioned earlier included all ownerships, not just National Forests). These numbers represented the minimum viable populations. In addition, four population levels representing different management alternatives were developed and Forest Supervisors were instructed to model at least the minimum and the minimum plus 30 percent when assessing the impacts on other resources. This direction was, in part, a result of a task force recommendation following the appeal of the Oregon Wilderness Coalition. This action brought a response from the Northwest Timber Association members who strongly protested the consideration of an area 1,000 acres in size.

On September 19, 1980, the Regional Forester clearly stated to Forest Supervisors in a memorandum (2670), that "...you not forgo your options to manage for owl population levels in your Forest Plan other than your tentative allocation in response to public involvement..." There will be a continuing public involvement process as Forest Plans are developed, and any long-term decisions concerning spotted owl habitat will follow this process.

In April 1983 Region 6 established a task force to address concerns about the assumptions of models that were used to simulate management that would meet minimum management requirements for wildlife benchmark assessments (a benchmark is a habitat base to which all alternatives are compared to show the effects of alternatives on other resources and on the population of a species selected). Reviews by the Chief and the Pacific Southwest Region of the Forest Service raised some questions about the two methods used to model spotted owl habitat management. The two approaches used were: (1) to dedicate the areas to spotted owl management and defer timber harvest as long as the area meets habitat requirements; and (2) to manage the areas for timber while meeting minimum requirements for the owls. The dedicated method simply sets the habitat aside and no programmed timber harvest occurs. The managed approach provides for timber harvest over a long rotation either as clearcuttings or harvesting individual trees.

The task force determined (unpublished report) that two variables affected the efficiency of timber management while managing spotted owls: (1) the definition of old growth, especially the rotation age; and (2) the size of the old-growth stand. Because of this and other studies for different Forests, Region 6 planning efforts will evaluate both methods or a combination where appropriate.

On February 9, 1983, the Regional Forester sent "Regional Guidelines for Incorporating Minimum Management Requirements in Forest Planning" [2] to the Forest Supervisors. The reason for Regional direction for minimum management

---

.&/Unpublished Administrative Document, 1984, "Regional Guide for the Pacific Northwest Region", on file, Pacific Northwest Regional Office, USDA Forest Service, 319 S.W. Pine Street, Portland, OR 97208.

z/Unpublished Administrative Document, 1983, "Regional Guidelines for Incorporating Minimum Management Requirements in Forest Planning," by Jeff M. Sirmon, Regional Forester, Pacific North-west Regional Office of the USDA Forest Service, 319 S.W. Pine Street, Portland, OR 97208.

requirements (MMR) for wildlife was to insure consistency across the Region in meeting National direction. MMRs also serve as baseline constraints for developing benchmarks and alternatives. These MMRs were not to be construed as alternatives in themselves. The number of spotted owls designated for each Forest was based on Region-wide information. Because these numbers were only approximate, each plan alternative would be measured against the MMRs and a determination made whether that alternative was meeting the intent of the law.

Using this direction, the Forests in Region 6 began to choose the areas that would be managed for spotted owls to meet the MMRs. They also began to develop distribution patterns that would provide for interaction between the owls. The guidelines incorporated the latest information from the Oregon-Washington Interagency Wildlife Committee.

Following a review of the approach to MMRs that several Region 6 Forests were using it was determined that some items needed clarification. On April 16, 1984, this clarification and some additional direction was sent to the Forests. Emphasis was placed on habitat distribution as a key to minimum viable populations. Criteria for distance between spotted owl habitats had been established. A requirement to connect three or more habitats whenever possible was added. Following this direction, the minimum viable population goal for spotted owls increased from 399 pairs to 530 pairs.

The MMRs were developed over several months using data from spotted owl research and the advice of professional wildlife biologists and planners from all levels of the Forest Service. A brief review of the planning of the forests with spotted owl habitat reveals the following:

1. All Forests are using a grid pattern as a planning model.

2. A few (41) habitats will be managed for timber over a long-term harvest plan.

3. Most (489) habitats will be dedicated to old-growth forest and will not be harvested so long as they are suitable for spotted owls.

4. Of the 530 sites, 413 currently contain enough old-growth forest to make them suitable as spotted owl habitat.

5. And, 117 sites have potential as owl habitat but are not currently suitable because of the age of the timber. The particular age used as a determining factor varies by forest but a forest generally becomes suitable for owl habitat between 140 and 170 years of age.

6. There are 374,417 acres of commercial forest affected by this management or about 4 percent of the commercial forest base of those Forests involved. (This data is tentative and subject to change during the planning process.)

Considerable refinement and expansion was done to plan for spotted owl habitat management in the final Regional guidelines. Following is a summary of some of the guidelines:

1. The northern spotted owl will be considered a "management indicator species" in Forest planning.

2. To ensure that viable populations will be maintained, habitat must be provided to support at least a minimum number of reproductive individuals, and that habitat must be well distributed so these individuals can interact with others in the planning area.

3. Each Forest is directed to:

    A. Analyze and display the economic effects of providing for a specified number of spotted owls.

    B. When additional spotted owls are discovered, include these owls in the range of alternatives considered in developing Forest plans.

    C. Incorporate management for spotted owls into the planning process at those Forests that discover owls subsequent to this direction.

    D. Establish new minimum population numbers for those Forests where habitat is determined incapable of meeting the assigned numbers.

4. The modeling procedures must meet the following criteria:

    A. Be silviculturally attainable.

    B. Be designed to ensure maintaining viable populations of owls.

    C. Provide for proper distribution.

    D. Meet habitat needs as defined in the proposed Spotted Owl Management Plan (March 6, 1981) and the Regional MMRs (February 9, 1983).

5. One of the following methods will be used to model the effects on timber yields:

    A. Dedicate the area to old growth.

    B. Designate the area to management over an extended rotation designed to meet habitat needs.

    C. Designate the area to uneven-aged timber management that meets habitat needs.

    D. Designate the area to some combination of the above systems or manage different areas under different systems.

6. At least two Forest plan alternatives relating to spotted owl management will be

evaluated. One alternative will evaluate the Forest's share of the minimum viable population for the Region and the second will evaluate the minimum plus 30 percent. Other alternatives will be considered where indicated to meet multiple-use objectives.

Following is a summary of events in the evolution of management direction for spotted owl habitat in Region 6.

A CHRONOLOGY OF PLANNING IN REGION 6

Pre-1973 Little interest in spotted owls. Rapid loss of habitat.

1973 Formation of Oregon Endangered Species Task Force and recommendations from task force to manage 300 acres around known nest sites; rejection of recommendations by Region 6.

1976 Direction from Regional Forester to protect known sites. Task force recommends 400 sites be protected in Oregon.

1977 First spotted owl management plan for Oregon; assignment of 290 pairs to National Forests.

1978 Direction by Regional Forester to meet intent of plan for 290 pairs.

1979 Region 6 spotted owl management guidelines developed; revised Oregon Interagency Spotted Owl Management Plan.

-4

1980 National Forests protecting all known nest sites and verifying location of owls.

1981 Revision of management plan. Issuance of draft Regional plan; 263 pairs of owls assigned to National Forests and in Oregon and 112 to National Forests in Washington.

1983 Regional direction for determining Minimum Management Requirements in Forest planning.

1984 Clarification and revision of 1983 direction; Forests establish new minimums of 530 pairs; Regional guide finalized (replaced document referred to as Regional plan).

RESEARCH

Spotted owl habitat often consists of mature or old-growth timber on highly productive sites capable of producing up to 90,000 board feet Per acre in a 60-year period. There is a lot of interest in how that land is allocated. Questions, that research can answer, about the conflict between the requirements of the owl and potential timber production have been identified:

How are old growth timber stands identified, inventoried and properly classified?

What happens to old growth when it is put under management?

What mix of old growth, mature, and other age classes is acceptable to the owl?

What are the upper and lower acreage limits that affect the suitability of the site for owl habitat?

What is the upper limit on acceptable disturbance before the site losses it habitat capability?

What is a minimum viable population of spotted owls and what is its distribution?

What are the dispersal rates and distances by sex and age of the spotted owl?

SUMMARY

The spotted owl jumped from obscurity to National prominence in a few years. The reason for this is the owl's affinity for old-growth timber along the west coast. Continued research is needed to determine the allocation of spotted owl habitat among the owl, other old-growth dependent species, and timber production. State and Federal agencies continue to plan these allocations. Cooperation between the agencies, private land owners, and persons with an interest in the owl and its habitat is essential if a balance between the timber productivity of these sites and a stable population of owls is to be achieved. The agencies involved are seeking and using all available information in planning for the future of these resources.

LITERATURE CITED

U.S. Department of Interior, Fish and Wildlife Service. Threatened wildlife of the United States. Resour. Publ. 114. Washington, D.C.: U.S. Department of Interior, Fish and Wildlife Service; 1973. 289 p.

IMPLEMENTING A SPOTTED OWL MANAGEMENT PLAN:
THE GIFFORD PINCHOT NATIONAL FOREST EXPERIENCE

William C. Ruediger

ABSTRACT : Managers faced with implementing a spotted owl management plan should anticipate the long-term realities of loss of habitat from natural and human induced causes, the necessity of building in flexibility to accommodate changes, the need to measure suitability of the actual habitat and use by spotted owls prior to making land allocations, and the role of monitoring.

INTRODUCTION

Over the last 6 years the Gifford Pinchot National Forest, Pacific Northwest Region, has been in the process of developing a spotted owl management plan. The objective of the plan is to maintain spotted owls, and other species that utilize or require mature or "old-growth forest conditions,' throughout their existing range in the Forest. During this period of change and exchange of facts and philosophies, certain realities have become evident and some far-reaching and complex challenges have surfaced. The conclusion is that the challenges are growing each year and the options for solving these challenges are decreasing. Decisions being made today are going to dictate options and success rates for tomorrow, and we cannot wait to make these decisions. Perhaps by looking at the experience in the Gifford Pinchot, other biologists and managers can evaluate their situations and make better decisions.

There are several critical elements land managers and biologists should consider when developing and implementing a spotted owl management plan. These critical elements may have universal application across the range of the spotted owl or , on a broader perspective, they seem to apply for any species being managed near minimum population levels.

The key features of a spotted owl management plan include:

1. The quantity of habitat provided.
2. The quality of habitat provided.
3. The distribution of habitat provided with emphasis on key axis habitats which if lost could isolate geographic populations.
4. Demonstrated use by spotted owls (verification).
5. The ability of the individual management areas and the overall plan to absorb unforeseen impacts.

WILLIAM C. RUEDIGER is a wildlife biologist, USDA Forest Service, Gifford Pinchot National Forest, Vancouver, WA.

The following documents how these critical elements have evolved from and affected the Gifford Pinchot National Forest's spotted owl management program between 1978 and 1984.

QUANTITY OF HABITAT

Both the number of spotted owl management areas provided and the size of each area are important. In 1978, the Gifford Pinchot National Forest was providing 40 acres of habitat around each spotted owl nest site. As only one nest site was known then, the total area managed for spotted owls was 40 acres.

In 1979, the policy was changed to provide habitat for 39 pairs of spotted owls. Each pair was allotted 300 acres of old growth or, if this was not present, mature habitat in the Douglas-fir/hemlock vegetative zone. The basis for 300 acres of habitat for each pair was the Oregon Spotted Owl Management Plan. 1/ Whenever possible, management areas where spotted owls were known to exist were given priority over adjacent areas without known pairs. The total area needed to sustain this population level was 11,700 acres.

In 1980, the Gifford Pinchot National Forest made a decision that all spotted owl management areas would be inventoried prior to selection to evaluate habitat suitability. During this time, Mount St. Helens erupted and destroyed approximately 24,000 acres of old growth and mature Douglas-fir/ hemlock type forest, much of it known to contain spotted owls. A new spotted owl management strategy was prepared, this time utilizing 45 pairs of spotted owls and 540 acres of habitat per pair (300 acre nesting core plus three 80-acre foraging areas). The basis for using this criteria was the Oregon Interagency Spotted Owl Management Plan. 2/ The total area necessary to sustain this population was 24,300 acres.

The Oregon Interagency Spotted Owl Management Plan was revised in 1981, 3/ reflecting the then-current consensus that 1,000 acres of old-growth habitat was necessary for each pair. In 1982 the Forest told Ranger Districts that 1,000 acres of habitat would be maintained for all pairs identified in the Spotted Owl Management Plan, and that 1,000 acres would be maintained for all new spotted owl pairs located until the Forest's plan was completed. The number of acres necessary to sustain the spotted owls identified in the Gifford Pinchot National Forest Spotted Owl Management Plan and the Mount St. Helens Land Management Plan was 47,000 acres. An additional 7,000 acres received temporary reprieve from timber harvesting as "pair protection areas" pending final disposition in the Forest's plan. The total acreage receiving management emphasis for spotted owls was 54,000 acres.

The situation as of 1984 is that there are now 14 "pair protection areas." The 47 pairs in the Gifford Pinchot Spotted Owl Management Plan and Mount St. Helens Land Management Plan are also being provided for, for a total short-term commitment of 61,000 acres.

There are several scenarios that could be provided for the future, but let me provide what I consider a minimal approach for the Gifford Pinchot National Forest. Recent analysis suggests that the lowest number of spotted owls that could be managed for over the long term, with a reasonable amount of risk, is approximately 52 pairs. At this level, there would be 10 habitats providing flexibility for situations described later in this paper.

There are two ways spotted owl habitat could be managed. The first option is referred to as "dedicated", whereby suitable areas of 1,000 acres would be identified and preserved. The total area necessary to sustain 52 pairs under this type of management would be 52,000 acres, some of which is already being preserved under such allocations as "wilderness" and *national monument".

The second option would consist of managing approximately 2,400 acres under a 240-year rotation to sustain 1,000 acres of habitat suitable for one spotted owl pair. If 80 percent of the spotted owl management areas were managed with an extended rotation and 20 percent managed as dedicated (in wilderness or national monument status), the acreage necessary to sustain 52 spotted owls would be 110,800 acres.

QUALITY OF HABITAT

Occupied spotted owl management areas were measured in the Gifford Pinchot National Forest and the following stand characteristics were observed:

1. Twenty to 40 large trees per acre (30-in. diameter at breast height (d.b.h.) or larger).
2. Eight or more large snags per acre (20-in. d.b.h. or larger).
3. Twelve or more downed logs per acre (12-in. d.b.h. or larger).
4. Multistoried stands with at least 80 percent canopy closure.

In 1980, the Forest planned to inventory habitat in all areas being considered for spotted owl management. The eruption of Mount St. Helens

---

1/ Oregon Department of Fish and Wildlife. 1978. Spotted owl work group meeting, plan on file at the NW Regional Office, Corvallis, OR.

2/ USDA Forest Service. 1984. Regional Guide for the Pacific Northwest Region. Appendix C, p. c-5/6/7. On file at USDA Forest Service, Region Six, 319 S.W. Pine, P.O. Box 3623, Portland, OR.

3/ USDA Forest Service. 1984. Regional Guide for the Pacific Northwest Region. Appendix F, p. F-2/3/4. On file at USDA Forest Service Region Six, 319 S.W. Pine, P.O. Box 3623, Portland, OR.

made inventorying impossible over much of the Forest; however, 23 areas were evaluated. Of the 23 areas inventoried, 3 (13 percent) were subsequently determined to be unsuitable because they lacked one or more of the previously described habitat components. The three areas considered unsuitable were replaced with more suitable areas nearby.

Between 1981 and 1984, approximately 25 additional potential habitat areas have been inventoried. Five (20 percent) of these were subsequently determined to be unsuitable and replaced with suitable areas. These areas had preliminary evaluations consisting of aerial photograph reviews and nonmeasurement ground reconnaissance.

Managers who have not measured actual spotted owl habitat parameters can likely assume that 15-20 percent of the areas being considered or managed as habitat may not meet minimum standards.

USE BY SPOTTED OWLS

A significant portion of management areas judged to be suitable habitat (even after a habitat inventory) may not be used by spotted owls. For example, in the Gifford Pinchot National Forest approximately 20 percent of the spotted owl management areas have either had to be replaced because use by owls could not be confirmed, or the areas continue to be managed as habitat without owls. If habitat inventories had not been the basis for locating management areas, an estimated 40 percent of the spotted owl management areas selected would not have been suitable.

Spotted owl management plans that are developed with little or no information on habitat or use can be expected to go through major revisions, or they may not sustain expected population levels.

DISTRIBUTION OF HABITAT

Distribution strategies must consider availability and suitability of habitat, home range and territory sizes, dispersal distances, and other pertinent behavioral and environmental factors.

In the Gifford Pinchot National Forest, habitat availability has necessitated managing spotted owls above the densities that could be sustained if habitat were uniformly distributed. Theoretically, if my mathematics are close, spotted owls could be managed at one pair per 40,000-42,000 acres, using maximum distances provided in the revised Oregon Interagency Spotted Owl Management Plan. Estimated minimum densities in the Gifford Pinchot National Forest are one pair per 30,000 acres. This density is about 25 percent greater than the theoretical minimum and results from the existing distribution of suitable habitat in the Forest.

When occupancy by spotted owls (verification) becomes a criterion for habitat suitability, many old-growth areas may be excluded. Each additional criterion further limits the selection of choices and will tend to increase the density of habitats managed.

Intermingled private and public land ownerships can also contribute to distribution, management, and other resource impacts. This is a significant problem on many Forest Service and Bureau of Land Management lands. Intermingled ownerships commonly create at least three problems for the land manager. First, the impact on timber resources is increased for the managing agency if all habitat requirements must be supported on half of the available land area, which is a common situation where there is railroad-ceded lands. Second, intermingled ownership may increase the density of owls that must be managed because of restricted availability or suitability of areas that can be selected. Third, management of habitat on federal lands can be hampered by factors such as blowdown and fragmentation, which can result from large areas cutover on adjacent lands.

ABILITY OF A SPOTTED OWL MANAGEMENT PLAN TO ABSORB UNFORESEEN IMPACTS

The experiences I have had over a relatively short period of time have convinced me that an important part of a spotted owl management plan is its provisions for absorbing unforeseen impacts such as natural disasters, land ownership or land use changes, and management mistakes. These impacts can be catastrophic, as in the case of the eruption of Mount St. Helens: more often they are subtle and cumulative.

The following are examples from the Gifford Pinchot National Forest of how these impacts can be widespread and significant, even over the relatively short timespan of 5 years.

Natural Disasters:

1. The eruption of Mount St. Helens eliminated approximately 25,000 acres of mature and old-growth forests on National Forest lands known to contain a high density of spotted owls.

2. The Christmas Day windstorm in 1983 caused 215 acres of blowdown in six spotted owl management areas, including 75 acres in one core area. This resulted in having to make adjustments in five areas, combine two other management areas into one, and relocate one management area. Blowdown appeared greatest adjacent to harvest units, particularly in locations where habitat had already been fragmented by timber harvesting.

Land Exchanges:

1. Land exchanges south and west of Mount St. Helens resulted in relocation of two management areas. The land ownership pattern was intermingled.

2. Land exchanges to the south and west of Mount Rainier National Park will likely result in the loss of one or more spotted owl management areas. The land ownership pattern is intermingled.

3

Management Problems:

An escaped slash fire in 1979 resulted in 1,200 acres of old-growth habitat being burned. A spotted owl management area tentatively planned for this area was moved to another, less suitable area.

SUMMARY

Viability and flexibility of spotted owl management plans and strategies will depend largely on:

1. Identifying suitable habitat based on habitat inventory data, verification of spotted owls and evidence of breeding success. If possible, radio telemetry should be used to focus on habitat used by owls in contrast to habitat that may appear suitable but does not receive use.

2. Providing management areas that are larger than the minimum necessary to maintain owls so there is flexibility to adjust for spatial needs and allow for habitat attrition. Reliance on minimum-sized management areas (1,000 acres) carries a high risk.

3. Considering distribution and land ownership patterns to identify key axis areas where geographic populations could be isolated if habitat were lost.

4. Providing an adequate number of management areas so that viability is maintained even if several areas are lost. Emphasis for additional areas should be placed at key axis locations to ensure distribution criteria are met over time. Management plans or strategies that rely on minimum population levels should be considered high risks.

5. Diligent monitoring of critical factors such as dispersal of young, mortality rates, breeding success, spatial and habitat requirements, and changes in habitat caused by natural and human induced causes.

OLYMPIC NATIONAL FOREST SPOTTED OWL HABITAT MANAGEMENT: TRANSLATING EVOLVING MANAGEMENT GUIDELINES INTO ACTIONS

Maureen A. Beckstead

ABSTRACT: Significant progress has been made in identifying the distribution, abundance, and habitat of spotted owls in the Olympic National Forest. Implementation of the Spotted Owl Management Plan has been complex due to the geography of the Olympic Peninsula, the vagaries of spotted owl behavior, and other resource conflicts. The Olympic National Forest is committed to a more complete, site-specific knowledge of spotted owl habitat use and continues to gather data through monitoring to help refine future management regimes.

INTRODUCTION

It is a task of personnel in Supervisors' Offices of National Forests to identify and clarify, to define and refine management direction and guidelines, and to oversee inclusion of the guidelines in land management planning and field operations. It is a task of personnel stationed at Ranger Districts to interpret and employ management direction and guidelines in project planning and field operations. These tasks are necessarily complex because they are often concurrent, usually iterative, and always interactive.

The implementation of spotted owl habitat management direction and guidelines has been complicated by the fact that this direction has been continually evolving, as has direction for development of Forest Land Management Plans. This evolution will continue as research and monitoring identify new or more refined information and as Forest Land Management Plans are completed, amended, and revised.

Direction to the Olympic National Forest (Olympic) to manage northern spotted owl habitat is less than 5 years old. Early direction specified that this Forest would maintain a specific number of "known" spotted owl habitats and guidelines were developed that indicated the size and distribution of suitable habitat within each Spotted Owl Management Area (SOMA). Following several changes, later direction specified size and distribution of suitable habitat within SOMAs, minimum and maximum distances between SOMAs, and a distribution that would allow owls in any one SOMA to disperse to at least three other SOMAs.

Implementation of management direction and guidelines for size and distribution of habitats is complicated by certain geographic features partitular to the Olympic. Major features include:

MAUREEN A. BECKSTEAD, former Olympic National Forest wildlife biologist, is Landowner Relations Program Manager for the Department of Game, Olympia, WA.

probable geographic isolation from suitable habitat in the Cascade Range; size and shape of lands managed by the Olympic; previous land management and fire history of the Olympic and adjacent landowners.

Add to these features the facts that little information is available regarding spotted owls or habitats on adjacent lands and that spotted owl behavior appears to vary from year to year and area by area. Implementation of a spotted owl management plan may have to employ large doses of "best professional judgment" to meet the intent, if not always the letter, of management direction.

The purpose of this paper is to discuss the techniques and procedures used, the progress to date, and the difficulties encountered in identifying and planning for SOMAs in the Olympic. Also important to discuss is the need for continuing to refine techniques, knowledge, and management direction through monitoring, evaluation, and revision. Because direction, procedures, difficulties, and progress were evolving at the same time, I have chosen a chronological format for this discussion for the sake of clarity.

IMPLEMENTATION

Ancient History Through 1977

The earliest direction received by the Olympic stressed inventory of spotted owls. All sightings, nest locations, and acres surveyed were to be reported to the Pacific Northwest Regional Office by July 1977. Interim to the completion of a Spotted Owl Management Plan by the Oregon Endangered Species Task Force, habitat diversity was to be maintained. More specifically, a complete range of successional stages was to be retained in areas of 8,000 to 20,000 acres.

To this time, no inventory of spotted owls had been performed in the Olympic by Forest Service personnel. Howard R. Postovit[1/] conducted the first survey in Washington in 1976. Several of his survey routes occurred in Olympic National Forest and in Olympic National Park.

Postovit surveyed areas of unharvested old-growth forest, mosaics of old-growth and second-growth stands, and uniform second growth. These were divided into five classes by proportion of old growth and 30 routes were randomly selected for survey in each class. Routeswalked were $2^{1/2}$ miles long; each route was walked twice while calling owls at 164-foot intervals. If an owl response was heard, Postovit moved three-quarters of a mile before calling again to avoid calling the same bird. Data collected within 327 feet of each owl location included elevation, topography, tree species, canopy density, approximate stand age, average diameter at breast height (d.b.h.) of overstory trees, and forest class.

Fourteen owls were located at 13 sites on the Olympic Peninsula and 8 owls were located at 7 sites in the Cascade Range. Almost all locations were in old growth; the majority of surrounding areas were more than 66 percent old-growth forest. On the Olympic Peninsula, 9 owls were found on National Forest lands and 5 owls on National Park land. Average slope was 55 percent; all owls were located on western and northeast slopes; elevation ranged from 752 to 3,188 feet on the west side of the Peninsula and from 1,488 to 2,747 feet on the northeast side.

Survey, 1978

William Brown, Jr., Forest Wildlife Biologist for the Olympic, contracted with Ken Dzinbal, Oregon State University, to conduct a spotted owl survey. The survey was designed to determine the existing geographic range of spotted owls in the Olympic, to provide preliminary information on habitat preferences and owl density, and to refine inventory techniques for future use.

Dzinbal, usually accompanied by Ranger District personnel, ran 417 miles of road transects in over 40,000 acres of suitable habitat; i.e., areas that contained predominantly old growth and that were under 4,000 feet in elevation. Nonroaded pristine old growth and areas predominantly in younger stands were not surveyed for practical reasons.

Owls were located by calling at night for 1 minute every one-quarter mile along a road transect. If a response was received, the observer moved 1 mile before calling again. Data collected at each response location or sighting included aspect, percent slope, elevation, time, percent cloud cover, moon phase, precipitation, wind speed, and temperature.

The survey resulted in a total of 51 responses and 3 sightings, of which 13 may have been male/female pairs, at 38 separate locations. Response locations indicated spotted owl use predominated at midelevation ranges on moderately steep slopes on northwest or southeast aspects. Owl use was different on west and east sides of the Olympic. On the east side, locations of owls averaged 2,750 feet in elevation and occurred only on south, southwest, and southeast aspects. On the west side, locations averaged 1,900 feet in elevation, and 70 percent occurred on north, northwest, and northeast aspects.

Density of owls, based on responses and sightings, were one owl (pair) per 8.9 miles of road surveyed. Area density was calculated from clusters of responses representing three or more owls (pairs). Area densities ranged from one owl (pair) per 1.96 square miles to one owl (pair) per 4.17 square miles. The assumption in 1978 was that spotted owls were rarely known to live separately so that each response was considered

---

[1/] Unpublished report, 1977, "A Survey of the Spotted Owl in Northwest Washington," by Howard R. Postovit, National Forest Products Association, 1619 Massachusetts Avenue, N.W., Washington, DC 20036 a pair location. More recent survey and research have cast doubt on this assumption.

Hiatus, 1979-1980

Though management direction and guidelines were evolving rapidly during this period, activity at the field level consisted of documenting accidental encounters with spotted owls and some nonstandardized surveying of proposed timber sale areas.

In 1979, for the first time, the State of Washington joined the spotted owl planning process and the Oregon-Washington Interagency Wildlife Committee revised the Spotted Owl Management Plan (SOMP) During 1980, a USDA Forest Service task force developed a process to determine various levels of viable spotted owl populations; it was assumed that all owls in Oregon and Washington were one interbreeding population. The Regional Forester adopted the SOMP and forwarded direction to the Olympic to maintain at least 17 SOMAs as a tentative, interim allocation. The Olympic National Forest Plan was to evaluate various alternative management levels. SOMAs were to encompass 1,200 acres of "known" spotted owl habitat and include a 300-acre contiguous old-growth core around a nesting site, plus at least three 80-acre feeding-perch patches nearby in order to implement the SOMP. The Olympic was directed to designate confirmed or suitable SOMAs by July 1981.

Standards for confirming SOMAs and verifying core nesting areas were also developed in 1980.[2/] Confirmation of general SOMA occupancy consisted of two or more visual observations or auditory responses of spotted owls in approximately the same area, 72 or more hours apart, anytime throughout the year. Verification of a core area must be made during the period from March 1 to August 31 and consist of one of the following: one or more visual observation or auditory response of an adult male and female within the same one-quarter square mile area; three or more visual observations or auditory responses of an adult bird in the same one-quarter square mile area, 72 or more hours apart; or location of a nest or recently fledged young-of-the-year birds.

Habitat for all known pairs was to maintained until the Olympic verified its minimum number of SOMAS. Further, once a SOMA was confirmed, no habitat modification was to occur until the core area was verified. Once the minimum number of SOMAs were verified, Forests were encouraged to maintain habitat for other known pairs to provide for alternative planning levels.

Implementation and Planning, 1981

The SOMP was revised in 1981 and the Olympic received direction to establish SOMAs containing a 300-acre core area with an additional 700 acres of old growth within $1^{1/2}$ miles. These SOMAs were to be distributed no more than 6 or 12 miles apart depending on whether they contained a single pair of owls or multiple pairs. Single-pair SOMAs were acceptable only to meet distribution requirements or where remnant habitat existed. Other direction continued, including the prohibition on habitat modification except that, now, timber sold previous to October 1980 was exempt and available for harvest.

I was transferred to the Forest Wildlife Biologist position in 1981, though I had been working on the Olympic Forest Plan during the previous year. It was already obvious that geography and topography were going to make implementation of the SOMP difficult, at best. The Olympic resembles an elongated doughnut, broken on the west side by extensive areas of State and Indian reservation lands and on the north by private lands that surround the Olympic National Park. Width of the Olympic in most areas is 12 miles or less and rarely exceeds 15 miles. Because of previous, intensive and extensive fire history, as well as a history of lowland timber harvesting, large areas were void of suitable spotted owl habitat, as defined by the Regional Office. Identifying potential SOMAs to provide well-distributed habitat throughout the historic range in the Olympic planning area was impossible. No SOMAs were yet verified, but managing only 17 potential areas out of over 40 response and observation locations caused them to be strung out like beads on a necklace at distances exceeding management direction. Previous inventory of owls and habitat indicated that clusters of owls for multiple-pair SOMAs were extremely rare except on one Ranger District, so that a 6-mile distribution of habitats was the norm. Because the previous survey was conducted only in roaded areas, most potential SOMAs were in conflict with existing or proposed timber sales and were often already fragmented to some degree.

Survey and attempts at verification of SOMAs were reinitiated in 1981. The Forest Supervisor's direction emphasized (1) survey of proposed timber sale areas to comply with the process required by the National Environmental Policy Act; (2) survey of roadless areas or lands dedicated to purposes other than timber management to reduce resource conflicts; and (3) reinventory and verification of areas with a previous owl history.

Surveys were conducted at night between March and September using recorded spotted owl calls amplified from a cassette tape player. Surveyors included personnel from any and every resource area in District and Supervisor's Offices. Crews of two or more drove a predetermined route, stopping every one-quarter mile and calling every few seconds for 5 to 10 minutes at each stop. On trail routes, calls were played every few minutes. Calling generally began 1 hour after sunset and lasted about 4 hours. Response locations or sightings were mapped; time, weather, and comments were recorded.

[2/] Horn, Kirk M, 1980, Information on file at the USDA Forest Service, Pacific Northwest Region, P.O. Box 3623, Portland, OR. 97208, 2 p.

Although 41 responses were received during 332 hours of survey, which compared favorably to 51 responses in 276 hours in 1978 with many locations repeats from 1978, no SOMAs were either verified or confirmed to the regional standards described above. It was noted in 1981 that moving 1 mile from a response or sighting was not always enough, as some observers were followed by owls for several miles, particularly early in the breeding season. Also, about half of the areas where owls were located in 1978 that were checked in 1981 did not produce owl responses.

Implementation and Planning, 1982

The Olympic issued direction that verification of at least 17 SOMAs was a high priority so that Forest Plan development could proceed based on site-specific information. The Olympic also agreed to participate in the L-year spotted owl census organized by the Department of Game, however, and was committed to run eight census routes in the Forest and Park. Funding for these activities was minimal so verification efforts were also limited.

Details regarding procedures used for the State census routes are presented elsewhere (Allen and Brewer 1985). Efforts at verification followed regional standards. Though 40 owl responses were received in 442 hours of survey, only three SOMAs were verified on two Ranger Districts by the end of the season. Two SOMAs were within 3 miles of one another, further complicating the distribution problem. Many response locations repeated those of either 1978 or 1981, or both, but some were new, and again resurvey of old locations produced responses only about half of the time. It was also apparent, through annual responses, that in at least one Ranger District owls were using habitat not considered "suitable" by Regional Office definition.

To proceed with the development of the Olympic Forest Plan, potential SOMAs were allocated to each District according to the following prioritized criteria:

1. SOMAs already verified;
2. Potential SOMAs with a history of previous responses or sightings;
3. Potential SOMAs with no history of occupation, that were needed to meet distribution criteria for suitable habitat, but with few resource conflicts; and
4. Potential SOMAs with no history of occupation that were needed to meet distribution criteria, but either had resource conflicts or habitat not considered immediately suitable.

These potential SOMAs were entered into the Olympic's Total Resource Inventory System (TRI System), which served as the data base for the Forest Plan and the automated mapping system, R-2 Map. From these systems, detailed information could be retrieved for each potential SOMA; information that included number of acres assigned inside and outside the core, elevation, aspect, vegetative ecoclass, stand tree size, and stand year of origin. Where there had been any silvicultural exams or inventory plots within a SOMA, data also included percent of area in trees, shrubs or grass-forb stages, major species, and a history of any management activity or direction.

Following allocation, the extent of conflict with other resource activities became more apparent. For instance, all three SOMAs verified in 1982 contained timber sales already sold as well as proposed sales. One SOMA had timber units sold prior to October 1980 (which were exempt) in the core, including the suspected nest tree. Locations of a radio-collared male from this SOMA showed him to be repeatedly using areas scheduled for harvest within 1 to 2 years. The Olympic is presently in the expensive and time-consuming process of modifying several sales to provide protection for areas of owl use.

The need for continuing refinement and interpretation of management direction coupled with large doses of "best professional judgment" arose along with the immediate and ongoing requests for boundary changes to accommodate other resource needs. A careful balance of priorities was needed to resolve resource conflicts that included theoretical knowledge of life history and habitat use of spotted owls weighed against the ability of managers to accomplish their timber managment activities elsewhere.

Semi-finally, 1983

The Forest Supervisor for the Olympic issued direction to Ranger Districts to complete verification of their minimum allocation of SOMAs plus one additional area by the end of the 1983 season. Again, the Forest's funding was minimal so that only half of the State's census routes were completed, as emphasis was placed on verification. This direction stemmed from the recognition that planning based on potential SOMAs was a major factor in the difficulties described previously, and that a site-specific knowledge of spotted owl use would lend more credibility to the decision-making process.

During an intensive effort involving 1,577 hours of field work, of which one-third was volunteered 77 responses or sightings were recorded. Fourteen SOMAs were confirmed and nine core areas verified within them. Though the total allocation of 17 SOMAs had been confirmed, the requirements for distribution of habitat could not be met because all but two seemed to be single-paired and because of the geography of the Forest.

Other possible anomalies appeared with the confirmation of two SOMAs in habitat previously considered "unsuitable)"' one of which produced two fledglings. Special attention was given to this SOMA due to the paucity of old growth within 11/2 miles of the nesting area. Much of the Ranger District, including the SOMA area, includes 90-year-old, or younger, stagnated stands ranging from 5,000 to 20,000 stems per acre. Some areas, however, contained old-growth elements such as interspersed larger trees and snags. In an effort to determine the appropriate size and shape of this SOMA, an attempt to determine the prey base, prey base density, and habitat use by the owls was begun. Department of Game captured, radio-collared, and monitored habitat use of the two fledglings through mid-1984, though the fledglings soon dispersed from their natal area. District personnel and I collected eight pellets from the fledgling roost area. These were analyzed by Murray Johnson, University of Puget Sound, and were found to include nine northern flying squirrels, two red-backed voles, and one adult and three immature bushy-tailed woodrats. I also observed a cached (partial) snowshoe hare while collecting pellets. Funds were requested to determine prey base density in order to estimate the amount of habitat necessary to support the dietary needs of an adult pair and two fledgling spotted owls.

Because of these anomalies, distribution difficulties, erratic occupancy of specific areas, and the long distances apparently traveled by curious, defending, or dispersing spotted owls, the Olympic in concert with the Mt. Baker-Snoqualmie and Gifford Pinchot National Forests cooperatively developed a SOMA monitoring plan with Forest Service research and the Washington State Department of Game. This plan is described in a paper by Carey and Ruggiero (1985).

Meanwhile, regional direction was refined and made more specific, and issued as minimum management requirements for establishing viable populations of spotted owls in the Forest planning process. This direction was used to establish the latest confirmed and verified SOMAs and core areas in the Forest Plan data base during the planning "pause" which followed the Ninth Circuit Court of Appeal's decision regarding evaluation of RARE II areas.

Existing Situation, 1984

A summary of the Olympic's data on spotted owl habitat use as of early 1984, included a total of 209 owl responses or sightings at 48 locations. Locations were considered "separate" if they were 2 to 3 miles from any other location. Of these locations, 17 had been confirmed as SOMAs and 12 core areas were verified. Breeding pairs or fledglings had been observed in three of these SOMAS. Field work involved 2,627 hours, which was estimated to be one-third to one-half of the total expended on implementation of the SOMP.

By including all 48 known locations and all potential suitable habitat on one map, it was apparent that there were still some weak links in the geographical distribution of spotted owls and habitats on the Olympic's east and south sides. These were due primarily to previous fire history on the east side and intensive and extensive timber harvest on the south side. I had repeatedly expressed concern to the Regional Office biologists that the probability existed that spotted owls on the Olympic Peninsula were genetically isolated from those occuring in the Cascade Range, and that this isolation may have begun in the very early 1900's when the lowlands in the Puget Trough were logged off within a 30- to 40-year period. An analysis of the risk involved in managing 17 habitats for spotted owls in the Olympic following the procedures of Salwasser [3/] indicated that this population, viewed in isolation, could become 50 percent inbred in only a few generations.

Recognizing that the Peninsula subpopulation of spotted owls included those on adjacent lands, the Olympic National Park was queried for any spotted owl use data and an estimate of the amount and location of potentially suitable habitat. Park personnel had very limited data and declined to make an estimate of habitat. I polled seven Forest Service and State biologists for an estimate of either spotted owl density or suitable habitat in the Park; estimates ranged from 42 to 109 pair. Risk analysis was again performed (including potential Park owls), which indicated long-term evolutionary fitness was unlikely for an isolated Olympic Peninsula subpopulation. Department of Game had data on three owl areas on adjacent Department of Natural Resources lands, but to date there has been no State agreement to manage spotted owl habitat.

Direction from the Regional Office was received in April and included recognition of the probable isolation of spotted owls on the Olympic Peninsula. It was suggested that, in the absence of protection for habitats linking the Olympic Peninsula and the Cascade Range, the Olympic subpopulation might be periodically enhanced through transplants in cooperation with Department of Game. Other direction stated that the number of SOMAs to be managed, at a minimum, would be determined by an appropriate distribution of habitats rather than by a number of owl pairs calculated to provide genetic viability.

The new distribution requiremeuts were mapped and SOMAs located such that any one SOMA was distributed within dispersal distance of at least three others, and so that no large area was void of habitat. The Olympic, being too narrow to accommodate this distribution, and having all but one SOMA distributed at 6 miles because of the single-pair situation, added potential Park habitats to the 28 or 30 needed for distribution on National Forest lands. These Park habitats were added where necessary to tie Olympic lands, fragmented by other landowners or unsuitable habitats into one continuous distribution. Suitable Park lands were taken from a map generated by remote sensing data, which included age and elevational criteria; none of these habitats have yet been examined on the ground or inventoried for owls.

During the 1984 field season, funds were requested to census the prey base in the stagnated timber stands within verified SOMAs. During monitoring, spotted owls were located in all 11 SOMAs evaluated, thereby validating procedures used to inventory and confirm these areas. Owls

[3]/ Contribution to Forest Service Handbook, FSH, 2609.14, draft November 25, 1983, Chapter 5.7, Viable Population Risk Analysis, 34 p., by H. Salwasser.

appeared to be spending as much time outside designated SOMAs as within, however, and some owls could not be located in the SOMA until late August after the breeding season. This preliminary information indicates the state of our imperfect knowledge of spotted owl habitats and habitat use.

TIPS FOR NEW PROGRAMS

There are a few hints I can provide to those contemplating the start of a program to manage spotted owls, or perhaps any species about which relatively little is understood:

1. Count on a long-term project. Identify and try to secure funding and personnel for a commitment of several years.
2. Concentrate surveys early in the breeding season. Spotted owls appear most territorial (responsive) before their young have fledged.
3. Don't waste your time. Visiting "perfect" habitat more than three to five times in a season appears to be nonproductive, though it should be visited in consecutive seasons and during the winter before being abandoned.
4. Recognize that suitable habitat is that which is occupied by spotted owls, not that which meets a standardized definition. Establishing habitat management areas in a generalized distribution pattern, then checking them for use causes constant readjustment and wastes time. General survey should be followed by habitat analysis, then future surveys refined to reflect such data.
5. A crew on contract is easier to standardize and supervise. I found that, in the Olympic, the *contract crew had a response rate per unit time spent of one response per 5 hours of survey; crews of various changing Forest Service personnel achieved one response per 9 hours of survey; and a combination of in-house personnel plus one-third volunteers produced one response per 21 hours of survey.
6. Lack of owl response does not necessarily indicate that owls aren't there. Responsiveness appears linked to the technique of the caller, weather, time of day and year, individual differences, number of times previously called, phase of the moon, and whether or not it's Thursday.
7. When managing a species at low population levels, where viability is a concern, supply the best habitat available. Marginal habitat may be only periodically occupied or may not be able to support a breeding pair plus young.
8. Avoid conflicting resource uses, such as timber harvest, within SOMAs even though more than sufficient habitat is available. Ongoing monitoring will continue to refine spotted owl habitat use, and at low population levels, use should define habitat.

FUTURE NEEDS

The Olympic has defined its needs for more information through participation in the cooperative SOMA monitoring study (Carey and Ruggiero 1985). Additionally, information is being gathered on specific habitat use by adult owls in stagnated timber stands to define the SOMA parameters for these anomalous situations. It would also be prudent to examine the suitability of Park lands and conduct a survey of spotted owls in habitats that were selected to geographically ensure a continuous distribution throughout the owls' range. Managing owls near minimum population levels allows little margin for error; assumptions regarding suitability and occupancy of several habitats imposes a very high risk.

Several years of observation and preliminary monitoring data indicate a need for more specific information regarding differences in "winter range" vs. "summer range" use by owls, differences in male vs. female use of the home range during nonbreeding years, home range size of fragmented SOMAS vs. contiguous ones, reproductive strategy, and fledgling survival. These require research efforts beyond the scope of an individual Forest to purse.

Finally, there is a continuing and future need for flexibility in management direction. Direction and guidelines need to be more immediately responsive to new or site-specific data in order for habitat to be managed to maintain pairs of spotted owls. Presently, habitats are assigned to owls and they must fit within those or perish. With continuing monitoring and refinement of data on habitat use and spotted owl biology, the opportunity exists to manage habitats selected by the owls.

SUMMARY

Information on spotted owl distribution, density, biology, and habitat use has been collected in the State of Washington for only a few years. Imperfect knowledge coupled with the commitment to maintain viable populations of this species, considered threatened in the State, caused the Regional Forester to adopt habitat management guidelines and issue direction for implementation of the SOMP. This direction has been revised or refined nearly annually since 1977, but throughout, has been highly specific and based on research conducted, largely, in the forests of western Oregon.

Implementation of management guidelines and direction was accomplished through the coordinated, interactive efforts of personnel from many resource disciplines at both the Supervisor's and Ranger District offices. Though significant progress has been made in identifying the distribution, abundance, and habitats of spotted owls in the Olympic, implementation of the SOMP was made complex due to the peculiar geography of the Peninsula, the vagaries of spotted owl behavior, and other resource conflicts.

The Olympic is committed to more complete, site-specific knowledge of spotted owl habitat use and continues to gather data through monitoring and administrative studies. The expectation is that management direction in the future will be flexible and responsible to new information, for after all, The ultimate result must be that we maintain viable populations of spotted owls, over time, such that we prevent the need for Federal listing.

R. E. Worthington
Regional Forester
October 28, 1980

LITERATURE

Allen, Harriet; Brewer, Larry W. A review of current northern spotted owl (Strix occidentalis caurina) research in Washington State. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture,' Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985; 55-57.

Carey, Andrew B; Ruggiero, Leonard F. Spotted owl management: meeting NFMA requirements through monitoring. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 34-38.

MANAGEMENT OF SPOTTED OWLS BY THE CALIFORNIA DEPARTMENT OF FISH AND GAME

Gordon I. Gould, Jr.

ABSTRACT: The California Department of Fish and Game must maintain populations of spotted owls for the intrinsic and ecological values of the owls. The Department performs this job through a coordinated effort with land management agencies to protect the old-growth and mature forest habitat required by the owl. Commercial logging dramatically reduces this habitat and jeopardizes the species' existence. Problems in current land management planning are discussed and research needed to improve management is identified.

INTRODUCTION

The California Department of Fish and Game (CDF&G) is charged with the conservation of all wildlife within the State, including species that are not harvested (Section 1801, Fish and Game Code). This specific legislative mandate calls for maintaining all species of wildlife and their habitat (1) for the use and enjoyment by all citizens of the state; (2) for the intrinsic and ecological values that all species have; and (3) for aesthetic, educational and other nonconsumptive uses. Management for species that are not used consumptively (15 species of owls and 622 species of other birds and mammals) centers around habitat preservation.

In 1970, the California legislature passed the Endangered Species Act, recognizing that destruction of wildlife habitat. reduction in the amounts of certain types of habitat, and severe modification of many natural environments were endangering many species, or subspecies, of native wildlife.

GORDON I. GOULD, JR., is a Nongame Wildlife Biologist for the California Department of Fish and Game, Sacramento.

Subsequently, CDF&G's management activities included monitoring populations, determining habitat requirements, preserving particular habitats, and assessing other land management agencies in their management of land and other resources to preserve habitat and to maintain or restore population levels of particular wildlife species.

In the process of surveying for the needs of endangered species, the spotted owl (Strix occidentalis) was identified as a species whose numbers were declining, possibly to the point of extirpation (Remsen l978). The major reason for the decline was a reduction in old-growth and mature forest, the habitat the owls require. The purpose of this paper is to report on the status of the spotted owl in California and to discuss the ways in which the CDF&G is attempting to maintain this species and its habitat.

CDF&G; ACTIVITIES

The first activity the CDF&G participated in was a State-wide survey to determine the distribution and habitat requirements of spotted owls (Gould **1974)**. Present activities include: continuously monitoring populations of spotted owls to determine how constant the occupancy of territories is, what the distribution of territories is across the State, and regional trends in populations; working with other government agencies to coordinate research on spotted owls, which includes the habitat requirements and the effects of land management on populations; compiling the results of research on owls and serving as a central source of information on the owl's status, biology, and management; assisting Federal, State, and private land managers in developing plans and guidelines that will preserve the habitat of spotted owls (Gould 1983); and reviewing plans for selling timber and timber harvests to ensure that the needs of spotted owls are considered.

CURRENT STATUS OF SPOTTED OWLS

The Department has classified the spotted owl as a "bird species of special concern." This designation carries no special legal status but only designates a species as one whose population has declined severely or is otherwise so low that extirpation is a real possibility.

Currently three geographically distinct populations that belong to two described subspecies are recognized (Grinnell and Miller 1944). The northern spotted owl (S. o. caurina) occurs from Marin County north along coastal California to the Oregon border and east to northeastern Shasta County. The California spotted owl (S. o. occidentalis) is found the length of the Sierra Nevada from southeastern Shasta County to northeastern Kern County; a second population occurs along California's south coast from Monterey County to San Diego County. The status of each population seems equally critical, although the nature of current threats vary.

Within this distribution there are 1,317 sites classified as territories (table 1) where (1) a pair has been observed; (2) young have been observed between May and September; or (3) a vocal defense of an area has been heard or solicited. However, this number doesn't represent the number of currently active sites as some sites have been abandoned and others may be yet undiscovered.

It's difficult to compare current densities of spotted owls with past densities. The lack of information on the distribution and density prior to 1973 can best be demonstrated by the Statewide estimate, made in 1971, of 30 pairs.[1] Therefore, I can only speculate about historical densities. Spotted owls have been reported from 549 different townships throughout California. Only one territory has been recorded for most townships. However, 6 to 11 territories have been recorded for 37 townships. Twenty-six of these townships are in north coast counties, 10 are in central Sierra Nevada counties, and only 2 are in south coast counties. Most of these areas are not pristine; I have personal knowledge of logging occurring in at least half of these townships, and logging probably has occurred in many of the others.

Table 1—Known distribution of spotted owl territories in California, June 1, 1984

County	Present number known	Nos. for northern spotted owls	Nos. for California spotted owls: Sierra Nevada	Nos. for California spotted owls: South coast
Alpine	3		3	
Amador	6		6	
Butte	19		19	
Calaveras	11		11	
Colusa	2	2		
Del Norte	41	41		
El Dorado	75		75	
Fresno	23		23	
Glenn	12	12		
Humboldt	117	117		
Kern	13		10	3
Lake	18	18		
Lassen	11		11	
Los Angeles	13			13
Madera	24		24	
Marin	18	18		
Mariposa	29		29	
Mendocino	38	38		
Modoc	1	1		
Mono	1		1	
Monterey	9			9
Napa	4	4		
Nevada	12		12	
Orange	2			2
Placer	40		40	
Plumas	83		83	
Riverside	4			4
San Bernardino	28			28
San Diego	21			21
San Luis Obispo	8			8
Santa Barbara	17			17
Shasta	36	22	14	
Sierra	27		27	
Siskiyou	250	250		
Sonoma	5	5		
Tehama	58	46	12	
Trinity	146	146		
Tulare	35		35	
Tuolumne	43		43	
Ventura	6			6
Yuba	8		8	
Totals	1317	720	486	111

One could infer that densities of five territories of spotted owls per township probably were not uncommon historically. Using a conservative historical density of 3.5, or 32 percent of the currently known maximum density, provides an estimate of the spotted owl population that existed in pristine times at almost 2,100 territories. This assumes that current distribution and historical distribution are the same and that historical density was 1.6 times current density.

[1] Personal communication, Ned Johnson, University of California, Berkeley.

There is good evidence that historical distribution was more extensive than the current distribution. Spotted owls are no longer present at at least 30 of approximately 125 historical sites (Gould 1974). This implies that the minimum historical range of spotted owls included at least 105 more territories than calculated above.

Population trends can be implied both from trends in the density of owls and from trends in the numbers of territories over a period of time. The trend of a reduction of density and range that was calculated above shows a reduction of at least 50 percent. Other evidence of a decrease in spotted owls was gathered in a survey in 1974; spotted owls were present at only 73 percent of the previously reported occupied sites (Gould 1974). Because the time between the first sighting and the most recent sighting varied, it was impossible to determine the rate of loss. However, over the last 10 years the Department has monitored 1,317 territories; at the It's visit, 58 of these sites were not occupied. possible that spotted awls were present but not detected or that the site was of marginal quality to begin with and isn't consistently occupied. I calculate that 1,259 of the 1,317 territories are presently occupied--a reduction of 4.5 percent over 10 years. This population size probably is smaller because those territories with the highest disappearance rate are those where only one report has been received for that territory and that report was of a single individual. Of the 1,259 occupied territories, 407 of these are single sightings of individual owls; pairs have been verified at only 41.6 percent of the territories.

As the number of territories increases the chance of adding new territories decreases. The USDA Forest Service has intensively surveyed 10 of the 17 National Forests in California; four other forests have been lightly surveyed. Surveys have covered from 50 to 85 percent of Forest Service lands, with most areas about 75 percent surveyed. Other lands were not as well surveyed; but these lands probably don't provide habitat for many spotted owls.

The California Region (Region 5) of the Forest Service controls 19,680,327 acres of land (USDA Forest Service 1979), much of it forested. Additional land is controlled by the Bureau of Land Management, but much less is forested. Large quantities of privately owned forest land exist but were the first areas logged; suitable owl habitat (old-growth and mature forest) is now scarce. Forests also *occur* in some State and Federal parks. On these lands, timber harvest does not occur and old-growth and mature forest habitat is usually the management objective.

More spotted owls are found on Forest Service land than on that in any other ownership (table 2) (Gould 1979); this clearly demonstrates the importance of Forest Service land to the preservation of this species in California. Currently, this land is being logged. It has been estimated that all commercially suitable old-growth forest habitat will be cut within 25 years. This logging will reduce owl habitat and spotted owl populations; it is doubtful that viable populations of this species will be maintained unless some accommodations are made. Similar logging is occurring on BLM and privately owned timber lands with few or no restraints to protect spotted owls.

Table 2--Land ownership of spotted owl territories in California, 1978

Ownership pattern	Percent territories by subspecies: Northern	California	Total percent
Completely private	4.5	4.0	4.2
Private near Federal land	1.5	10.9	6.2
Completely Forest Service	40.6	44.6	42.6
Forest Service with private land nearby	31.2	26.2	28.7
Bur. of Land Mgmt. with private land nearby	5.4	1.0	3.2
Jointly owned by Federal agencies	2.5	4.5	3.5
Ccmpletely National Park Service	3.0	5.9	4.5
NPS with private land nearby	2.5	0	1.2
Completley State park land	0.5	2.0	1.2
State park land with private land nearby	6.4	1.0	3.7
Other	2.0	0	1.0

The preference of spotted owls for old-growth habitat has been well documented (Forsman 1976, 1980; Forsman and others 1977; Gould 1974; Marcot 1978; Marcot and Gardetto 1980; Solis and Gutie'rrez 1982).[2] Old growth functions as the thermal cover necessary for the owl's survival (Barrows 1980, 1981; Barrows and Barrows 1978). The general biology and seasonal habitat use of the northern spotted owl has been described (Forsman 1976,1980; Solis and Gutiérrez 1982). Ongoing research is documenting the winter habitat use of the northern spotted owls and the dispersal of young.[3] Also, year-round habitat use, occupation patterns, and the dispersal of young are being studied in a central Sierra Nevada population of the California spotted Owl.[4]

[2] Unpublished Progress Report, 1981, "Habitat use by radio-tagged northern spotted owls on the Six Rivers National Forest," by David M. Solis, Jr., and Chuck Sisco, Six Rivers National Forest, Eureka, CA.

[3] Personal communication, Chuck Sisco and Ralph Gutigrrez, Wildlife Department, Humboldt State University, Arcata, CA.

[4] Personal communication, Stephen Laymon, School of Natural Resources, University of California, Berkeley.

COORDINATION IN LAND MANAGEMENT

The Department has collaborated with the USDA Forest Service and the State Board of Forestry in an effort to manage spotted owls. Both efforts involved trying to establish land management plans and regulations.

In 1983, under the California Forest Practices Act, the Board of Forestry listed species that must be considered in the planning of timber sales on private land. This list contains the species designated as “rare” or “endangered” by California or designated as a species of special concern by the Board. The Department made recommendations to the Board for establishing the list of species and the timber management activities that should be required to protect these species. The Department also acted in an advisory capacity to the Board in their deliberations. The Board didn’t list the spotted owl as a species of concern because of a lack of information, and because of the large territory size and the amount of potential timber that might be tied up by any single spotted owl territory.

Collaboration with the Forest Service at the field level has involved input and comment on individual timber sale plans by Department biologists. These area biologists review proposed sales and comment on the effects of the proposed sale on wildlife resources and suggest mitigation or alternatives to reduce the impact.

At the staff level, collaboration has involved the exchange of survey and research data, establishment of guidelines for spotted owl management, and the review of individual forest plans to determine if these plans comply with the guidelines. To date, 36 surveys have been performed by individual forests or ranger districts. These surveys have provided more records of spotted owls than has any other survey effort.

In 1981, the Department assisted the Pacific Northwest Region (Region 6, Portland) of the Forest Service by participating in a workshop assessing regional spotted owl management guidelines. Similar assistance was given to the Pacific Southwest Region (Region 5, San Francisco).

The Department has a representative on the Forest Service’s regional review team (Region 51 that evaluates the land management plan for each forest. Both Department staff and area biologists review and comment on the wildlife portion of each forest plan. Spotted owls are a major concern in the Department’s review of these plans.

IMPROVEMENTS NEEDED IN COLLABORATIVE EFFORTS

The Department is a single purpose agency and precise agreement with other agencies and private groups on land management decisions is not always possible. This is especially true when dealing with agencies that are either single purpose or have a very dominant purpose that is not compatible with the complete maintenance of the wildlife resource.

Because of conflicts in resource use, compromises Often must be made. With compromises wildlife always loses something. In the case of the spotted owl, compromise results in a decrease in available habitat and in putting the species in an ever more precarious position. Under such circumstances it is difficult to achieve the State’s objectives of maintaining intrinsic and ecological values, providing use and enjoyment to the citizens of California, and maintaining aesthetic, educational, and nonappropriative uses. There must be limits to compromise once the resource no longer adequately provides these attributes.

There are several problems concerning spotted owls that result when land management agency objectives don’t fully coincide with wildlife resource objectives:

1. The State Board of Forestry didn’t designate the spotted owl as a species of concern. As a result it lacks the protection that it and many other old-growth forest species need on private lands. Spotted owls are among the best indicators of old-growth forest quality still found in the state’s forests.

2. Although the Forest Service considers spotted owls in their land management planning effort, the plans, their guidelines and the manner in which they are being implemented may not offer adequate protection to maintain viable populations throughout California. More specifically:

a. The planning process is biased towards the timber resource so that the preservation of other resources is jeopardized regardless of what alternative is chosen (CHEC 1984).[5]

b. The plans are supposed to maintain a viable population of spotted owls but much of the information needed to determine what constitutes a viable population hasn’t been gathered.

c. There is no level of viability (probability of species survival) set in the planning process. Since a viab e population level is not fixed through time,[6] the level of viability set in the management plans must accommodate the worst possible situation; the plans don’t make this accommodation.

d. An inordinate delay is occurring between the establishment of guidelines, the development of plans, and the implementation. Because the harvest of old-growth forests is

---

[5] Correspondence, H. E. Hodgdon, The Wildlife Society, letter of 4/9/84 to T. E. Hamilton, Director, RPA, U.S.D.A. Forest Service, Bethesda, MD, 5 p.

[6] Unpublished Administration Report, 1983, "Wildlife population viability--a question of risk,” by Hal Salwasser and Stephen P. Mealey, USDA Forest Service, Pacific Southwest Region, San Francisco, CA.

continuing, it is likely that the plans will not be able to be implemented as written and Planning guidelines will not be met.

3. The Bureau of Land Management, National Park Service, California State Board of Forestry, California Department of Parks and Recreation, and California Department of Forestry do not have any State-wide, long-term planning efforts that consider spotted owls.

The Department also needs to develop a plan for preserving old-growth and mature forest ecosystems. It has already done this type of planning for coastal wetlands. A plan for old growth forests should include an inventory of the remaining old growth, a list of species that must be accommodated in forest preservation, a description of the current and the desired status of the forest wildlife in California, and procedures for working with land management agencies to carry out the plan. To be effective, the plan must be implemented promptly because all the commercially available old-growth forest may be harvested within 25 years, and the sales for those harvests are likely to be planned within the next **10** years.

INFORMATION NEEDS

It's obvious that the multiple use of forests can't stop for spotted owls. But, the Department must demand, and other land management agencies must provide for, the preservation of all species throughout their ranges at ecologically sound population levels.

A species can% be preserved throughout its range without adequate surveys to delimit the range and to show patterns of abundance within the range. Surveys of habitat facilitate the population surveys, provide information on the potential range of the species, and the future potential area available for the species. Survey work isn't complete in the species' believed range in California. However, in many areas, particularly in a few National Forests, it is nearly complete.

The most important information that's needed concerns the population dynamics of spotted owls. Data is needed to prepare a life table for a viable population of owls; specifically needed are age-specific reproductive rates, age at first breeding, mortality causes, and age-specific mortality rates. This information could be used to model the normal functioning of spotted owl populations and to predict the population's ability to reproduce itself and sustain the population. What is required to sustain the population could be compared to what occurs under different regimes of habitat disturbance and distribution patterns. The future course of any subpopulation could be estimated and changes in population size and distribution could be predicted. Only then can land management plans be made that would provide a solid basis for maintaining viable populations.

Finally, the pattern of site occupancy must be studied to understand and determine the causes and rates of local extinctions and recolonizations. An extensive monitoring system would have to be established throughout the species' range to collect this information.

REFERENCES

Barrows, Cameron Wallace. Summer roost selection by spotted owls: an adaptation to heat stress. Long Beach, CA: California State University; 1980. **51** p. M.S. dissertation.

Barrows, Cameron W. Roost selection by spotted owls: An adaptation to heat stress. Condor. **83: 302-309; 1981.**

Barrows, Cameron; Barrows, Katherine. Roost characteristics and behavioral thermoregulation in the spotted owl. Western Birds. 9: l-8; **1978.**

CHEC. Review of the **1985** RPA Program. Eugene, OR: Cascade Holistic Economic Consultants; **1984. 31 p.**

Forsman, Eric. A preliminary investigation of the spotted owl in Oregon. Corvallis, OR: Oregon State University; **1976. 127 p. M.S.** dissertation.

Forsman, Eric D. Habitat utilization by spotted owls in the west-central Cascades of Oregon. Corvallis, OR: Oregon State University; 1980. 95 p. Ph.D. dissertation.

Forsman, Eric D.; Meslow, E. Charles; Strub, Monica J. Spotted owl abundance in young versus old-growth forest, Oregon. Wildlife Society Bulletin. 5(2): **43-47; 1977.**

Gould, Gordon I., Jr.; The status of the spotted owl in California. Sacramento, CA: California Department of Fish and Game, Wildlife **Management** Branch; 1974; Admin. Rep. 74-6. 56 p.

Gould, Gordon I., Jr.; Status and management of elf and spotted owls in California. In: Schaeffer, P.; Ehlers, S., eds. Owls of the West; 1979 January 20; San Frncisco, CA. Tiburon, CA: National Audubon Society, Western Education Center; 1979:86-97.

Gould, Gordon I., Jr.; Owl nest territory monitoring program. Sacramento, CA; California Department of Fish and Game, Nongame Wildlife Investigations; 1983; Progress Rep. Project W-54-R-15, Job II-3. 6 p.

Grinnell, Joseph; Miller, Alden H. The distribution of the birds of California. Pacific Coast Avifauna. 27: 203-205; **1944.**

Marcot, Bruce G. Prolegomena of the spotted owl (Strix occidentalis) in Six Rivers National Forest. Eureka, CA: Six Rivers National Forest; 1978; Tech. Rep. 48 p.

Marcot, Bruce G; Gardetto, Jeffrey. Status of the spotted owl in Six Rivers National Forest, California. Western Birds. 11: 79-87; **1980.**

Remsen, J.V., Jr. Bird species of special concern in California. Sacramento, CA: California Department of Fish and Game, Wildlife Management Branch; 1978; Admin. Rep. **78-l. 54** p.

Solis, David **M.,** Jr; Gutirrez, Ralph J. Spotted owl habitat use on the Six Rivers National Forest, Humboldt County, California. Eureka, CA: Six Rivers National Forest; 1982; Final Rep. 230 p.

USDA Forest Service. Land Areas of the National Forest System as of September 30, 1979. Washington, DC: Department of Agriculture, Forest Service; **1979.**

STATUS OF SPOTTED OWL MANAGEMENT IN OREGON AS PERCEIVED BY OREGON DEPARTMENT OF FISH AND WILDLIFE

Richard D. Carleson and William I. Haight

ABSTRACT: The Oregon Department of Fish and Wildlife has a legal mandate to prevent serious depletion of wildlife species indigenous to Oregon. Because the population of spotted-owls appeared to be threatened by timber harvesting, the Department took the lead in organizing an interagency wildlife committee. The committee, composed of representatives of land and wildlife management agencies, developed a Spotted Owl Management Plan. The plan calls for maintaining a minimum of 400 pairs of spotted owls in Oregon; the present population is l,OOO-1,200 pairs. But cooperation and coordination among the land management agencies must be increased to accomplish this plan. And many questions, such as what constitutes a viable population, need to be answered.

INTRODUCTION

We estimate the present population of spotted owls (Strix occidentalis) in Oregon to be l,000-1,200 pairs based on recent research by Forsman and others (1984). The Spotted Owl Management Plan recommended by the Oregon-Washington Interagency Wildlife Committee calls for maintaining 400 pairs in Oregon. Comparing the two numbers, it appears that the present population is high enough to maintain a viable population of spotted owls throughout most of their range in Oregon if sufficient habitat can be retained.

RICHARD D. CARLESON and WILLIAM I. HAIGHT are wildlife biologists, Oregon Department of Fish and Wildlife, Portland, Oreg.

SPOTTED OWLS ON BLM AND PRIVATE LAND

Although the present statewide population is around l,000-1,200 pairs, there probably is not sufficient habitat to support that number, even in the short term. Timber harvest patterns have incrementally nibbled away at what were once vast acreages of old growth, creating a high interspersion of clearcutting with old growth in some ownerships, particularly the checkerboards of private and Bureau of Land Management (BLM) lands in western Oregon. There the remaining old growth is highly fragmented with few l,OOO-acre blocks of good spotted owl habitat. The gross acreage of old growth remaining in western Oregon is high enough to give the mistaken impression that there is plenty of habitat available. The fragmented habitat appears to allow existing spotted owls to survive in the short term, it is unclear whether they will be able to reproduce well enough to persist indefinitely. For example, 16 Spotted Owl Management Areas (SOMA) on the Coos Bay BLM District were surveyed in 1984 and only eight were occupied by spotted owls. Only one pair produced offspring. Spotted owl habitat on private land is, for the most part, already gone. Most of the old-growth stands large enough to contribute to a comprehensive spotted owl management plan were already harvested or committed to timber harvest before the Spotted Owl Management Plan was written.

The BLM lands in western Oregon offer better promise of maintaining spotted owl habitat than on private lands. Although sections of BLM land alternate with sections of private lands, BLM land still contains spotted owls and old-growth forest.

Four out of five western Oregon BLM districts (Coos Bay, Salem, Eugene and Roseburg) completed ten-year timber management plans in 1983. Inventory data presented in the BLM impact statements showed the existing population of spotted owls to be 177 pairs: the timber management plans protect the habitat of 64 pairs for 10 years. The protective standards, however, maintain only 300 acres of old-growth forest per spotted owl pair. According to the environmental statement, only 17 of the 64 SOMAs meet the minimum standards of the Spotted Owl Management Plan (SOMP) recommended by the Oregon-Washington Interagency Wildlife Committee. Because the BLM plans were regarded by the Department to need better protection of spotted owls, the department and BLM signed a cooperative agreement to provide needed protection for at least the first five years of the plans. The cooperative agreement is described later in this paper.

SPOTTED OWLS ON FOREST SERVICE LANDS

The spotted owls on the National Forests have more potential for survival. The forests haven't been as extensively harvested as BLM lands, so bigger blocks of old-growth habitat remain. A desirable distribution of SOMAs may be difficult to obtain, because the Forest Service ownership is not continuous from border to border (north and south) in the Coast Range. The planning process for the Forest Service is only partly completed, but there seems to be acceptance of the need to protect the habitat for owl pairs in close compliance with Oregon's Spotted Owl Management Plan. The Forest Service was allocated 290 pairs out of the 400 pairs recommended as minimum to maintain a viable population in Oregon throughout their range.

ODFW And The Spotted Owl

The overriding statement directing the Oregon Department of Fish and Wildlife (ODFW) is in the Wildlife Policy (Oregon Revised Statutes 496.012) adopted by the Oregon legislature in 1973. The appropriate part of the law is as follows: "It is the policy of the State of Oregon that Wildlife shall be managed to provide the optimum recreational and aesthetic benefits for present and future generations. of the citizens of this state...maintain all species of wildlife at optimum levels and prevent the serious depletion of any indigenous species...". The law does not define what the "optimim levels" are, nor does it establish what constitutes "serious depletion". The statutes authorize the Governor to appoint a seven member Commission to develop and implement policies and programs of the State for the management of wildlife and to promulgate rules to carry but the provisions of the wildlife laws. The wildlife laws relate mostly to the management and use of wildlife species. Traditionally, management of the land and its value as habitat has been at the discretion of the landowner. The end result is that the Commission can, by rule, regulate the taking or molestation of a species, but has only limited authority to regulate habitat management on the lands of others. The department does seek habitat protection through laws and regulatory mechanisms of other agencies such as Oregon Forest Practices Act and National Forest Management Act. The Commission did pass an administrative rule prohibiting the taking of sensitive wildlife, including State-listed threatened and endangered wildlife, and all nongame birds except sparrows and starlings. The ODFW was given authority to manage nongame wildlife by the 1971 legislature. Prior to that time authority was limited to game mammals and gamefish. A chronology of ODFW actions concerning the spotted owl follows:

May 1973.--John W. McKean, Director, Oregon Game Commission, proposed that a professional task force be formed and that its initial emphasis be placed on the identification of habitat requirements for the northern spotted owl (S. *occidentalis caurian*).

The Oregon Endangered Species Task Force was established and recommended the adoption of statewide guidelines by June 30, 1974. Protection of 300 acres around each known northern spotted owl location was recommended as an interim protective measure pending the completion of a management plan. At that time there was no information on the extent of acres used for forage by spotted owls. For this reason, the 300-acre guideline was adopted only as an interim measure, to be altered, if necessary when additional data became available.

October 1974.--The Sikes Act, Public Law 93-452, became law and provided for the protection for fish and wildlife, "officially classified as threatened or endangered pursuant to Section Four of the Endangered Species Act of 1973 or considered to be threatened, rare, or endangered by the State agency."

January 1975.--The Oregon Wildlife Commission adopted a list of threatened and endangered wildlife in Oregon. The northern spotted owl was listed as a threatened species on the official State list. Federal land managers were expected to provide protection for those species under the Sikes Act.

In 1977 the Oregon Endangered Species Task Force was reorganized into the Oregon-Washington Interagency Wildlife Committee, a multiagency group formed to coordinate the activities of wildlife and land management agencies. It appointed a Spotted Owl Subcommittee. At this time ODFW's previous role as being solely responsible for formulating a spotted owl management plan became a shared responsibility with the other agencies.

The Spotted Owl Subcommittee completed a Spotted Owl Management Plan in late 1977. Through the Wildlife Committee the plan was transmitted to concerned agency administrators for review and comment. The objective of the plan was "to maintain a population of at least 400 breeding pairs of northern spotted owls distributed throughout the known range in Oregon". The Bureau of Land Management accepted responsibility for the protection of 90 pairs; the USDA Forest Service, 290 pairs; and combined, state lands (Department of Forestry, Oregon Department of Fish and Wildlife, and Parks Division), county lands, Crater Lake National Park and private lands were to protect 20 pairs. Eash SOMA was to be at least 1,200 acres in size and to include at least 300 acres of old-growth forest. The Forest Service and BLM both agreed to implement the SOMP on an interim basis.

In 1981, after telemetry research on spotted owls indicated that the SOMP might not protect enough old-growth habitat, the subcommittee revised the SOMP to increase the old growth in each SOMA to 1,000 acres.

March 1981.--In March 1981, the Oregon-Washington Interagency Wildlife 'Committee adopted the Spotted Owl Subcommittee's revision to the Oregon SOMP. Robert M. Stein, chairman of the committee, forwarded the revised SOMP to the
4 Regional Forester, Pacific Northwest Region, USDA Forest Service; State Director, BLM; and the Oregon State Forester for use in forest land planning. Formal acknowledgement of the acceptability of these revisions was not forthcoming from the Bureau of Land Management or the Oregon Department of Forestry. The Forest Service agreed to incorporate the revised standard into its planning activities.

September 1982.--When the first of five BLM timber management plans was proposed in September 1982, the Oregon Fish and Wildlife Commission found the proposal to be in violation of Oregon's Wildlife Policy, the Federal Sikes Act, and the Oregon Coastal Management Plan. One of the deficiencies in the plan was that only 300 acres of old growth per SOMA were to be protected instead of the 1,000 acres called for in the Spotted Owl Management Plan.

October 1983.--In the summer of 1983 all five BLM Timber Management Plans were adopted by the Bureau with the additional deficiency that the number of spotted owl pairs to be protected was less than called for in the SOMP.

After a series of negotiations involving several agencies and media exposure, an agreement was reached between the ODFW and BLM. The BLM agreed to manage spotted owl habitat in accordance with the best available scientific information for a period of 5 years and ODFW would not pursue a legal challenge to the timber management plans. The agreement will provide sufficient habitat protection in the interim, but long-term protection requires successful completion of present research and reevaluation of the SOMP and timber management plans at the end of the five year period. ODFW and the BLM are presently evaluating implementation of the agreement.

'The distributional requirements of the spotted owls are as important as habitat quality and quantity, and we are in the process of coordinating the disribution of SOMAs between the USFS and BLM.

There are no ongoing discussions with private landowners about maintaining spotted owl habitat. Most private holdings have been harvested, are too small to make a habitat unit, or have not been inventoried for spotted owls. Further, the bulk of the SOMAs (380 out of 400) have been allocated to the most extensive land managers (BLM and Forest Service); it seems reasonable to first secure protection on those lands, and then try to fit the remaining 20 SOMAs into the distribution provided by federal lands.

State lands do hold some spotted owl habitat, but population inventories have not been made. State lands are managed by various State agencies each having differing legal mandates. The majority of State lands are managed for timber production by the Oregon Department of Forestry.

Needed Collaboration

Development of the Spotted Owl Management Plan provided a necessary tool for protection of spotted owl habitat. It was intended to give land managers a recipe for protection that, if implemented, would maintain a minimum viable spotted owl-population throughout its native range in Oregon. The SOMP represents minimum standards and the responsibility for success of the plan depends on implementation of the plan by each of the major landowners. There needs to be more coordination among the agencies responsible for implementing the plan. The coordination is difficult because the agencies have differing schedules for completing their land use plans. The plans of one land manager will affect the outcome of the plans of another agency. To make certain that spotted owl habitat units are distributed properly there must be continuous discussion among the agencies. Since the Spotted Owl Subcommittee has become more active, the interagency coordination has improved. It is expected that continued coordination by members of the Spotted Owl Subcommittee will provide updated direction to the land management agencies

The Spotted Owl Management Plan is dynamic and needs to reflect new research findings. The Subcommittee is expected to continuously evaluate the SOMP to see that it is state-of-the-art and to monitor its implementation by land managers.

INFORMATION NEEDS

Many papers end with the statement that more research is needed; this paper is no exception. More answers are needed and are needed soon to such questions as: What is needed to ensure the continued existence of spotted owls? Is the population in Oregon isolated from the one in Washington? If so, is there a potential link somewhere in the Columbia Gorge? Can old-growth habitat be successfully managed to provide timber and old-growth-dependent wildlife? Can spotted owl habitat be created? How much fragmentation of old-growth habitat can be tolerated within a SOMA? Does a fragmented SOMA need more acreage of old growth than an unfragmented SOMA, and if so, how much? Some of the SOMAs being selected by land managers appear to be in marginal habitat; can the parameters of the SOMP be successfully applied to marginal habitat? The questions could go on and on. Unfortunately it's easier to find the questions than it is to find the money to fund the answers.

LITERATURE CITED

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Distribution and biology of the spotted owl in Oregon. Wildlife Monograph No. 07; 1984. 64 p.

MANAGING NORTHERN SPOTTED OWLS IN WASHINGTON: THE POSITION OF THE WASHINGTON DEPARTMENT OF GAME

Tom Juelson

ABSTRACT : The northern spotted owl is classified as threatened by the Washington Department of Game. The Department considers the Olympic Peninsula spotted owl population to be isolated from all others and considers the Washington Cascade Range population to be genetically isolated from Oregon spotted owls by the Columbia River. The principal responsibilities of the Department are to protect and improve wildlife habitat, and to preserve, protect, and perpetuate wild animals in the best interest of the people of Washington. The responsibility of the Department to spotted owls is implicit under these guidelines. The Department is involved in independent research as well as interagency cooperative research regarding the spotted owl. Further collaboration among agencies is needed, particularly in managing the Olympic Peninsula spotted owl population. There are additional research needs in reference to the spotted owl which should be addressed.

STATUS OF THB SPOTTED OWL

The Washington Department of Game has classified the northern spotted owl as a threatened species in Washington. The State's definition of "threatened" is the same as that of the U.S. Fish and Wildlife Service. This spotted owl classification is currently under review for a possible change to "endangered". The final decision on the status is pending completion of research in Washington.

TOM JURLSON is the nongame program manager, Washington Department of Game, Olympia, Washington.

Department biologists currently perceive the spotted owl population in Washington as divided into two gene pools. One exists on the Olympic Peninsula. These spotted owls are isolated from genetic interaction with others because of large expanses of water and nonforested areas. The habitat there is severely fragmented for the most part and in short supply. It may be too late to provide enough habitat on the Peninsula to support a viable population, and it is highly unlikely that a forested corridor will be established linking the Peninsula with the Cascade Range in Washington. Some biologists consider the long-term existence of this segment of the spotted owl population to be endangered by any criteria.

The second spotted owl gene pool in Washington is in the Cascade Range. This range includes the wet-type forests of western Washington and the dry-type coniferous forests of the eastern slopes of the Cascades.

The Department believes the Washington Cascades spotted owl population may be genetically separated from the Oregon population by the Columbia River and by adjacent land use in the river valley. The Washington Cascades population is continuous with the British Columbia spotted owl population; however, current information indicates that the British Columbia segment of the population is probably very small.[1] Management considerations for the Washington Cascades spotted owl population, along with members of that population in British Columbia, should be based on a viable population level separately derived for the geographic area north and west of the Columbia River. Department biologists do not believe a satisfactory viable population level has been determined.

DEPARTMENT OF GAME POLICY

The policy manual of the Washingtn Department of Game provides a "statement of purpose" for each administrative division within the agency. Two of these divisions share the principal responsibilities with regard to the northern spotted owl: the Habitat Management Division and the Wildlife Management Division. The goal of the Habitat Management Division is "to protect and improve land and water habitats to assure optimal numbers, diversity, and distribution of wildlife for the welfare of people of Washington State." The goal of the Wildlife Management Division is "to preserve, protect, and perpetuate wild animals and to provide optimum wildlife oriented recreation for citizens of Washington through management, surveys, and research of birds, mammals, reptiles, and amphibians and their habitat." The spotted owl is a native species of Washinton and the responsibility of the Department toward management of this species is implicit in these two statements.

COLLABORATIVE EFFORTS

The Department initiated independent research on spotted owl ecology in 1981 (Allen and Brewer 1985) which has stimulated a number of cooperative efforts between state and federal agencies and interactions between state and private industry in Washington. The Department is cooperating with three National Forests in Washington in an administrative study of the effectiveness of spotted owl management areas (Carey and Ruggiero 1985). USDA Forest Service, Burlington Northern Railroad, Weyerhaeuser Company, and USDI National Park Service personnel cooperated with the Department in completing a statewide spotted owl survey. Department biologists are interacting with USDA Forest Service district biologists on many aspects of spotted owl information sharing (for example, location information, home range data, and habitat data). Department personnel are negotiating with the Washington Department of Natural Resources regarding Natural Resources policy on spotted owl management. Department research biologists are cooperating with wildlife management biologists from British Columbia in setting up spotted owl censuses in British Columbia that are targeted for spring 1985. The Department is conducting radio-telemetry monitoring of spotted owls on two ranger districts for the USDA Forest Service. This work is funded by timber sale revenues (Knutson-Vandenberg Act funds).

ADDITIONAL COLLABORATION NEEDED

A generally acceptable determination of a viable population level for spotted owls in the Washington Cascade Range and in the British Columbia populations should be made through an interagency approach. The U.S. Fish and Wildlife Service should consider reviewing the spotted owl population on the Olympic Peninsula to see if it should be declared endangered. If it is, cooperative efforts should be initiated to develop and carry out a maintenance program of the current population level. The Oregon-Washington Interagency Wildlife Committee and its Spotted Owl Subcommittee are developing means for interagency collaboration.

INFORMATIONAL NEEDS

To complete the evaluation of the size and distribution of the Washington and British Columbia spotted owl populations, we need good data on the British Columbia population. Genetic research to determine the extent of inbreeding in current populations would further facilitate the evaluation of species status.

The effects of habitat fragmentation and the size and distribution of habitat blocks on population should be more clearly defined, particularly with regard to predation and interspecific competition.

An analysis of habitat use in dry-type coniferous forests is needed to define the limits of spotted owl range in eastern Washington. This is particularly important in deciding the location of Spotted Owl Management Areas in dry-type forests.

Additional information on the relationship bewteen prey species and spotted owl habitat use is needed to assess the merits of alternative forest practices (that is, selective harvest).

1/ Personal communication, D. Dunbar and D. Wilson, B.C. Fish and Wildlife Management, Parliament Bldg., Victoria V8V 1X5.

LITERATURE CITED

Allen, Harriet; Brewer, Larry W. A review of current northern spotted owl (Strix occidentalis caurina) research in Washington State. In: Gutiérrez, Ralph J.; Carey, Andrew B, tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 55-57.

Carey, Andrew B.; Ruggiero, Leonard F. Spotted owl management: meeting NFMA requirements through monitoring. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service; Pacific Northwest Forest and Range Experiment Station; 1985: 34-38.

SPOTTED OWLMANAGEMENT: MEETING NFMA REQUIREMENTS THROUGH MONITORING

Andrew B. Carey and Leonard F. Ruggiero

ABSTRACT: In 1983, biologists from USDA Forest Service research, three National Forests in Washington, and the Washington Department of Game collaborated to design and implement an extensive program for monitoring the effectiveness of the management area system for spotted owls-a designated management indicator species and key vulnerable species. The program will evaluate the success of the management system as well as current standards and guidelines for management. This kind of collaborative effort may be the only practical way to effectively monitor a species that is possibly in jeopardy from the reduction of its habitat.

INTRODUCTION

The USDA Forest Service is charged with the authority and responsibility for managing the National Forests. Accompanying papers (Beckstead 1985, Carrier 1985, Lee 1985, Ruediger 1985) relate the procedures used and the difficulties encountered in planning for and making decisions about northern spotted owls (Strix occidentalis caurina). What, then, are the risks of making such decisions with incomplete information? For the spotted owl, wrong decisions or unexpected results could place in jeopardy the subspecies' existence, lead to a change in its legal status (for example, it could be placed on the Federal Endangered Species List), and incur stringent constraints on future forest management. Worse, the subspecies could be extirpated from much of its range. Both situations would be failures in meeting management objectives as well as legal requirements.

What can be done to reduce the risks associated with making decisions based on incomplete information? Conservative decisions-those that assume the worst case-can be made. Advice can be obtained from persons most knowledgeable about the species. Research can continue to produce new information. Most importantly, however, the effects of the decisions can be monitored to determine if the objectives and expected results are being attained. The purpose of this paper is to discuss monitoring and to describe a monitoring program recently implemented in the National Forests in Washington to determine how well the Spotted Owl Management Area (SOMA) system is working.

ANDREW B. CAREY is research coordinator and LEONARD F. RUGGIERO is program manager, Old-Growth Forest Wildlife Habitat Program, Pacific Northwest Forest and Range Experiment Station, USDA Forest Service, Olympia, WA.

MONITORING

Monitoring is an integral part of modem management systems. It provides information on the quality and quantity of the products of management and on the degree of attainment of goals and objectives. Monitoring provides an evaluation of the reasonableness of objectives and the efficacy and suitability of the processes (management actions) used to achieve the objectives. And monitoring provides information for future management.

The USDA Forest Service has adopted a goal-oriented approach to its management of wildlife and fish (Nelson and others 1983). Now the National Forest System is developing monitoring systems that are in accordance with legal requirements and management needs. Carey (1983) and Verner (1983) provide examples of how monitoring systems might be developed and advice on experimental design and sampling considerations for monitoring. Legislative mandates for monitoring the attainment of goals and objectives of wildlife and fish management were reviewed by Salwasser and others (1983). The National Environmental Policy Act of 1969 (NEPA), the subsequent regulations formulated by the Council on Environmental Quality, and, later, Executive Orders provide the basis for most of the requirements for monitoring by Federal agencies.

The regulations stemming from the National Forest Management-Act (MacCleery 1982) provide the most explicit direction for monitoring by the National Forest System. The regulations require that monitoring be "addressed" in both the regional guide and forest plan. "On a sample basis", monitoring is to periodically determine and evaluate the effects of management practices, how closely management standards and guidelines have been applied, and how well objectives have been met. An important "minimum specific management requirement" is to provide for adequate habitat to maintain viable populations of existing native vertebrate species and to ensure that habitat for management indicator species is maintained or improved to the degree consistent with the multiple-use objectives established in the forest plan. The population trends of management indicator species must be monitored and relationships to habitat changes determined. Monitoring of populations is to be done in cooperation with State fish and wildlife agencies, to the extent practicable.

The Pacific Northwest Region (R-b-the National Forests in Oregon and Washington) of the National Forest System lists the northern spotted owl as a management indicator species and as a "key vulnerable species"--a species possibly in jeopardy because of reductions in its limiting habitat. [1]/ Thus, minimum management requirements (including monitoring) for management indicator species and for minimum viable populations apply to the spotted owl.

SPOTTED OWL MANAGEMENT IN R-6

Detailed information on spotted owls in the Pacific Northwest was first collected in the 1970's. The owl's association with old-growth Douglas-fir forests was documented and declines in populations were noted. In 1973 an interagency committee of biologists from the USDA Forest Service, USDI Bureau of Land Management, USDI Fish and Wildlife Service, Oregon State University, and the Oregon Department of Fish and Wildlife drafted a management plan for spotted owls. Later, biologists from the Washington Department of Game (WDG) joined the committee. R-6 accepted the recommendations of the committee and subsequent revisions (Forsman and others 1982).

In 1983, R-6 minimum management requirements (see footnote 1) for each pair of spotted owls in a Spotted Owl Management Area (SOMA) were 1,000 acres of old-growth forest with 300 contiguous acres constituting a nest grove (core area) and 700 acres within 1.5 miles of the nest, in patches greater than 30 acres, constituting a foraging area. If 1,000 acres of old-growth were not available, the next oldest stands were to be substituted for the old growth. Each SOMA was to encompass the home ranges of at least three pairs of owls. Single-pair SOMAs were acceptable only to improve the geographic distribution of SOMAs or where remnant habitat existed. SOMAs of three or more pairs were to be less than 12 miles apart; the core areas of multipair SOMAs were to be separated by l-3 miles. Single-pair SOMAs were to be less than 6 miles from other SOMAs (core center to core center). The National Forests, with the Bureau of Land Management, were to maintain SOMAs for 400 pairs of owls west of the Cascade Range crest in Oregon; the National Forests in Washington (west of the Cascade Range crest) were to provide sufficient SOMAs to maintain 108 pairs of owls.

Proposed SOMAs were located using owl distribution maps and habitat descriptions, and through coordination with other land uses. The distribution of spotted owls in the National Forests was determined by eliciting vocal responses from spotted owls by broadcasting tape recordings of owl calls at night from roads and trails in mature and old-growth forest (see Forsman 1983 for procedures). A SOMA was considered verified (established) when occupancy was determined by repeated nocturnal surveys or when immature owls were observed. In April 1984 the minimum management requirements for the spotted owl were expanded to reflect the most recent information on the biology of spotted owls (see the paper by Lee in this symposium).

The procedures used to choose and verify SOMAs had several weaknesses, especially when they were applied in the National Forests in Washington. First, most research on the spotted

[1]/ Jeff M. Sirmon. 1983. Regional guidelines for incorporating minimum management requirements in forest planning. Written directive to Forest Supervisors, Region 6, National Forest System, on file at Pacific Northwest Region, P.O. Box 3623, Portland, OR.

owl's habitat requirements had been done in Oregon and was not specific to Washington. Second, nocturnal surveys do not precisely determine an owl's home range and may be misleading because owls often move towards the caller before responding. And third, few nestling or fledgling owls were seen by National Forest System biologists. For these three reasons, an extensive monitoring program for spotted owls in National Forests in western Washington was developed jointly in 1983 by Forest Service and WDG biologists. Andrew Carey and Len Ruggiero represented Forest Service research; Bill Ruediger, the Gifford Pinchot National Forest (NF); Dick Dearsley, the Mount Baker-Snoqualmie NF; Maureen Beckstead and Kelly Coon, the Olympic NF; and Harriet Allen and Larry Brewer, the WDG. Earlier, Eric Forsman (Oregon State University) and Rocky Gutiérrez (Humboldt State University) had provided the group with unpublished reports and technical advice. Funds to implement the monitoring in 1984 were provided by R-6 and the WDG. WDG personnel are conducting the monitoring with assistance from the personnel at the National Forests and under the guidance of the ad hoc committee of biologists listed above. Total costs for a 3-year program are estimated to be $380,000.

MONITORING SOMAS IN WASHINGTON

Objectives

The ad hoc committee formulated 2 primary objectives and 14 secondary objectives for the monitoring.

<u>Objective I: Determine if the SOMA system is working</u>.--It is presently assumed by R-6 that each SOMA will provide the necessary habitat to maintain at least one pair of spotted owls. At least the following will be determined:

1. The proportion of SOMAs occupied by spotted owls.
2. The proportion of SOMAs occupied by one or more pairs (male and female) of spotted owls.
3. The proportion of SOMAs occupied by breeding pairs of spotted owls.
4. The average number of spotted owls (and owl pairs) per SOMA.

<u>Objective II: Determine if current standards and guidelines are appropriate</u>.--At a minimum, two aspects of current standards will be evaluated: size of SOMAs and characteristics of SOMAS. For evaluating size standards, the following will be determined:

5. The proportion of the SOMA being used by spotted owls.
6. The amount of areas adjacent to the SOMA being used by owls.
7. The home range of owls using SOMAs.
8. The home range of pairs of owls using SOMAs.

For evaluating characteristics, the following will be determined:

9. The age of stands used by owls in the SOMAs.
10. The proportion of time spent in old growth by the owls.
11. The proportion of time spent in young forests by the owls.
12. The habitat characteristics (canopy layers, diameter at breast height, abundance of snags, and others) of areas used by owls.
13. The habitat characteristics of areas not used by owls, but in or adjacent to the SOMAS.
14. The differences between used and unused areas.

Study Areas

Population objectives were 49 pairs of spotted owls for the Mount Baker-Snoqualmie NF, 42 pairs for the Gifford-Pinchot NF, and 17 pairs for the Olympic NF. Each Forest biologist provided us with a sequentially numbered list of SOMAs equal in number to that Forest's population objective. We used a random numbers table to select the SOMAs to be evaluated: 19 SOMAs were chosen for the Mount Baker-Snoqualmie NF, 17 for the Gifford-Pinchot NF, and 10 for the Olympic NF. A list of alternate SOMAs was also selected for each Forest in the event one or more SOMAs had to be eliminated from the sample.

Methods

<u>Determination of occupancy</u>.--Forest Service personnel have surveyed most of the SOMAs for spotted owls. Thus, for some SOMAs, the primary center of activity or core area is known. Because owls range widely and may travel far to respond to calls at night, the core areas and actual occupants of many other SOMAs are not well documented. WDG monitoring crews will determine occupancy each year for at least 3 years. When the core area is known, the crews will visit the SOMA during the day to locate the resident owls. Nocturnal surveys will be made throughout the other SOMAs. If no owls are found it will be assumed that the SOMA is unoccupied that year. If owls are observed, then the center of activity will be located and visited during the day. All surveys will be done from March to August. Up to seven daytime visits will be made to each SOMA. If owls can't be found on seven visits, the SOMA will be classified as unoccupied for that year. If owls are found, the number, age, and sex of the owls and their roosting and nesting trees will be noted. If only one owl is observed at a time, it will be assumed that the SOMA was not occupied by a pair. If a pair of owls is seen or if young owls are seen, it will be assumed that the SOMA was occupied by a pair of owls. Occupancy will be determined in each of 3 years.

<u>Use and home range</u>.--Ten occupied SOMAs were selected for evaluation. Resident owls were trapped in early spring (1984) and fitted with radio transmitters. Each owl is being monitored

through radiotelemetry at least 1 day per week and l-3 nights per week throughout the year. Areas used for foraging, roosting, and nesting are being determined. Movements and use (activity) will be plotted on aerial photographs or orthophoto quadrangle maps. Altogether, the proportion of SOMA used, habitats used, and home range will be determined by season for l0-20 spotted owls.

Description of habitat.--A standard sampling procedure developed by the Old-Growth Forest Wildlife Habitat Program for analyzing wildlife habitat will be used to describe used and unused areas in, and adjacent to, the SOMAs, with use determined by radiotelemetry. Both vegetation and environmental structure will be described.

Results

SOMA effectiveness will be measured by the following statistics: proportion of SOMAs occupied, proportion occupied by pairs, and number of owls per SOMA. Because the sampling (choice of stands) was random, average effectiveness will be calculated forestwide and statewide. Effectiveness will be evaluated as follows: if on the average (over 3 years) 41 of the 46 SOMAs were occupied by pairs and over the 3 years every SOMA surveyed was occupied by a pair in at least 1 year, it would be concluded that the SOMA system was working very well. The conclusion has an implicit assumption that adult owls have a life expectancy of more than 3 years, during which at least two young would be produced. But if 23 of the 46 SOMAs were occupied by pairs with 15 of 46 never occupied, then effectiveness would be low and adjustments (such as replacing the 15 never used with new SOMAs) would be indicated.

Habitat descriptions will be compared to current standards and guidelines to test their appropriateness. These results could be used to assess, and, if necessary, adjust the kind and amount of land managed for spotted owls. It may be possible to contrast the areas used by single owls with the areas used by pairs. Thus, definitive information on the habitat required to maintain a population could be provided.

Coordination

The results of the monitoring program will be augmented by research being done by the Old-Growth Forest Wildlife Habitat Program and the WDG. The Old-Growth Program is collecting detailed information on the prey of spotted owls, the structure and composition of young, mature, and old-growth forests, the reproductive attainment of adult spotted owls, and the dispersal of juvenile spotted owls. The WDG has been conducting a statewide inventory of spotted owls, relating spotted owl distribution to land use patterns, and studying adult owl habitat use and juvenile owl dispersal. By the third year of the monitoring program substantial new information. relating to spotted owl management will be available.

CONCLUSION

Federal regulations call for monitoring populations of management indicator species. Monitoring is a complex and costly procedure. In Washington, Forest Service research, three National Forests, the Pacific Northwest Region of the National Forest System, and the Washington Department of Game have collaborated in designing and implementing a program for monitoring the attainment of the Forest Service's objectives in managing for spotted owls and for evaluating the standards and guidelines to manage habitat for spotted owls. Such collaborative efforts have much promise and may be the only way to accomplish effective monitoring of key sensitive species. This monitoring system model is a prototype for all monitoring in the National Forest System; the level of investment, however, must be matched to significance of the land use issue for other species. [2]

ACKNOWLEDGMENTS

We thank Maureen Beckstead, Larry Brewer, Richard Pedersen, Hal Salwasser, and Jared Verner for their comments on an earlier version of this paper.

LITERATURE CITED

Beckstead, Maureen. Olympic National Forest spotted owl habitat management: translating evolving management guidelines into actions. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 14-20.

Carey, Andrew B. Monitoring diurnal, cavity-using bird populations. In: Snag habitat management: proceedings of a symposium; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-99. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1983: 188-199.

Carrier, W. Dean. Planning and managing for the spotted owl in the National Forests, Pacific Southwest Region. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 2-4.

[2] Personal communication, Hal Salwasser, U. S. Department of Agriculture, Forest Service, Wildlife and Fisheries Staff, 3825 E. Mulberry, Fort Collins, CO.

Forsman, Eric D. Methods and materials for locating and studying spotted owls. Gen. Tech. Rep. PNW-162. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1983. 8 p.

Forsman, Eric D.; Horn, Kirk M.; Neitro, William A. Spotted owl research and management in the Pacific Northwest. Transactions of the North American Wildlife and Natural Resources Conference. 47: 323-331; 1982.

Lee, Philip I. History and current status of spotted owl (Strix occidentalis) habitat management in the Pacific Northwest Region, USDA-Forest Service. In: Gutiérrez, Ralph J.: Carey, Andrew B., tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 5-9.

MacCleery, Douglas W. National Forest System land and resource management planning. Federal Register. 47(190): 43026-43052; 1982.

Nelson, Robert D.; Black, Hugh, Jr.; Radtke, Robert E.; Mumma, John. Wildlife and fish management in the Forest Service: a goal oriented approach. Transactions of the North American Wildlife and Natural Resources Conference. 48: 87-95; 1983.

Ruediger, William. Implementing a spotted owl management plan: the Gifford-Pinchot National Forest experience. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 10-13.

Salwasser, Hal; Hamilton, Carole K.; Krahn, William B.; Lipscomb, James F.; Thomas, Carl H. Monitoring wildlife and fish: mandates and their implications. Transactions of the North American Wildlife and Natural Resources Conference. 48: 297-307; 1983.

Verner, Jared. An integrated system for monitoring wildlife on the Sierra National Forest. Transactions of the North American Wildlife and Natural Resources Conference. 48: 335-366; 1983.

AN OVERVIEW OF RECENT RESEARCH
ON THE SPOTTED OWL

R. J. Gutigrrez

ABSTRACT: The recent literature on the northern spotted owl (Strix occidentalis caurina) is reviewed and the salient features of the owl's natural and life history are presented. The conclusion is that northern spotted owls are dependent upon old-growth conifer forests of the Pacific Northwest.

INTRODUCTION

The spotted owl (Strix occidentalis) occurs as three recognized subspecies (S. o. caurina, S. o. occidentalis, and S. o. lucida) distributed from southern British Columbia south into Mexico (American Ornithologists Union 1957). The northern spotted owl (S. o. caurina) is thought to be closely associated with old-growth Douglas-fir (Pseudotsuga menziesii (Mirb.) Franco) forests throughout the Pacific Northwest (Forsman and others 1977, 1984; Gould 1974; Grinnell and Miller -1944; Gutigrrez and others 1984; Solis 1983). The importance of these forests to both the timber industry and the spotted owl is the center of a growing controversy over the disposition of old-growth forests and the future of the owl (Heinrichs 1983, 1984).

Spotted owls appear to be declining with the continued logging of old-growth forests (Forsman and others 1977, 1982, 1984; Gould 1977, 1985; U.S. Department of the Interior, Fish and Wildlife Service 1982). Most of the remaining old-growth areas occur in National Forests (Forsman and others 1984; Gould 1979, 1985). The National Forest Management Act of 1976 (U.S. Laws, Statutes, etc. 1976), which requires maintenance of viable populations of vertebrate species on all National Forests, is being invoked as a reason for intensive investigation and management of spotted owls and other old-growth wildlife species (Carey 1984, Carrier and others in press, Gutiérrez and others 1984, Ruggiero and Carey 1984).

In this paper, I will summarize the recent research on northern spotted owls within the context of natural history and life history characteristics that are particularly important for the management of this species. Campbell and others (in press) have provided an extensive bibliography on the spotted owl. I will therefore not attempt to incorporate obscure agency reports unless they are particularly germane.

NATURAL HISTORY

General Comments

Prior to 1970, most observations and research on spotted owls had been anecdotal (Campbell and others in press), and the bird was thought to be rare and secretive. Forsman (1976, 1980) was the first to record extensive natural history observations of the spotted owl and to summarize usable field study techniques (Forsman 1983). His work was especially timely with passage of the National Forest Management Act of 1976. In the following natural history review I will first present information on vocal and morphological

R. J. Gutiérrez is associate professor and chairman of the Wildlife Department, Humboldt State University, Arcata, Calif.

characteristics that have been found useful in spotted owl studies. Then I will summarize salient features of spotted owl habitat, home range and movements, and food habits.

Vocalizations

Spotted owls are territorial and actively defend their home range, particularly the nest grove (Forsman 1976, 1980; Forsman and others 1984). Thus, they can be located through imitation of their calls. Males can be distinguished from females by the male's lower-pitched, four-note hoot (see Forsman and others 1984 for a more complete description of the owl's vocal repertoire).

Molt and Sexual Characteristics

The molt of the spotted owl has been described by Forsman (1981). Of particular interest to biologists is the fact that three age classes can be distinguished: juveniles can be identified by the presence of downy plumage until about 3 months postfledging; immature/subadult birds can be distinguished by the presence of pointed, white-tipped middle rectrices from their first autumn of life until midsummer of their third year; and adults have rectrices with rounded tips. Barrows and others (1982) describe a method for determining the sex of spotted owls by retrix barring pattern. Miller and Meslow (1985) have reported this method to be accurate.

Females are, on the average, larger than males (Earhart and Johnson 1970); however, the overlap in weights, between large males and small females, does not allow sexual determination. Similarly, juveniles are usually at or near adult weight soon after they are able to fly (personal observation); thus weight cannot be used as a criterion for either age or sex determination. Tail-barring pattern may be the best future method for determining the sex of juveniles.

Habitat

Perhaps the most important contribution of recent work has been the analysis of habitat and home range (the latter will be discussed in the next section). This information has been critical to the delineation of appropriate habitat for Spotted Owl Management Areas (SOMAs in the Pacific Northwest Region, USDA Forest Service) and Spotted Owl Territories (SOTs in the Pacific Southwest Region).

Forsman and others (1984), Gutigrrez and others (1984), Sisco and Gutigrrez (1984) and Solis (1983) demonstrate a significant association of the owls with old-growth forests. Solis' work is particularly useful in that it describes not only an affinity for old growth, but also describes the forest structure in detail. Although Douglas-fir old growth is-the most important habitat type, much old growth (and mature, unmanaged conifer forests) below the high elevation subalpine conifers also is occupied by spotted owls (Forsman and others 1984, Solis 1983).

Several interesting features of habitat use are emerging from the studies. First, although spotted owls can be found within second-growth conifer forest, and in other habitats, it is unknown if they are reproductively successful; this aspect needs further research (Forsman and others 1977, 1984). Neither presence-absence nor abundance of owls alone should be used as an indicator of habitat quality (Van Horne 1983). Fitness, when measured as breeding success, should be used as one of the primary criteria for the quality of habitat (Van Horne 1983). Second, not all old- growth stands appear to be equally used by the owls[1] (Solis 1983). Use may be related proximately to habitat structure per se, or ultimately to food resources (see also Hilden 1965 for a theoretical discussion of these concepts). Third, male and female owls appear to be using habitat of different structure (Sisco and Gutiérrez 1984, Solis 1983, see footnote 1).

In general, spotted owls use old-growth forests that are characterized by multistoried stands of large-diameter (> 91 cm in diameter at breast height [d.b.h.]) conifers with hardwood understories in northwestern California. In Oregon, the understory may be either hardwood or conifer (Forsman and others 1984, p. 16). The stands in California have high canopy closure (approximately 80-90 percent) and they are old (> 150 years) with a high degree of stand decadence (Sisco and Gutiérrez 1984, Solis 1983). Spotted owl habitat 3.
in Washington appears to closely resemble Cascade Oregon habitats but has 90 percent canopy closure (Garcia 1979).

Tables 1, 2. and 3 present data that more specifically define the owl's habitat in northwestern California. The multistoried pattern of spotted owl habitat is easily discerned from tabulation of tree density and basal area (table 1). Douglas-fir dominates the upper canopy and hardwoods the lower strata (that is, diameter classes). There are, however, conifers and hardwoods represented in all diameter classes.

A comparison of table 1 with table 2 shows the average age of trees in the largest diameter class (≥ 91 cm d.b.h.) is 268 years; the tree diameter class 53-91 cm d.b.h. averaged 142 years. There is much variation in ages among trees of a particular size class as a result of the influence of site factors, elevation, and exposure. Table 3 indicates that these stands also have a high degree of decadence associated with them. Stands used by spotted owls in northwestern California may therefore contain relatively small diameter (53-91 cm d.b.h.) trees but exhibit properties of stands that are much older. Such properties include (1) a multiple canopy of hardwoods and

---

[1] Manuscript in preparation by David Solis, Wildlife Department, Humboldt State University, Arcata, CA 95521.

Table 1--Some tree characteristics within spotted owl habitat in northwestern California [1]/

Diameter size class [2]/	Mean density	Mean basal area
	stems/ha	m^2/ha
Hardwoods:		
I	46.20	0.48
II	154.14	4.40
III	47.54	5.26
IV	9.80	3.27
V	1.26	1.30
Subtotal	258.96	14.71
Conifers:		
I	17.98	0.18
II	74.47	2.27
III	48.28	5.68
IV	25.67	9.81
V	27.57	35.74
Subtotal.	193.99	53.70
(Douglas fir)	171.73	49.65
Total trees	452.95	68.41

[1]/ Data from Solis (1983) and Sisco and Gutiérrez (1984) and represent 723 vegetation plots 0.02 ha in size.

/Diameter size class: I = 10.16-12.44 cm d.b.h. (diameter at breast height); II = 12.7-27.68 cm d.b.h.; III = 22.94-53.08 cm d.b.h.; IV = 53.34-91.19 cm d.b.h.; V = >91.44 cm d.b.h.

Table 2--A sample of Douglas-fir (Pseudotsuga menziesii) tree ages within spotted owl habitat in northwestern California [1]/

Diameter size class [2]	Mean-	S.D.	Sample size
	years		
I	47.3	13.0	3
II	51.8	8.5	5
III	114.1	57.2	70
IV	142.0	65.3	84
V	268.66	108.3	86

[1]/ Data is from Sisco and Gutiérrez 1984.

[2]/ Diameter size class: I = 10.16-12.44 cm d.b.h. (diameter at breast height); II = 12.7-27.68 cm d.b.h.; III = 27.94-53.08 cm d.b.h.; IV = 53.34-91.19 cm d.b.h.; V = >91.44 cm d.b.h.

Table 3--Summer habitat characteristics of spotted owl habitat in northwestern California [1]/

Habitat characteristics	Summer
Snag density (stems/ha)	53.54
Canopy closure [2]/	87%
Decadence [3]/	
I	.28
II	.24
III	.48

[1]/ Data are from Solis (1983) and Sisco and Gutiérrez (1984) and represent 723 vegetation plots, 0.02 ha in size.

-?-/Canopy closure is a measurement of both conifer and hardwood components of the stand.

/Decadence: See Solis (1983) for a complete description of decadence; however, level III has highest snag incidence, indicating a more decadent stand.

conifers and (2) advanced decadence including dead and down debris and snags. Decadence plays a very important role in spotted owl habitat. First, suitable cavity nest sites are-formed as a result of the decay and aging process. In addition, snags, decadent and rotting trees, and downed woody debris may provide cover and habitat for flying squirrels and wood rats, the spotted owl's major prey.

Removal of woody debris and understory vegetation may alter the foraging patterns of spotted owls. Solis (1983) reports that a radio-telemetered bird foraged within a shelter-wood cut until the understory was burned as part of a silvicultural prescription. The owl was not observed to forage in this area after the prescribed burn until the understory vegetation had begun to grow again.

The pattern of habitat use in summer and in winter is similar (Forsman and others 1984, Sisco and Gutiérrez 1984). Winter habitats resemble summer habitat structurally (Sisco and Gutiérrez 1984) in spite of the large -increases in winter home range area (Forsman and others 1984, Sisco and Gutiérrez 1984). Extensive analysis of plant species composition and structural analysis of northwestern California owl habitats is given by Sisco and Gutiérrez (1984) and Solis (1983). The old-growth habitat used by spotted owls are also the most valuable timber on public lands in the Pacific Northwest. One of the major questions that managers and biologists ask is whether the spotted owl is indeed dependent on old growth

(Carey 1984). There are several aspects of their habitat ecology that strongly indicate that spotted owls are dependent on old growth:

1. Habitat use patterns demonstrate the owl's association with old growth (Foreman and others 1984, Forsman and Meslow 1985, Gutiérrez and others 1984, Sisco and Gutiérrez 1984, Solis 1983; see footnote 1).

2. Spotted owl habitat characteristics demonstrate agreement between forest scientists and wildlife biologists that this habitat is classified as old growth (for example, Franklin and others 1981, Franklin and Spies 1984, and reference immediately above).

3. Habitat analysis demonstrates there is a statistical difference in forest structure between intensively used and available habitat (Solis 1983).

4. The decline of spotted owl populations as old growth is logged demonstrates an association between the owls and these particular forests (Forsman and others 1984, U.S. Department of the Interior, Fish and Wildlife Service 1982).

5. The correlation between home range size and the amount of old growth in the range demonstrates the importance of old growth in influencing home range size (Sisco and Gutigrrez 1984; see footnote 1).

6. Spotted owl behavioral response to heat stress by roosting in old growth demonstrates the importance of old growth for thermoregulation by owls (Barrows 1981).

7. The general absence of spotted owls on heavily cutover lands demonstrates a qualitative, negative impact on owl populations with loss of old growth (Forsman and others 1977).

Home Range and Movements

Adult northern spotted owls are considered sedentary animals (Forsman 1980, Forsman and others 1984, Sisco and Gutiérrez 1984, Solis 19831, even though some populations show migratory behavior (Layman 1985). In contrast, juvenile spotted owls are highly mobile (Gutiérrez and others 1985, Miller and Meslow 1985).

Movements within the home range usually do not exceed 1.5 km (measured as straight distance from beginning to end of sample period) within a 24-hour period. Movements may, however, involve use of large areas (about 300 ha) within a relatively short period (3-4 weeks) (Forsman and others 1984; see footnote 1).

One interesting aspect of the home range is that it is large (x = 785 ha in Sisco and Gutiérrez 1984; x = 1713 ha, table 1, in Forsman and others 1984). Forsman and others (1984) state that an average of 131 days of observation was needed to determine 80 percent of an owl's home range area. The data from northwestern California probably underestimate the home range size for most of the owls radio tagged there because the monitoring period was less than 131 days. The owl's home range often increases substantially in size with winter range expansion (Forsman and others 1984, Gutiérrez and others 1984, Sisco and Gutiérrez 1984; see footnote 1). Home range size has been shown to be positively correlated with the amount of old growth within the range and not with other seral stages (see fig. 13 in Sisco and Gutiérrez 1984). Owls in fragmented forests sometimes have very large or very small home ranges relative to other owls (Forsman and others 1982, 1984; Gutiérrez and others 1984). Perhaps in the former case the owls use larger areas to encompass fragments of old growth (Forsman and others 1984, p. 54), and in the latter case they may be isolated by adjacent territorial owls or are constrained by inhospitable habitat (for example, clearcuts and grasslands) (see footnote 1).

The relationship among home range size, habitat dispersion, and habitat quality is still not well understood (Gutiérrez 1985). Owls in fragmented forests have limited access to old growth and may have reduced fitness (lower reproduction); this needs to be studied (Gutiérrez 1985). There is some indication that some owls with only limited old growth available to them have low reproductive output. [2]/

Food Habits

Although spotted owls capture a variety of prey, numerous food habit studies have shown that mammals are their major food resource--particularly flying squirrels, *Glaucomys sabrinus*, and woodrats, *Neotoma* sp. (Barrows 1980, 1985; Forsman and others 1984; Kertell 1977; Marshall 1942; Solis 1983). Earhart and Johnson (1970) suggest that spotted owls are more insectivorous than current data indicate. Forsman and others (1984) and Sisco [3]/ believe that flying squirrels may predominate in the diet of owls living in mesic habitats and woodrats may predominate in more xeric environments. Habitat structure or food availability within these habitats may influence which prey species is most abundant. It is interesting that woodrats in northwestern California have a bimodal distribution of abundance; their greatest populations are found in early and late seral stage forests (that is, brushy clearcuts and old-growth forests) and the lowest populations are found in intermediate-aged forests (Raphael and Barettt 1984).

Barrows (1985) presents data that suggest spotted owls may breed in years when their larger prey

[2]/ Unpublished data by R. J. Gutiérrez and others on file, Wildlife Department, Humboldt State University, Arcata, CA 95521.

[3]/ Manuscript in preparation by C. Sisco, Wildlife Department, Humboldt State University, Arcata, CA 95521.

are either more abundant or more available. Barrow&/has data on *Peromyscus* populations in his study area that suggest spotted owls do not appear to be tracking large *Peromyscus* populations. His idea is certainly plausible when one observes the large talons these birds possess. The large talons indicate evolutionary selection for handling large prey. The ecology of the spotted owl's major prey is not well understood but may ultimately be important in predicting reproductive biology and demography of the spotted owl (Gutiérrez 1985).

LIFE HISTORY

Little is known of the demography or other life history characteristics of spotted owls. Studies of population dynamics require the construction of life tables. Although spotted owl demographic data are limited to first approximations, subject to modification with new information, life table construction is possible (Barrowclough and Coats 1985). In the following brief review I will describe those life history features that are particularly important to the demography of spotted owls.

Reproductive Biology

There is substantial yearly and geographic variation in the proportion of an owl population that breeds (Barrows 1985, Forsman and others 1984, Gutiérrez and others 1984, Laymon 1985). Gutiérrez and others (1984) report general breeding failure throughout the Pacific Northwest. Forsman and others (1984), in analyzing 130 nesting attempts over 5 years, found on the average that 62 percent (range, 16-89 percent) of their pairs attempted to nest each year but Gutiérrez and others (see footnote 2) have noted a lower frequency of nesting attempts in northwestern California. They found an average of 36 percent of 92 pairs (range, 0-45 percent) attempted to nest over a 3-year period. Some pairs appear to nest far more frequently than others; for example, Miller (1974) reports a pair, (presumably the same birds) that nested in 5 of 7 years. Conversely, Barrows (see footnote 4) and Gutiérrez and others (see footnote 2) have monitored some nonnesting pairs for 5 years. These unsuccessful pairs were located in nonold-growth habitat or in fragmented habitat. Reproductively successful pairs may provide clues for isolating habitat quality or individual variation parameters responsible for that success. Yet Forsman and others (1977) correctly point out the need to study those few owls in second-growth forests (see also Gutiérrez 1985).

Clutch Size

The modal clutch size was two in Forsman and others (1984). They refer to other historical studies that report four-egg clutches although the maximum brood size (an index to clutch size) they observed was three. Forsman and others (1984) found no evidence for renesting by wild spotted owls, although captive birds have laid two clutches in one season (Forsman and others 1984). Because the birds are physiologically and genetically capable of laying two clutches, failure to renest may be related to food availability or some other factor.

Because males feed their incubating mates, females are dependent on the male's foraging ability (Forsman 1976). When foraging conditions are poor and the female is forced to leave the nest to search for food, the clutch may be lost. Poor food resources probably do not improve soon enough to allow a female to renest.

Age At First Reproduction

Barrows (1985) reports a second-year female breeding and Miller [5]/ has observed a second-year female breeding. My field crew has also observed at least two second-year females paired with adult males. Because juveniles have a high mortality rate, second-year breeding, at least by females, may not be uncommon.

Survivorship And Mortality

Juvenile owls have a low first-year survivorship (Forsman and others 1984, Gutiérrez and others 1985, Miller and Meslow 1985). Young *Strix* owls die for many documented reasons, such as avian predation, starvation, accidents, and human predation (Gutiérrez and others 1985, Southern 1970). Young spotted owls are especially vulnerable during development following fledging and during early dispersal (Forsman and others 1984, Gutiérrez and others 1985, Miller and Meslow 1985).

Forsman and others (1984) suggest that spotted owls are long lived. Data on adult demography will be slow in accumulating and will require extensive banding and monitoring to determine adult survival rates. Adults are susceptible to predation, starvation, disease, and accidents, but the influence of these forces on survival is unknown.

Density

There are few published accounts of density estimations in the strict sense of the term (Burnham and others 1980). Forsman and others (1977) published an "index of density," and Marcot and Gardetto (1980) published nearest neighbor distances and other estimates

[4]/ Unpublished data by Cameron Barrows on file, North Coast Preserve, Banscomb, CA 95417.

[5]/ Manuscript in preparation by Gary Miller, Oregon Cooperative Wildlife Research Unit, Oregon State University, Corvallis, 97331.

of density. The assumptions and applications of nearest neighbor distance has been discussed by Clark and Evans (1954) and Poole (1974). This technique is unsuitable for demographic (density) analysis. Barrowclough and Coats (1985) approximate the density of spotted owls across all habitats to be 0.037 owls/km^2 (based on calling surveys compiled by the California Fish and Game Department).

Population boundaries need to be delineated to arrive at some area suitable for census. I would predict spotted owl densities are likely to vary substantially with habitat quality and quantity. Forsman and others (1977) found spotted owls substantially more abundant (approximately 12 times, according to their index) in old growth than in second growth. One of my study areas of 10,000 ha has 22 owls and a nearby area with good census data has 12 owls in 20,000 ha. The latter area has undergone extensive logging.

Dispersal

Dispersal ecology has been the subject of recent intensive research (Gutiérrez and others 1985, Miller and Meslow 1985). Preliminary results show that juvenile spotted owls are aggressive dispersers capable of moving long distances. They appear to move directionally and rapidly (Gutiérrez and others 1985). It is unknown from published data whether this pattern is consistent with other areas (Allen and Brewer 1985, Miller and Meslow 1985). Observations of the 1984 cohort of juvenile spotted owls in northwestern California suggest that this pattern may not continue (see footnote 2). As dispersal data continue to accumulate, managers will gain a critical piece of information for spatially distributing spotted owl territories and calculating demographic parameters for spotted owls (Barrowclough and Coats 1985).

Other Life History Features

Some important parameters of life history evolution are almost entirely unknown for spotted owls but ultimately may play a role in predicting the effect of management plans on the owls. Some of these are their interspecific competitive ability, variation in parental care among pairs, environmental stability, and population genetics (see also Stearns 1976, 1977, for a discussion of life history characteristics).

HYPOTHESES ON DEPENDENCE ON OLD GROWTH

Recent research has led to some interesting hypotheses concerning the spotted owl's dependence on old-growth forests. These hypotheses are:

1. Nesting hypothesis,
2. Thermoregulation hypothesis,
3. Predation hypothesis,
4. Prey hypothesis, and
5. Adaptation hypothesis.

Carey (1985) discusses these hypotheses elsewhere in this symposium. I have combined his two hypotheses on prey under one category because they are often interrelated. The implications of these hypotheses for management will be discussed as will their potential for explaining the evolutionary relationships of spotted owls and old-growth forests. It is undoubtedly a combination of factors that have led to the spotted owl's role or dependence on old-growth forests. I have, therefore, expanded and reinterpreted Carey's (1985) adaptation hypothesis.

Nesting Hypothesis

Spotted owls, like most other owls, do not construct their own nests (Burton 1973). They depend on the natural occurrence of suitable nesting sites within their habitat. The location, structure, and type of nesting sites used by spotted owls are typically found in old, decadent forests (Forsman and others 1984). They are generally high above the ground ($\bar{x}$ = 27.3 m; $\bar{x}$ = 24.3 m); in cavities or broken-top snags (64 percent; 92 percent); and in large diameter trees ($\bar{x}$ = 135cm d.b.h.; $\bar{x}$ = 170cm d.b.h.) (Forsman and others 1984 and LaHaye,[6/] respectively). Old-growth forests are often decadent and provide the greatest number of trees suitable for nesting sites. It is unlikely that the need for nesting sites is the evolutionary force behind the dependence of spotted owls in old-growth forests for the following reasons. First, spotted owls do nest in abandoned stick nests built by other birds and in accumulations of organic debris in the tree canopy. Forsman and others (1984) report 36 percent of their spotted owl nests were of debris or were nests of other species. Both of these conditions can occur in younger aged forests, although accumulations of organic debris probably occur more frequently in old-growth forests (Forsman and others 1984). 'Second, residual, decadent trees are often left behind after fires or other natural environmental perturbations. Yet, spotted owls apparently seldom use these residual old-growth trees in younger forests (only 6 percent of the nests found by Forsman and others 1984, p, 30, were in young forests with scattered residual trees). Finally, open-canopied hardwood stands within old-growth areas often provide presumably suitable structural nest sites but are rarely used by spotted owls (see footnote 6).

From a management perspective, nesting sites can probably be created through manipulation. Live trees can be topped or cavities created in several ways to create structurally suitable nesting sites (see footnote 6). One pair of owls has been observed to use an artificial cavity in the Six Rivers National Forest (personal observation). The tawny owl (*Strix aluco*) of Europe responds readily to artificial nest boxes

---

[6]/M.S. thesis in progress by W. LaHaye, Humboldt State University, Arcata, CA 95521.

(Southern 1970). Nest boxes have been placed in old-growth forests in California by Forest Service biologists without success (personal observation). The sites chosen for box placement may have already had abundant or traditional nesting sites. For example, my research crew discovered an active owl nest within 150 m of a nest box after the box had been placed in an old-growth tree. Because this pair had successfully nested in 2 out of 4 years at the natural site, it was unlikely that they would abandon their traditional site for the artificial one. The successful placement and construction of nesting boxes will depend heavily on adequate models of nesting sites and nesting habitat (see footnote 6).

Thermoregulation Hypothesis

Barrows and Barrows (1978) and Barrows (1981) first quantified the relationships between roosting site microclimate and heat stress in spotted owls. Spotted owls choose cool and shady microclimates that provide relief from high ambient temperatures (Forsman 1976, Solis 1983).

Because natural selection has favored the evolution of a plumage that is adapted to withstand winter conditions (Barrows 1981, Barrows and Barrows 1978), it is possible that use of the cool microclimate, which multistoried old-growth forests provide, is the counterbalance to the plumage. There are, however, several natural history observations that suggest that even though selection for old-growth roosting sites may be an indication of dependency on old-growth forests, it probably does not explain the dependency on large tracts of old growth.

Ward [7] analyzed microhabitat selection and behavioral positioning in response to variation in ambient temperatures. He concluded that the position an owl chooses within the foliage is as important as the selection of actual roosting habitat. Sisco and Gutiérrez (1984) demonstrate that the old-growth forests are still the most important habitats for spotted owls when heat is not a factor. Alternatively, old-growth forests may provide more protection from inclement weather and, thus, may be important for winter thermoregulation (Forsman and others 1984).

This hypothesis is important to management. Spotted owls need adequate thermal cover in all seasons. Many areas of potential spotted owl habitat may not provide relief from heat without old-growth. In some areas access to old-growth roosting sites may energetically constrain the owls to a finite distance from the roosting site. Because owls can and do select roosting sites in cool, moist, shaded canopies within canyons to relieve heat stress, they may have some alternative habitats to use. Also, the small patches (24 ha) of old-growth forest required as a minimum patch size for spotted owl management areas in California will probably provide an adequate microclimate to relieve heat stress. Yet SOMAs and SOTs without old growth on south-facing slopes or in areas where alternative habitats are not located will probably not be used by spotted owls.

Predation Hypothesis

Great horned owls (Bubo virginianus) and goshawks (Accipiter gentilis) will prey on juvenile spotted owls (Forsman and others 1984, Gutiérrez and others 1985, Miller and Meslow 1985; see footnote 1). Presumably, spotted owls are more vulnerable in open habitats than in the forests. The many observations of juvenile spotted owls moving through open areas (that is, grasslands, savannas, clearcuts, and oak woodlands) (see Gutiérrez and others 1985) suggest that the potential for predation does not, in general, deter these birds from using open areas when they are juveniles. Forsman and others (1984, p. 54) suggest adult spotted owls may also be preyed upon by great horned owls. Yet great horned owls are found throughout the range of spotted owls and often occupy areas adjacent to or overlapping spotted owl home ranges with little predation occurring (personal observation). I have recorded spotted owls temporarily avoiding an area when a great horned owl vocally established its presence, but the birds again used the area at some later date. Thus predation has probably occurred opportunistically at low levels for adults and at higher levels among juvenile spotted owls. This predation pressure has probably not been strong enough to explain the spotted owl's association with old-growth forests.

From a management point of view, predation could become a serious factor. If great homed owls increase in response to forest fragmentation, then the opportunity for their preying upon spotted owls will increase.

Prey Hypothesis

I have chosen to combine the prey abundance and prey availability hypotheses of Carey (1985) and Forsman and others (1984) into one hypothesis because I believe the hypotheses are closely related.

Raphael and Barrett (1984) suggest a bimodal abundance distribution for wood rats in northwestern California. These rodents are plentiful in shrub-sapling stages and in older aged forests. Raphael and Barrett (1984) demonstrate an increase in relative abundance of wood rats with increasing age of old-growth stands. Thus the spotted owl's primary prey, in northwestern California, is more abundant as the forest increases in age.

The reason that owls do not forage in shrub-sapling habitats probably is the inability of the owls to hunt effectively in these densely vegetated habitats (Forsman and others 1984). Solis

[7] Unpublished senior thesis by J. P. Ward on file, Department of Wildlife, Humboldt State University, Arcata, CA 95521.

(1983) and Sisco and Gutiérrez (1984) demonstrate significant differences in foraging habitat between male and female owls. The differences in the structure of foraging habitat is probably related to-the wing loading of the birds. The smaller, more maneuverable males use denser forests. Differential habitat use by the sexes may reflect an avoidance of competition. These differences persist in winter when home ranges expand and the birds forage independently (Sisco and Gutiérrez 1984, see footnote l). Because shrub-sapling stages are far more dense than habitats normally used by foraging owls, one might expect that the owls cannot maneuver well enough therein to effectively prey on wood rats. Although Raphael and Barrett (1984) did not adequately sample flying squirrels, these animals are rare in shrub-sapling stages and in pole-sized timber.

The ecology of wood rats and flying squirrels within Pacific Northwest forests is not well understood. If their populations fluctuate asynchronously, or by habitat type and age, then it would help explain not only the foraging of owls within large areas but also the owls' use of a variety of stands greater than 150 years of age.

Hilden (1965) points out that food is one of the ultimate factors in habitat selection of a species, not only because of short-term physiological maintenance but also because of reproductive needs. It is probably the interplay of abundance, availability, and distribution of the spotted owls food base that explains the birds historical dependence on large tracts of old-growth forests. As its habitat becomes increasingly fragmented, the bird's needs for thermoregulation, for nest sites, and to avoid predators and competitors will become more important factors in the population ecology of spotted owls.

The prey hypothesis is probably the most important hypothesis for managers because it may explain the spotted owl's use of large tracts of old-growth forest. If the owl's major prey is geographically variable in abundance, distribution, or availability, spotted owls may have to forage widely through the year to find adequate prey populations. Thus the increased energy needed to exploit habitat patches in a fragmented forest may negatively affect reproductive output. The interrelationship between prey, territory size, and foraging patterns needs to be investigated to predict the impact of habitat fragmentation on the species (see also Gutiérrez 1985).

Adaptation Hypothesis

Carey (1985) discusses this hypothesis, which proposes that spotted owls have coevolved with old-growth forest and thus are behaviorally or physiologically adapted to these forests. In reality, this hypothesis is a combination of all other hypotheses and unknown natural selection forces. I will expand this hypothesis differently than does Carey (1985).

Biologists could engage in endless discussion over the coevolution of spotted owls and old-growth forests. Spotted owls may have even secondarily invaded old-growth forests although this is unlikely. Nevertheless, there is considerable data, just presented, that old-growth is important if not critical for thermoregulation, nesting, and foraging. Although ecologists are currently engaged in serious debate concerning the nature of competition (Salt 1984), one potential factor in the relationship of old growth and spotted owls might have been the competitive relationship with the larger and more widespread and aggressive great horned owl. One potential way of avoiding competition is through differential habitat use.

Through time the spotted owl's success in using old growth may have favored adaptive response to old-growth habitation regardless of the original pressure to use old growth. Forest fragmentation in the Pacific Northwest may also favor the spread of a potential competitor in the barred owl (Strix varia) (Gutiérrez and others 1984, Taylor and Forsman 1976). The interaction of these closely related species is now being studied by Allen. [8] Introducing competitors, as well as changing the nature of the environment spotted owls have shown strong adaptive responses to, could have serious consequences for spotted owls. Studies of spotted owls and their reproduction under varying environmental conditions will help tremendously in understanding the nature of the spotted owl's adaptability in a changing world.

CONCLUSIONS

Wildlife biologists have gained a great deal more information on the natural history than on the demography of the northern spotted owl. There are several reasons for this. First, natural history data are needed to establish a research foundation; second, natural history features are more easily observed in nature and often require only direct observation; third, natural history information provides the manager with the raw data for management (for example, habitat requirements and nest site selection). Life history characteristics provide the manager with the tools necessary for developing predictions of population viability. Many life history features, particularly demographic and, to a lesser extent, dispersal information, take a great deal of time, energy, and money to quantify. Barrowclough and Coats (1985) and Shaffer (1985) point out the importance of this information for predicting the long-term viability of spotted owls. The need for specific research is outlined elsewhere in this symposium by Gutiérrez (1985).

Old-growth forests provide the food and cover essential for the survival and breeding success of northern spotted owls. The impact of habitat loss through logging over time must be assessed

[8]/ Manuscript in preparation by H. Allen, Washington Department of Game, 600 North Capitol Way, Olympia, WA 98504.

both in terms of natural and life history characteristics. Clearly habitats with known, consistently reproductive pairs must be chosen as the SOMA. The ultimate numbers of owls to be, maintained will depend upon demographic and dispersal information that-is, at present, lacking. First order approximations are possible (Barrowclough and Coats 1984) but will undoubtedly change as our understanding of the spotted owl increases.

ACKNOWLEDGMENTS

I would like to thank Cameron Barrows, Andy Carey, Sadie Coats, Alan Franklin, Ann Franklin, Ned K. Johnson, William LaHaye, Bruce Marcot, David Solis, and James P. Ward for critically reviewing this paper.

LITERATURE CITED

Allen, Harriet; Brewer, Larry W. A review of current northern spotted owl (Strix occidentalis caurina) research in Washington State. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 55-57.

American Ornithologists Union. Checklist of North American birds. Baltimore, MD: The Lord Baltimore Press; 1957. 691 p.

Barrowclough, George F.; Coats, Sadie L. The demography and population genetics of owls, with special reference to the conservation of the spotted owl (Strix occidentalis). In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 74-85.

Barrows, Cameron W. Feeding ecology of the spotted owl in California. Raptor Research. 14(3): 73-78; 1980.

Barrows, Cameron W. Roost selection by spotted owls: an adaptation to heat stress. Condor. 83(3): 302-309; 1981.

Barrows, Cameron W. Breeding success relative to fluctuations in diet for spotted owls in California. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 50-54.

Barrows, Cameron; Barrows, Katherine. Roost characteristics and behavioral thermoregulation in the spotted owl. Western Birds. 9(l): l-8; 1978.

Barrows, Cameron W.; Bloom, Peter H.; Collins, Charles T. Sexual differences in tail barring of spotted owls. North American Bord Bander. 7(4): 138-139; 1982.

Burnham, Kenneth P.; Anderson, David R.; Laake, Jeffrey L. Estimation of density from line transect sampling of biological populations. Wildl. Mongr. 72. Washington, D.C.: The Wildlife Society; 1980. 202 p. Supplement to Journal of Wildlife Management. 44(2): 1980 April.

Burton, John A. Owls of the world: their evolution, structure and ecology. New York; E.P. Dutton: 1973. 216 p.

Campbell, R. Wayne; Forsman, Eric D.; Van Der Raay, Brigitta M. An annotated bibliography of literature on the spotted owl (an old-growth dependent species). Victoria, BC: British Columbia Provincial Museum; in press. [586 references].

Carey, Andrew B. A critical look at the issue of species-habitat dependency. In: Proceedings of the convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 346-351.

Carey, Andrew B. The scientific basis for spotted owl management. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 100-114.

Carrier, W. Dean; Solis, David M.; Toth, Edward M. Providing habitat for spotted owls through a managed forest ecosystem on California's National Forests. In proceedings of a workshop on management of non game species and ecological communities; 1984 June 11-12; Lexington, KY. Lexington KY: University of Kentucky, Department of Forestry; (in press).

Clark, Philip J.; Evans, Frances C. Distance to nearest neighbor as a measure of spatial relationships in populations. Ecology. 35(4): 445-453. 1954.

Earhart, C.N.; Johnson, N.K. Size dimorphism and food habits of North American owls. Condor. 72(3): 251-264. 1970.

Forsman, Eric D. A preliminary investigation of the spotted owl in Oregon. Corvallis, OR: Oregon State University; 1976. 127 p. M.S. dissertation.

Forsman, Eric D. Habitat utilization by spotted owls in the west-central Cascades of Oregon. Corvallis, OR: Oregon State University; 1980. 95 p. Ph.D. dissertation.

Forsman, Eric D. Molt of the spotted owl. Auk. 98(4): 735-742. 1981.

Forsman, Eric D. Methods and materials for locating and studying spotted owls. Gen. Tech. Rep. PNW-162. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1983. 8 p.

Forsman, Eric D.; Horn, Kirk M.;.Neitro, William A. Spotted owl research and management in the Pacific Northwest. In: Transactions, 47th North American wildlife and natural resources conference; 1982 March 29-31; Portland, OR. Washington, DC: Wildlife Management Institute; 1982: 323-331.

Forsman, Eric D.; Meslow, E.C, Old-growth forest retention for spotted owls--how much do they need? In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 58-59.

Forsman, Eric D.; Meslow, E. Charles; Strub, Manic J. Spotted owl abundance in young versus old-growth forests, Oregon. The Wildlife Society Bulletin. 5(2): 43-47; 1977.

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Distribution and biology of the spotted owl in Oregon. Wildl. Monogr. 87. Washington, DC: The Wildlife Society; 1984. 64 p. Supplement to Journal of Wildlife Management. 48(2): 1984 April

Franklin, Jerry F.; Cromack, Kermit, Jr.; Denison, William; [and others]. Ecological characteristics of old-growth Douglas-fir forests. Gen. Tech. Rep. PNW-118. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1981. 48 p.

Franklin, Jerry F.; Spies, Thomas A. Characteristics of old-growth Douglas-fir forests. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters: 1984: 328-334.

Garcia, Ernest R. A survey of the spotted owl in southwestern Washington. In: Schaeffer, Philip P.; Ehlers, Sharyn M., eds. Proceedings of the National Audubon Society's symposium on owls of the West: their ecology and conservation. 1979 January 20; San Francisco CA. Tiburon, CA: National Audubon Society Western Education Center; 1979: 18-28.

Gould, Gordon I., Jr. The status of the spotted owl in California. Pittman-Robertson Federal Aid Project W-54-R-6. Sacramento, CA: California Department of Fish and Game, Non-Game Wildlife Investigations: 1974: 56 p.

Gould, Gordon I., Jr. Distribution of the spotted owl in California. Western Birds. 8(4): 131-146, 1977.

Gould, Gordon I., Jr. Status and management of elf and spotted owls in California. In: Schaeffer, Philip P.; Ehlers, Sharyn M., eds. Proceedings of the National Audubon Society's symposium on owls of the West: their ecology and conservation; 1979 January 20; San Francisco CA. Tiburon, CA: National Audubon Society, Western Education Center; 1979: 86-97

Gould, Gordon I., Jr. Management of spotted owls by the California Department of Fish and Game. In: Guttierrez, Ralph J.; Carey, Andrew B., tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 21-26.

Grinnell, Joseph; Miller. Alden H. The distribution of the birds of California. Pacific Coast Avifauna. 27: 608 p.; 1944.

Gutiérrez, R.J. Information and research needs for spotted owl management. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 115-118.

Gutiérrez, R.J.; Franklin, Alan B.; LaHaye, William; Meretsky, Vicky J.; Ward, J. Patrick. Juvenile spotted owl dispersal in, northwestern California: preliminary results. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 60-65.

Gutiérrez, R.J.; Solis, David Muñoz; Sisco, Charles. Habitat ecology of the spotted owl in northwestern California: implications for management. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters; 1984: 368-373.

Heinrichs, Jay. The winged snail darter. Journal of Forestry. 81(4): 212-214, 262; 1983.

Heinrichs, Jay. The owl and the old growth. American Forests. 90: 22-23 and 54-56; 1984.

Hildén, 0. Habitat selection in birds, a review. Annales Zoologicae Fennicae. 2: 53-75; 1965.

Kertell, D. The spotted owl at Zion National Park, Utah. Western Birds. 8(4): 147-150; 1977.

Laymon, Stephen A. General habitats and movements of spotted owls in the Sierra Nevada. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest

Forest and Range Experiment Station; 1985: 66-68.

Marcot, Bruce G.; Gardetto, Jeffrey. Status of the spotted owl in Six Rivers National Forest, California. Western Birds. ll(2): 79-87; 1980.

Marshall, Joe T., Jr. Food and habitat of the spotted owl. Condor. 44(l): 66-67; 1942.

Miller, Grace M. Grace M. Miller on spotted owls. In: Walker Lewis Wayne, ed., The book of owls. New York: Alfred A. Knopf; 1974: 130-146.

Miller, Gary S.; Meslow, E. Charles. Dispersal data for juvenile spotted owls: the problem of small sample size. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 69-73.

Poole, Robert W. An introduction to quantitative ecology. New York: McGraw-Hill Book Co.; 1974. 532 p.

Raphael, Martin G.; Barrett, Reginald H. Diversity and abundance of wildlife in late successional Douglas-fir forests. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 352-360.

Ruggiero, Leonard F.; Carey, Andrew B. A programmatic approach to the study of old-growth forest-wildlife relationships. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 340-345.

Salt, G.W., ed. Ecology and evolutionary biology: a round table on research. Chicago: University of Chicago Press; 1984. 130 p.

Shaffer, Mark L. The metapopulation and species conservation: the special case of the northern spotted owl. In: Gutiérrez, Ralph J.; Carey Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment; Station; 1985: 86-99.

Sisco, Chuck; Gutiérrez, R-J. Winter ecology of radio-tagged spotted owls on Six Rivers National Forest, Humboldt Co., CA. Final Rep. Eureka, CA: U.S. Department of Agriculture, Forest Service, Six Rivers National Forest; 1984. 140 p.

Solis, David M., Jr. Summer habitat ecology of spotted owls in northwestern California. Arcata, CA: Humboldt State University; 1983. 168 p. M.S. dissertation.

Southern, H.N. The natural control of a population of tawny owls (Strix aluco). Journal Zoology London. 162(2): 197-285; 1970.

Stearns, Stephen C. Life history tactics: a review of the ideas. Quarterly Review of Biology. 51: 3-47. 1976.

Stearns, Stephen C. The evolution of life history traits. Annual Review of Ecology and Systematics. 8: 145-171. 1977.

Taylor, Avery L.; Forsman, Eric D. Recent range extensions of the barred owl in western North America, including the first records for Oregon. Condor. 78(4): 560-561; 1976.

U.S. Department of Interior, Fish and Wildlife Service. The northern spotted owl: a status review. Portland, OR: U.S. Department of Interior, Fish and Wildlife Service Regional Office; 1982. 29 p.

U.S. Laws, Statutes, etc.; Public Law 94-588. National Forest Management Act of 1976. Act of Oct. 22, 1976. 16 U.S.C. 1600 (1976).

Van Horne, B. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. 47(4): 893-901; 1983.

BREEDING SUCCESS RELATIVE TO FLUCTUATIONS IN DIET
FOR SPOTTED OWLS IN CALIFORNIA

Cameron W. Barrows

ABSTRACT: This paper describes infrequent, successful breeding in spotted owls (Strix occidentalis) and the relationship between breeding and diet. When spotted owls do breed, large prey such as dusky-footed woodrats and flying squirrels are predominate in their diet. The availability of these large prey items may be important in the breeding frequency and success of spotted owls. The relationship between breeding success and prey populations should be considered in the development and implementation of habitat-suitability models for spotted owls.

INTRODUCTION

Recently there has been a substantial growth in the knowledge of spotted owl (Strix occidentalis) habitat requirements. Forsman's work in Oregon (Forsman 1976, 1980) provides an initial foundation for spotted owl research. For northern California, Solis (1983) and Sisco and Gutiérrez (1984) provide detailed analyses of seasonal habitat use by spotted owls. Barrows and Barrows (1978) and Barrows (1981) describe microhabitat selection related to the owls' thermoregulatory constraints.

Data from the studies mentioned above have been incorporated into spotted owl management plans by the USDA Forest Service and used to develop habitat suitability models (Laymon and Barrett 1982). There remains a serious void in knowledge about spotted owl habitat that precludes a well-informed application of these plans and models. For example, the factors that influence the reproductive success of spotted owls are poorly understood. Forsman (1976) first described the irregular breeding of spotted owls. Although Barrows (1980) alludes to mechanisms responsible for breeding irregularity in spotted owls, the causative factors are not documented.

In this paper, I present results of ,a study designed to examine the causes of the lack of successful breeding in spotted owls. It should be noted that this is a multifaceted problem and only one aspect is examined here.

Newton (1979) has shown that breeding rates in raptors are positively correlated with food suPPlY- Most studies examining this relationship have dealt with relatively simple predator-prey systems consisting of a single primary prey source (Adamick and others 1978, Hamerstrom 1979, Pitelka and others 1955, Smith and others 1981). Spotted owls take a broad spectrum of prey (Barrows 1980); any one of four major mammalian prey species can be the most prevalent in the owls' diet in a given year. My analysis examined the relationship between fledging success and the relative frequency of these mammalian prey species in the diet of spotted owls.

METHODS AND STUDY AREA

I collected regurgitated pellets below diurnal roost sites of spotted owls during 1977 through 1984. The pellets contained approximately 1,500 individual prey items. To facilitate comparisons over much of the spotted owls' range in

CAMERON W. BARROWS is a preserve director at the Northern California Coast Range Preserve, The Nature Conservancy, Branscomb, Calif.

California, I categorized prey species into two size groups: small prey -- animals that weigh less than 100 g, and large prey -- animals that weigh 100 g or more. Only mammalian prey were considered in this grouped analysis because mammals comprise over 90 percent of the biomass consumed by spotted owls (Barrows 1980). I also calculated mean prey weight of all prey species for each of my study areas.

For this study, I defined fledging success as the percent of occupied territories in each area in which spotted owl pairs fledged young over the 8-year period. Each year I observed owls in a territory was designated a potential breeding attempt. I recorded 47 breeding attempts in 21 spotted owl territories. Five of these territories were found in the Peninsular Range of southern California; the other 16 territories were located in Marin, Mendocino, Humboldt and Trinity Counties of northern California. My largest sample came from three occupied territories observed for 4, 6, and 7 years (17 breeding attempts) in The Nature Conservancy's Northern California Coast Range Preserve in Mendocino County.

RESULTS AND DISCUSSION

Forsman and others (1984) record spotted owl fledging success for Oregon over a 5-year period (1972-1976). They observed 130 breeding attempts with a fledging success of 44 percent. My data from California were similar with 47 breeding attempts over 8 years and a fledging success of 45 percent. Individual territories varied considerably in fledging success. Three territories in northern Mendocino County had a fledging success of 0 percent, 33 percent, and 29 percent, for 4, 6, and 7 years, respectively. One territory in central Humboldt County had a fledging success of 100 percent based on 6 years of observation. Barrett and Laymon (1982, 1983) report a fledging success of 6 percent based on 32 breeding attempts over 2 years in the Sierra Nevada of California. Miller (1974) reported a fledging success of 80 percent in 5 years of observation of one territory in Marin County, California.

The generally low and variable fledging success of spotted owls shows marked yearly trends. A broad regional failure in spotted owl breeding success was observed in 1982 (Gutiérrez and others 1983). Fledging success approached 0 percent for Oregon (Miller and Meslow 1984) and northern California.[1/] Breeding success improved in 1983. Of 63 occupied territories checked in Oregon, 48 percent successfully fledged young; on those territories with known pairs of owls, 62 percent successfully fledged young (Miller and Meslow 1984). In northern California in 1983, 17 percent of 87 occupied spotted owl territories successfully fledged young; of those territories with confirmed pairs, 45 percent successfully fledged young (Gutiérrez and others 1984). Similar year to year fluctuations were noted by Forsman and others (1984).

The year to year variations in the diet of representative pairs of spotted owls are shown in table 1. An increase in the frequency of large prey in the diet during breeding years was characteristic for all of the pairs of owls included in the analysis. Overall mean prey weights for breeding spotted owls ($\bar{x}$ = 115 g, S.D. = 31) are significantly greater (one-tailed t test, P(0.01) than for nonbreeding owls ($\bar{x}$ = 79 g, S.D. = 25) for 16 spotted-owl pairs I studied intensively. A comparison of the frequency of spotted owl prey species, grouped by size, taken in breeding and nonbreeding years is depicted in figure 1.

Table 1--Percent occurrence of prey species in regurgitated pellets of spotted owls, collected from two owl territories in California

AREA/PREY SPECIES	1977	1980	1981	1982	1983
	- - - -	- Percent	- - - -	-	
Northern Coast Range A [1/]			*		
Neotoma fuscipes	43		14	8	16
Glaucomys sabrinus	17		8	3	32
Arborimus longicaudus	9		35	50	32
Peromyscus maniculatus	9		20	26	8
Other mammalian prey [2/]	1		3	0	1
Nonmammalian prey [3/]	21		20	13	11
Northern Coast Range B			*		
Neotoma fuscipes	18	18	14	9	3
Glaucomys sabrinus	13	18	29	16	24
Arborimus longicaudus	24	32	20	38	42
Peromyscus maniculatus	15	12	10	14	14
Other mammalian prey	4	3	7	7	2
Nonmammalian prey	26	17	20	16	15

1/ Northern Coast Range A and B are located on the Northern California Coast Range Preserve, Mendocino County, CA.

2/ Other mammalian prey include: *Clethrionomys californicus, Microtus californicus, Scapanus latimanus, Neurotrichus gibbsi, Sorex trowbridgii*, Lasiurus *cinereus*, Mustela *erminea*, *Tamias* sp., and *Sylvilagus* sp.

3/ Nonmammalian prey include various species of arthropods and birds.

* Indicates year of successful breeding.

1/ Personal communication, R. Gutiérrez, Humboldt State University, Arcata, CA 95521.

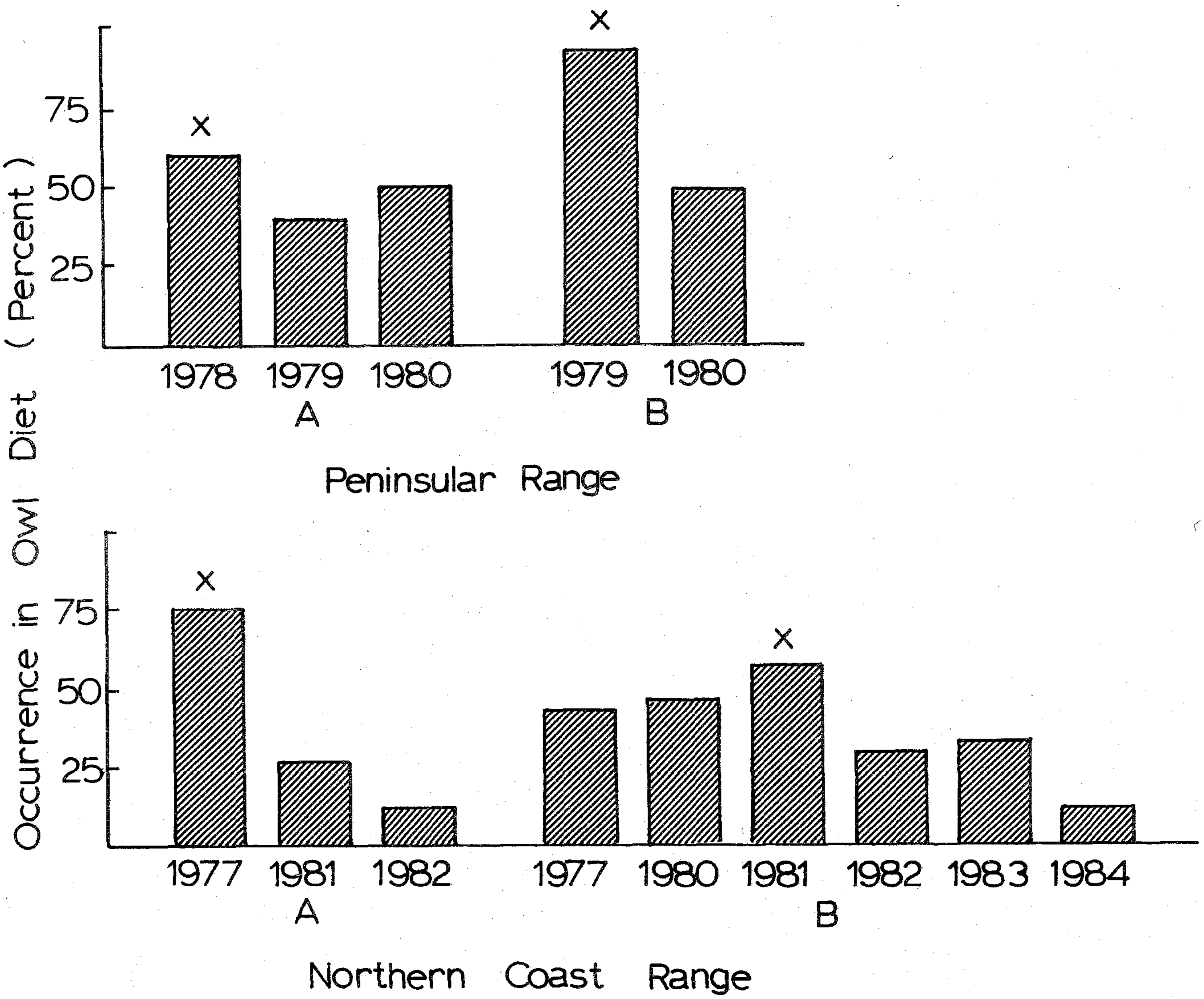


Figure 1. Prey frequencies in the diet of four representative pairs of breeding and nonbreeding spotted owls. Successful breeding years are denoted by an "X" above the histogram. Mammalian prey are grouped in two size classes; small prey -- less than 100 g; large prey -- 100 g or more. (Northern Coast Range pairs A and B are located on the Northern California Coast Range Preserve, Mendocino County, CA; Peninsular Range pairs A and B are located in Cuyamaca Mountains State Park, San Diego County, CA).

Differential breeding success rates in spotted owls may relate to basic habitat quality and varying habitat conditions. Habitat features, such as shrub cover, snag density, volume of dead and down wood, and canopy cover, are correlated with prey density and vulnerability (Maser and others 1979, Southern and Lowe 1968). These characteristics vary through the forest and so might account for some interterritorial differences in spotted owl breeding success. Fruit and mast production and weather-related effects on prey vary among years and sites.

Food supply is most often cited as the ultimate cause in determining breeding success in raptors (Newton 1979). Other factors such as the individual owl's breeding experience certainly have some effect (for example, see Southern 1970); in at least one case, however, I found a second-year female spotted owl successfully breeding. Small mammal density estimates for northern California in 1982 and 1983[2] support a correlation between breeding success of spotted owls and fluctuations in rodent populations. This correlation must be viewed with skepticism as the primary prey species of spotted owls in northern California (Barrows 1980) are not sampled effectively by a single trapping method, Dusky-footed woodrats (Neotoma fuscipes), northern flying squirrels (Glaucomys sabrinus), red tree voles (Arborimus longicaudus), and deer mice (Peromyscus maniculatus) are important prey of spotted owls, but their dissimilar ecologies and behaviors require vastly different sampling methods for estimating their densities. Often densities can't be estimated and population indices are not comparable among species.

The energetic demand on a spotted owl pair feeding one to three owlets has not been measured but *it* must be considerably greater than that for nonbreeding pairs. The average weight of dusky-footed woodrats (269 g) or northern flying squirrels (115 g) (Forsman and others 1984) is four to twelve times that of deer mice (22 g) and red tree voles (27 g). The energetic benefits of taking larger prey, which require fewer trips to the nest, must be balanced against possible costs, such as greater difficulty of capture and a lower encounter rate, that result in longer search times for these larger animals.

For the spotted owl pairs I studied, the presence of large prey, such as dusky-footed woodrats and northern flying squirrels, is important to breeding success. The high frequency of large prey in the diet of breeding spotted owls could be a function of either the availability of the large prey or the owls' prey selection. Prey availability, however, partly determines prey selection. This distinction is important but is beyond the scope of the present paper. Understanding the ecology of the prey is fundamental to understanding the ecology of the predator. For the spotted owl, predator-prey relationships seem closely linked to reproductive success. Managing for spotted owls, therefore, should include consideration of those animals that serve as owl prey; ecological data on these prey species is required before we can understand the process behind the breeding pattern of spotted owls,

Current spotted owl management plans and habitat suitability models focus on habitat use by spotted owls, not on the owls' productivity. Habitat use alone is but one measure of habitat quality (Van Horn 1983). Breeding success is perhaps the best measure of habitat quality (Hilden 1965). Individual spotted owls and spotted owl pairs do occupy habitats that are apparently inadequate for consistent successful reproduction. Without immigration from areas that allow high reproductive output, spotted owl populations in poor environments may not be able to persist.

Habitat suitability models for spotted owls need to be tested using the frequency of successful breeding, Such tests could be conducted by applying the models to the territories of pairs for which reproductive attainment has been measured. If the models cannot distinguish between the territories of reproducing and nonreproducing owls in terms of viability, then the models must be reexamined and refined. The models could also include terms reflecting the suitability of the territory for the owls' major prey species. The importance of regular breeding success in a population cannot be overstated. Factors that contribute to breeding success should be integral parts of habitat models. Such factors may vary temporally (for example, density) and long-term ecological studies may be necessary before good models can be developed.

[2] Personal communication, Martin Raphael, University of California, Berkeley, CA 94720.

Unpublished data on file, Northern California Coast Range Preserve, 42101 Wilderness Road, Branscomb, CA 95417.

ACKNOWLEDGMENTS

Katherine Barrows, Bill Block, Lenny Brennan, Andrew Carey, Rocky Gutiérrez, Pat Manley, and David Solis offered critical suggestions that improved this paper. Katherine Barrows, Alan Franklin, Rocky Gutiérrez, Bill LaHaye, and Pat Ward augmented my prey analysis with numerous owl pellets collected from throughout northwestern California.

LITERATURE CITED

Adamick, R.S.; Todd, A.W.; Keith, L.B. Demographic and dietary responses of great horned owls during a snowshoe hare fluctuation. Canadian Field Naturalist. 92(2): 156-166; 1978.

Barrett, Reginald H.; Laymon, Stephen A. Analysis of habitat preference and use by dispersing juvenile spotted owls: progress report 1982. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1982. 53 p.

Barrett, Reginald H.; Laymon, Stephen A. Analysis of habitat preference and use by dispersing juvenile spotted owls: progress report 1983. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1983. 4 p,

Barrows, Cameron W. Feeding ecology of the spotted owl in California. Raptor Research. 14(3): 73-78; 1980.

Barrows, Cameron W. Roost selection by spotted owls: an adaptation to heat stress. Condor. 83: 302-309; 1981.

Barrows, Cameron W.; Barrows,-Katherine B. Roost characteristics and behavioral thermoregulation in the spotted owl. Western Birds. 9: 1-8; 1978.

Forsman, Eric D. A preliminary investigation of the spotted owl in Oregon. Corvallis, OR: Oregon State University; 1976. 127 p. M.S. thesis.

Forsman, Eric D. Habitat utilization by spotted owls in the west-central Cascades of Oregon. Corvallis, OR: Oregon State University; 1980. 95 p. Ph.D. dissertation.

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs. 87; 1984. 64 p.

Gutiérrez, Ralph J.; Franklin, Alan; LaHaye, William S.; Meretsky, V.J.; Ward, J.P. Juvenile spotted owl dispersal: progress report #3 (1 September to 15 November 1983). Arcata, CA: Humboldt State University Foundation, Humboldt State University; 1983. 10 p.

Gutiérrez, Ralph J.; Franklin, Alan; LaHaye, William S.; Meretsky, V.J.; Ward, J.P. Juvenile. spotted owl dispersal: progress report #4 (16 November 1983 to 15 June 1984). Arcata, CA: Humboldt State University Foundation, Humboldt State University, 1984. 7 p.

Hamerstrom, Francis N. Effect of prey on predators: voles and harriers. Auk. 96(2): 370-374; 1979.

Hilden, 0. Habitat selection in birds, a review. Annals Zoologica Fennica. 2: 53-75; 1965.

Laymon, Stephen A.; Barrett, Reginald H. Administrative study of relationships between wildlife and management of mature and overmature (old-growth) tree stands: supplemental report on a test of a spotted owl habitat suitability model. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station; 1982. 31 p.

Maser, Chris; Anderson, R.C.; Cromack, Kermit, Jr.; Williams, J.T.; Martin, R.E. Dead and down woody material. In: Thomas, Jack Ward, ed. Wildlife in managed forests - Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture, Forest-Service; 1979: 78-95.

Miller, Grace M. Grace Miller on spotted owls. In: Walker, L.W., ed. The book of owls. New York, NY: Alfred A. Knopf; 1974: 130-146.

Miller, G.S.; Meslow, E. Charles. Juvenile spotted owl dispersal project: 1983 annual report (April 15, 1983 - January 31, 1984). Corvallis, OR: Oregon Cooperative Wildlife Research Unit, Department of Fisheries and Wildlife, Oregon State University; 1984. 11 p.

Newton, I. Population ecology of raptors. Vermillion, SD: Buteo Books; 1979. 399 p.

Pitelka, Frank A.; Tomick, P.Q.: Treickel, G.W. Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. Ecological Monographs. 25: 85-117; 1955.

Sisco, Chuck; Gutiérrez, Ralph J. Winter ecology of radio-tagged spotted owls on Six Rivers National Forest, Humboldt County, CA. Eureka, CA: U.S. Department of Agriculture, Forest Service, Six Rivers National Forest; 1984. 140 p.

Smith, D.G.; Murphy, J.R.; Wolfinden, N.F. Relationships between jackrabbit abundance and ferruginous hawk reproduction. Condor. 83: 52-56; 1981.

Solis, David M. Summer habitat ecology of the northern spotted owl. Arcata, CA: Humboldt State University; 1983. 230 p. M.S. thesis.

Southern, H.N.; Lowe, V.P.W. The pattern of distribution of prey and predation in tawny owl territories. Journal of Animal Ecology. 37: 75-97; 1968.

Southern, H.N. The natural control of a population of tawny owls (Strix aluco). Journal of Zoology, London. 162:197-285; 1970.

Van Horn, Barbara. Density as a misleading indicator of habitat quality. Journal of Wildlife Management, 47(4): 893-901; 1983.

A REVIEW OF CURRENT NORTHERN SPOTTED OWL (*Strix occidentalis caurina*) RESEARCH IN WASHINGTON STATE

Harriet L. Allen and Larry W. Brewer

ABSTRACT : Two spotted owl research efforts are underway in Washington. One is a study of spotted owl population and ecology and is being conducted and funded by the Washington Department of Game. The other is a study to evaluate the effectiveness of the Spotted Own Management Area (SOMA) concept and is funded jointly by the USDA Forest Service and the Washington Department of Game.

INTRODUCTION

The northern spotted owl was classified as "sensitive" by the state of Washington in 1982; this classification was changed to "threatened" in 1983. The Department of Game is currently conducting two research projects on the spotted owl.

The first project was initiated in 1982 and was funded by the Nongame Program of the Department of Game. It was established to provide facts about spotted owl ecology that either added to existing knowledge or clarified unique management questions in Washington. The objectives were to:

1. Determine the population distribution and status of spotted owls in Washington;
2. Monitor habitat use patterns of adult spotted owls;
3. Analyze habitats used by adults; and
4. Develop management recommendations for spotted owls in Washington.

A fifth objective, to monitor the dispersal of juvenile owls, was added during the second year of the study.

The second research project began in 1983 in cooperation with the USDA Forest Service to evaluate the effectiveness of the Spotted Owl Management Area (SOMA) concept. The cooperators are the USDA Forest Service Pacific Northwest Region, including the Mount Baker-Snoqualmie National Forest, the Gifford Pinchot National Forest, and the Olympic National Forest; the Pacific Northwest Forest and Range Experiment Station Old Growth Research and Development Project, Olympia, WA; and the Washington Department of Game. Objectives of the study were to:

1. Determine occupancy rates of SOMAs;
2. Determine how owls are using SOMAs; and
3. Determine how used areas differ from unused areas.

An overview of the methods and preliminary results of these two projects will be discussed individually.

SPOTTED OWL ECOLOGY STUDY

Population Levels and Status

We began our work on population evaluation by conducting a random survey throughout the potential range of the spotted owl in Washington. This included coniferous forests in both western Washington and on the eastern slopes of the Cascade Range. 'We divided the study area into

---

LARRY W. BREWER and HARRIET L. ALLEN are Wildlife Research Biologists with the Washington Department of Game, Olympia, WA.

20-km (12.5 mi) square cells and then randomly selected 53 cells in which to run surveys. The surveys were conducted along 32-km (20-mi) routes on roads or trails nearest the center of the cells. Routes were surveyed twice between May and September in both 1982 and 1983. Approximately 40 cooperators from State and Federal agencies and private organizations worked on the spotted owl survey each year.

Along the routes, cooperators stopped every 0.8-km (0.5 mi) and played a tape of a spotted owl call. The call was played at specified intervals over a B-minute period at each listening station. All owl responses and the direction from which the responses were heard were recorded at each station.

Prior to the spotted owl surveys, each listening station was evaluated for habitat characteristics. Data were gathered for a 400-m-radius circle at each listening station and were recorded in a computer format. The data will be used to compare habitat among areas where spotted owls responded and areas where no owls responded.

In spring 1982 we called owls at 1,772 stations along 48 routes. During this effort we heard 44 spotted owls and 5 barred owls. In spring 1983 we surveyed 1,289 stations over 35 routes. We heard 33 spotted owls and 16 barred owls. We will attempt to estimate a minimum spotted owl population level from the census results. Data on barred owls will be used in a separate evaluation of barred owl distribution in Washington.

The sites where spotted owls were located during the surveys will be used as a random sample to help evaluate the classification status of the spotted owl in Washington. At each of these sites we will determine the habitat types, habitat fragmentation, land ownership, and future land use plans of an area 3.2 km (2 mi) square centered on the survey listening station.

The information from these analyses will be combined with other pertinent data to make a final determination of the status of the spotted owl in Washington. There are no plans to repeat the survey in future years.

Monitoring Habitat Use

The movement and habitat use patterns of 17 spotted owls have been monitored via radio telemetry for varying lengths of time within the Z-year study period. Seasonal and overall home ranges for adult male and female owls are being identified. Roosting and foraging concentration areas within the home ranges are being mapped.

To date, the home range size for the three most northerly pairs of owls have been evaluated. Two of these pairs were located near Mount Baker in the Mount Baker-Snoqualmie National Forest and one was in the Early Winters Creek drainage, Okanogan National Forest. The average home range for these pairs was 2499 ha (6,176 acres). The average home range for each individual owl was 1648 ha (4,071 acres).

These three preliminary home range estimates are conservative figures. The owls were monitored for periods of 120 to 300 days and may represent as little as 60 percent of the total home range (Forsman 1984). Preliminary evaluations suggest that home ranges are larger at the northern end of the species' range. We have made preliminary estimates of the total area of old growth within the home ranges of these three owl pairs using 1979 classified Landsat satellite imagery (Brewer and Eby 1983). The three home ranges evaluated contain an average of 749 ha (1,850 acres) of old growth per pair.

Analysis of Habitats Used by Adults

Habitat analyses of use areas will be compared to habitat analyses of randomly selected plots. We will also look for disparities in habitats selected by males vs. females. These habitat evaluations will be conducted in wet coniferous forest types in western Washington and in dry coniferous forest types on the eastern slopes of the Cascade Range. A major emphasis of this work will be to compare habitat needs of the northern spotted owl from the southern limits to the northern reaches of the species' range.

Throughout the project, spotted owl pellets have been collected at nesting and roosting sites and will be used to analyze food habits. Prey species will be identified and results compared with results from similar studies in California and Oregon.

Monitoring Juvenile Dispersal

Six juvenile spotted owls were trapped and equipped with raio transmitters in August 1983. These young birds dispersed from their nest areas in September and early October and were monitored throughout the following year by spot checks from aircraft. Dispersal routes of the juvenile birds were plotted; distance, direction, habitat selection, and mortality during dispersal are being evaluated.

The juveniles had a known mortality rate of 67 percent; as of June 1984, four of the six juveniles were dead. We were unable to locate two of the owls after extensive searches in May and suspect that the transmitters failed. Preliminary review of the data indicates that dispersal by juvenile spotted owls is random in both direction and habitat use. We tracked juvenile owls through a variety of habitats; only a few of them fit the current concept of adult spotted owl habitat. Dispersal distances exceeded 48 km (30 mi) in some cases. In those instances where two siblings were radio equipped, the birds dispersed from the nest area in generally opposite directions. The sample size in this study is small; however, the results should add to the understanding of juvenile dispersal when combined with the results of similar research conducted in Oregon and California.

Management Recommendations

The final objective of this research is to provide recommendations regarding the population status and management of the northern spotted owl in Washington. The target date for written completion of this research effort is July 1985.

EVALUATION OF THE SPOTTED OWL MANAGEMENT AREA (SOMA) CONCEPT

Occupancy Rates of SOMAs

A total of 46 SOMAs were randomly selected for the monitoring study: 19 in the Mount Baker-Snoqualmie National Forest; 17 in the Gifford Pinchot National Forest; and 10 in the Olympic National Forest. During the first field season (March - September 1984), we surveyed these 46 SOMAs to determine occupancy. Emphasis of surveying was to locate owls within the SOMAs during the day rather than at night. SOMAs were surveyed at night when we were unable to elicit daytime responses. If after 7 surveys throughout the season we were unable to elicit a response, we considered the SOMA unoccupied.

We obtained at least one response from a spotted owl in 43 of the 46 SOMAs. We found no spotted owls in 3 of the 46 SOMAs. Of the 43 SOMAs with responses, we got daytime confirmations of a pair of owls in 12 SOMAs; and daytime confirmations of a single owl in 11 SOMAs. We got only night-time responses from owls in 20 SOMAs. Of these, seven were confirmed (according to Forest Service guidelines of three responses more than 72 hours apart) to contain at least one spotted owl. Thirteen SOMAs had at least one response, but were not verified to contain owls. We obtained barred owl responses in or near eight of the 46 SOMAs. We found no reproduction in any of the 46 SOMAs surveyed.

Owl Use of SOMAs

We monitored five owls during the first field season. Preliminary results indicated an average summer range area of 968 ha (2,391 acres) (range: 257 ha (634 acres) to 1765 ha (4,362 acres)). From 0 to 85 percent ($\bar{x}$ = 35.5 percent) of the locations were within the SOMAs; summer ranges overlapped the SOMAs by 0 to 44 percent ($\bar{x}$ = 20.5 percent). Winter tracking is continuing on these SOMAs during 1984-85. We will monitor nine pairs of birds (three SOMAs on each forest) during 1985.

Comparison of Used vs. Unused Areas

Habitat analyses of used vs. unused areas will begin during the 1985 field season. Vegetation analysis that incorporates concentric circular plots (Spies 1983) randomly located in used and unused habitat, will be conducted in each of the home ranges of monitored owls. This effort will concentrate on those portions of home ranges that fall within the SOMAs.

LITERATURE CITED

Brewer, Larry; Eby, James. A Washington state LANDSAT ground cover classification. Washington Department of Game Pitman-Robertson Report, Project W-92-R. Olympia. 1982. 121 p.

Forsman, Eric. Distribution and biology of the spotted owl in Oregon. Wildl. Monogr. No. 87. 1984. 64 p.

Spies, Thomas. Draft study plan: Characterization of old-growth douglas-fir forests of western Oregon and Washington. USDA Forest Service Unpublished Report, Oregon State University, Corvallis. 1983. 37 p.

OLD-GROWTH FOREST RETENTION FOR SPOTTED OWLS--HOW MUCH DO THEY NEED?

Eric D. Forsman and E. Charles Meslow

ABSTRACT: Pairs of adult owls in Oregon were studied by radiotelemetry to determine their home ranges and the acreages of old-growth forest in the home ranges. Six pairs were studied for 3 to 13 months. The pairs used 1,008-3,786 acres of old growth, averaging 2,264 acres per pair. The 1,008-acre figure provided the basis for management recommendations.

INTRODUCTION

In 1980 the Oregon-Washington Interagency Wildlife Committee recommended that the amount of old-growth forest retained for individual pairs of spotted owls be increased from 300 to 1,000 acres (121-405 ha) (Oregon-Washington Interagency Wildlife Committee 1980). This recommendation was based on data gathered during radio-tracking studies of spotted owls in Oregon between 1975 and 1980 (Forsman 1980, 1981; Forsman and others 1984). During these studies, 14 adult spotted owls were fitted with radio transmitters and tracked for periods ranging from 3 to 13 months. In 6 cases, we were able to track both members of a resident pair of owls.

ERIC D. FORSMAN is a wildlife biologist residing at 580 S.E. Corliss Ave., Corvallis, OR. E. CHARLES MESLOW is leader, Cooperative Wildlife Research Unit, Oregon State University, Corvallis, OR.

At the end of the tracking period, the total home range of each pair of owls was determined, and the amount of old growth within each home range was determined from orthophotos. The minimum amount of old growth within the home ranges of the 6 pairs studied was 1,008 acres (405 ha) as reported by Forsman (1981) and Forsman and others (1984).

Subsequent to the 1980 revision of the spotted owl management plan, we received a number of requests to display all the data relating to the amount of old growth within the home ranges occupied by the pairs of owls that we studied (only the minimum acreage figure was cited in our initial reports). The purpose of this report, therefore, is to display the complete set of data concerning the amount of old growth within the home ranges of the 6 pairs of owls.

OLD GROWTH PER PAIR

The area of old-growth forest in the home ranges of the radio-tagged pairs is shown in table 1. As described in Forsman (1980, 1981) and Forsman and others (1984), data from the lA and 2C pairs (table 1) should be viewed with caution because there was some question about the stability of those pairs. The other 4 pairs, however, appeared to be comprised of well-established individuals.

Table l--Amount of old-growth forest within home range areas utilized by 6 pairs of radio-tagged spotted owls in northwestern Oregon

Pair no.	Home range size 1/	Old-growth area
	- - - - - - - Acres	- - - - - - - - -
IA	10,146	3,786
2A	3,945	2,092
5A	3,969	2,248
1c	10,440	2,262
2c	8,343	2,191
3c	2,840	1,008
Mean	6,614	2,264
Std. Dev.	3,419.5	886.5

1/ Areas given indicate the total home range area used by each pair of owls. Home ranges utilized by individual owls were described in Forsman and others (1984).

The old-growth acreages used by the pairs of spotted owls in our studies do not appear unusual. Recent studies in California and Washington indicate that pairs of spotted owls use extensive areas of old-growth and mature forest in those areas as well (Sisco 1984; Solis 1983; Harriet Allen, pers. comm. 1984 1/).

A/Washington State Game Department study in progress. Data on file with Harriet Allen, Washington State Game Department, Olympia, WA.

Because of economic concerns, the approach to spotted owl management in Oregon has been to manage for the minimum number of pairs necessary to sustain a genetically viable population and to provide each pair with a minimum amount of old-growth habitat. This approach involves a high degree of risk because it is unlikely that any species will prosper if it is reduced to minimum numbers and, at the same time, provided with a minimum amount of suitable habitat. To mitigate the effects of minima1 numbers and minimal areas of habitat, managers should attempt to ensure that old-growth habitat that is retained for spotted owls is of the highest quality available.

LITERATURE CITED

Forsman, Eric D. Habitat utilization by spotted owls in the west-central Cascades of Oregon. Corvallis, OR: Oregon State University; 1980. Ph.D. dissertation. 95 p.

Forsman, Eric D. Habitat utilization by spotted owls on the Eugene District of the Bureau of Land Management. Portland, OR: Bureau of Land Management; 1981. 63 p.

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Biology and management of the spotted owl in Oregon. Wildlife Monograph No. 87; 1984. 64 p.

Oregon-Washington Interagency Wildlife Committee. Oregon spotted owl management plan. Portland, OR: Oregon Department of Fish and Wildlife; 1980. 2 p.

Sisco, C.; Gutiérrez, R. J. Winter ecology of radio-tagged spotted owls on Six Rivers National Forest, Humboldt Co., CA. Eureka, CA: U.S. Department of Agriculture, Forest Service, Six Rivers National Forest; 1984. 139 p.

Solis, David M., Jr. Summer habitat ecology of spotted owls in northwestern California. Arcata, CA: Humboldt State University; 1983. M.S. thesis. 168 p.

JUVENILE SPOTTED OWL DISPERSAL IN NORTHWESTERN CALIFORNIA: PRELIMINARY RESULTS

R. J. Gutiérrez, Alan B. Franklin, William Lahaye,
Vicky J. Meretsky, and J. Patrick Ward

ABSTRACT: Dispersal ecology of juvenile spotted owls was studied in northwestern California during 1982 and 1983. Breeding spotted owls were not found in northwestern California in 1982. In 1983, we radio-marked 13 juvenile owls. Eleven owlets survived to disperse between 2 September and 23 October 1983. The total dispersal distances for these owlets ranged from 30 km to 156 km ($\bar{x}$ = 78 km). The final dispersal distance measured as a straight line from the nest to the location of juvenile mortality or transmitter failure ranged from 20 km to 98 km ($\bar{x}$ = 45 km). An analysis of dispersal directions using circular statistics showed that, as,a group, juveniles dispersed in a southerly direction (154°). We lost radio contact with four of the owls, while the remaining seven died. Causes of mortality included a presumed accident (1), animal predation (1), starvation (3), undetermined (4). The management implications for these preliminary results are discussed.

INTRODUCTION

The northern spotted owl (*Strix occidentalis caurina*) is closely associated with old-growth Douglas-fir (*Pseudotsuga menziesii* (Mirb.) Franco) forests from southwestern British Columbia through northwestern California (Forsman 1980, Solis 1983). The rapid harvest of these forests in the Pacific Northwest has led to a population decline of the northern spotted owl (Forsman and others 1984, U. S. Fish and Wildlife Service 1982). In response to this decline, the USDA Forest Service established Spotted Owl Teritories (SOTs) that are developed from habitat and home range studies conducted by Forsman (1980) and Solis (1983). Although data exist for establishing guidelines for SOT habitat quality and quantity, no data exist for determining an appropriate distribution of SOTs.

The maintenance of effective population size (Barrowclough and Coats 1985) and the correct spatial organization of SOTs cannot be adequately predicted without an understanding of dispersal. The importance of animal dispersal to demography, genetics, and social behavior has

R. J. GUTIÉRREZ is an associate professor of wildlife management and chairman of the Dept. of Wildlife at Humboldt State University, Arcata, CA. ALAN FRANKLIN, WILLIAM LAHAYE and VICKY MERETSKY are graduate students in wildlife management and J. PATRICK WARD is an undergraduate student in wildlife management at Humboldt State University, Arcata, CA.

been documented for a wide variety of taxa (Greenwood 1980, Lidicker 1962, Lidicker and Caldwell 1982, Southwood 1962). For this paper, dispersal is defined as nonmigratory movement by an individual beginning with its departure from the natal area and ending with the establishment of a breeding territory. In this paper, we present some initial observations on the dispersal of juvenile spotted owls in northern California and discuss the implications for the management of this species.

MATERIALS AND METHODS

The dispersal ecology of northern spotted owls was studied in northwestern California from 1982 to 1983. Because of a region-wide breeding failure of spotted owls in 1982, data on dispersing juveniles were not collected until 1983.

Our study area encompasses portions of the Six Rivers, Klamath, and Shasta-Trinity National Forests in northwestern California. The area is dominated by rugged topography and numerous river and stream systems. Elevations of the study area range from 300 m to 1500 m. The climate is typically wet and cool in winter, with snow at higher elevations; summers are hot and dry. Average yearly precipitation for the study area is approximately 142 cm.

The study is limited to Douglas-fir forests because spotted owls appear to be more abundant in this habitat (Forsman and others 1984); this vegetation type is also the most extensive and valuable of the old-growth forests in northwestern California. The vegetation seres are more completely described by Sawyer and others (1977) and Solis (1983).

Nests and juveniles were located in the manner described by Forsman (1984). Juveniles were captured using a dip net constructed of mist netting. Each captured juvenile was banded with a U. S. Fish and Wildlife Service aluminum leg band and outfitted with a radio transmitter attached to a backpack of 5-mm teflon ribbon (Solis 1983). The birds were released within 18 min and observed to determine behavioral reactions.

Radio-marked owls were monitored using the methods outlined by Solis (1983). Owl locations were plotted on U. S. Geological Survey topographic maps (1:24000) using a minimum of three compass bearings from monitoring points with the bearing describing the peak radio signal (Springer 1979).

Juvenile owls were initially monitored at least once a week to determine location or mortality prior to dispersal. We tracked dispersing juveniles from the ground as closely as terrain and weather conditions permitted. Telemetry-equipped aircraft were used to relocate owlets lost during ground tracking and for monitoring owlets in inaccessible areas.

Dispersal directions and direction-distance vectors were analyzed using circular statistics (Batschelet 1981).

Table 1--Summary of dispersal distances and fates of 13 juvenile spotted owls, _Strix occidentalis caurina_, from northwestern California, 1983

Owl	Sex[1/]	Date Sighted	Date Banded	Date Died	Total Distance km (mi)	Final Distance km (mi)	Fate
Tonto	M	30 Jun	26 Jul	22 Sep	0 (0)	0 (0)	Dead
Fang	U	1 Jul	7 Jul	9 Oct	32 (19)	26 (16)	Dead
Titus	U	30 Jun	6 Jul	25 Nov	128 (77)	99 (62)	Dead
Bertha	U	18 Aug	23 Aug	2 Feb	45 (27)	22 (13)	Unstable[2/]
Merlyn	U	11 Aug	19 Aug	20 Mar	163 (98)	67 (41)	Dead
Ranger	M	22 Jun	6 Jul	29 Mar	63 (38)	44 (27)	Dead
Cheech	U	23 Jun	11 Jul	17 Jan	77 (46)	42 (26)	Stable[3/]
Chong	U	23 Jun	13 Jul	21 Nov	73 (44)	56 (35)	Dead
Jake	U	24 Jun	20 Jul	20 Dec	138 (86)	42 (26)	Dead
Elmo	U	24 Jun	14 Jul	25 Nov	60 (36)	53 (32)	Dead
Sugarbaby	U	17 Jun	12 Jul	2 Sep	0 (0)	0 (0)	Dead
Harpy	U	17 Jun	8 Jul	3 Jan	45 (27)	23 (14)	Unstable
Shrew	U	6 Jul	21 Jul	17 Jan	70 (42)	35 (22)	Unstable

[1/]Sex M = male; U = unknown.
[2/]Unstable = dispersal in progress when transmitter failed.
[3/]Stable = settled in a restricted area before transmitter failed.

RESULTS AND DISCUSSION

Dispersal Patterns

All marked, surviving juveniles dispersed between 2 September and 23 October 1983 (table 1). Sixty-four percent (7 juveniles) dispersed within a 9-day period from 19 September to 27 September. The degree of parental care at the time of dispersal was not known, but after a bird left its natal area, it did not return.

Dispersal distance and direction.-The total dispersal distance, which is the sum of dispersal movements for an individual owl, ranged from 30 km to 156.km (19 mi to 97.6 mi) with a mean of 78 km (48.4 mi) (table 1). The final distance measured as a straight line from the nest to the location of the juvenile mortality or transmitter failure ranged from 20 km to 98 km (12 mi to 61.5 mi) with a mean of 45 km (28.3 mi).

The directions in which dispersing owlets traveled were averaged and represented as vectors of dispersal (fig. 1). The r values associated with each vector represent the measure of concentration of the individual directions taken by each bird. The higher the r value, the more consistently the juvenile moved in a single direction. Observations from all of the birds were combined to calculate a group direction or vector **(0).** The group direction for all juveniles was 0 = 154° with r = 0.35. The low r value indicated that directions taken between dispersal movements were variable. Rayleigh and Rao's spacing tests (Batschelet 1981) showed that five birds were heading in a particular compass direction. The remaining birds' movements were. not shown to be significantly different from a random distribution. The group direction (0), however, was significantly different from a random distribution according to both the Rayleigh and Rao's spacing tests. As a group, the juveniles therefore appeared to be moving in a southerly direction (0 = 1540; fig. 1).

For each owl, a bivariate vector was plotted using distance and direction from the nest to the owl's final known location (fig. 2). A mean vector (M) of 188° and 34 km (21.1 mi) was calculated for the sample of vectors. Again, as a group, the juveniles appeared to be moving in a southerly direction.

Hotelling's confidence ellipse (Batschelet 1981) was calculated to determine the area covering

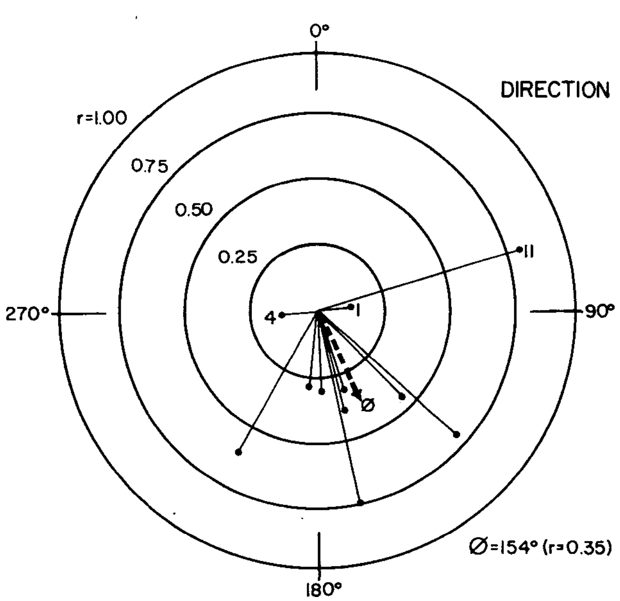


Figure 1.--Direction vectors for 11 dispersing juvenile spotted owls, Strix occidentalis caurina, from northwestern California, 1983. 0 = an overall group direction; r = the measure of concentration of 0 (Batschelet 1981).

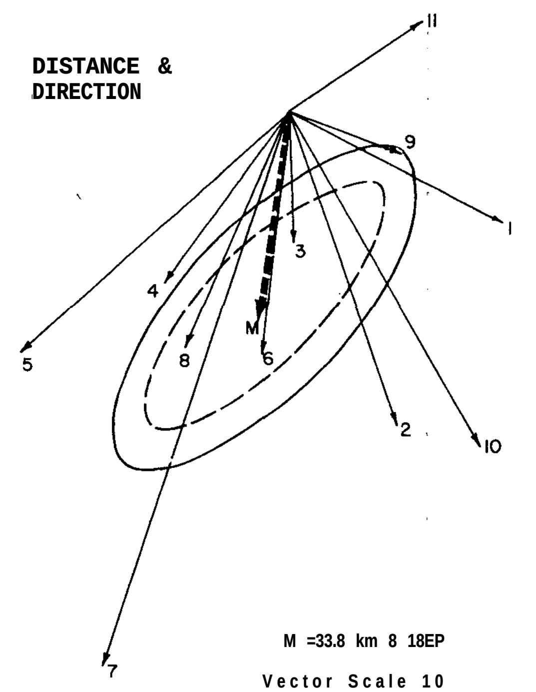


Figure 2.--Bivariate vectors using distance and direction from nest to final location for 11 dispersing juvenile spotted owls, Strix occidentalis caurina, from northwestern California, 1983. M = the sample mean; the **outer ellipse is one standard deviation around the mean; the inner, a 95% Hotelling's** confidence ellipse (Batschelet 1981).

the true population center of dispersing juvenile owls with 90 percent probability. In other words, with the starting point at the nest (origin) there is a 90 percent probability that the population mean of final dispersal locations of juvenile spotted owls would be included within this ellipse.

When the circumstances allowed us to closely follow individuals that were dispersing, we found that these birds typically moved rapidly and unidirectionally. The average rate of movement for all birds was 8 km/day (5.03 mi/day), with a range of 1.6-17 km/day (l-10.9 mi/day).

After an initial rapid movement from the natal area, most (n = 8) of the owlets attempted to settle. Three of these owlets, which were monitored closely, had home ranges of 362 to 461 ha (882 to 1125 acres>. After settling, six of the owlets died or their transmitters failed. Two continued to disperse after remaining four to seven weeks in their respective areas. One owl roosted and foraged for several days in the same area on three separate occasions and made two round trips of 6 and 50 km (4 and 31 mi). The owlet died 19 km (12 mi) from the area during its third departure.

Effect of barriers and habitat on dispersal.--Geographic and topographic barriers did not noticeably affect direction of dispersal. Owlets frequently crossed major ridges and rivers during dispersal; for example, one bird crossed three large rivers (75-100 m width) and two major ridges (1200-1500 m elevation) during its dispersal.

Juvenile owls readily crossed habitats in northwestern California that would be classified as unsuitable for spotted owls (Gutiérrez and others 1984, Solis 1983). Although owlets frequently entered these areas, they often died there as well. Unsuitable habitats (for example, clearcuts and oak woodlands) may be effective barriers to dispersal, but this does not seem to deter the birds from entering them.

Juvenile Mortality

All of our marked juveniles (n = 7) that survived to disperse, and whose transmitter batteries did not fail, died during dispersal. Causes of mortality included predation (11, starvation (31, and undetermined (3). Four transmitter batteries failed before they could be replaced. Two juveniles died before dispersing, one from an apparent accident (punctured eye) and the other from unknown causes. Because none of the juveniles survived to established breeding territories, the distances recorded in our study cannot be considered net effective dispersal distances.

It has long been known that dispersing animals incur high mortality rates (Howard 1960, Lidicker and Caldwell 1982). Juvenile tawny owls (*Strix aluco*) exhibited average first-year mortality rates between 47 and 66 percent under normal conditions (that is, without decreasing habitat limitations) (Southern 1970), Barrowclough and Coats (1985) calculated an expected first-year Surivorship for spotted owls to be 19 percent.

A population of owls could, clearly, not maintain itself with a mortality of 100 percent such as we observed. Our sample size is small enough that one might expect the entire group to die by chance alone (Barrowclough and Coats 1985). An larger sample size may be needed to detect the 19 percent survivorship. Despite such a high first-year mortality rate, spotted owls may be sufficiently long-lived that they could replace themselves within their reproductive lives.

MANAGEMENT IMPLICATIONS

There are three important implications of our preliminary findings. First, our study demonstrates that juvenile spotted owls move considerably farther than previously observed (Forsman and others 1984). Yet, our data are consistent with those reported in this symposium by Miller and Meslow (1985). Owlets are aggressive dispersers and travel rapidly over topographic barriers and into or through unsuitable habitat. Inter-SOT distances should not, however, be increased to reflect these long dispersal distances. Because owlets move directionally, the probability of a juvenile owl encountering a SOT would decrease as the inter-SOT distance increases.

Second, we do not know how long-term population viability will be affected if adequate dispersal sinks (as defined by Lidicker 1962, habitats where nonbreeding owls can persist until breeding habitat becomes available) are not available for juvenile owls. Because spotted owls are probably long-lived, SOTs may be occupied for a long time. A SOT management scheme without consideration for dispersal sinks must depend almost entirely on the current year's productivity to fill available SOTs. Thus, the most productive habitat or pairs of owls should be maintained to ensure adequate productivity. We believe that establishing SOTs with pairs of owls that show sporadic or no productivity are inadequate for maintaining a viable population. The reasons for this are: (1) adults have a variable reproductive pattern (Gutiérrez 1985, Gutiérrez and others 1984); (2) juveniles have a low survivorship (Barrowclough and Coats 1985, Forsman and others 1984, Miller and Meslow 1985); and (3) there is continuing habitat deterioration.

Third, the influence of dispersal on the survivorship of juvenile spotted owls and effective population size is presented by Barrowclough and Coats (1985). If the high juvenile mortality we observed is, in part, due to deteriorating habitat (that is, increased patchiness and loss of old growth), then we might predict (1) lower survivorship of juveniles as this deterioration continues and (2) an increase in dispersal distance required to reach suitable habitat. In turn, effective population size is strongly influenced by these dispersal distances (Barrowclough and Coats 1985). Ultimately, the long-term viability of spotted owls in the Pacific Northwest will be a function of effective population size and colonization of habitat patches that are partially dependent on dispersal ecology (Barrowclough and Coats 1985, Frankel and Soulé 1981, Gutiérrez and others 1984, Schaffer 1985). SOTs should be established with appropriate habitat characteristics, as described by Forsman and others (1984) for mesic Oregon, by Solis (1983) and Gutiérrez and others (1984) in northwestern California, and by Layman (1985) in the Sierra Nevada. SOTs should not be designated solely on their value (or lack thereof) as a timber resource. Many of the most productive habitats appear to be in valuable timber stands. If adequate protection is to be provided for spotted owls, SOTs must be placed in these stands, commercial values notwithstanding. Above all, spotted owl management plans must be allowed some flexibility (Gutiérrez and others 1984) to accommodate new and relevant findings on spotted owl dispersal.

ACKNOWLEDGMENTS

We would like to thank Don Kudma, Jeff Mattison, Rolando Mendez, Jan Stevenson, David Solis, Marilyn Stoll, Ed Toth, and Becky Oz of the Six Rivers National Forest; Edie Asrow, Don Bright, Alan Scott, and Lou Waltering of the Klamath National Forest; Terry Brumley, Lynn Shipley, Kim Stokely and Paul Weeden of the Shasta-Trinity National Forest; Jim Decker of the Bureau of Land Management; and Gordon Gould of the California Department of Fish and Game. All of these people were extremely helpful with our field efforts. We also thank Len Ruggiero for his support in funding. Andrew Carey, Hal Salwasser, Carl Marti and Jared Verner kindly reviewed the manuscript. Jay Brown made the illustrations and Bruce Garlinger provided air service.

Funding for this project was provided by the Old-Growth Forest Wildlife Habitat Program, USDA Forest Service, Forestry Sciences Laboratory, Olympia, Washington. This is contribution 84-2 of the College of Natural Resources, Humboldt State University, Arcata, California.

LITERATURE CITED

Batschelet, Edward. Circular statistics in biology. New York, NY: Academic Press; 1981. 371 p.

Barrowclough, George F.; Coats, Sadie. The demography and population genetics of owls, with special reference to the conservation of the spotted owl (Strix occidentalis). In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 74-85.

Forsman, Eric D. Habitat utilization by spotted owls in the west-central Cascades of Oregon. Corvallis, OR: Oregon State University; 1980. Ph.D. dissertation. 95 p.

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Biology and management of the spotted owl in Oregon. Wildlife Monograph No. 87; 1984. 64 p.

Frankel, O. H.; Soulé, Michael E. Conservation and evolution. Cambridge, England: Cambridge University Press; 1981. 327 p.

Greenwood, P. J. Mating systems, philopatry and dispersal in birds and mammals. Animal Behavior. 28: 1140-1162; 1980.

Gutiérrez, R. J. An overview of recent research on the spotted owl. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 39-49.

Gutiérrez, R. J.; Solis, David M.; Sisco, Charles. Habitat ecology of the spotted owl in northwestern California. In: Proceedings of the convention of the Society of American Foresters; 1983 October 16-20; Portland, OR: American Society of Foresters; 1984: 368-373.

Howard, W. E. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist. 63: 152-161; 1960.

Layman, Stephen A. General habitats and movements of spotted owls in the Sierra Nevada. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owls in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985:66-68.

Lidicker, W. Z., Jr. Emigration as a possible mechanism permitting the regulation of population density below carrying capacity. American Naturalist. 96: 29-33; 1962.

Lidicker, W. Z., Jr.; Caldwell, R. L., eds. Dispersal and migration. Benchmark papers in Ecology 11. Stroudsberg, PA: Hutchinson Publishing Co.; 1982. 309 p.

Miller, Gary S.; Meslow, E. Charles. Dispersal data for juvenile spotted owls: the problem of small sample size. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 69-73.

Sawyer, John O.; Thornburgh, D. A.; Griffen, J. R. Mixed evergreen forest. In: Barbour, M.; Major, J., eds. Terrestrial vegetation of California. New York, NY: John Wiley and Sons, Inc.; 1977: 359-415.

Schaffer, Mark L. The metapopulation and species conservation: the special case of the northern spotted owl. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 86-99.

Solis, David M. Summer habitat ecology of spotted owls in northwestern California. Arcata, CA: Humboldt State University; 1983. 168 p. M.S. thesis.

Southern, H. N. The natural control of a population of tawny owls (Strix aluco). Journal of zoology. 162: 197-285: 1970.

Southwood, T. R. E. Migration of terrestrial arthropods in relation to habitat. Biological Review 37: 171-175; 1962.

Springer, J. T. Some sources of bias and sampling error in radio triangulation. Journal of Wildlife Management. 43: 926-935; 1979.

U.S. Fish and Wildlife Service. The northern spotted owl: a status review. Portland, OR: U.S. Department of Interior, Fish and Wildlife Service; 1982. 29 p.

GENERAL HABITATS AND MOVEMENTS OF SPOTTED OWLS IN THE SIERRA NEVADA

Stephen A. Layman

ABSTRACT: This paper reports a summary of a 3-year research project on the California spotted owl in the central Sierra Nevada of California. Owls with radio transmitters were tracked and vegetation parameters were measured on summer, autumn, and winter roosting plots and on randomly located plots within the owl's home range. The discovery of downslope migrational movements and establishment of winter home ranges in the foothill woodland was a significant finding which may indicate a subspecies difference and which raises previously unthought of management problems. The ramifications of these new management issues are discussed.

INTRODUCTION

A great deal of research has been undertaken on the northern spotted owl (Strix occidentalis caurina). Forsman and others (1484) completed eight seasons of field work in west-central Oregon, including two years of radio telemetry on two study sites. Gutiérrez and associates at Humboldt State University, Arcata, California, have conducted a 5-year research effort to examine winter and summer habitat use and juvenile dispersal of spotted owls in northwestern California. The California subspecies, Strix occidentalis occidentalis, which ranges from northeastern Tehama Countv south through the Sierra Nevada and the high mountain ranges of southern California, and in the Coast Range from southern California north to Monterey County, has received little attention from researchers. The only published information consists of work on thermoregulation (Barrows 1981) and on food habits (Barrows 1480, Marshall 1942).

STEPHEN A. LAYMON is a research assistant, Department of Forestry and Resource Management, the University of California, Berkeley, Berkeley, Calif.

The current study, from 1982 to 1984, was' designed to fill in gaps in the knowledge of the natural history, life history,, habitat selection, and juvenile dispersal in the Sierra Nevada population of the California spotted owl, and to determine if there were differences between the northern and California subspecies. Presented here is an outline of the general accomplishments and progress of the study.

STUDY AREA

The study was conducted primarily between the middle. and south forks of the American River in El Dorado and Placer Counties, California. Elevation was 300-2000 m and the study area encompassed 500 km^2. University of California at Berkeley Blodgett Forest Research Station, near Georgetown, California, was the base of operations for the study. Habitat types in the study area included mixed conifer forest, red fir forest , yellow pine forest, pine-oak woodland, and oak Savannah.

METHODS

Radio Telemetry

A total of 13 adults and 12 juveniles were equipped with radio transmitters during the 3-year study. Adult foraging sites and winter roosting sites were located using triangulation methods from known locations. Summer and autumn roosting sites for both adults and juveniles were located visually with the aid of radio telemetry.

Vegetation Sampling

Vegetation was sampled on 15-m-radius plots centered on roosting, foraging, and random trees. All trees greater than 10 cm diameter at breast height (d.b.h.), total height, height of first foliage, and average radius of foliage. Additionally, tree species, shape, and condition were recorded. Canopy closure was estimated using an inverted monocular with plastic prism grid. Shrubs and trees smaller than 10 cm d.b.h. were sampled with a 0.5-m-wide belt transect. Dead and down material was sampled with line intercept methods (Brown 1974). Slope and aspect were also measured. Sampling was done at randomly selected roost and foraging sites and at sites determined by coordinates randomly selected from a grid placed over a map of each pair's home range.

RESULTS

Vegetation Sampling

Vegetation was measured at 10 summer (June-August) roosting sites and 10 summer foraging sites for each of 12 paired adults. Roosting sites and foraging sites were characterized for nine adults during the autumn (September-October). Twenty random points were surveyed within the home range of each pair. Vegetation was also sampled at 15 roosting sites and at 15 random points in winter-use areas of four birds. Sampling on a total of 50 vegetation plots was also completed at juvenile roosting sites. Analysis of vegetation data is not yet complete. A cursory look at the data shows little similarity along summer roosting sites, foraging sites, and randomly selected sites, and between winter roosting and winter randomly selected sites. Great similarity is found between autumn roosting and autumn foraging sites.

Food Habits

Approximately 800 pellets of regurgitated, undigested portions of prey items have been collected and analyzed. A much higher diversity of prey items by species has been found in this study than in others. The 1982 data, based on eight pairs of owls and 522 food items, show an almost equal division of biomass eaten: northern flying squirrels (Glaucomys sabrinus), 30 percent; dusky-footed woodrats (Neotoma fucipes), 22 percent; western gray squirrels (Sciurus griseus), 22 percent; and birds, 16 percent. The 1983 data show a similar pattern.

Reproductive Success

Reproductive success has been quite low for the three years of the study. During 1482 and 1983 only 1 of 14 pairs produced young (7 percent). In 1984, 3 of 12 pairs produced young in the Eldorado National Forest study site and 3 of 10 pairs produced young in the Stanislaus National Forest -- a success rate of 27 percent.

Juvenile Mortality

I observed 11 juveniles during the post fledging-predispersal period. Seven of the the juveniles died; three dispersed. I am currently monitoring one juvenile that has not yet dispersed. Of the seven deaths, four were attributed to predation and three to starvation.

Migratory Movements

I monitored four adult owls by radio telemetry during autumn 1983. In late October the four owls began moving downslope to the southwest. One bird was tracked daily during this time. It moved 3-6 km each night, traversing the 29 km between breeding and wintering sites in seven nights. This bird dropped in elevation from 1600 to 930 m. The other three owls moved from 19 to 32 km and dropped in elevation an average of 700 m. All four owls circulated through areas of 300-2000 ha, which appeared to be a winter home range. The birds remained in the wintering areas until at least late February. All four birds returned by mid-April to their nest sites used the previous year.

The areas occupied during the winter were pine-oak woodlands in contrast to the mixed conifer forest used during the summer. All wintering areas were below the level of persistent winter snow, which is approximately 1300 m in this part of the Sierra Nevada.

DISCUSSION

All findings from the study indicate that natural history patterns of the California spotted owl in the central Sierra Nevada differ significantly from those of the northern spotted owl in northwestern California and Oregon. The migratory movement is of special interest. It indicates a significant behavioral difference that may be linked to subspeciation. Migration also creates significant management complications because it takes owls from summer home ranges primarily in USDA Forest Service jurisdication to winter home ranges which are primarily in areas that are privately owned. In addition, the winter home ranges are in the elevational and geographical area that is growing faster in human population than any other area in California.

The migratory movement underscores the importance of multiple studies on a species in different geographical areas to determine the range of a species' behavior. It also points out the dangers of imposing a management plan for a species in a geographical region other than the one where the ecological data, on which the plan was based, was gathered. On the west slope of the Sierra Nevada, USDA Forest Service management plans designed to maintain breeding populations of spotted owls may not be adequate if the majority of the owls are dependent on winter habitats in the foothill zone, which is growing fast in human population. A much more complicated management effort involving USDA Forest Service, United States Department of the Interior Bureau of Land Management, California Department of Fish and Game, California Department of Forestry, county Boards of Supervisors, and the California State Legislature may be necessary to provide year-round habitat for the spotted owls. Factors such as fuelwood harvest, clearing woodland areas for cattle grazing, and subdivision of land for housing are all impacts on the foothill zone; these impacts will certainly become more serious in the future. This study has pointed out a previously unknown problem that makes the management of spotted owls in the Sierra Nevada a much more difficult task than previously thought. Whether management agencies can meet this challenge will be seen in the years ahead.

ACKNOWLEDGMENTS

This study was funded by USDA Forest Service, Pacific Southwest Forest and Range Experiment Station, Berkeley, California, under a cooperative agreement with the University of California at Berkeley, Department of Forestry and Resource Management, and a contract with California Department of Fish and Game. Special thanks must go to the 14 volunteers and near-volunteers without whom this study would not have been possible. Special mention goes to Janice A. Reid who contributed to all aspects of the project and to Regina1d H. Barrett who has provided equipment, encouragement, and counsel throughout the project.

LITERATURE CITED

Barrows, Cameron W. Feeding ecology of the spotted owl in California..Raptor Research. 14:73-77; 1980.

Barrows, Cameron W. Roost selection by spotted owls: an adaptation to heat stress. Condor. 83:302-309; 1981.

Brown, J. K. Handbook for inventorying downed woody material. Gen. Tech. Rep. INT-16. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 1974. 24 p.

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Distribution and biology of the spotted owl in Oregon. Wildlife Monograph. 87:1-67; 1984.

Marshall, Joe T., Jr. Food and habitat of the spotted owl. Condor. 44:66-67; 1942.

DISPERSAL DATA FOR JUVENILE SPOTTED OWLS: THE PROBLEM OF SMALL SAMPLE SIZE

Gary S. Miller and E. Charles Meslow

ABSTRACT: Collection and interpretation of dispersal data for juvenile northern spotted owls (Strix occidentalis caurina), based on preliminary information from Oregon, are discussed. Criteria for determining when dispersal ends and methods of measuring dispersal distances are examined. Small sample sizes, caused by unpredictable reproduction and high juvenile mortality, account for much of the problem in studying juvenile dispersal.

INTRODUCTION

Dispersal, on some scale, is an attribute of most animals. Dispersal and its patterns are basic to a species' life history strategy and affect nearly all aspects of a species' ecology and behavior (Horn 1983). Dispersal is the mechanism that brings about colonization of unoccupied areas and gene flow between populations. Dispersal has also been proposed as an important factor in population regulation (Lidicker 1962). While the importance of dispersal has been recognized for some time, the ability to obtain detailed dispersal information has been limited for most species.

Dispersal has been defined differently by various investigators. Howard (1960) defines it as "the movement the animal makes from its point of origin to the place where it reproduces or would have reproduced if it had survived and found a mate." Others simply define dispersal as the movement of an individual from its natal area to a new area or succession of areas (Greenwood 1980, Shields 1982). These later authors add, however, that successful dispersal requires the individual to reproduce following dispersal movements. We will distinguish between dispersal and successful dispersal.

GARY S. MILLER is a research assistant with the Cooperative Wildlife Research Unit, Oregon State University, Corvallis. E. CHARLES MESLOW is leader of the Cooperative Wildlife Research Unit, Oregon State University, Corvallis.

Information on avian dispersal has historically come from band returns or sightings of marked individuals (Erickson 1938, Gibb 1954, Johnston 1956, Kluijver 1951). Dispersal information, for owls in particular, has been gained from various banding studies (Houston 1978, Stuart 1952, Van Camp and Henny 1975), and although helpful in determining some aspects of dispersal, the information relies on band returns from the public and is therefore somewhat biased. Information on an individual's movements is not available, and locations where bands are recovered probably do not accurately portray the individual's total movements. Biases occur with the area the dispersing birds move through. In more populated areas, the chances are higher that a bird will be recovered or sighted. Bands as identification marks have also been used in retrapping efforts on specified study areas to determine dispersal between birthplace and breeding place (Newton and Marquiss 1983). Such studies use data both from band returns from the general public and from birds retrapped on the study areas. Studies with confined sampling areas provide an appraisal of juvenile dispersal that is biased toward short-distance dispersers.

A distinct improvement is provided by radio telemetry, which reduces much of the bias of band return studies by eliminating the reliance on a confined study area and band returns from the public. Radio telemetry has been used successfully for a number of years to study dispersal of mammals (Phillips et al. 1972, Shirer 1968; Storm and others 1976). Only recently has telemetry been employed to gather detailed dispersal information on birds.

We discuss some of the problems encountered when attempting to collect and interpret dispersal data gathered in Oregon from juvenile northern spotted owls (Strix occidentalis caurina). Actual data used are preliminary and represent primarily a single year's effort.

SPOTTED OWL DISPERSAL STUDY

Results from recent studies have shown that northern spotted owls depend on old-growth forests and are declining in numbers as these forests are harvested (Forsman and others 1984, Solis 1983). As the number of spotted owl pairs decreases and the habitat becomes more sparse, the chances increase for pairs or groups of pairs to become reproductively isolated. Isolated owls do not contribute to the maintenance of a diverse gene pool. The distance between adjacent pairs or groups of breeding owls must be such that dispersal and recruitment can replace losses (deaths or emigrations) among existing pairs and provide for colonization of suitable unoccupied habitats. A study of dispersal should help formulate better criteria for minimal spacing between pairs. Some limited work on juvenile dispersal of spotted owls has been reported from both Oregon and California (Forsman and others 1984, Solis 1983). There are studies currently underway in both California and Washington (see respectively, Gutiérrez and others 1985 and Allen and Brewer 1985), as well as our study in Oregon, to examine dispersal of juvenile spotted owls in more detail.

In spring 1982, a radio-telemetry study was initiated in Oregon to obtain dispersal information about the northern spotted- owl. Study areas (fig. 1) were in the western hemlock (Tsuga heterophylla [Raf.] Sarg.) zone of western Oregon, an area dominated by Douglas-fir (Pseudotsuga menziesii [Mirb.] France) and western hemlock - (Franklin and Dyrness 1973). Specific study sites within the western hemlock zone were necessarily determined by locations of nesting owls. Two broad regions were chosen (the Cascade and Coast Ranges), but specific study locations within these regions necessarily changed from year to year. Forests in the Cascades were less fragmented than were those in the Coast Ranges.

In addition to addressing appropriate interpair spacing, this dispersal study provided an opportunity to document other components of the species' life history, such as breeding frequency, nesting success, juvenile survivorship, and recruitment Mortality of juvenile spotted owls has been examined only briefly (Forsman and others 1984). Age at first breeding and rates of recruitment to the breeding population are unknown.

Collection of Dispersal Data

Life history characteristics of the spotted owl create many of the limits to the study of dispersal. For example, spotted owls lay relatively small clutches (l-3) and do not breed every year (Forsman and others 1984). As a result, researchers must work with small sample sizes of

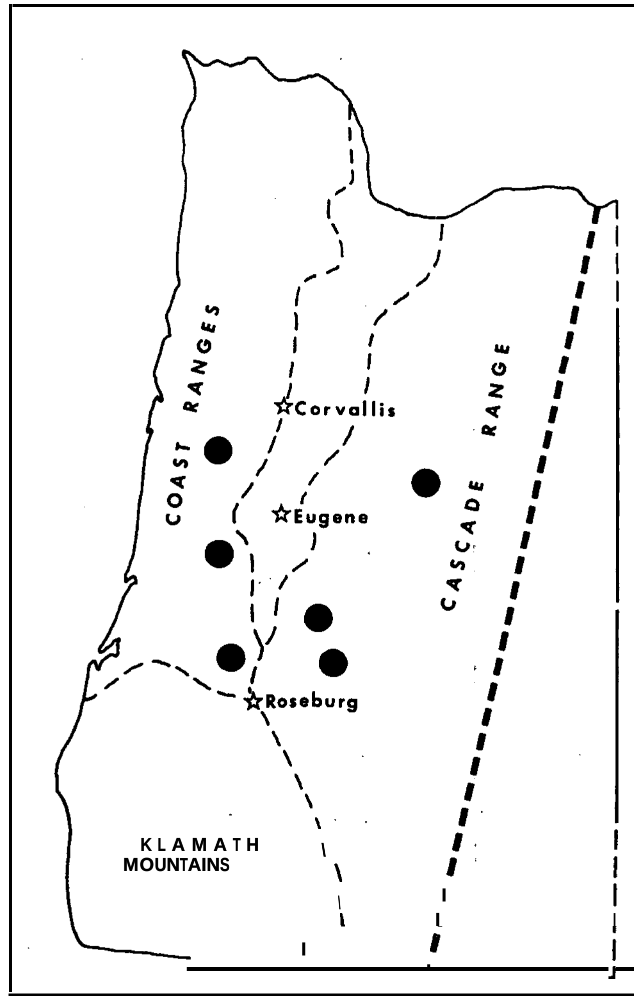


Figure l--Northern spotted owl study areas in western Oregon.

dispersers. In addition, substantial mortality occurs prior to dispersal (Forsman and others 1984), making it very difficult to follow significant numbers of dispersing juveniles. Forsman and others (1984) document the fate of 29 young between the time of fledging and the end of August; 19 survived the interval, yielding a mortality rate of 35 percent. We found mortality rates to be the same with a similar sample size for an equivalent time period. Use of radio transmitters also allowed documentation of mortality for almost an additional month up to the time of dispersal (young owls began dispersal between 7 September and 4 November). Mortality following fledging rose to about 45 percent for this total predispersal period.

Thus, with a mean of two young fledged per successful nest (Forsman and others 1984), coupled with the high predispersal mortality rate, an average of one successful nest per "useful" dispersing juvenile must be located. This is a formidable task, especially if study design dictates partitioning of the sample into various categories (for example, habitat fragmentation and stand ages). In 1983 we located 33 young that fledged from 19 successful nests. We relocated these young at least weekly until young were large enough to carry the transmitters. Twenty-five young were still alive at the time transmitters were put on (July-August) and 18 survived to disperse.

Mortality seems to continue at a relatively high rate during dispersal. Of the 18 juveniles that survived to disperse, only 3 were still alive the following May. Three other dispersers could not be located, status undetermined.

When radio signals for dispersing juvenile owls were lost, extensive aerial searches were initiated to relocate them. If relocation was unsuccessful, we could not establish with certainty whether the owls dispersed beyond the range of the aerial searches (unlikely) or if their transmitters failed. Radio failure, although uncommon, does occur. When a radio-marked disperser disappeared, for whatever reason, we faced a dilemma: how to employ dispersal data for such individuals up to the time of disappearance. The conservative approach was to eliminate from the sample of dispersers any owls that could not be accounted for (disappear). Data gathered from such individuals could be incorporated into any summary of dispersal so long as the bird was located throughout the period examined. Also, because such owls were not necessarily dead, they could not be incorporated into most mortality calculations except under similar time constraints. The value of all data acquired on any individual that eventually "disappeared" was greatly diminished because there was no documented end point--successful dispersal or death.

3

Short-term studies amplify the impact of the above life history attributes. When trying to examine dispersal in a quantitative rather than qualitative way, the small sample size limits the significance of any statistical differences.

MEASURING DISPERSAL

End of Dispersal

Because of biological, logistic, and budgetary limitations, projected sample sizes for a study of owls will be small: An annual goal, for a 3-person field team, of 20-25 dispersing juveniles is realistic. If the level of mortality we observed is typical, few successful dispersers will be documented. If an adequate number of successful dispersers is not available, then criteria must be set to evaluate the level of resolution of dispersal at hand. Various levels of defining when dispersal ends can be adopted. Of these, the most restrictive definition that the data will permit should be selected. The following are examples in decreasing order of resolution: (1) owl is paired, breeds, and fledges one or more young; (2) owl is paired during the breeding season; (3) owl is settled in a definable area (3 months or longer) during the breeding season; (4) owl is settled in a definable area (3 months or longer) during the nonbreeding season; and (5) owl disperses but dies before it has settled for 3 months.

In our study there are no juveniles in the first two categories. Three juveniles fall into category 3, two into category 4, and eleven into category 5. As is evident from the data, it will take several years of field study to obtain any sort of sample size in the first two categories. Thus, it may be necessary to adopt a less restrictive definition of dispersal in order to have a reasonable sample to work with and to base management recommendations on. Both researchers and forest managers need to recognize these limitations and jointly participate in deciding the level of resolution acceptable for management decisions.

Measuring Dispersal Distances

How to effectively measure dispersal distances or to express dispersal depends on which role of dispersal is examined. One role of dispersal is as the mechanism that brings about gene flow. Although all movements between birth site and breeding site are important, as they contribute to survival or lack thereof, only straight-line distances between these sites measure dispersal as it contributes to gene flow. In our study, juveniles have moved up to 76.8 km (straight-line distance) from their birth site. But survival of such long-distance dispersers has been low. Dispersal, as it relates to gene flow, is functional only if the owl survives to breed. The appropriate measure is the straight-line distance between birth site and breeding site.

The other role of dispersal is the colonization of vacant habitats. To determine encounter rates of potentially vacant habitats by dispersing juveniles, total distance moved between birth site and breeding site (summation of day-to-day movements) are more appropriate than the straight-line distance. If daily movements are determined, these could be related to the type of habitats encountered. Consideration of daily movements allows other important characteristics of dispersal to be documented as well. Patterns of dispersal, such as the use or nonuse of major drainage systems, can only be plotted through the total movements of the juvenile.

Effective dispersal distance--Other researchers have expressed dispersal distances in terms of the number of home ranges moved across (Greenwood and others 1979; Shields 1982). Shields (1982) states that "dispersal distances are normally reported as population averages of the absolute distances individual propagules move. This erroneously implies that dispersal is a continuous phenomenon, ignoring the contributions of normal individual spacing to dispersal." The individual spacing that effects dispersal can be estimated from the size of the home range. Effective dispersal distance is the median dispersal distance divided by the average diameter of the area occupied exclusively by sedentary individuals (that is, home range diameters). It is a term describing dispersal in relation to home range size (Greenwood 1980, Shields 1982). Effective dispersal distance thus does not provide a measurement of distance but rather provides an index of population with respect to other populations or

Table l--Median and mean straight-line distances moved by spotted owls in west central Oregon (from natal area to death or settling)

Categories	Sample Size	Dispersal Distances		
		Median	Mean	Minimum-maximum
		-------------Kilometers-------------		
Successful dispersers (fledged 1 or more young)	0	--	--	
Owl is paired (breeding season)	0	--	--	
Owl is settled (breeding season)	3	10.8	26.3	(4.8-57.9)
Owl is settled (nonbreeding season)	2	-	17.8	(14.8-20.8)
Owl disperses but dies before settling	11	24.0	33.4	(4.8-76.8)

species. Studies employing effective dispersal distances have dealt with a more homogeneous environment without the large gaps between pairs of birds that are typical of the spotted owl. The fragmented environment of the spotted owl does not lend itself to expressing dispersal distance in this manner.

Mean vs. median dispersal distances--When straight-line distances are used to express dispersal, should they be averaged? Shields (1982) points out that by averaging the distances, the few long-distance dispersers inflate the mean dispersal distance. This leads to an overestimation of the distance the typical individual moves. He suggests using the median dispersal distance instead. Using our 1983 sample, we calculated both mean and median dispersal distances (table 1) for the categories discussed in determining when dispersal ends. Median dispersal distances were substantially less than the mean, and we feel the median better represented the typical individual's movements.

Dispersal-Related Questions

Other dispersal-related questions requiring attention include differential dispersal by sex, population density effects on dispersal distances and success, initiating and terminating factors for dispersal, and yearly variation in dispersal. In a short-term study, some of these questions cannot be adequately addressed. For the spotted owl in particular, an especially important question might be "what effect does fragmentation of the habitat have on dispersal and the foraging behavior, habitat use, and survival of dispersers?" One of the main problems with determining fragmentation effects is devising an appropriate measure of fragmentation. Work with habitat fragmentation presents the investigator with all the problems associated with an uncontrolled experiment: The various arrays of fragmentation were not designed.

If active nests are located in a variety of fragmented regimes, a control area should exist that has little or no fragmentation. Spotted owl movement capabilities seem, unfortunately, to be great enough to thwart any attempt to utilize existing landscape patterns, even national parks or wilderness areas. Dispersing juveniles are likely to pass through several levels of habitat fragmentation, thereby frustrating attempts to differentiate which fragmentation pattern has what effect.

Many investigators have documented that for most birds, females predominate among long-distance dispersers. To test whether or not this is also the case for the spotted owl, one must be able to correctly identify the sex of juveniles. Criteria used in the past to identify the sex of juvenile spotted owls (weight and wing measurements) are not particularly reliable. In a recent paper, Barrows and others (1982) suggest determining sex of spotted owls by inspection of the barring pattern on the middle tail feathers. Of 11 carcasses for which we were able to check tail feathers against an internal examination, the pattern of tail feathers correctly identified the sex of the juvenile in each case. The success of this technique should help answer the differential-dispersal-by-sex question for the spotted owl.

SUMMARY

The problems presented here are not new and are common to any study of dispersal. The spotted owl, because of its low density, sporadic reproduction, and small clutch sixes, presents a significant problem to dispersal studies --small sample size or high cost per unit of data.

The acceptable resolution level of dispersal and measurement of dispersal distances are closely tied to sample size. With a limited sample, it may not be possible to focus only on the successful dispersers. The longer the issue is studied on a continuous basis, the more the above-mentioned problem will be alleviated.

Especially in short-term studies, the major question becomes how much information is enough. There must be a consensus among researchers and managing agencies, such as the State and Federal fish and wildlife agencies, USDA Forest Service, and the Bureau of Land Management, as to what constitutes an acceptable data set to base management decisions on. The agencies that will employ the information are necessarily responsible for determining the longevity of the studies and the size of the sample.

ACKNOWLEDGMENTS

Robert Anthony, Ruth Brandt, Andrew Carey, Eric Forsman, and R. J. Gutiérres reviewed various drafts. Paul Opler, U.S. Fish and Wildlife Service, provided a constructive review as well. Their comments added greatly to the manuscript. This study was conducted under the auspices of the Oregon Cooperative Wildlife Research Unit with Oregon State University, Oregon Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and the Wildlife Management Institute cooperating. Funding for this research was provided by the Old-Growth Forest Wildlife Habitat Program, USDA Forest Service, Pacific Northwest Forest and Range Experiment Station, Contribution No. 26. This is Oregon State University Agricultural Experiment Station Technical Paper 7264.

LITERATURE CITED

Allen, H.; Brewer, L.W. A review of current northern spotted owl (Strix occidentalis caurina) research in Washington State. In: Gutiérrez. Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 55-57.

Barrows, C.W.; Bloom, P.H.; Collins, C.T. Sexual differences in the tail barring of spotted owls. North American Bird Bander. 7: 138-139; 1982.

Erickson, M.M. Territory, annual cycle, and numbers in a population of wren-tits (Chamaea fasciata). University Calififornia Publication Zoology. 42: 247-334; 1938.

Forsman, E.D.; Meslow, E.C.; Wight, H.M. Distribution and biology of the spotted owl in Oregon. Wildlife Monograph. 87; 1984. 64 p.

Franklin, J.F.; C.T. Dyrness. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1973. 417 p.

Gibb, J. Population changes in titmice, 1947-1951. Bird Study. 1: 40-48; 1954.

Greenwood, P.J. Mating systems, philopatry, and dispersal in birds and mammals. Animal Behavior. 28: 1140-1162; 1980.

Greenwood, P.J.; Harvey, P.H.; Perrins, C.M. The role of dispersal in the great tit (Parus major): the causes, consequences and heritability of natal dispersal. Journal of Animal Ecology. 48: 123-142; 1979.

Gutiérres R.J.; Franklin, Alan B.; LaHaye, William; Meretsky, Vicky J.; Ward, J. Patrick. Juvenile spotted owl dispersal in northwestern California: preliminary results. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 60-65.

Horn, H.S. Some theories about dispersal. In: Swingland, I.R.; Greenwood, P.J., eds. The ecology of animal movement. Oxford University Press; 1983. 54-59.

Houston, C.S. Recoveries of Saskatchewan-banded great horned owls. Canadian Field-Naturalist. 92: 61-66; 1978.

Howard, W.E. Innate and environmental dispersal of individual vertebrates. American Midland Naturalist. 63: 152-161; 1960.

Johnston, R.F. Population structure in salt marsh song sparrows. Part 1. Environment and annual cycle. Condor. 58: 24-44; 1956.

KLuijver, H.N. The population ecology of the great tit, Parus m.major L. Ardea. 39: 1-135; 1951.

Lidicker, W.Z. Emigration as a possible mechanism permitting the regulation of population below carrying capacity. American Naturalist. 96: 29-33; 1962.

Newton, I.; Marquiss, M. Dispersal of sparrowhawks between birthplace and breeding place. Journal of Animal Ecology. 52: 463-477; 1983.

Phillips, R.L.; Andrews, R.D.; Storm, G.L.; Bishop, R.A. Dispersal and mortality of red foxes. Journal of Wildlife Management. 36: 237-248; 1972.

Shields, W.M. Philopatry, inbreeding and the evolution of sex. Albany, NY: State University of New York Press; 1982. 245 p.

Shirer, H.W.; Downhower, J.F. Radio tracking of dispersing yellow bellied marmots. Transactions of the Kansas Academy of Science. 71: 463-479; 1968.

Solis, D.M. Summer habitat ecology of the northern spotted owl. Arcata, CA: Humboldt State University; 1983. M.S. thesis. 168 p.

Storm, G.L; Andrews, R.D.; Phillips, R.L.; Bishop, R.A.; Sinoff, D.B.; Tester, J.R. Morphology, reproduction, dispersal, and mortality of midwestern red fox populations. Wildlife Monograph. 49; 1976. 82 p.

Stuart, P.A. Dispersal, breeding behavior, and longevity of banded barn owls in North America. Auk. 69: 227-245; 1952.

VanCamp, L.F.; Henny, C.J. The screech owl: its life history and population ecology in northern Ohio. North American Fauna No. 71; 1975. 65 p.

THE DEMOGRAPHY AND POPULATION GENETICS OF OWLS, WITH SPECIAL REFERENCE TO THE CONSERVATION OF THE SPOTTED OWL (*Strix occidentalis*)

George F. Barrowclough and Sadie L. Coats

ABSTRACT: Data are summarized on the density, dispersal, demography, and genetic structure of several species of owls. Life history traits for the majority of these species are such that the effects of variance in reproductive success and overlapping generations act to reduce effective population size with respect to census size by as much as 50 percent. Estimates of effective deme sizes vary over several orders of magnitude; for four of six species, the effective sizes are on the order of 10^2 to 10^3. The genetic structure of spotted owl, *Strix occidentalis*, populations in the Pacific Northwest consists of a continuum of neighborhoods isolated by distance from each other. We estimate that currently there are approximately 10 such units, each composed of about 220 effective individuals, in the range of the subspecies *caurina*. A management plan to preserve the species in that region will result in the preservation of a network of habitat patches. The effects such a plan will have on genetic structure and level of inbreeding depend critically on the level of occupancy of the preserved areas. Estimates of this occupancy rate are not available, but a method is outlined to evaluate genetic structure given such estimates or a model of population dynamics. A "best case" example is given along with some recommendations for data that are critically needed for evaluating the actual effects of a spotted owl management plan.

INTRODUCTION

The purpose of this paper is to describe and analyze, to the extent possible, the patterns of demography and population genetics of owls. Special emphasis is placed on the spotted owl, *Strix occidentalis*, a subject of current interest because of concern about the species' status in old-growth forests of the Pacific Northwest.

GEORGE F. BARROWCLOUGH is Assistant Curator and SADIE L. COATS is Associate in the Department of Ornithology of the American Museum of Natural History, New York, N. Y.

It appears likely that much of the old-growth forest that constitutes the prime habitat for the spotted owl will be regularly harvested for timber; thus, the survival of the bird in this part of its range may depend on the maintenance of Spotted Owl Management Areas (SOMAs) in the National Forests of the region. The efficacy of these habitat patches as a mechanism for preserving the spotted owl in the Pacific Northwest will depend not only on the number, size, geographical location and quality of these areas, but also on the demographics (survivorship, fecundity, and dispersal schedules) and genetics of the species (Shaffer 1981). These aspects of the biology of a species can be analyzed using the techniques of population ecology and population genetics. Population ecologists can aid wildlife managers by investigating the way a species' demography, dispersal patterns, and geographic distribution may interact with environmental factors and ecological perturbations. Models can then be developed for predicting long-term probability of survival. Shaffer (1985) addresses these issues. Geneticists use these same variables and the equations of population genetics to investigate the genetic structure and likely pattern of inbreeding in the population. We address that topic here.

It is widely understood that inbreeding can be detrimental. It can lead to reduced numbers of offspring, poorer quality offspring, and a generally reduced vigor of the individuals in a population. These effects are discussed in Frankel and Soulé (1981). A general conclusion of such analyses is that inbreeding, if severe, can lead to inviability of a population and to its eventual extinction. Hence, an important goal of any attempt to maintain a natural population through management must be the monitoring and regulation of inbreeding.

The extent of inbreeding in a. population can be measured directly--for instance -by using molecular genetics techniques such as. electrophoresis (for example, Patton and Feder 1981); however, these methods only yield estimates of the current level of inbreeding. To predict how inbreeding will progress, a model of the genetic structure of the population must be developed. By genetic structure, we refer to the geographic continuity of populations--over what geographic area a population can be considered randomly mating, and how many individuals can be found in that area. The models used to develop guidelines, such as preserving 50 individuals to prevent inbreeding in excess of 1 percent per generation (Frankel and Soulé 1981), are based on the assumption of no geographical structure; that is, on complete panmixia of the population. Such an assumption is reasonable for zoos, but not necessarily for a wild population spread over large expanses of a continent.

Researchers concerned with the population dynamic aspects of conservation have explicitly examined the role of geography on the probability of long-term maintenance of a population (see, for example, Shaffer 1985). However, population geneticists concerned with conservation genetics have not devoted equivalent attention to this problem. In this study we begin a first attempt to incorporate this important biological reality into conservation genetic analysis.

Much remains to be learned about the natural and life histories of owls,. including the spotted owl. In spite of this lack of complete data, however, management plans are now being developed. To assess whether any particular proposed Spotted Owl Management Plan (SOMP) will be successful over some extended period of time, it is necessary to predict the response of the owls to the details of the plan. This necessitates the rapid development of models for the population dynamics and genetics of spotted owls. Thus, it seems requisite to beqin organizing our knowledge of owl demographics and genetics now, even though data are limited. Data from future studies, as well as from projects currently underway, will no doubt refine estimates of parameters and lead to some modifications of results and conclusions; nevertheless, it is equally true that the simple, preliminary results of these analyses and models will identify key life history parameters that require immediate intensive investigation.

Finally, we believe it is important to summarize inferences that currently can be made about the demography and genetics of owls in general and to make these data available to the community of researchers interested in the dynamics and genetics of natural populations.

METHODS AND RESULTS

Our analysis of the demographics of owls requires the estimation of population density and the distributions of three life history parameters--survivorship, fecundity, and dispersal. From these data, a life table can be constructed; such a table is essential for most approaches to modeling population dynamics. These same data are needed for modeling the genetic structure of a population.

Several models of geographic population structure may be relevant to avian species. The various models and instances of their use in studies of birds have been reviewed by Barrowclough (1980) and Rockwell and Barrowclough (in press). A basic distinction must be made between species that are geographically isolated in colonies or "islands" of habitat, and those that are more or less continuously distributed throughout their range. For the spotted owl, as well as for most other owls, the latter model appears to be more reasonable. For such cases, even though the species' distribution is considered continuous, there is expected to be some genetic differentiation across the range simply because dispersal of young birds, from their natal site to the location where they breed as adults, is finite. Depending on the strength of the tendency for offspring to nest in the vicinity of the site where they were raised (philopatry), it may take several, or even many, generations for genes to "flow" across the range of the species. Continuously distributed populations of birds are therefore said. to be "isolated by distance." The genetic structure of such species is modeled by determining the geographical area over which allelic frequencies should be nearly uniform--this requires information about dispersal--and estimating the number of birds in such an area--which requires estimates of density. The "effective population size" (N_e) of this area of the total species' range is derived by estimating how such factors as population fluctuations, sex ratio, and life expectancy and fecundity schedules affect the dynamics of genes within the local population.

The effective population size of the local unit (deme) is the number of genetically ideal (randomly mating, discrete generations, Poisson variance of offspring numbers, etc.) individuals that would have evolutionary properties equivalent to those of the actual individuals in the deme with their real, biologically complicated demographic schedules. Once the theoretical effective size of a deme of continuously distributed organisms is known, it is possible to make some predictions about the extent of inbreeding in the population.

The estimation of the genetic structure of natural populations using demographic data, as with any complicated modeling approach, is based on a 'number of biological and mathematical assumptions. These assumptions are discussed in some detail in Rockwell and Barrowclough (in press).

Calculations. The specific method used to obtain statistics describing. the genetic structure of spotted owl populations originated with Dobzhansky and Wright (1943, 1947), who worked on Drosophila. The method subsequently was modified for use on avian populations by Barrowclough (1980). We estimate the effective size, N_e, of current spotted owl demes as the number of randomly mating individuals equivalent to the number of owls actually present in a circle with a radius twice the dispersal distance of juveniles. In summary:

$$N_e = 4 \pi p\, s^2 F_R F_{RS} F_{GT} \;;$$

where p is the density of spotted owls throughout the area over which dispersal occurs, σ is the root-mean-square dispersal distance for juveniles, and F_{RS} and F_{GT} are factors that correct for departures from the random transmission of genes from generation to generation caused by the effects of variation among pairs in reproductive success, and the influence of overlapping generations, respectively. F_K corrects the geographical size of the deme for the effects of non-normality of the dispersal distribution.

A. Dispersal.--Spotted owls are nocturnal and difficult to study; consequently, quantitative data for the species are just starting to be accumulated, and we were forced to use data and estimates of life history parameters from a number of different sources. Data resulting from radio-tracking juvenile and adult spotted owls in northern California for several (Gutiérrez and others 1985, unpubl. data 1/), allow estimation of the dispersal distribution of juveniles and information on survivorship of both juvenile and adult spotted owls.

Table 1--Summary of dispersal distances of juvenile spotted owls, based on radio-tagging within northwestern California

Distance, d_i (km)	0-25	26-50	51-75	76-100
Number, n	3	6	3	1

If the distances juveniles moved (between the sites where they were hatched and where they breed as adults) were random with respect to direction and normally distributed with respect to distance, then approximately 87 percent of all genes at a particular point would come from within two standard deviations of the distribution of dispersal distances from that point. Thus, a standard measure of N_e for continuously distributed organisms is the effective size of the population within a circle of radius 2 σ (Wright 1969). The root-mean-square dispersal distance, σ, is the standard deviation of juvenile dispersal distances about their nest site (origin); σ^2 is the variance of such distances. Dobzhansky and Wright (1947) showed that:

$$s = \sqrt{[(1/2N) \Sigma d^{2/1}]}:$$

where N is the total number of juvenile owls studied and d_i is the distance dispersed by the i^{th} juvenile. For the study by Gutiérrez and others (1985), the distribution of juvenile dispersal distances is summarized in table 1. σ, computed as described above, was found to be 33.56 km for the 13 radio-tagged juveniles. These data may somewhat underestimate true dispersal distances because some of the owls in the study may have died before finishing their dispersal; additionally, the batteries in some of the transmitters may have failed before dispersal was ended. More dispersal data are needed; at present these are the best data available and suggest that actual dispersal is roughly 30-40 km. It would be desirable to have dispersal distances based on a large sample of birds followed from their birth site to their actual breeding site.

B. Density.--To obtain a realistic estimate of effective deme size, one should have an estimate of density from the same region from. which the dispersal distance data were obtained. This is because there is the possibility that density and dispersal may covary. That is, dispersing birds may tend to move further in areas of low density (poor habitat). Data on the density of spotted owls in northern California where the radio-tagging is being performed were obtained. 2/

1/ Data on file with R. J. Gutiérrez, Department of Wildlife Management, Humboldt State University, Arcata, CA 95521.

2/ Data compiled by G. I. Gould, Jr., Wildlife Management Branch, Department of Fish and Game, 1416 Ninth St., Sacramento, CA 95814.

There are approximately 558 territories in the area bounded by the Pacific Ocean on the west, the Oregon border on the north, the northern border of Mendocino County on the south, and a line on the east running north-south through the town of Yreka. It was estimated that 90 percent of the 558 territories were occupied by pairs of owls and the remaining 10 percent by single birds: in 28,990 km^2 of northern, coastal California, there are about 1060 owls, or an approximate density of 0.037 owls per km^2. This estimate is of average density over good, poor, and completely unsuitable habitat. It is necessary to use this estimate rather than one for strictly good habitat because the dispersal of juveniles takes them through mixes of habitat types, and the geographical area occupied by a single deme of spotted owls will include unsuitable habitat.

C. Life table.--A life table *is* perhaps the most important abstraction required in modeling the population dynamics of a species. It is also needed for modeling population genetics because it provides the information requisite for estimating the effects of delayed breeding and overlapping generations. There are two critical aspects to the estimation of a life table: data are needed on year-to-year survivorship and on fecundity.

1. Survivorship.--Survivorship was estimated using the results of the radio-tagging undertaken by Forsman and others (1984) and by Gutiérrez and others (1985). First, for adult spotted owls, it was noted that there were five deaths in 33 owl years of monitoring; this is based on 20 owls that were tracked for periods of 1 to 3 years and six others that were tracked for periods of roughly 4 months. Thus, year-to-year survivorship was approximately 0.85. We assumed that avian lifespans are exponentially distributed (for example, Deevey 1947); survivorship was therefore assumed to be constant for the second year of life on.

Survivorship of juveniles was more difficult to estimate. We again used data from radio-tracking of juveniles in northwestern California. Because of the short timespan over which owls have been tagged, and the high mortality rate, we estimated survivorship separately for each 3-month period of the first year, beginning at the time of fledging. For the first 3 months, 3 out of 13 tagged birds died: this is a period of time when the juveniles are still partially dependent on their parents for food. Survivorship (s_x) during this interval was estimated as 10/13, or 0.77. During the next 3-month period, when dispersal occurs and winter begins, 4 of 10 tagged birds died: thus, we took s_x to be 8.60. For the winter months, 3 of 6 birds apparently died: consequently, s_x was assumed to be 0.50. No data were available for the last 3 months of the first year of life. During this period of time, spring, prey should become abundant; hence we estimated that the probability of death would be of the order of one-half the rate during the previous 9 months. The average death rate, per 3-month period over the first 9 months, was 0.38; the average s_x over this period was 0.62. Thus, for the last 3-month period, we estimated the death rate to be 0.19; this yields an s_x of 0.81. Consequently, we estimate first year survivorship of spotted owls as (0.77)(0.60)(0.50)(0.81) or 0.19. This estimate has an unknown, but probably substantial, standard error associated with it; it is likely that only about one out of five to one out of ten fledged spotted owls survive their first year.

Table 2--Distribution of reproductive success among pairs of spotted owls

No. of fledglings (x)	0	1	2	3	4
No. of pairs (p)	73	16	26	4	0

Source: Forsman and others (19841.

2. Fecundity.--We estimated a mean and a variance of fecundity using the data reported by Forsman and others (1984), which was based on their study of the spotted owl in Oregon. We measured fecundity as the number of fledged, or nearly fledged, offspring observed at a nest. This measure of fecundity conforms to the survivorship period of the life table, which starts at the time of fledging. The numbers of offspring produced by 119 pairs are shown in table 2; a total of 80 young were produced. Thus, each pair produced an average of 0.67 offspring per year. If a 1:l sex ratio is assumed, then this is equivalent to 0.34 female offspring per female per year. The variance of reproductive success among pairs, computed from the same distribution of fecundities, is:

$$^{V}RS = [\,\Sigma px^2 - (\Sigma\ px)^2/N] = (N-l) = 0.87;$$

where x is the number of fledglings produced by a pair, p is the number of pairs producing that number of fledglings, and N is the total number of nests observed. We assume spotted owls do not breed their first or second spring: this is generally consistent with life history studies and other, anecdotal information in the literature. It is probably true that some 2-year-olds attempt to breed: also, however, probably not all 3-year-olds do: further study of radio-tagged, known-age birds is warranted.

We stress that the life table for the spotted owl, based on these calculations (table 3), must not be taken as definitive, given the uncertainty associated with much of the data. Nevertheless, it should prove useful as a first approximation in initiating analyses of the dynamics and genetics of the species.

D. Generation time.-- Age-structure will influence the effective size of a local population. For example, Dobzhansky and Wright (1943) explicitly discuss this problem, and human demographers have devoted much effort to analyses of the magnitude of the effect (for example, Emigh and Pollack 1979). Emigh and Pollack present an algebraic method for

Table 3--Life table for the spotted owl: fecundity is measured as number of female offspring per female

Age (x)	0	1	2	3	4	5	6	7	8	9	10
Survivorship (s_x)	1.00	0.19	0.85	0.85	0.85	0.85	0.85	0.85	0.85	0.85	0.85
Fecundity (b_x)	0	0	0	0.34	0.34	0.34	0.34	0.34	0.34	0.34	0.34

correcting estimates of effective population size for the effects of age-structure, delayed breeding, and overlapping generations.

We have used the life table for spotted owls (table 3) as input to a computer program that calculates the magnitude of this effect. The result is a factor, ^{F}GT, that represents the ratio between effective size and the census number of individuals. For the spotted owl, the result is ^{F}GT = 0.69. The fraction, for this life table, is considerably less than one, indicating an important effect. This is because we have assumed that the density figures are for territorial, but not necessarily breeding, birds; that is, some 1- and 2-year-old birds are present in the population, respond to calling (and so are included in the density estimates), but do not breed. The ^{F}GT factor corrects for the fact that the census density includes prereproductives, and consequently is greater than the number of individuals contributing to the gene pool at any given time. In theory this factor can vary from zero to two; if only reproducing individuals were included in the density figures, then ^{F}GT for this life table would be close to one.

E. <u>Variance in reproductive success</u>.--An underlying assumption of estimates of effective population size is that the variation in reproductive success among pairs of individuals has a Poisson distribution; that is, that the variance of the distribution is equal to its mean. This is an empirical question, however, and it appears that in a number of species, at least of birds, the variance exceeds the mean. Such is the case for the spotted owl, in which our estimate of the mean fecundity is 0.67, and its variance is 0.87 (see above). Again, as with the problem of age-structure, it is possible to compute a correction factor to estimate the effective size of a population with a given distribution of fecundities. The formula is given by Crow and Kimura (1970): the ratio of effective to actual number of individuals is computed as:

$$^F\mathrm{RS} = x/[x-1+(^V\mathrm{RS}/x)];$$

where x is the mean number of fledglings per pair, and ^{V}RS is its variance. For the spotted owl, x is 0.67, ^{V}RS is 0.87, and ^{F}RS is 0.69.

F. <u>Kurtosis of dispersal</u>.--An additional assumption that requires attention in the computation of effective deme size is that of a normal distribution of juvenile dispersal distances. In fact, as Bateman (1951) points out, dispersal distance distributions depart to some degree from normal in almost all organisms. (Distributions may be characterized as leptokurtic or platykurtic. In a leptokurtic distribution, there are more short- and long-distance dispersers and fewer intermediate-distance dispersers -than would be expected in a normal distribution. In a platykurtic distribution there are an excessive number of intermediate-distance dispersers over the expectation of a normal distribution, but fewer short- and long-distance dispersers.) The distribution of dispersal distances for the spotted owl (table 1) is slightly platykurtic, with a coefficient of kurtosis of -1.07. Using the above estimate of kurtosis, we estimate a deme of owls, due to this departure from normal dispersal of juveniles, actually occupies an area slightly smaller than the circle of radius 2 σ. The actual size of this area is reflected in the kurtosis factor, ^{F}K, computed using the relationship developed by Wright (1969, p. 304-305). For the spotted owl, we obtain an estimate of ^{F}K of 0.81.

G. <u>Effective deme size</u>.--Given the results of the above analyses, it is possible to compute an estimate of effective population size of a deme or neighborhood using the formula presented earlier:

$$N_e = 4\,\pi\,\sigma\,{}^F\mathrm{K}\ {}^F\mathrm{RS}\ {}^F\mathrm{GT}.$$

Thus,

$$N_e = 4\,\Pi\,(0.04\mathrm{km}^{-2})(33.56\mathrm{km})^2(0.81)(0.69)(0.69) = 218.23.$$

This is an estimate of the effective size of local populations of spotted owls under current conditions.

An additional point is worth noting. ^{F}RS was defined as the ratio of effective size to census size that corrected for the effect of a nonrandom (non-Poisson) contribution of genes from individuals of one generation to the next because of variance among individuals in reproductive success. ^{F}GT was defined as the ratio of effective size to census size that corrected for the fact that generations are not discrete and that prereproductive owls are included in estimates of density. Consequently, the overall ratio of genetical effective population size to census number for spotted owls must be the product of ^{F}RS and ^{F}GT, or 0.48. This implies that to have an effective population size of any particular number of spotted owls, it is necessary to have a census number of

Table 4--Estimates of density for several species of owls

Species	p (km^{-2})	Reference
Tyto alba	0.08	Sharrock (1976)
Otus asio	0.30	Craighead and Craighead (1969)
Bubo bubo	0.01	Olsson (1979)
B. virginianus	0.15	Craighead and Craighead (1969)
Strix aluco	0.40	Sharrock (1976)

adults l/0.48, or 2.10, times as large. For example, an effective population of 500 owls would require a census number of 1,042 owls.

The fact that the effective size of populations is usually substantially less than the census size has now become widely recognized by geneticists and wildlife managers [Frankel and Soule 1981). Thus, the result reported above should not be particularly surprising. Two additional factors with potential effects on this same ratio have not been considered here, but should be kept in mind. First, we have implicitly assumed a 1:1 sex ratio for breeders. If the sex ratio differs from this, then effective size will decrease further. Second, we have assumed that the owl populations are numerically constant and do not fluctuate. If they do fluctuate, about some mean, then the overall N_e to N_c ratio will again be reduced and will be biased toward the minimum size (for example, Crow and Kimura 1970, p. 109-110).

H. Genetic structure and inbreeding.--Inbreeding is a complex, hierarchical topic. The general, underlying concept concerns the correlation of individual alleles within individuals. That is, in diploid organisms, such as birds, each individual has two copies of each gene. If more than a single allele segregates at a locus in the species, then the probability that the two genes in an individual will be identical can be computed, for a randomly mating population, based on the frequencies of the alleles. If there are departures from random mating, however, then the probability of the two copies of the gene being identical may increase and the individual is said to be inbred; that is, there is a positive correlation of identity of the two copies of a gene within an individual. The departures from random mating may be of two types. First, there may be an increased likelihood of close relatives mating: this is the notion of inbreeding in common usage. It is sometimes identified by the symbol F_{is}. Second, if the entire population of the species is not panmictic, but rather is organized into isolated colonies or even more or less continuously distributed neighborhoods (demes), then the copies of the same gene in an individual will be correlated merely due to the geographic structure of the population inhibiting the thorough mixing of genotypes in each generation. Here we refer to the magnitude of this effect by the symbol F_{st}.

Our computations suggest that the genetic structure of spotted owl populations in the Pacific Northwest is characterized by neighborhoods of approximate effective size of 220 individuals. These demes are not discrete entities, but continuously grade into each other; they each occupy a geographical area of diameter $4\sigma\sqrt{FK}$, or approximately 120 km. Thus, in the range of the subspecies *S. o. caurina* in Washington, Oregon, and California, there are probably on the order of 10 demes. This is a very rough approximation based on geographical distance and area. It is consistent with a current total census population of about 5,000, and a total effective size, summed over demes, of about 2,500. These estimates are probably correct to within a factor of two or so, and will be sufficient for illustrative calculations.

Wright (1969, p. 299-303: see also Rockwell and Barrowclough in press) provides a method for estimating levels of correlation of genes within demes (F_{st} inbreeding) that are isolated by distance, relative to the total population. For a series of 10 demes each of size 220, F_{st} is estimated to be about 0.007.

DEMOGRAPHY AND GENETICS OF SELECTED SPECIES OF OWLS

We examined literature on life history, ecology, and behavior of birds to obtain comparative results for other species of owls. This survey was made partly to ascertain whether our estimates of spotted owl parameters were reasonable, but also to explore the demography and genetics of a number of species of an avian order and make the results available to ornithologists and population ecologists.

We found sufficient data to compute estimates of life tables and effective deme sizes for five additional species of owls: *Tyto alba*, *Otus asio*, *Bubo virginianus*, *B. bubo*, and *Strix aluco*. Of necessity, data from more than one study had to be combined in the analysis of some of these species. Where possible, data used for a species were all from the same geographic region. Data for *Tyto alba*, the barn owl, are from England, except for fecundity and survivorship values which come from studies in the United States. Data for *Otus asio*, the eastern screech-owl, come from northern Ohio and southern Michigan. Data for *Bubo bubo*, the Old World eagle owl, derive from studies in southeastern Sweden, and Germany and adjacent northern Austria. Density figures for *Bubo virginianus*, the great horned owl, come from southern Michigan; the data for productivity, dispersal, and survivorship are from birds breeding in Saskatchewan. All data for *Strix aluco*, the tawny owl, are from near Oxford,

Table 5--Distribution of dispersal distances for selected species of owls

Species		Distance and number dispersing [1]								Reference
Tyto alba	x	5	30	75	150	250				Bunn and others (1982)
	f(x)	98	68	9	8	1				
Otus asio	x	8	24	40	56	105	185	233	298	Van Camp and Henny (1975)
	f(x)	25	21	3	2	1	1	1	1	
Bubo bubo	x	25	50	75						Olsson (1979)
	f(x)	8	5	3						
B. virginianus	x	5	26	81	185	315	710	908	1062	Houston (1978)
	f(x)	18	17	23	11	3	4	3	2	
Strix aluco	x	0.7	1.5	3.5	7.2	20				Southern (1970)
	f(x)	3	1	2	1	2				

[1] f(x) is the number of individuals banded as nestlings and recovered, when old enough to breed or hold a territory, x kilometers from their nestsite.

Table 6--Mean and variance of reproductive success among pairs in selected species of owls

Species	Number of young fledged per pair									Reference
	0	1	2	3	4	5	6	x	V_{RS}	
Tyto alba	31	11	18	22	22	10	1	2.23	3.02	Bunn and others (1982)
Bubo bubo	22	10	8	7	0	0	0	1.00	1.26	Frey (1973)
B. virginianus	82	78	121	84	6	0	0	1.61	1.23	Henny (1972)
Strix aluco [1]	8	3	2	3	1	0	0	1.18	1.90	Southern (1970)

[1] Data from 1947 study year.

England, except the density figures, which are an average over all of England, Scotland, and Wales.

Data for density, dispersal, and reproduction are listed, with their sources, in tables 4, 5, and 6. Tabulated values were mostly taken directly from the literature, but in some cases estimates of requisite parameters were not available and were calculated using published information. σ, V_{RS}, and factors F_K and F_{RS} were computed as for the spotted owl. Dispersal distances in table 5 are not uniform across species because of the way that data are reported in the original literature. The values shown are the midpoints of the reported intervals. Data for among-pair variation in number of fledglings produced by *Otus asio* were lacking, so the mean of the other five V_{RS} estimates was used for that species.

Estimates of life tables for the five species of owls are shown in table 7. All are arbitrarily truncated at 10 years. The estimates of fecundity are based on data in table 6 except for *Otus asio* and *Strix aluco*; a 1:1 sex ratio is assumed and b_x is given as female offspring per female. For *Otus*, the complete life table is that computed by Ricklefs (1983). For *Strix*, the data in table 6 are for a single year, 1947, of Southern's study (1970). The estimate of b_x in table 7 represents an average for the tawny owl over 13 study years. To compute year-to-year survivorship, we computed ratios of returns of banded birds from consecutive *years*. Juveniles were treated as a separate class. In cases for which adequate returns were available, first year birds were also treated separately. These life tables are all rough approximations, but are adequate for the calculation of F_{GT}, which was their intended purpose.

Table 8 contains estimates of effective deme sizes and several other parameters relevant to the genetics of natural populations. The estimates were computed as described above for the spotted owl. There is substantial variation of the estimates of N_e among species. The principal factors contributing to the variation appear to be dispersal distances, density, and the factor reflecting variance in reproductive success among pairs (F_{RS}). The results for the great horned owl indicate an exceptionally large value of N_e; this reflects the estimate of dispersal that is an order of magnitude greater than those for the other species. The sample sizes in Houston's (1978) study were not small; however, the result is influenced by a few very long distance dispersers. Thus, the estimate is probably a bit on the high side. For example, if

Table 7--Life tables for selected species of owls

Species		Age (x) 0	1	2	3	4	5	6-10	Reference
Tyto alba	s_x [1]	0.35	0.57	0.63	0.63	0.63	0.63	0.63	Stewart (1952)
	b_x [2]	0.00	1.12	1.12	1.12	1.12	1.12	1.12	Bunn and others (1982), Henny (1969)
Otus asio	s_x	0.31	0.59	0.63	0.67	0.75	0.75	0.75	Ricklefs (1983)
	b_x	0.00	1.04	1.30	1.30	1.30	1.30	1.30	Ricklefs (1983)
Bubo bubo	s_x	0.44	0.67	0.67	0.67	0.67	0.67	0.67	Rockenbauch (1978)
	b_x	0.00	0.00	0.50	0.50	0.50	0.50	0.50	Frey (1973)
B. virginianus	s_x	0.42	0.56	0.67	0.67	0.67	0.67	0.67	Houston (1978)
	b_x	0.00	0.00	0.80	0.80	0.80	0.80	0.80	Henny (1972)
Strix aluco	s_x	0.47	0.79	0.82	0.82	0.82	0.82	0.82	Southern (1970)
	b_x	0.00	0.35	0.35	0.35	0.35	0.35	0.35	Southern (1978)

1/ Year-to-year probability of survival.
2/ Female offspring per female per year.

dispersal and density covary (that is, if dispersal distances are greater for owls that travel through unsuitable habitat), then the estimate of N_e would be exaggerated because, for this species, our estimate of density is for an area of farms and eastern deciduous woodland (that is, generally good habitat).

An important point evident in table 8 is that the results for the spotted owl do not stand out or otherwise seem unreasonable compared with the other five species. Additionally, with the exception of ***Bubo virginianus***, the values of N_e for these owls, including ***S. occidentalis*** , fall in the same range as the values computed for an assortment of passerine birds by Barrowclough (1980). As pointed out by Barrowclough and Shields (1984), such values are also in general agreement with the results of karyological and electrophoretic analyses.

A final comment concerns the influence of kurtosis of the dispersal distribution and the pair-to-pair variance in reproductive success on the calculation of deme size. Neither of these factors have previously been computed for analyses of N_e for birds. Shields (1981), for example, suggests that correcting for kurtosis of the dispersal distribution might result in a significant reduction in the estimate of N_e. This seems not to be the case for these owl species: the size of the effect varies from 0 to at most 25 percent. The reproductive variance factor (F_{RS}) is of greater importance, ranging from about 0.6 to 1.2. No generalization seems possible concerning this effect: its influence may be to decrease, increase, or leave unchanged an estimate of N_e derived in the absence of data requisite for estimating the factor.

EFFECTS OF THE SPOTTED OWL MANAGEMENT PLAN

A major effect of managing National Forest land in the Pacific Northwest for timber harvesting is a reduction of suitable foraging and nesting habitat for the spotted owl. The object of the spotted owl management plans developed by the USDA Forest Service is to preserve a gridwork of suitable habitat patches for the owls (SOMAS) in the National Forests of California, Oregon, and Washington. Although the precise details of the overall SOMP are not clear, it appears that about 800 to 1,000 SOMAs will be set aside for pairs of spotted owls in the 3-State area. Unfortunately, a complete estimate of the effects a SOMP will have on the genetics of spotted owls would require a model of the population dynamics of the owl/habitat patch interaction under the plan. Because such a model is not available, we must limit our analysis to the genetical effects of the SOMP under unrealistic "best case" conditions, and can only outline an approach to the analysis of actual future conditions.

Best Case. The best case, from a genetical point of view, would be a condition in which all the SOMAs were used by breeding pairs; that is, if occupancy were 100 percent. In reality, of course, this is not possible as a long-term equilibrium situation because individual owls will eventually die and, depending on the nature of age-structure and patterns of dispersal through patchy habitat, it will take a finite time for any patch to become reoccupied by a breeding pair. Nevertheless, if the best case of 100 percent occupancy were realized, then there would be about 850 pairs of owls spread over the Pacific Northwest.

Table 8--Estimates of population genetics parameters[1] for selected species of owls

Species	σ (km)	ρ (km^{-2})	Nc	F_K	F_{RS}	F_{GT}	N_e
Tyto alba	31.14	0.08	974.85	0.93	0.86	0.87	678.33
Otus asio	44.03	0.30	7308.50	0.90	0.84[2]	0.78	4309.68
Bubo bubo	32.78	0.01	135.03	0.75	0.79	1.30	104.01
B. virginianus	216.35	0.15	88229.72	0.96	1.17	0.67	66396.75
Strix aluco	6.99	0.40	245.60	1.00	0.66	0.72	116.71
S. occidentalis	33.56	0.04	566.13	0.81	0.69	0.69	218.23

1/ Root-mean-square dispersal distance (σ), density (p), census number per neighborhood (N_c), correction factors for kurtosis (F_K), variance in reproductive success (^{F}RS), and generation time (^{F}GT), and effective population number per neighborhood (N_e).
2/ Mean for other 5 species (data for **Otus asio** not available).

At present, the data from California and Oregon suggest that the density of owls in the Coast Ranges and the Cascade Range is of the order of 0.03 to 0.04 owls per km^2. This is an average density over prime, fair, and unusable habitat. A management plan with approximately 500 SOMAs in Oregon plus Washington and about 400 in California would translate into 1,800 adults in approximately 110,000 km^2 of equivalent area. Thus, the overall density of the birds would fall to 0.016 owls per km^2. If life history traits of the birds were unaltered by the patchy habitat, then effective size would decrease correspondingly from the current value of about **220**. In particular, we can estimate that N_e, per local deme, would be reduced to:

$$4\ \pi\ (0.016,(33.56)^2 0.81(0.69)0.69 = 87.33.$$

Inbreeding at two levels must be considered in determining the effects the best case scenario of the management plan would have on the genetic structure of the spotted owl. First, the effects on the rate of loss of variation and increase of inbreeding over the entire range must be found and, second, the change in local inbreeding, F_{st}, caused by reduction in the effective size of local neighborhoods must be computed. With regard to the first problem, there is a question of whether the entire population can be considered panmictic for purposes of calculating the rate of increase of inbreeding. Unfortunately, that problem appears not to be well studied theoretically for realistic models. For example, the generalization that a series of populations can be considered panmictic if they 'exchange one or more individuals per generation is explicitly based on an "island" model of population structure: it does not apply to more biologically reasonable "stepping-stone" and "isolation-by-distance" models. Maruyama (1977) reports, however, that for a two-dimensional, continuous space model the entire population can be considered panmictic if p σ^2>l. For this case, P σ^2 = 0.016(33.56)^2 is of the order of 20, so the roughly 10 demes each of effective size 85 can be considered a single panmictic population of size 850 for computation of loss of variability. Expected overall inbreeding will therefore increase at a rate of $1/2N_e$, or 0.0006 per generation. (If the spotted owl distribution is considered one-dimensional, essentially the same result is obtained for the "best case.")

In order to compute how F_{st} will change with the implementation of the management plan, we compute the expected value, again using the procedure of Wright (1969), for a series of 10 demes each of size 85. For such a case, F_{st} is 0.017. This, however, is not a per generation increase of inbreeding of demes relative to the entire population: it is the equilibrium level. Wright (1969) indicated that the amount of time required to achieve this equilibrium is of the order of magnitude of the total number of neighborhoods in the population. Consequently,. local correlation of genes within individuals is expected to rise from the current estimated level of 0.007 to 0.016 over a period of about 10 generations.

Under the "best case" situation, the management plan would result in an increase in local inbreeding, relative to total variation, of about 1 percent, and a slow loss of overall variability, at a rate probably of the same order as replenishment by mutation (Franklin 1980).

A GENERAL METHOD FOR ASSESSING GENETIC EFFECTS OF A MANAGEMENT PLAN

The method outlined above should enable an interested researcher to compute the genetic effects of any particular management plan, given a set of estimates of the key variables. The particular calculations are for the unrealistic case of 100 percent occupancy of the management sites. A more realistic result could be obtained if estimates of mean occupancy rate **were** available. An estimate of density based on the anticipated mean occupancy, if used in the above equations, would yield an average value for the effective size of the managed population; from this, estimates of inbreeding could be obtained easily. Such an exercise ought to be performed before any management plan is implemented.

A more sophisticated but more useful way of realistically evaluating the genetic effects of a management plan requires the development of a model of the population dynamics of the species including, especially, a model of death and recolonization of the habitat patches or SOMAs. Repeated simulation of such a stochastic model would yield predictions of the time course of effective deme size for the owl-habitat system. From this a probability distribution of inbreeding rates could be obtained.

RECOMMENDATIONS

The statistics that have been recommended for management purposes and discussed by Frankel **and** Soulé (1981)--total effective population sizes of 50 individuals for short-term preservation, 500 for long-term, and a maximum of 1 percent inbreeding per generation--must be regarded as only guidelines. The models on which they are based are quite simplistic. Nevertheless, they must be taken as the most reasonable minimal goal in the absence of more specific analysis of the needs of any given species with its own population ecology, age structure, and social and mating system.

Our analysis of the "best case' scenario for the management plan for spotted owls outlines a method for evaluating the effects of any management plan, given estimates of several important parameters. Estimates of these are now critically needed, therefore we believe that it is imperative to:

1. Devote research effort to investigating those key aspects of the spotted owl's biology that are relevant to the development of a model for the dynamics of the owl's population.

2. Develop such a model and use it to investigate both the long-term stability of the owl's population under various SOMPs and the probable genetic effects of the SOMP.

3. Proceed with extreme caution in timber harvesting until the above results are obtained.

Our particular recommendations in regard to the first item are:

1. To study the effects of patch size and habitat composition on occupancy and fecundity.

2. To study intensively the dispersal of juveniles to get information on whether (and with what probability) isolated patches of suitable habitat are found.

3. To estimate, by using surveys, the current occupancy rates of isolated patches of good habitat.

Additionally, more data on fecundity, adult and juvenile survivorship, and dispersal are needed to confirm **or** modify **our** preliminary estimates. Finally, blood or tissue samples should be taken from 20 to 25 juveniles at a couple geographical locations during routine banding or radio-tagging activities for later electrophoresis. The laboratory results could be used to assess current levels of inbreeding (F_{is} and F_{st}) and genic heterozygosity of the species.

ACKNOWLEDGMENTS

A number of colleagues assisted us during the course of this study. Eric Forsman, Gordon Gould, and Rocky Gutiérrez generously provided data from their own studies of spotted owls. In addition, we thank Eric Forsman, Mark Shaffer, J. L. David Smith, and Jared Verner for useful conversations. Andrew Carey, Rocky Gutiérrez, Charles Meslow, and Robert Zink offered helpful comments on preliminary versions of the paper.

LITERATURE CITED

Barrowclough, George F. Gene flow, effective population sizes, and genetic variance components in birds. Evolution. 34: 789-798; 1980.

Barrowclough, George F.; Shields, Gerald F. Karyotypic evolution and long-term effective population sizes of birds. Auk. 101: 99-102; 1984.

Bateman, A. J. Is gene dispersion normal? Heredity. 4: 353-363; 1951.

Bunn, D. S.; Warburton, A. B.; Wilson, R. D. S. The barn owl. Vermillion, SD: Buteo Books: 1982. 264 p.

Craighead, John J.; Craighead, Frank C., Jr. Hawks, owls and wildlife. New York: Dover Publications: 1969. 443 p.

Crow, James F.; Kimura, Motoo. An introduction to population genetics theory. New York: Harper and Row; 1970. 591 p.

Deevey, Edward S., Jr. Life tables for natural populations of animals. Quarterly Review of Biology. 22: 283-314; 1947.

Dobzhansky, Th.: Wright, Sewall. Genetics of natural populations. X. Dispersion rates in Drosophila pseudoobscura. Genetics. 28: 304-340; 1943.

Dobzhansky, Theodosius; Wright, Sewall. Genetics of natural populations. XV. Rate of diffusion of a mutant gene through a population of **Drosophila pseudoobscura.** Genetics. 32: 303-324: 1947.

Emigh, Ted H.; Pollak, Edward. Fixation probabilities and effective population numbers in diploid populations with overlapping generations. Theoretical Population Biology. 15: 86-107: 1979.

Forsman, Eric D.: Meslow, E. Charles: Wight, Howard M. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs. 87: l-64: 1984.

Frankel, 0. H.; Soulé, Michael E. Conservation and evolution. Cambridge, England: Cambridge University Press: 1981. 327 p.

Franklin, Ian Robert. Evolutionary change in small populations. In: Soulé, Michael E.; Wilcox, Bruce A., eds. Conservation biology. Sunderland, Massachusetts: Sinauer Associates; 1980: 135-149.

Frey, Hans. Zur ökologie niedercsteröeichischer uhupopulationen. Egretta. 16: l-68: 1973.

Gutiérrez, R.J.; Franklin, Alan B.; LaHaye, William; Meretsky, Vicky J.; Ward, J. Patrick Juvenile spotted owl dispersal in northwestern California: preliminary results. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 60-65.

Henny, Charles J. Geographical variation in mortality rates and production requirements of the barn owl **(Tyto alba** spp.). Bird-Banding. 40: 277-290; 1969.

Henny, Charles J. An analysis of the population dynamics of selected avian species. Washington, DC: Bureau Sport Fisheries and Wildlife; 1972. 99 p.

Houston, C. Stuart. Recoveries of SaskatchewanT-banded great horned owls. Canadian Field-Naturalist. 92: 61-66; 1978.

Maruyama, Takeo. Stochastic problems in population genetics. Berlin: Springer-Verlag: 1977. 245 p.

Olsson, Viking. Studies on a population of eagle owls, ***Bubo bubo*** (L.), in southeast Sweden. Viltrevy. 11: l-99: 1979.

Patton, James L.; Feder, Juliana H. Microspatial genetic heterogeneity in pocket gophers: non-random breeding and drift. Evolution. 35: 912-920; 1981.

Ricklefs, Robert E. Comparative avian demography. Current Ornithology. 1: l-32; 1983.

Rockenbauch, Dieter. Untergang und wiederkehr des uhus Bubo bubo in Baden-Württemberg. Anzeiger der Ornithologischen Gesellschaft in Bayern. 17: 293-328; 1978.

Rockwell, Robert F.: Barrowclough, George F. Gene flow and the genetic structure of populations. In: Cooke, Fred.: Buckley, Paul A., eds. Avian genetics. New York: Academic Press; [in press].

Shaffer, Mark L. Minimum population sizes for species conservation. Bioscience. 31: 131-134; 1981.

Shaffer, Mark L. The metapopulation and species conservation: the special case of the northern spotted owl. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 86-99.

Sharrock, J. T. R. The atlas of breeding birds in Britain and Ireland. Berkhamsted, England: T. and A. D. Poyser, Ltd.: 1976. 477 p.

Shields, William M. [Review of] Gene flow, effective population sizes, and genetic variance components in birds. Journal of Field Ornithology. 52: 89; 1981.

Southern, H. N. The natural control of a population of tawny owls, (*Strix aluco*). Journal of Zoology, London. 162: 197-285: 1970.

Stewart, Paul A. Dispersal, breeding behavior, and longevity of banded barn owls in North America. Auk. 69: 227-245; 1952.

Van Camp, Laurel F.: Henny, Charles J. The screech owl: its life history and population ecology in northern Ohio. North American Fauna. 71: l-65; 1975.

Wright, Sewall. Evolution and the genetics of populations. Chicago: University of Chicago Press; 1969. Vol. 2.

THE METAPOPULATION AND SPECIES CONSERVATION: THE SPECIAL CASE OF THE NORTHERN SPOTTED OWL

Mark L. Shaffer

ABSTRACT: The conservation of patchily distributed species presents a complex problem for land-use planning and wildlife management. A new paradigm of population structure will be necessary to understand the extinction-persistence dynamics of such species both for site-specific and regional conservation efforts. The metapopulation model provides a beginning conceptual framework for solving this problem.

The model is reviewed in light of the problem of avoiding stochastic extinctions and illustrated with the current problem of conserving the northern spotted owl *(Strix occidentalis caurina)* in the Pacific Northwest. Major theoretical and empirical research needs are identified both for the applicability of the metapopulation model in general and for the northern spotted owl in particular.

INTRODUCTION

The equilibrium theory of island biogeography (MacArthur and Wilson 1967) has had a significant impact on biogeography, population ecology, community ecology and conservation. Currently, controversy persists on the validity of the theory (Gilbert 1980, Simberloff 1983) and the applicability of principles derived from the theory for the design of nature reserves (Margules and others 1982, Simberloff 1983). Irrespective of the outcome of these controversies, the theory, and the studies it has spawned, have led to three realizations of fundamental and continuing importance to conservation:

1. Local extinctions and colonizations, in ecological time, may be common events.

2. Extinctions and colonizations may, in many cases, be the products of stochastic events.

3. The simple geometric variables of habitat area and interhabitat distance, through their relationship with stochastic events, may be important determinants of the rate of local extinctions and colonizations.

These realizations raise key issues that must. be addressed if certain conservation efforts are to be successful. The importance of these realizations does not hinge on the validity of any particular theory of the interplay of the extinction and colonization processes. The fact that equilibrium theory remains inadequately validated as a general description of nature simply means that the relationship of the extinction and colonization processes remains unclear, particularly their relative frequencies and subsequent balance for various scales of time, size, and population structure. In fact, some of the studies necessary for conservationists to deal effectively with the issues raised by these realizations will help in further vali--dating, refuting, or refining equilibrium theory.

To date, most efforts to apply equilibrium theory to conservation have involved postulating principles on the size, configuration, and dispersion of nature reserves that will maximize the species

Mark L. Shaffer is a nongame staff specialist for the Office of Migratory Bird Management, U.S. Fish and Wildlife Service, Washington, D.C.

richness they contain and minimize the loss of species over time (for a review, see Margules and others 1982). An equally challenging problem is that of assessing the probabilities of persistence for species that are patchily distributed and whose patchwork of habitat **is** undergoing alteration. An example is an old-growth-dependent species in a National Forest where the natural successional mosaic is undergoing alteration due to both natural disturbance and resource management activities such as timber harvest. Here the question is how the probability-of species persistence on the forest responds to various regimes of patchwork alteration (that is, reduction in either the number or size of habitat patches and their increased isolation, or both). Managers need to know how many old-growth stands of what size and what distance from similar neighbors must be maintained to assure the persistence of the species in the forest to meet some acceptable management criterion (for example, 95 percent probability of persistence on the forest for one successional or rotational cycle). The solution to this complex problem relies on various areas of biological and ecological knowledge that are not yet fully developed theoretically, empirically, or experimentally. These areas include stochastic population dynamics and the roles of temporal and spatial environmental heterogeneity, dispersal, and-genetic diversity in population regulation and, hence, persistence. The tone of this paper **is**, therefore, necessarily speculative. My goal is to establish a frame of reference, identify key processes and variables, and point to potentially fruitful approaches for further work in this important area. My specific objectives are;

1. Reiterate the probabilistic component of extinction and, hence, conservation.

2. Introduce conservationists to the concept of the metapopulation as a basic frame of reference for conserving patchily distributed species.

3. Review a simple model of metapopulation dynamics.

4. Outline the potential relationships of the factors affecting metapopulation extinction dynamics **to** the spatial configuration of habitat.

5. Examine the implications of these relationships for conservation of the northern spotte owl *(Strix occidentalis caurina)* in terms of both management options and research needs.

THE STOCHASTIC COMPONENT OF EXTINCTION

Populations may go extinct from a variety of factors, but almost any factor can operate in two very different ways. *Systematic pressures,* despite temporal or geographic variation, show a significant trend over time that negatively impacts the population. Long-term climatic changes are one example. In such a situation, the size of the population bears only on the length of time the population persists, but extinction is a foregone conclusion provided the trend does not change. *Stochastic perturbations* show **no** significant trends with time but still may force a population to extinction if sufficiently frequent or severe. Drastic, intermittent variations in climate are **an** example of this mode of extinction. In this case, the population's size and distribution may be critical determinants of its persistence through the temporary period of unfavorable **con**ditions.

Once systematic pressures have been identified and solutions instituted for a species in jeopardy , the question of stocahstic perturbations remains. One essential goal for effective conservation is the minimization of extinctions due to stochastic perturbations. The northern spotted owl provides an example of the relationship of these two modes of extinction. The species is currently of concern because of its apparent dependence on old-growth coniferous forests (Forsman and others 1984, Gutiérrez and others 1983), a habitat which has steadily declined over the years due principally to timber harvest. Further habitat declines are anticipated due to the high economic value of the timber that provides suitable habitat. Determining that habitat preservation is critical to the species survival is the answer to the systematic pressure threatening this species. But determining how much habitat to preserve and how it is distributed must address the species' viability in the face of the stochastic perturbations to which it may be **subject.** Land is a precious resource. So is biotic diversity. When the conservation of a species conflicts with alternative land uses, the first question to arise is what is the minimum land area necessary to achieve conservation. Given that localized extinctions are, in part, the results of stochastic events, and the probability of such extinctions increases with time and decreasing population size, determining the amount of land necessary to achieve the conservation of a species must address three key issues:

1. The types of stochastic perturbations to be anticipated.

2. The time frame to use in conservation planning.

3. The degree of security sought for the unit being conserved.

These issues are addressed for a single, isolated population in an earlier paper (Shaffer 1981). The northern spotted owl represents a different problem--a species distributed on a patchwork of habitat. A new perspective on population structure is necessary to deal with the conservation of such species.

THE METAPOPULATION

The Metapopulation Concept

Most species are patchily distributed and can be viewed as a population of populations (Levins 1970) or a metapopulation (Wilson 1975). Wilson (1975) provides a metaphorical description of the metapopulation as ".. . .a nexus of patches, each patch winking into life **as** a population **colonizes** it and winking out again as extinction occurs. At equi-

Figure 1.--A hypothetical metapopulation at two different time steps: (A) T=1; (B) T=2.

librium the rate of winking and the number of occupied sites are constant, despite the fact that the pattern of occupancy is constantly shifting" (fig. 1). For such a patchily distributed species, global extinction is equivalent to its extinction on all patches. Effective conservation of such species thus requires an understanding of the processes of local extinction and colonization and the factors affecting these processes.

Levins' Model

Levins (1970) provides an initial treatment of metapopulation dynamics (table 1). His model considers three parameters: the proportion of patches occupied by populations at some particular time (N_x), the proportion receiving immigrants (prospective colonizers) in an instant of time (m), and the proportion of patches whose populations are going extinct in an instant of time (e). The model states that the Change in occupancy of patches over time is a function of the rates of immigration and extinction.

Levin's model, although a general one, is oversimplified. It is formulated in continuous time. It assumes either equal size patches or no relationship between patch size, population size and extinction probabilities. Nevertheless, the model provides a conceptual beginning for a more detailed consideration of the determinants of metapopulation persistence.

Table 1--Levins (1970) model of metapopulation dynamics

Let:

(t) = proportion of patches occupied by populations at time

m = proportion of patches receiving migrants in an instant of time (whether occupied or not).

e = proportion of populations becoming extinct in an instant of time.

Then:

$$dN_x/dt=mN_x(l-N_x)-eN_x \qquad (1)$$

and, at equilibrium:

$$N_x=l-e/m \qquad (2)$$

Levins' (1970) analysis of this model reveals several important findings. First, for the metapopulation to persist, the proportion of patches receiving immigrants (or the rate of immigration, m) must exceed the rate of extinction $(\bar{e})$. If the equilibrium proportion of occupied patches $(\hat{N}_x)$ is close to 1, a change in extinction rate has relatively little effect on $\hat{N}_x$. If $\hat{N}_x$ is small, however, $\hat{N}_x$ is more sensitive to changes in extinction rate. When extinction rate shows random variation through time the immigration rate must exceed the extinction rate by more than the variance of the extinction rate for the species to persist (that is, $m-\bar{e} > \sigma_e^2$). If the variation in extinction rate is autocorrelated, the persistence of the metapopulation is further reduced.

If the immigration rate (m) is large, then the persistence of the metapopulation is very sensitive to changes in m. Different species are likely to have different distributions of immigration probabilities (compare passive, wind-dispersed seeds to actively dispersing birds). Levins (1970) and MacArthur and Wilson (1967) argue that an exponential decline of dispersing individuals with distance is a reasonable qualitative description for passive dispersing species. In this case, a change that doubles the distance between patches will square the immigration rate and will have a greater effect on the chances of persistence than would doubling the extinction rate. Consequently, increased patch separation, as this affects dispersal probabilities, may be the limiting factor in determining metapopulation persistence for passively dispersing species. Though based on a simplistic model, this is an important finding as, in Levins' words, it:

> . . .forces us to change our notion of suitable habitat. If there is always a finite probability of extinction of a local population even in the best of circumstances, a region will be suitable or unsuitable depending on the density of appropriate sites and a species will fail to survive even if its optimal habitat is present.

Thus, habitat (patch) density may be as fundamental to conservation as habitat quality and management actions that reduce habitat density may lead to the regional extinction of a species even if habitat of suitable quality remains. An important management corollary of this result is that effective conservation of patchily distributed species may require the preservation of suitable but intermittently, perhaps currently, unoccupied habitat.

The minimal objective of metapopulation conservation is simply its continued existence; that is, persistence in one or more patches $(N_x > 0)$. This requires maintaining an immigration rate greater than the extinction rate $(m > \bar{e})$. This can be achieved either by increasing the immigration rate or decreasing the extinction rate. Aside from the foregoing consideration of the effects of interpatch distance on immigration, Levins' model does not explicitly incorporate the spatial dimensionality of the metapopulation in terms of patch number or size and their effects on immigration or extinction rates. Yet, if population size correlates with area, probability theory would indicate that patch number is an important consideration for both immigration and extinction rates; and both probability theory and empirical studies (Gilpin and Diamond 1981, Jones and Diamond 1976, Simberloff 1976) indicate that patch size should be an important determinant of extinction rate. To go further requires incorporation of this spatial dimensionality and an examination of its effects on metapopulation persistence. First, it is necessary to more clearly define the specific objectives of metapopulation conservation.

Metapopulation Structure and Conservation Objectives

From a conservation standpoint, the interest is in estimating certain probabilities of the extinction-persistence of the metapopulation or parts thereof. These probabilities may be defined as shown in table 2 for a metapopulation starting from saturation (that is, all patches occupied).

Table 2--Definitions and relationships of metapopulation probabilities

Let:

e_i = probability of extinction on patch i;

p_i = probability of persistence on patch i;

E = probability of extinction everywhere (that is, all patches);

P = probability of persistence everywhere;

e_x = probability of extinction somewhere (that is, $\geq$ 1 patch);

p_x = probability of persistence somewhere.

Then:

$$e_i = 1-p_i$$
$$p_i = 1-e_i$$
$$E = \prod_{i=1}^{N} e_i$$
$$P = \prod_{i=1}^{N} p_i$$
$$e_x = 1-P = 1-\prod_{i=1}^{N} p_i$$
$$p_x = 1-E = 1-\prod_{i=1}^{N} e_i$$

If the metapopulation under consideration is a closed system (that is, it is not connected to or embedded in another metapopulation) and patches are fixed, permanent, and independent with regard to stochastic events, then these extinction-persistence probabilities may be calculated as shown in table 2. For conservation purposes interest is most likely to be in determining the probabilities of (1) extinction in certain patches (e_i), (2) over all patches (E), or (3) of persistence of the species somewhere within the patchwork $(p_x,\ x \geq 1)$.

Clearly, once the site-specific extinction probabilities $(e_i$'s$)$ are estimated all other probabilities can be calculated. Equally clear is that we generally do not know, nor can we expect to estimate, site-specific extinction probabilities over a short time with much meaning for long-term planning (but see Gilpin and Diamond 1981). Moreover, estimating site-specific extinction probabilities for an existing metapopulation configuration does not necessarily allow prediction of the e_i schedule that will pertain to a new metapopulation configuration, because this value is, in part, a function of the configuration in which it is estimated. Even on a qualitative basis these relationships raise an important management issue: the specific objective of metapopulation conservation. Is the objective to assure the persistence of the species:

1. On a particular patch or set of patches (minimize e_1 and/or e_2, etc.)?

2. On all patches (minimize e_i's and E)?

3. On at least one or some preselected percentage of unspecified patches (maximize p_x, $x \geq 1$)?

In the absence of an answer to this question, no definition of a minimum patchwork can be offered. The answer chosen may make a difference in which land-use pattern(s) will be acceptable.

In the remainder of this paper, the focus will be on minimization of site-specific (e_i) and overall (E) extinction probabilities as the conservation objective probabilities. This is an arbitrary choice. Because $E = \prod_{i=1}^{N} e_i$ anything reducing site-specific extinction probabilities will automatically reduce overall extinction probabilities, but the chances of overall extinction may be reduced simply by increasing patch number (N). Though considering both site-specific and overall extinction probabilities may introduce a certain redundancy, the factors affecting these probabilities can operate at different levels of metapopulation structure. The discussion will be more comprehensive if both types of probabilities are included. It should also be useful to contrast site-specific conservation versus patchwork conservation.

It should be noted that because $p_x = 1 - E$, minimizing the overall extinction probability automatically maximizes the probability of persistence somewhere, which will usually be the real objective of metapopulation conservation.

METAPOPULATION CONFIGURATION AND STOCHASTIC EXTINCTION DYNAMICS

There are four categories of stochastic perturbations that may be factors in the extinction of a population (Shaffer 1981):

1. Demographic stochasticity caused by chance events in the survival and reproduction of a finite number of individuals.

2. Environmental stochasticity resulting from temporal variation of habitat and niche parameters such as weather, food supply, predators, etc.

3. Natural catastrophes such as floods, fires, hurricanes, etc.

4. Genetic stochasticity, or changes in gene frequencies with negative effects on demographic parameters resulting from founder effect, random fixation, or inbreeding.

It is reasonable to reduce this organization to three categories by recognizing natural catastrophes as merely an extreme form of environmental stochasticity. One important distinction within this new composite categorization is that of stochastic events that are contagious by nature (for example, epizootics). It is anticipated that such events may have spatial dynamics that differ from noncontagious events such as floods, drought, etc. Ruediger (1985) presents examples of these phenomena relevant to the northern spotted owl.

All these categories of stochastic perturbations increase in importance with decreasing population size. Moreover, they are likely to interact, as for example an environmental perturbation that reduces population size over time to the point where inbreeding depression may become a factor by negatively impacting the demographic parameters of survival and fecundity. Though increased attention has recently been focused on the importance of genetic stochasticity (Frankel and Soulé 1981, Schoenwald-Cox, and others 1983, Soulé and Wilcox 1980), there is still no theoretical or empirical guidance on which category of stochastic perturbation sets the lower limit to population viability. This may well vary from one type of population to another (for example, density-independent populations with nonoverlapping generations vs. density-dependent populations with age structure).

To better understand how the geometric distribution of habitat may affect metapopulation extinction dynamics, it is necessary to consider how changes in the metapopulation configuration variables (that is, patch number, size, and isolation) may affect the objective probabilities $(e_i,\ E)$ caused by the various categories of stochastic perturbations (demographic, environmental, genetic). Because habitat management chiefly controls the metapopulation configuration variables, this discussion is organized with each variable considered separately. The discussion is condensed in table 3 where, for a particular change in each configuration variable, the expected change in site-specific and overall extinction probabilities caused by various stochastic perturbations, acting through various conditions, is given. This dicussion assumes a strong, positive correlation between habitat area and population size.

Table 3--Expected changes in site-specific *(e_i)* and overall *(E)* extinction probabilities with changes in metapopulation configuration variables caused by various types of stochastic perturbations.

Metapopulation configuration variable	Change	Objective probability	Change	*Caused by*	*Acting through*
Patch #	↑	e_i	↓	demographic stochasticity	sources of immigrants
			↓	noncontagious stochastic events	sources of immigrants
			↑↓	contagious stochastic events	sites for initiation, sources of immigrants
			↓	genetic stochasticity	sources of immigrants
		E	↓↓	demographic stochasticity	number of realizations, sources of immigrants
			↓↓	noncontagious stochastic events	environmental correlation, sources of immigrants
			↑↓	contagious stochastic events	sites for initiation, sources of immigrants
			↓↓	genetic stochasticity	number of realizations, sources of immigrants
Patch Size	↑	e_i	↓↓	demographic stochasticity	
			↓↓	noncontatious stochastic events	
			↓↓	contagious stochastic events	
			↓↓	genetic stochasticity	inherent resilience, number of immigrants
		E	↓↓	demographic stochasticity	
			↓↓	noncontagious stochastic events	
			↓↓	contagious stochastic events	
			↓↓	genetic stochasticity	
Isolation	↑	e_i	↑	demographic stochasticity	distance for immigrants
			↑	noncontagious stochastic events	distance for immigrants
			↓↑	contagious stochastic events	distance for infectives, distance for immigrants
			↑	genetic stochasticity	distance for immigrants
		E	↑	demographic stochasticity	distance for immigrants
			↑↓	noncontagious stochastic events	distance for immigrants, environmental correlation
			↓↑	contagious stochastic events	distance for infectives, distance for immigrants
			↑	genetic stochasticity	distance for immigrants

Further, the entire discussion is intuitive and is based on common sense expectations. Unless otherwise stated, all cause-effect statements come with the caveat of, "all else being equal." This is not intended as a comprehensive, exhaustive discussion, but rather as an indication of the major relationships and potential complexity of the interplay between various stochastic perturbations and metapopulation configurations.

Patch Number

Increasing the number of patches should decrease both site-specific *(e_i)* and overall *(E)* extinction probabilities for two reasons. First, e_i should be reduced because more patches constitute more sources of immigrants that may bolster a patch population temporarily failing because of demographic, environmental, or genetic stochasticity. This is the so-called "rescue effect" (Brown and Kodric-Brown 1977). This phenomenon deserves much more theorectical and empirical attention.

Second, because the overall extinction probability is equal to the product of all site-specific extinction probabilities ($E=\prod_{i=1}^{N} e_i$; if e_i's are independent), the chances of overall extinction can be reduced simply by adding to patch number even if the site-specific extinction probabilities remain unchanged. The larger site-specific extinction probabilities are, however, the more patches must be added to achieve a certain specified overall extinction probability. For example, if $e_1=e_2=e_3$, etc., and the objective is to achieve $E \leq 0.10$, then for $e_i=0.5$, N must be ≥ 4. If $e_i=0.9$, however, N must be ≥ 22 to achieve the specified level of E. The key point here is the extent to which patches are independent with respect to the stochastic perturbations affecting populations. The greater this independence, the greater the benefit of adding additional patches. If patches are not independent with regard to environmental or genetic stochasticity, then adding additional patches is equivalent to simply adding the individuals they contain to an aggregate population size. That is, the metapopulation behaves as one unsubdivided population. This pattern is potentially very complex as the degree of correlation between patches may well vary from one type of environmental perturbation to another.

The one potential negative aspect of increasing patch number concerns contagious stochastic events. For example, consider forest fires as a form of contagious environmental stochasticity. The more patches there are, the more likely at least one will be affected by a forest fire during any particular time period (if patch number adds area) The larger the number of sites for initiation of a contagious disturbance, the more likely that any particular patch may be disturbed given that the degree of isolation-does not change. How important a consideration this may be is, of course, unknown and is likely to be quite variable for species and from one habitat to another.

Patch Size

Because all forms of stochastic perturbations decrease in importance with increasing population-size, increasing patch size should significantly reduce both site-specific and overall extinction probabilities. An important question is the form of the functional relationship between population size and e.. Several theoretical models (MacArthur and Wilson'1967, Richter-Dyn and Goel 1972, Wright and Hubbell 1983) have demonstrated that, considering demographic stochasticity alone, the expected time to extinction in relation to population size for an isolated population takes the general form of an exponentially increasing function (fig. 2a). That is, starting from a population of one, the expected time to extinction increases so rapidly with an increase in population size (here expressed as K) that, in the case of Richter-Dyn and Goel's model, by the time K=20 (individuals) the population is essentially immortal with respect to any time period of potential interest to managers. This relationship is very sensitive to changes in r, the intrinsic rate of increase. Extreme caution should be used in interpreting the results of these models because they do not incorporate the effects of age-structure or environmental or genetic stochasticity. Shaffer and Samson (in press) show that incorporating age structure and environmental stochasticity drastically reduces the predicted population viability obtained. from Richter-Dyn and Goel's model. More importantly, it must be remembered that the expectation of extinction even in a viable environment approaches one as time approaches infinity. Larger population size merely makes this approach more gradual (fig. 2b). Further, incorporating genetic stochasticity would likely have an equally significant effect, at least to some species. Thus, the whole class of models dealing with only demographic stochasticity becomes suspect for application to real world problems.

From a genetic standpoint, Franklin (1980) has argued that a minimum effective (in the genetic sense) population of at least 50 breeding adults is necessary to avoid the short-term deleterious consequences of inbreeding and that an effective population size of 500 may be necessary for long-term genetic adaptability. This argument suffers

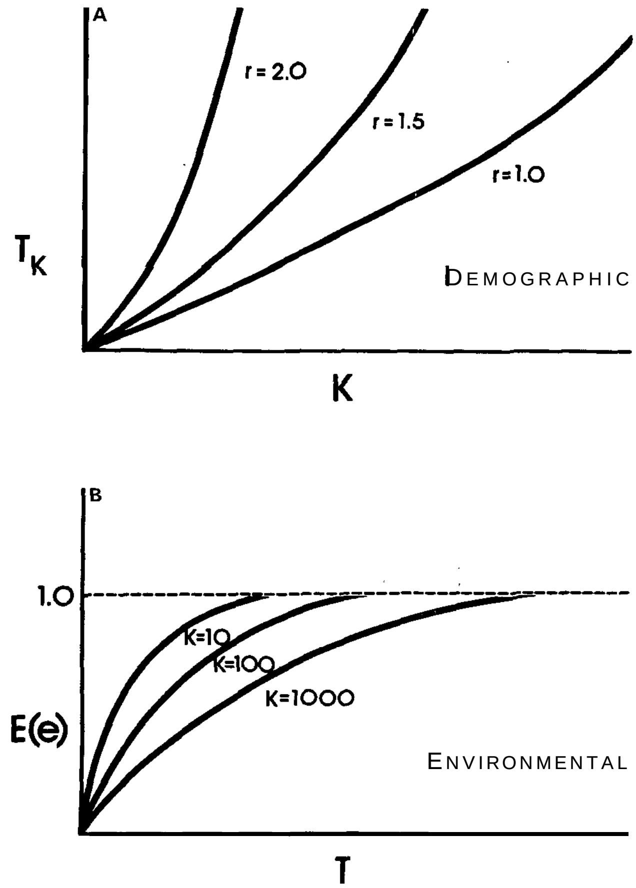


Figure 2: (A) The functional form of the expected time to extinction caused by demographic stochasticity for a population of size *K* (T_K) as a function of population size (*K*). This relationship is shown for three different intrinsic rates of increase (*r*) (adopted from MacArthur and Wilson 1967).

(B) Hypothetical functional form of the expectation of extinction (*E*(*e*)) caused by environmental stochasticity for a population size *K* as a function of time (*T*). This relationship is shown for three different population sizes (*K*=10, 100, 1,000).

many of the shortcomings found in the demographic models cited above. It does not include the effect of age-structure or environmental stochasticity. In fact, there do not seem to be any comprehensive theoretical models that integrate the various categories of stochastic perturbations. This is a crucial need for management and may prove an enlightening exercise for basic ecological theory.

Different species are likely to show different sensitivities to the various types of perturbations. For example, Karr (1982) presents evidence that, amongst forest birds in tropical undergrowth, the variability in population size is a better predictor of extinction than population size itself. Karr interprets the coefficient of variation (CV) in population size as a first approximation of environmental variability. This result applies only to a subset of species sufficiently abundant to be considered immune to extinction from demographic stochasticity alone. This would seem to indicate that demographic stochasticity sets the lower limit on species survival but that environmental stochasticity is the most important factor above this lower limit.

Ehrlich (1983), based on his work with Bay checkerspot butterfly populations *(Euphydryas editha bayensis)*, believes most local extinctions in this species are the result of catastropic weather events and the effects on host food plants rather than "normal" variation in weather patterns.

Rails and Ballou (1983) present evidence that, for zoo populations of mammals, inbreeding depression has had a significant deleterious effect on demographic viability and suggest similar effects may occur in wild populations that become much reduced.

This is by no means a comprehensive review, but work with three different major taxonomic groups (birds, butterflies, mammals) has yielded three different indications of- which type of stochastic perturbation may be most important in determining population viability. This area is rife with potential for theoretical, empirical, and experimental work.

Patch Isolation

The distance between patches is important because of its potential effects on the probability-of interpatch movements and, thus, the operation of the rescue effect, the frequency of recolonizations, and the rate of immigration in maintaining a species' genetic variability, and the avoidance of inbreeding. Reduced isolation is a two-edged sword because, though it may produce the benefits mentioned above, it may also entail a high degree of inter-patch correlation with regard to noncontagious environmental stochasticity and the facilitation- of the spread of contagious environmental events. The relative importance of this mixed blessing is, of course, unknown and, again, likely variable.

Several efforts at modelling the importance of dispersal to population regulation and persistence (Roff 1974a, 1974b, 1975; Vance 1984) have produced some interesting results. Roff (1974a) demonstrates that, for populations with a stochastic exponential growth rate, increasing environmental stochasticity greatly reduces the probability of population persistence. If such a population is subdivided and there is movement of individuals between patches, persistence of this metapopulation configuration may be increased several orders of magnitude over the original undivided configuration.

Vance (1984), examining a number of population models, shows that, for a wide variety of dispersal patterns, dispersal tends to stabilize population fluctuations. In some circumstances, however, dispersal does not increase population stability. He further argues that the details of patch location do not alter the qualitative stabilizing effect of dispersal. But the scenario of his spatial argument (that is, equispaced patches all connected or all isolated) is too simplistic to be of interest for application.

The value of Roff's models, beyond their obviously important heuristic value, *is* limited by their consideration only of exponential growth. Vance's results are much more robust but suffer from an inadequate consideration of spatial effects.

Moreover, neither model incorporates the negative and potentially destabilizing aspects of dispersal, namely the effects of contagious stochastic events. As with the relationship of population size and extinction, assessing the effects of metapopulation configuration on persistence awaits the development of comprehensive, realistic models characterizing various life-history types.

The Trade-offs of Size, Number, and Distance

An examination of table 3 and the foregoing discussion summarize an intuitive expectation that many, large patches, which are close together, will usually minimize site-specific and overall extinction probabilities. Any conservation effort will necessarily be limited to some fixed amount of habitat and the question immediately arises of how best to distribute the habitat available.

If total habitat area is fixed then an increase in average patch size must correspond to a decrease in patch number. If the regional boundaries of the metapopulation are fixed then an increase in patch number may correspond to a decrease in patch isolation. If area and regional boundaries are fixed then an increase in patch size must correspond to a decrease in patch number and may entail an increase in isolation.

A small number of patches may be compensated for by large size and reduced isolation. Small patch size may be compensated for by increased patch number and decreased isolation. Increased isolation may be mitigated by increased patch number and increased patch size. Which strategy, or what mix of strategies, to use in any particular circumstance will depend on the particulars of that situation and the functional form of the relationships between the objective probabilities and metapopulation configuration variables, Without comprehensive models of the relationship of population size and configuration to extinction probabilities under the effects of all sources of stochastic perturbations, rational decisions on acceptable metapopulation configurations will not be possible. Even without such models, however, some preliminary guidance may be obtained from table 3. First, whether the objective is to minimize site-specific or overall extinction, increasing patch size should uniformly reduce the chances of extinction to all sources of stochastic perturbations. Neither patch number nor isolation is expected to have such an unambiguous effect on site-specific or overall extinction. This agrees with the results of Roff's (1974b) theoretical simulation models.

Second, additional patches should reduce both e_i's and E but should have a more dramatic effect on the latter, contingent upon the degree of independence of the patches with regard to stochastic environmental perturbations. The hazards of increased patch number enhancing the probability of extinction caused by contagious stochastic events is unknown but probably minor.

Third, because isolation will often correlate inversely with the environmental independence of patches but correlates directly with the ease of transmission of contagious stochastic events, lack of isolation is not an unambiguous blessing. A better knowledge of the prevalence and importance of the rescue effect and recolonizations relative to these potential disadvantages is necessary to better assess isolation's likely importance for minimizing site-specific and overall extinction. If the benefits of proximity outweigh the risks, then there is likely some tradeoff of distance with size, such that one configuration *(A)* of a certain patch size (x) and interpatch distance (y) behaves (that is, has the same persistence/extinction schedules) as another configuration *(A')* of smaller patches (x') closer together (y') (fig. 3). Determining the existence and form of such a trade-off should be of great importance in maximizing management options for land-use planning.

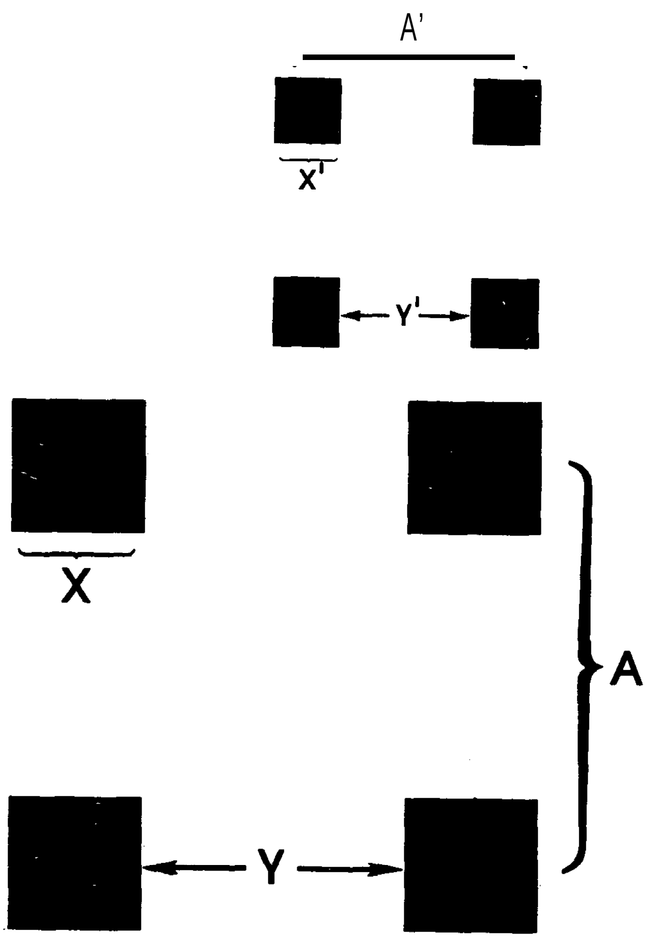


Figure 3.--The tradeoff of size and distance x' = x/2 y' = y/2 (not to scale). If there is a linear relstionship of the effects of size and distance on extinction probabilities, site-specific and overall extinction probabilities should be equal in these two configurations.

What all of this means is-that extinction/persistence probabilities are the result of the interplay of numerous forces, some opposing, that are determined, at least in part, by the configuration of the habitat patchwork. Thus, there is likely no simple prescription for patchwork configuration that will universally maximize persistence or minimize extinction probabilities. It also means that-the objective of metapopulation conservation must be explicit because the effects of various alterations may have differing effects on differing extinction/persistence probabilities. In other words, what's best to reduce the overall extinction probability (E) may not be best to reduce site-specific extinction probability (e_i). For example, to minimize e for a given i, may require one very large patch, but minimizing *E* may require numerous, smaller patches of intermediate isolation.

A crucial corollary of the tradeoff of size and distance, involves the twin dangers of metapopulation restriction and diffusion (fig. 4). In most scenarios conservationists will have to accept less than all of the remaining habitat for a species of concern. One goal of conservation is to maintain the representative distribution of a species. Yet specialized management can be administratively burdensome. The dilemma may then be one of choosing a dispersion-pattern either to maximize the species' geographical representation or to minimize the administrative burden. These may be opposing goals. Minimizing administrative burdens may require dedicating a number of patches close together and not having to deal with the species elsewhere. Geographic representation may require that patches be widely dispersed. The closer patches are, the more likely they are to behave as one. Thus, the potential to lose the species increases due to a contagious stochastic event or the fact patches are-so close (for example, all in one watershed) that they are essentially one with regard to environmental perturbations. This is the danger of restriction. On the other hand, maximizing dispersion may lead to a patchwork whose interpatch distances are so great that each patch behaves as an isolate (that is, dispersing individuals cannot reach another patch), and there is no realized benefit in terms of the rescue effect, recolonization, or gene flow. This is the danger of diffusion.

Clearly, this "stew" of processes, variables, and probabilities would be rendered more meaningful, if:

1. Data were available to derive the functional relationship of the objective probabilities to the various processes as these change with the various metapopulation configuration variables.

2. Theoretical models integrating the four types of stochastic events were available for both a single population and a metapopulation configuration for a variety of life-history types.

It would seem that realistic; theoretical models, be they analytical or numerical, could aid in determining the sensitivity of metapopulation persistence to various changes in metapopulation configurations. In table 3 I've indicated a postulated qualitative effect with a directional arrow. A next level of understanding would be to know which arrows are large and which small. Theoretical models may provide this. Eventually arrows could

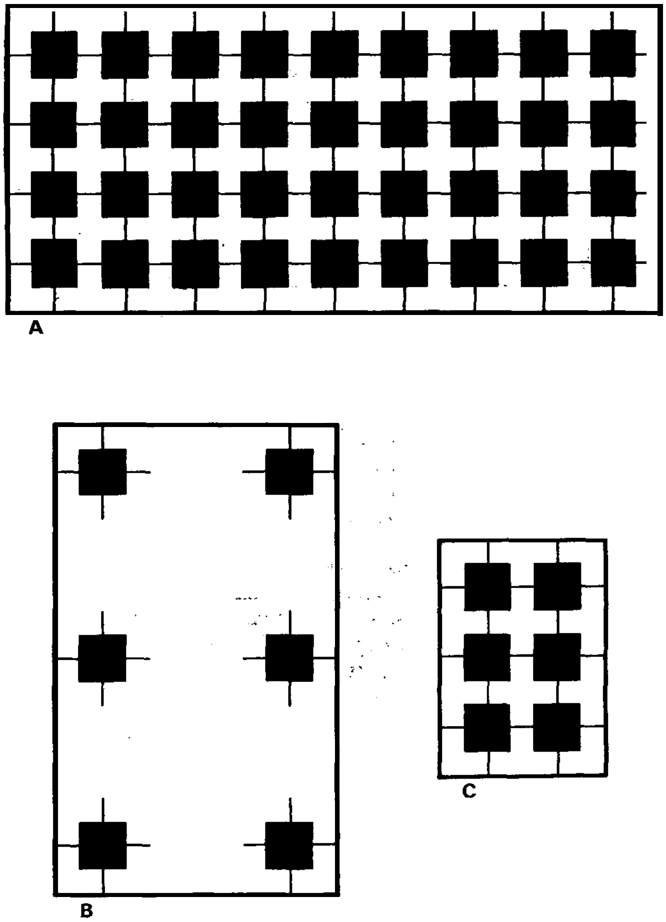


Figure 4.--The dangers of restriction and diffusion. 4A represents an *original, unaltered metapopulation, most of which is scheduled for* alteration. Management must be careful not to spread patches so thin that patch interactions are lost and each patch goes extinct relatively rapidly (4B), nor leave so few patches so close together that, despite patch interaction, all patches are eliminated by one catastrophic event (4C).

be replaced with equations but this will require extensive empirical and experimental work.

THE SPECIAL CASE OF THE NORTHERN SPOTTED OWL

How does the foregoing discussion relate to the current problem of conserving the northern spotted owl in public forest lands in the Pacific Northwest? From the reports on current research and management programs, much important data are being gathered on this species, particularly with regard to dispersal and the survivorship of young. In addition, research to date (Forsman and others 1984, Gutiérrez and others 1983) has shown the species' preference for mature and old-growth timber for foraging, roosting, and nesting; revealed a large home range size; demonstrated the varialbe success of the species' reproductive performance; and provided some estimate of overall population size and distribution. All this information is necessary, but it is not yet sufficient for comprehensive conservation planning. Still lacking are sex- and age-specific mortality and fecundity rates; sex and age structure (which may be derived from the preceding); some measure of the variability of these rates from year to year, and data on the genetic and breeding structure of the species. Thus, there are insufficient data with which to construct a comprehensive quantitative population model.

In the absence-of sufficient data to develop corn-prehensive quantitative approaches to assessing - the viability of various spotted owl habitat configurations, two management approaches have emerged. The first is what might be termed a qualitative approach; using available information on population size, distribution, habitat preference, home range size, and an intuitive appreciation of the importance of dispersal, to develop guidelines for management (Oregon Interagency Spotted Owl Management Plan). The other approach incorporates the above but is based on the growing use of genetic arguments to assess minimum viable population sizes (Salwasser and others in press). With regard to the former approach, its chief weaknesses are the need for a better-understanding of how home range size and the relative composition of mature and old-growth (that is percent composition - a rough measure of habitat quality) impinges on reproductive success, adult survivorship, and their variability; and the apparently arbitrary choice of distances between spotted owl management areas (SOMAs). Current work on dispersal should help correct the latter weakness fairly quickly, while extensive studies of reproductive success across a gradient of home range size and percent composition can partially alleviate the first weakness. For the temporal component of variation in SOMA suitability by size and percent composition there is simply no substitute for long-term monitoring. Certainly, using minimum-sized home ranges for long-term management guidelines would be courting failure as would a spacing regime for SOMAs based on maximum dispersal abilities. Combining these hazards with a dedication of a minimum number of SOMAs of low quality would further reduce the species survival probabilities.

The genetic approach represents a conceptual advancement based on both theoretical and empirical knowledge. However, several cautionary notes need to be sounded. First the 50/500 rule (Franklin 1980, Soulé 1980) discussed earlier, which seems to be emerging as a standard of application, is based on the simplest of analytical population genetics models, which do not take into account either age-structure or environmental stochasticity. Based on previous work on modelling grizzly bear (Ursus arctos) populations, the inclusion of age structure can dramatically affect the results of projecting population survivorship based on demographic stochasticity alone (Shaffer 1978). To the extent that genetic diversity directly affects demographic parameters (for example, mortality, fecundity), and this is the heart of the inbreeding depression argument, the inclusion of age-structure in determining effective population sizes may dramatically increase estimates of minimum viable population sizes. Make no mistake, there is no doubt that inbreeding depression poses a grave risk to small, isolated populations. What remains in doubt is what constitutes small for organisms of varying genetic structure and life-history patterns.

In this regard, Barrowclough and Coats (1985) estimate that the likely effective population size (in the genetic sense) for this species would approximate 2.1 of the census population size. This means that to achieve the goal of long-term adaptability (500 breeding adults, Franklin 1980) may require a census population goal of 1050 breeding adults or 525 pairs. This is very close to the current management objective of 500 pairs for Washington and Oregon (Salwasser and others in press).

A second point reiterates what emerged from the preceding consideration of metapopulation extinction dynamics. There currently exists no integrated theoretical model providing guidance on which class of stochastic events sets the lower limit to population viability. Implicit in the assumption of the 50/500 rule is that, if these sizes are sufficient to overcome the dangers of drift and inbreeding depression, all is well. This remains to be demonstrated. In fact, for density independent populations occupying variable environments, environmental stochasticity may be the limiting factor for population persistence, as appears to be the case in certain checkerspot butterfly populations (Ehrlich and others 1980). On the other hand, for large-bodied, long-lived, adaptable species with low genetic variability and some tolerance to inbreeding, demographic stochasticity may be the key factor in determining population persistence. How much demographic considerations or environmental conditions would modify the current management objective for the northern spotted owl is unknown, but it is highly probable an increase in the objective would be required.

MANAGEMENT OPTIONS AND RESEARCH NEEDS

It is clear from the discussion in the section, "Metapopulation Configuration and Stochastic Extinction Dynamics," that projecting the survivability of various metapopulation configurations is a daunting task. It is safe to say there are insufficient time and resources available to determine, empirically, all the requisite data over a sufficient period to ensure developing an accurate predictive capability for projecting population persistence of the spotted owl. This is a general and fundamental problem in conservation biology today; being asked to determine the long-term viability of wildlife species based on short-term studies. Nevertheless, the issue must be addressed. A reasonable strategy involves three components:. (1) theoretical research, (2) short-term empirical studies and (3) integration of a long-term monitoring-research program with current management action (Salwasser and others in press).

Theoretical Research

As discussed above, theoretical ecology lacks the detailed models necessary to provide sound guidance on the interplay of the factors affecting stochastic extinctions for populations of different life history patterns. It seems reasonable that the management agencies in need of such guidance should seriously consider instituting a program of basic research to address this weakness. In my judgment a few representative simulation models of various major life hisotry types would go a long way toward providing at least sound qualitative guidance on the likely persistence of various populations in relation to various stochastic factors and various land-use patterns. Such generalized models would also be useful in generating hypotheses for empirical field or experimental laboratory studies. There can only be a growing need for such guidance in the future. We may as well start now. In this regard it is very encouraging to learn of efforts by the USDA Forest Service to develop an interactive computer simulation model of vertebrate population dynamics that incorporates demographic, environmental and genetic stochasticity (Salwasser pers. comm.) [1] Such a modelling effort can be expected to make a major contribution in wringing the most value from the data at hand and helping to pinpoint the most crucial data gaps. Expansion of this model from a single isolated population format to a metapopulation configuration should provide a truly useful tool, not only- for management but for theoretical studies as well.

Short-Term Empirical Studies

For the northern spotted owl, short-term empirical studies should focus on assessing reproductive variability across a gradient of home-range sizes by percent composition; some measure of the genetic variability of the species; further work to determine dispersal behavior and success; and monitoring of suitable habitat, occupied and vacant, to assess the relative frequency of pair extinction and the recolonization of patches. Work on the latter item is underway (Carey 1985). Efforts should also be made to determine why this species prefers old growth. There is some suggestion that prey availability may be the greatest in old growth but that prey are abundant, yet unavailable, in early successional stages (Gutiérrez and others 1985). If this proves true, silvicultural options may be available to enhance the species' use of a wider variety of habitats.

Long-Term Monitoring of Management Actions and a Research Program

To the extent that agencies must act now to determine the species' habitat needs, the following guidelines may serve as a reasonable approach provided they are linked to the long-term monitoring research program specified.

Patch Number. The goal of 500 breeding pairs (Oregon Interagency Spotted Owl Management Plan), in the absence of better guidance, should be increased to 1,000 pairs for the subspecies. This goal of 1,000 pairs would apply to Washington, Oregon and northern California. While this number may seem large, it represents a 60 percent reduction from the most recant range-wide estimate of the subspecies' abundance (U.S. Fish and Wildlife Service 1982). Moreover, given our current

[1] Hal Salwasser, National Wildlife Ecologist, Washington Office, Wildlife and Fish Ecology, 3825 E. Mulberry Street, Ft. Collins, CO 80524.

understanding of the species genetic characteristics (Barrowclough and Coats 1985) this increase represents roughly a doubling of what would be necessary to meet the admittedly rough minimal requirements for long-term adaptability (Franklin 1980) currently employed by the USDA Forest Service. In addition, it should be noted that the emerging SOMA patchwork will result in localized populations of a size that will be extremely vulnerable to demographic stochasticity. Thus e_i's can be expected to be high. The low rates of survivorship and pair establishment of juveniles during dispersal (Allen and Brewer 1985, Gutiérrez and others 1985, Wilson and Meslow 1985) indicate a low m value can be anticipated. Recall that, for the species to persist m must be greater than e. Adding SOMAs should help assure this condition is met.

Further, if a management program is based on 1,000 pairs and no suitable unoccupied sites are reserved, it is unlikely that 1,000 sites will always be occupied (Salwasser and others in press). Thus some effort should be made to determine the current percentage of occupancy of suitable habitat and then use this percentage to correct for the number of patches necessary to actually maintain 1,000 pairs. All of these considerations point to a need to increase the SOMA objective for the species, at least until better information is available.

Patch size.--In the absence of better guidance, SOMA size should be based on mean size and percent composition of those areas sampled so far where the subspecies has successfully bred. This could be adjusted based on further sampling and the results of the reproductive variability studies.

Distribution.--SOMAs should be located no more than the median (Miller and Meslow 1985) distance of documented successful dispersals. This is conservative but until more data are available it's probably the prudent course to follow. Corridors of mature or old-growth forest, particularly riparian corridors, might aid inter-SOMA dispersal. It is of concern that, to date, radiotelemetry studies in Oregon and northern California have shown very low survivorship rates for dispersing juveniles (Allen and Brewer 1985, Gutiérrez and others 1985, Miller and Meslow-1985). This inevitably raises the question of whether habitat fragmentation has already produced a metapopulation configuration where $m < e$. These findings highlight the need for more work on dispersal and adult survivorship, and patch extinction and colonization rates.

A long-term monitoring research program should focus on estimating adult survivorship; further monitoring pair extinction and colonization rates; and reproductive success across a gradient of SOMA size/percent composition over time. Work should also be instituted to determine what habitat manipulation techniques may be effective and feasible to actively manage the species if it appears the network of reserved areas is failing. It is encouraging that the Pacific Southwest and Pacific Northwest Regions of the USDA Forest Service are actively pursuing the latter recommendation (Salwasser, pers. comm.) [2]/

SUMMARY

The importance of island biogeographic theory to conservation is the attention it has focused on the importance of understanding localized extinctions and colonizations, and the factors affecting these processes, as determinants of the distribution and persistence of species. This focus has triggered an increased appreciation of the role of chance in determining the patterns manifest in nature. The indications that such simple variables as habitat size and isolation may play key roles in determining population persistence in the face of chance events is of crucial importance in an increasingly fragmented world where the land-use patterns imposed by man are often inimical to the survival of certain species. Nowhere is this more evident than in considering the fate of a species whose patchwork of habitat is undergoing alteration. If persistence hinges on the number, size, and interrelationship of patches, at what point will the fabric of habitat be stretched too thin and the species lost? The northern spotted owl in the Pacific Northwest is one current problem that fits this scenario. A new paradigm, or perspective, on population structure and dynamics is essential to deal effectively with the conservation of such species. The metapopulation concept seems an appropriate frame of reference for this class-of problem, yet ecological theory has yet to provide a realistic model to assess even the qualitative behavior of such a population configuration under the influence of all the various types of stochastic perturbations that are likely to affect populations. Even without such models, common sense would indicate that a large number of large patches close together should minimize the loss of species both from particular patches and over all patches. Yet further reasoning from common sense indicates that there may be more subtle effects and these may produce tradeoffs in habitat configurations which, though spatially different, confer the same probability of persistence to the species in question. Determining the existence and form of such tradeoffs is crucial to maximizing management alternatives to "fit nature in."

In the case of the northern spotted owl, valuable data have been gathered but the effectiveness of this information is constrained by the lack of theoretical models to provide qualitative guidance about which data are most important. The current USDA Forest Service approach to the management of this species (Salwasser and others, in press) is encouraging but will benefit by expanding its focus on genetic arguments to include the effects of demographic and environmental effects. The northern spotted owl highlights the whole issue of land-use planning for the conservation of viable populations. This issue is complicated by the lack of a scientific consensus on standards for what constitutes such a population and by the inescapable reality that we are being asked to project

[2]/ Hal Salwasser, National Wildlife Ecologist, Washington Office, Wildlife and Fish Ecology, 3825 E. Mulberry Street, Ft. Collins, CO 80524..

the dynamics of a system without being given the time to examine it empirically or experimentally. I see no solution to this except that pointed out by Salwasser and others (in press): to stimulate theory to provide guidance and generate hypotheses that may be tested in the context of the management programs which will be implemented without complete knowledge. I hope **management will be allowed to** adapt in the future in the light of the experience thus gained.

ACKNOWLEDGMENTS

I thank R. J. Gutiérrez, L. Ruggiero, H. Salwasser, J. Nichols, M. Fuller, J. Ruos, E. C. Meslow, and P. Opler for their helpful reviews of this manuscript. I would also like to thank P. Holt for her tireless and proficient typing.

LITERATURE CITED

Barrowclough, George F.; Coats, Sadie L. The demography and population genetics of owls, with special reference to the conservation of the spotted owl (Strix occidentalis). In: Gutiérrez. Ralph J.: Carey, Andrew B.: tech. eds. Ecology and Management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 1985:74-85.

Brown, J. H.; Kodric-Brown, A. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology. 58:445-449; 1977.

Carey, Andrew B.; Ruggiero, Leonard F. Spotted owl management: meeting NFMA requirements through monitoring. In: Gutiérrez, Ralph J.; Carey, Andrew B.; tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 1985:34-38.

Ehrlich, Paul R. Genetics and the extinction of butterfly populations. In: Schonewald-Cox, Christine M.; Chambers, Steven M.; MacBryde, Bruce; Thomas, Larry, eds. Genetics and conservation: a reference manual for managing wild animal and plant populations. Menlo Park, CA: Benjamin/Cummings Publishing Company: 1983 : 158-163.

Ehrlich, P.; Murphy, D. D.; Singer, M. C.; Sherwood, C. B.; White, R. R.; Brown, I. L. Extinction, reduction, stability and increase: the responses of Checkerspot butterflies to the California drought. Oecologia. 46:101-105; 1980.

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Distribution and biology of spotted owl in Oregon. Wildlife Monograph 87:1984. 64 p.

Frankel, O. H.; Soulé, Michael E. Conservation and evolution. Cambridge, England: Cambridge University Press; 1981. 327 p.

Franklin, Ian Robert. Evolutionary changes in small populations. In: Soulé, Michael E.; Wilcox, Bruce A., eds. Conservation biology: an evolutionary - ecological perspective. Sunderland, MA. Sinauer Associates; 1980:135-149.

Gilbert, F. S. The equilibrium theory of island biogeography: fact or fiction? Biogeography. 7:209-235; 1980.

Gilpin, M. E.; Diamond, J. M. Immigration and extinction probabilities for individual species: relation to incidence functions and species colonization curves. Proceedings National Academy Science USA. 78:393-396; 1981.

Gutiérrez, R.J.; Franklin, Alan B.; LaHaye, William; Meretsky, Vicky J.; Ward, J. Patrick. Juvenile spotted owl dispersal in northwestern California: preliminary results. In: Gutiérrez, Ralph J.; Carey, Andrew B.; tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 1985: 60-65.

Gutiérrez, R. J.; Solis, David Munoz; Sisco, Charles. Habitat ecology of the spotted owl in northwestern California: implications for management. In: Proceedings of Convention of Society of American Forester's: 1983 October 16-20; Portland, OR: Bethesda, MD: Society of American Forester's; 1984:368-373.

Jones, H. L.; Diamond, J. M. Short-time-base studies of turnover in breeding bird populations on the California Channel Islands. Condor. 78:526-549; 1976.

Karr, James R. Population variability and extinction in the avifauna of a tropical land-bridge island. Ecology. 63(6):1975-1978; 1982.

Levins, Richard. Extinction. In: Gerstenhaber, M., ed. Some mathematical questions in biology. Vol. II. Providence, RI: American Mathematical Society. 1970:77-107.

MacArthur, Robert H.; Wilson, Edward O. The theory of island biogeography; Princeton, NJ: Princeton University Press; 1967. 203 p.

Margules, C.; Higgs, A. J.; Rafe, R. W. Modern biogeographic theory: are there any lessons for nature reserve design. Biological Conservation. 24:115-128; 1982.

Miller, Gary S.; Meslow, E. Charles. Dispersal data for juvenile spotted owls: the problem of small sample size. In: Gutiérrez, Ralph J.; Carey, Andrew B.; tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 1985: 69-73.

Ralls, Katherine; Ballou, Johnathon. Extinction: lessons from zoos. In: Schonewald-Cox, Christine M.; Chambers, Steven H.; MacBryde, Bruce; Thomas, Larry, eds. Genetics and conservation: a reference manual for managing wild animal and plant populations. Menlo Park, CA: Benjamin/Cummings Publishing Company; 1983:164-184.

Richter-Dyn, Nira; Goel, Narendra S. On the extinction of a colonizing species. Theoretical Population Biology. 3:406-433; 1972.

Roff, D. A. Spatial heterogenecity and the persistence of populations. Oecologia. 15:245-258; 1974a.

Roff, D. A. The analysis of a population model demonstrating the importance of dispersal in a heterogenous environment. Oecologia. 15:259-275; 1974b.

Roff, D. A. Population stability and the evolution of dispersal in .a heterogenous environment. Oecologia. 19:217-237; 1975.

Ruediger, William C. Implementing a spotted owl management plan: the Gifford Pinchot National Forest Experience. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 10-13.

Salwasser, Hal; Nealey, Stephen P.; Johnson, Kathy. Wildlife population viability - a question of risk. Transactions North American Wildlife and Natural Resources Conference. 49:[in press].

Schonewald-Cox, Christine M.; Chambers, Steven M.; MacBryde, Bruce; Thomas, Larry, eds. Genetics and conservation: a reference manual for managing wild animal and plant populations. Menlo Park, CA: Benjamin/Cummings Publishing Company; 1983. 722 p.

Shaffer, Mark L. Determining minimum viable population sizes: a case study of the grizzly bear. Durham, NC: Duke University; 1978. 192 p. Ph.D. thesis.

Shaffer, Mark L. Minimum population sizes for species conservation. Bioscience. 31(2):131-134; 1981.

Shaffer, Mark L.; Samson, Fred B. Population size and extinction: a note on determining critical population sizes. American Naturalist. [in press].

Simberloff, Daniel. Experimental zoogeography of islands: effects of island size. Ecology. 57:629-648; 1976.

Simberloff, Daniel. Biogeography: the unification and maturation of a science. In: Brush, Alan H.; Clark, George A., Jr., eds. Perspectives in ornithology. Cambridge, England: Cambridge University Press; 1983:411-455.

Soulé, Michael E.; Wilcox, Bruce A., eds. Conservation biology: an ecological-evolutionary perspective. Sunderland, MA: Sinauer Associates; 1980. 395 p.

U.S. Fish and Wildlife Service. The northern spotted owl. A status review. Portland, OR: Endangered Species Program, U.S. Fish and Wildlife Service; 1982. 29 p.

Vance, Richard R. The effect of dispersal on population stability in one-species, discrete-space population growth models. American Naturalist. 123(2):230-254; 1984.

Wilson, Edward 0. Sociobiology: the new synthesis. Cambridge, MA: Belknap Press; 1975. 697 p.

Wright, S. Joseph; Hubbell, Stephen P. Stochastic extinction and reserve size: a focal species approach. Oikos. 41:466-476; 1983.

A SUMMARY OF THE SCIENTIFIC BASIS FOR SPOTTED OWL MANAGEMENT

Andrew B. Carey

ABSTRACT: This paper is based on the presented papers and discussions at the symposium "Ecology and Management of the Spotted Owl in the Pacific Northwest: Conflicts and Opportunities" held in Arcata, California, in 1984. Additional information is drawn from published scientific reports and unpublished administrative study reports. The information is synthesized into a summary of the basis for managing spotted owls. Management for spotted owls has generated controversy because of conflicts with timber production and because there was little information on the ecology of the owl prior to the 1970's. Substantial information on the spotted owl has now been accumulated although much of this information has not been published. The accumulated information shows that spotted owls need old-growth forest to maintain healthy populations. Between 2,000 and 2,500 acres of old growth are used, on the average, by a pair of spotted owls. Existing information suggests that at least 1,000 pairs of northern spotted owls are necessary to maintain a viable population. This will require maintaining more than 1,000 spotted owl management areas because not all SOKAs will be occupied. Existing guidelines for distributing spotted owl management areas seem adequate. Major informational needs include an inventory of old growth, an assessment of how well present management is accomplishing goals for spotted owls, quantitative data on spotted owl demography. and a greater understanding of what constitutes a viable population. Monitoring the results of spotted owl management will be essential to ensure that population goals are met.

INTRODUCTION

A major problem for the resource management agencies in the Pacific Northwest is ensuring that there is sufficient information for managers about the spotted owl (*strix occidentalis*). During the 1970's management for spotted owls achieved regional prominence among wildlife issues because of the owl's apparent dependence on old-growth coniferous forests that also have high value as timber. The spotted owl was described as declining in numbers because of harvesting of timber and was accorded special status by California, Oregon, and Washington (Carleson and Haight 1985, Forsman and others 1982, Gould 1985, Heinrichs 1983, Juelson 1985). Because of its special status, its role as a surrogate for other wildlife associated with old-

ANDREW B. CAREY is research coordinator, Old-Growth Forest Wildlife Habitat Program, Pacific Northwest Forest and Range Experiment Station, Forestry Sciences Laboratory, 3625 - 936 Ave.. S.W., Olympia, Washington 98502.

growth forests, and its prominence in the public arena, the owl was designated a management indicator species by the USDA Forest Service (Carrier 1985, Lee 1985): During the 1980's the spotted owl achieved national prominence because of the conflict between harvesting timber and ensuring that spotted owl populations remain viable as required by the National Forest Management Act (Forsman and others 1982, Heinrichs 1983, Meslow and others 1981). The controversy over the spotted owl was exacerbated by the lack of information available in the 1970's on spotted owl habitat requirements (Heinrichs 1983). Prior to 1977, the only published information was either very general in nature or anecdotal and dealt with individual observations of the bird and its habitat, nests, and food habits. The first quantitative study appeared in a scientific journal in 1977 (Forsman and others 1977). The results of many studies are still in unpublished reports, manuscripts in preparation, or manuscripts in press (Campbell and others, in press). Reviews of the owl's ecology that were used to prepare management recommendations (for example, Zarn 1974, Department of the Interior 1982) had to be based on theses, anecdotes, unpublished reports, and personal communications. Even now there is only one major, published, scientific treatment of the spotted owl in the Pacific Northwest (Forsman and others 1984) and only a few research reports in journals that require rigorous technical review before publication (Barrows 1981, Forsman and others 1977, Marshall 1942. for example). The symposium _Ecology and Management of the Spotted Owl in the Pacific Northwest: Conflicts and Opportunities_ was convened in 1984 (Gutiérrez and Carey 1985) to bring together the rapidly accumulating information on the spotted owl. This paper summarizes the papers in that symposium and other published and unpublished information to analyze the sufficiency of information available to managers.

What Constitutes Sufficient Information?

To determine what constitutes sufficient information for management purposes, six things must be considered: (1) The objectives of the managing agency. (2) The present management situation and the options available to the agency. (3) The accumulated information. (4) Forthcoming information. (5) The state of wildlife science in terms of the development of theory and reliable predictive models. (6) Research needed and the costs, difficulty, methods, and likelihood of obtaining additional useful information in the near future. Each of these is discussed. Much of this analysis is directed towards the Pacific Northwest Region of the USDA Forest Service because it contains a majority of the remaining habitat for northern spotted owl (S. o. _caurina_) habitat. Habitat is also being managed by the Pacific Southwest Region of the Forest Service, and by the National Park Service, and Bureau of Land Management in the U.S. Department of the Interior.

OBJECTIVES OF THE MANAGING AGENCIES

Of all the laws relating to Forest Service activities (U.S. Department of Agriculture 1983). the National Forest Management Act of 1976 provides the clearest, most comprehensive direction both for overall policy and objectives and for managing forests for wildlife. The regulations implementing the act (MacCleery 1982) provide even more specific guidance: the dominant principle of Forest Service planning and management is to "provide for multiple use and sustained yield of goods and services from the National Forest System in a way that maximizes long-term net public benefits in an environmentally sound manner." This balance between producing goods and services and protecting the environment is maintained throughout the act and the regulations and is exemplified in specific, minimum requirements for management. These requirements include maintaining the diversity of plant and animal communities to meet multiple-use objectives and providing habitat adequate to maintain viable populations of existing native vertebrate species.

Both the Pacific Southwest Region and the Pacific Northwest Region of the Forest Service recognize that the spotted owl has special habitat needs and that changes in its population may reflect the effects of management activities. Both regions have adopted plans to maintain viable populations of spotted owls (Carrier 1985, Lee 1985). And both have recognized the value of old-growth coniferous forests as habitat for the spotted owl and other wildlife and as an integral component of natural diversity (Franklin and Spies 1984, Kerrick and others 1984, Salwasser 1984, Sirmon 1984, Teeguarden 1984). Simply stated, the Forest Service objective for spotted owls is to provide an environment that will maintain viable populations of spotted owls throughout their existing range across the National Forests. But the situation facing managers is not simple.

Because the spotted owl depends on mature and old-growth forests, maintaining an environment that is amenable to spotted owls will affect the level of sustained yield of wood products. Viable populations of spotted owls probably would be maintained if mature and old-growth forests were not harvested. But long-term net public benefits might not be maximized. Although the National Forest Management Act of 1976 emphasizes production of goods and services, it also states that multiple use is "not necessarily the combination of uses that will give the greatest dollar return or the greatest unit output." Viable populations of spotted owls must be maintained within a management arena that dictates minimum impact on the harvest and production of timber. Additional information on spotted owls is required primarily because of the need to balance spotted owl populations and wood products.

What kind of information do managers need to achieve this balance? To a major extent, the need for information is conditioned by the options that are available. If, in the current management situation, there is a great surplus of owls and owl habitat, managers will have many choices. If the spotted owls and their habitat are already near minimum levels, few choices are left. If suitable habitats can be created in a short time, more options are available than if a long time is required o- if habitat cannot be recreated.

If the management situation is favorable (many options exist), then precise and accurate descriptions of the requirements of spotted owls could be used to select habitat management areas. But if few options exist, then the information that is more qualitative than quantitative would be sufficient because few choices could be made. The situation is complicated further by the lack of a clear understanding of what constitutes a viable population. Information on the spotted owls must be placed in a theoretical framework that defines "viable population." The theory is relatively undeveloped as is the concept of dependency of a species on particular types and amounts of habitat (Barrowclough and Coats 1985; Carey 1984; Shaffer 1981, 1985).

THE PRESENT MANAGEMENT SITUATION AND OPTIONS AVAILABLE

Old Growth and Spotted Owls

Of the 15 million acres of old-growth (250-750 years old) forest (forests 250 to 750 years old) present in the Pacific Northwest in the l800's, about 5 million acres remain. About 1 million acres are reserved in national parks, wilderness areas, and research natural areas in western Washington and Oregon (Franklin and Spies 1984). About 25 percent of the National Forests in the Pacific Northwest west of the crest of the Cascade Range consist of forests more than 250 years old and amount to 2-l/2 million acres (Sirmon 1984). Some of the old growth is subalpine forest not suitable for spotted owls. The distribution of old-growth (and mature) forest is not even. Old growth is concentrated in the national parks and in the National Forests along the west slope of the Cascade Range. Old growth is not abundant in the valleys and mountains west of the Cascade Range except in parts of Olympic National Park. The State of Washington, Department of Game, feels that the remaining habitat on the Olympic Peninsula is insufficient to support a viable population of spotted owls (Juelson 1985). Certainly the amount of old growth remaining in the Olympic National Forest is insufficient (Beckstead 1985). The State of Oregon, Department of Fish and Wildlife, is concerned about the population in the Oregon Coast Range because of the relatively small amounts of old growth that remain and because plans are to remove much of the remaining old growth (Carleson and Haight 1985). The present populations of spotted owls are about 1,200 pairs in Oregon (Carleson and Haight 1985), 1,000 pairs in Washington (U. S. Department of the Interior 1982), and 1,260 pairs (of two subspecies) in California (Gould 1985). These populations will probably decrease with continued harvesting of mature and old-growth timber (Forsman and others 1982).

The Spotted Owl Management Plan

Present management of spotted owls in National Forests in Oregon and Washington is based on the "Spotted Owl Management Plan" (unpublished) prepared by the Oregon-Washington Interagency Wildlife Committee. The committee based its recommendations on the preliminary results of research conducted by Eric Forsman of Oregon State University; the plan and the events relating to the formulation of the plan are summarized by Forsman and others (1982). Forsman's research has been published (Forsman and others 1984, Forsman and Meslow 1985). The final recommendations of the committee were adodpted by the Pacific Northwest Region (Lee 1985) and the Pacific Southwest Region (Carrier 1985) of the Forest Service but not by the Oregon State Office of the Bureau of Land Management (Carleson and Haight 1985). Initially both Federal and State agencies were reluctant to adopt the committee's recommendations because of the lack of information on spotted owls. The state forestry agencies of California, Oregon, and Washington still have not accepted the recommendations. Even so, there is concern about whether or not the Federal agencies are doing enough (or conversely, doing too much at the expense of other resources) for the spotted owl (Carleson and Haight 1985, Gould 1985, Heinrichs 1983, Juelson 1985, La Follette 1979. Lee 1985).

Current management plans of Federal agencies (Forest Service, National Park Service, and Bureau of Land Management) would preserve the habitat of 800 to 1,000 pairs of northern spotted owls in the Pacific Northwest. The Forest Service has set goals of maintaining 530 pairs of spotted owls in Washington and Oregon (Lee 1985) and 500 pairs (of all subspecies) in California (Carrier 1985).

Options

What options are there for managers? The Pacific Northwest Region considered 533 pairs for its minimum goal and 690 pairs as an alternative high goal. Thus the managers in the Region had a fair range of options available. But the Region is reassessing the range of options, and the associated risks, through preparation of a supplemental environmental impact statement on the regional guide for forest plans. Individual National Forests in the Pacific Southwest Region are also considering alternative goals. The options available to the Bureau of Land Management are not clear. The National Park Service is charged with maintaining a natural environment, a charge that is compatible with maintaining spotted owl populations.

A full exploration of the options available to the Federal management agencies has not been possible because there is no inventory that contains the locations, sizes, and characteristics of the mature and older stands not scheduled for harvest. It is not possible without such an inventory for researchers to determine the present distribution of stands and the possible arrays that could form alternative networks for maintaining spotted owls. It also is not possible to select stands of specific structural characteristics, sizes, and distributions to ensure that if a minimum number of owls are maintained, they will be maintained in the highest quality environment.

THE ACCUMULATED INFORMATION

Spotted Owl Distribution

Bent (1938) reported that the spotted owl inhabited a variety of forested environments in western North America ranging from dense, coniferous forests in British Columbia to pine-oak woodlands in Mexico. However no sightings of spotted owls have been reported in British Columbia in recent years (Howie 1980). Until 1970, the spotted owl was thought not to commonly occur in the Pacific Northwest; only 24 sightings of spotted owls in Oregon had been recorded (Forsman and others 1982). Since 1972 numerous surveys for spotted owls have been conducted by biologists employed by Federal and State agencies, industry, and private organizations. Some results have been published (Erckman 1982; Forsman and others 1977, 1982, 1984; Garcia 1979; Gould 1977; Marcot and Gardetto 1980; Postovit 1979); others have not (many are listed by Campbell and others in press); and some surveys are ongoing (for example, Allen and Brewer 1985). Forsman and others (1982) tabulated many of the 1972-81 surveys: spotted owls had been located at over 400 sites in California, 600 sites in Oregon, and 200 sites in Washington. The population size for the northern spotted owl (S.o. caurina, the subspecies in the Pacific Northwest) was estimated to be roughly 2,500 pairs (U. S. Department of the Interior 1982).

Spotted Owl Habitat

Survey results.--Although many of the sites surveyed by biologists have not been described using standard, quantitative measures, the records show the most spotted owls were found in late seral forests; this substantiates the observations of naturalists during the early 20th century that the spotted owl was associated with old, virgin forest.

Forsman and others (1984) describe 595 sites in Oregon that were occupied by spotted owls, perhaps 50 percent of the occupied sites in Oregon. Most (98 percent) of the sites were old-growth (more than 200 years old) coniferous forests or virgin forests that were mixtures of mature stands (100 to 200 years old) and old-growth stands. The salient features of the occupied sites were: an overstory composed of trees 230 to 600 years old; an understory of trees 30 to 200 years old, canopy closure averaging 65 to 80 percent as a result of the uneven-aged, multilayered structure; and the presence of broken tops, deformed limbs, and heart rot in large trees. Of 47 nests located. 90 percent were in the classic old growth just described; the remainder were in younger forests that contained scattered old-growth trees. Nest trees averaged 49 inches in d.b.h. (diameter at breast height) and none were less than 29 inches in d.b.h. Nests were 39 to 180 feet above the ground averaging 75 feet in cavities or broken tops of trees or on platforms of sticks and debris on tree limbs.

Other, less extensive surveys gave the same results as Forsman's. Cordano and Cordano,1/ surveyed dense stands of mature to old-growth timber near streams in northern California. They found owls in 80 percent of the stands. Marcot and Gardetto (1980) surveyed a variety of stands in northern California: 95 percent of the owls they encountered were in mature or old-growth stands, which occupied only one-third of the area surveyed. Spotted owls were three times more abundant in old-growth forests than in mature forest. Gould (1977) describes 192 sites where he found spotted owls in northern California. The owls were found in dense, virgin, coniferous forests between 98 feet and 7,500 feet elevation. The sites contained mature forests with trees greater than 33 inches d.b.h., a variety of tree species, a multilayered canopy, canopy closure greater than 40 percent, and a moderate degree of decadence. In Oregon, Forsman and others (1977) surveyed areas in the Cascade and Coast Ranges, including extensive areas of second-growth forests 40-90 years old. Owls were 12 times more abundant in old growth than in forests that were less than 80 years old. Postovit (1979) surveyed extensive areas, including unbroken second growth, in the Cascade Range and the Olympic Mountains of northwestern Washington. Spotted owls were five times more abundant in old-growth forests than in younger forests. Only one owl was found in unbroken second growth. Abundance rapidly declined with declining proportions of old growth. Garcia (1979) surveyed stands of various ages in the Gifford Pinchot National Forest in southwestern Washington. He found owls in stands ranging in age from 60 to over 200 years old, but his data were too few for comparing age classes. Erckman (1982) found spotted owls to be widely distributed in old-growth forests in the Mount Baker-Snoqualmie National Forest in northwestern Washington. He concluded that all old growth was not of equal value to spotted owls. Areas below 3,200 feet in elevation and containing major creek drainages had higher owl densities than higher, drier sites. Forsman and others (1984) and Gould (1977) also found altitudinal limits and commented on the need for water.

Radio telemetry results.--Radio telemetry studies of adult spotted owls in mosaics of old-growth, mature, and young stands in western Oregon (Forsman and others 1984) and northern California (Gutiérrez and others 1984) confirmed the association of spotted owls with mature and old-growth stands. Ongoing studies in Washington are obtaining similar results (Allen and Brewer 1985).

In Oregon, home ranges of individual spotted owls encompassed 1,356 to 8,349 acres, averaging 2,907 acres in the Cascades where 55 percent of the area studied was in old growth and 4,725 acres in the

---

1/ Unpublished administrative study report, 1981, "A Preliminary Study of the Spotted Owl on the Corning Ranger District," by Anette Cordano and Marty Cordano, U. S. Department of Agriculture, Forest Service, Mendocino National Forest, 420 E. Laurel Street, Willows, CA 95988.

Coast Range where 20 percent of the area studied was in old growth The amount of old growth encompassed in the home ranges was 741 to 2,878 acres, averaging 1,988 acres in the Cascades and 1,245 acres in the Coast Range. None of the six pairs of spotted owls studied had less than 1,008 acres of old growth in its range (Forsman and others 1984, Forsman and Meslow 1985). The average amount of old growth in a pair's range was 2,264 acres (Forsman and Meslow 1985). These figures and all the figures for owls in the Coast Range are based on only 4 months of study during summer. In the Cascade Range, owls were studied from 9 to 13 months; the data indicated that 4 months of study are insufficient to adequately determine total home range use. The owls used old growth for foraging 64 to 99 percent of the time despite the low proportions of their ranges in old growth (20 to 66 percent). Owls spent 0 to 16 percent of their time foraging in mature stands and 0 to 36 percent in young (61 to 80 year old) stands. The owls also foraged in 25- to 35-year-old forests in the Coast Range (0 to 31 percent of the time) but not preferentially (up to 47 percent of the home ranges were 25- to 35-year-old forests). The only preference (use out of proportion to occurrence) demonstrated was for old growth. More than 1,600 roosts were located; 91-98 percent were in old-growth forest; 90 percent of the nests located were in old-growth forest.

Preliminary results of two northern California studies were reported by Gutiérrez and others (1984). Home range sizes for six owls were 741 to 3,705 acres or an average 2,245 acres. Home ranges of adult pairs exceeded 3.000 acres and contained more than 2,000 acres of mature and old-growth forests. Mature and old-growth forests comprised 22 to 52 percent of summer home ranges and 11 to 66 percent of winter home ranges. Mature forests in the California study area were more than 150 years old and had multilayered canopies; dominant trees were larger than 39 inches d.b.h. [2]/[3]/ Late seral stage forests were used out of proportion to their occurrence. Data analysis is incomplete, but results to date agree with the results reported by Forsman and others (1984) (Gutiérrez and others 1984). In both studies home range size increased as the proportion of old growth decreased, further substantiating the need for some minimum area of mature and old-growth forest.

A correlation was also found in radio telemetry studies in Washington between home range size and the amount of old growth contained in the home range. Three adult pairs had an average of 1,850 acres of old growth in their home ranges (Allen and Brewer 1985).

Laymon (1985) is conducting radiotelemetry studies on California spotted owls (S. o. occidentalis) in the Sierra Nevadas. He has observed a marked altitudinal shift in home range from summer to winter. The four owls he monitored moved 12 to 20 miles to areas that were an average of 2,296 feet lower in elevation than were the summer home ranges. These owls returned to their summer home ranges in the spring. Seasonal adjustments in home range have been noted by all the biologists studying the northern spotted owl, but none of these adjustments approached the migratory nature of the California spotted owl observed by Laymon. Laymon's research underscores the importance of studying a species throughout its range.

Radio telemetry studies have shown that dispersing juvenile spotted owls will frequent young forests and even clearcuttings. But mortality rates of juveniles are very high. Juveniles have the capability to disperse long distances before dying (up to 61 miles, but averaging 15 to 28 miles, depending on the area). There is no such information on successful dispersers (owls that disperse, establish a territory, mate, and produce offspring). The juveniles do not cross large bodies of water (for example, reservoirs or Hood Canal). They will cross rivers 246 to 328 feet wide. They often disperse along forested corridors, such as riparian areas, and they will cross ridges. Studies of dispersing juveniles are being conducted in California, Oregon, and Washington (Allen and Brewer 1985, Gutiérrez and others 1985, Laymon 1985, Miller and Meslow 1985).

A test of a habitat model.--Laymon [4]/ developed a Habitat Suitability Index model for spotted owls based on Forsman's research with some consideration of other studies. The model includes tree size, canopy closure, vertical layers of vegetation, and area. The model was tested on the Eldorado National Forest in California. The test confirmed the association of spotted owls with large trees (greater than 36 inches d.b.h.), high canopy closure (70 to 100 percent), and multilayered understory.

Summary of spotted owl habitat.--Spotted owls in the Pacific Northwest use all the major coniferous forest associations except subalpine forests and forests of ponderosa pine (*Pinus ponderosa* Dougl. ex Laws), lodgepole pine (p. *contorta* Dougl. ex Loud.), or sitka spruce (*Picea sitchensis* (Bong.) Carr.). Some hardwood stands are used. Spotted owls are most abundant in old-growth forests characterized by an uneven-aged, multilayered canopy with a high composite canopy closure. Dominant trees are large (39 inches d.b.h. or larger) and old (over 230 years) and many have broken tops. cavities, or deformed, platform-

---

2/Personal communication, R. J. Gutiérrez. Humboldt State University, Arcata, CA 95521.

3/ Unpublished administrative study report, "Winter Ecology of Radio-Tagged Owls on Six Rivers National Forest, Humboldt County, CA," by Chuck Sisco. Humboldt State University, Arcata, CA 95521.

b/Unpublished Administrative Study Report, "A test of a spotted owl habitat suitability model," by Stephen A. Laymon, University of California, Berkeley, College of Natural Resources, Berkeley, CA 94721.

forming branches. Understory trees are 30 to 200 years old. Some of the understory trees are small, often are deciduous (such as vine maple, Acer circinatum Pursh.) and provide perches-almost to the forest floor. Abundance of spotted owls varies with the proportion of old growth in the forested landscape. But the owls can do well in mosaics of old-growth, mature, and young stands. In extensively harvested forests, spotted owls expand their home ranges as fragmentation increases, presumably to maintain some minimum amount of old growth within their ranges. Averages (depending on area) are 1,850 to 2,265 acres of old growth per pair. Obviously, the owls cannot expand their range indefinitely (observed ranges are 1,356 to 8,349 acres); as they reach the higher limits their ability to survive and reproduce must be diminished. The average home range size in highly fragmented forests is around 4,693 acres and can be used as a basis for management. An area of 4,849 acres is encompassed by a circle with a radius of 1.5 miles. Forsman and others (1984:57) felt that 988 acres of old growth within 1.5 miles of a nest tree would be adequate habitat for a pair of spotted owls, even when the remaining acreage was covered by stands less than 80 years old. The 988-acre recommendation was based on the least amount of old growth in the home ranges of the pairs of owls Forsman studied. One pair, studied for 4 months, had 1,008 acres of old growth in its home range. No other pair had less than 2,092 acres of old growth in its home range (Forsman and Meslow 1985). Habitat management for spotted owls could be based on the average amount of old growth used by pairs in the Pacific Northwest (1,850 to 2,265 acres). For example, if 2,470 acres of old growth were maintained along with stands of a variety of other ages (including 80- to 200-year-old trees) within a 1.5 mile-radius-SOMU (spotted owl management unit-habitat for one pair), the chance of maintaining a pair of spotted owls in a SOMU would be substantially improved. If use of the SOMU by a pair of owls were documented, the manager could then be reasonably confident that the SOW was contributing to maintaining a viable population of spotted owls.

How reliable is the above information? Forsman's studies (Forsman and others 1977, 1984) and Gould's studies (1977, 1985) were based on unusually large sample sizes compared to other studies of raptors. The results of these studies were confirmed by smaller studies and by the preliminary results of two recent studies in California (Gutiérrez and others 1984, Gutiérrez 1985) and ongoing studies in Washington (Allen and Brewer 1985). But only a dozen pairs of adult owls have been studied with telemetry. Additional quantitative data will be forthcoming (Carey and Ruggiero 1985). It is unlikely that the description of suitable environments and the minimum recommendations will be lowered by forthcoming data, but data specific to a state or region are being gathered. Some tailoring of habitat management to local conditions may be possible.

Determinants of Habitat

Why are spotted owls associated with old-growth forests in the Pacific Northwest? A number of reasons have been proposed; they can be grouped into six loosely-formulated hypotheses that are not mutually exclusive: nesting hypothesis, heat-stress hypothesis, prey-abundance hypothesis, prey-availability hypothesis, predation hypothesis, and adaptation hypothesis.

Nesting hypothesis.--Old-growth forests are more likely to contain trees that are structurally suited for nests than are young forests. The spotted owl does not construct a nest. It must therefore find natural platforms that are suited for holding the female, eggs, and young birds. Because the spotted owl is a large bird, the platform must be large. To safeguard the eggs and young from terrestrial and semiarboreal predators the nest must be high above ground. Thus the platform must be part of a large tree. Suitable platforms include large cavities in trees, depressions in the broken tops of trees, and platforms resulting from the accumulation of organic material on the fan-shaped branches of old-growth trees. This hypothesis is supported by the descriptions of the nests of spotted owls that have been found in Pacific Northwest forests (Forsman and others 1984).

Heat-stress hypothesis.--Spotted owls are intolerant (compared to many other owls) of high temperatures and are stressed at temperature above 27 to 31°C (depending on wind speed). This temperature intolerance is a function of the owl's plumage which is adapted for withstanding the stress of cold winter temperatures (Barrows 1981, Barrows and Barrows 1978). The tall, multilayered canopy of old-growth forests results in a larger gradient in temperature (and amount of direct solar radiation) than exists in forests with shorter, simple, canopy structure. The multi-layered canopy provides roost perches that range from high in the canopy down to ground level. In particular, hardwoods in the understory (such as vine maple) allow roosting close to the ground. Field studies of roosting behavior and heat stress have employed meterological equipment, radio telemetry, direct observation, and characterization of roosts and roost-stands. Owls change roosts (especially height) and body posture to avoid direct sunlight in the summer and to find ambient temperatures lower than 27 to 31°C. Stands in California used for roosting were often on north-facing slopes and in canyons. Owls in California have also been observed to change roosting locations to be near water and, when heat stress still resulted in physiological reactions (gular flutter), to bathe (Barrows 1981, Barrows and Barrows 1978). Owls in Oregon exhibit similar behavior, but unexpectedly most owls in the Coast Range roosted in stands on south-facing slopes (Forsman and others 1984). The putative association of spotted owls with old-growth stands that contain streams or seeps lends further support to the heat-stress hypothesis, as does the association of spotted owls with caves and canyons in the Southwest. Laymon (1985) observed altitudinal shifts in home range in the Sierra Nevada with the owls using higher elevations in the summer than in the winter; the reasons for these shifts are net known at this time but the phenomenon does fit this hypothesis. The hypothesis does not explain why spotted owls are not known to occur at high elevations in Oregon and Washington.

Prey-abundance hypothesis.--Spotted owls prey on a wide variety of animals. They specialize in small mammals such as red tree voles (*Arborimus longicaudus*), deer mice (*Peromyscus maniculatus*), dusky-footed woodrats (*Neotoma fuscipes*), and northern flying squirrels (*Glaucomys sabrinus*); the latter two species are preferred--the woodrat in mixed conifer forests in California and Oregon and the flying squirrel in Washington and most of Oregon (Barrows 1985, Forsman and others 1984). A greater diversity of prey is eaten by spotted owls in the Sierra Nevada, with gray squirrels (*Sciurus griseus*) and birds assuming importance (Layman 1985). Barrows (1985) has noted that owls that eat a high proportion of large prey (flying squirrels and woodrats) have greater success in breeding than do owls that eat small prey. Owls expend less energy per unit of food in capturing the large prey, thus presumably more energy is available for reproduction than when the majority of the prey is small animals. A hypothesis has been advanced that the preferred prey is more abundant in old-growth forests than in younger forests. Raphael and Barrett (1984) found small mammals, as a group, more abundant in "large timber" than in "medium timber" or "small timber." Dusky-footed woodrats and deer mice were more abundant in forests older than 250 years than in forests 150-250 years old or younger than 150 years. Both species were also abundant in shrub-sapling stages. Raphael and Barrett did not, however, adequately sample northern flying squirrels. Thus there are few data to support the hypothesis. Ongoing studies by the Forest Service (Ruggiero and Carey 1984) will answer the questions about prey abundance across the sere of forest development.

Prey-availability hypothesis.--The prey-availability hypothesis differs from the prey-abundance hypothesis by stating that the prey of the spotted owl is abundant in old growth, but not necessarily more abundant there than elsewhere. The key feature is 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. Gutiérrez and others (1984) mention this hypothesis. Foraging perches are more available in old growth, and patchiness in the understory and gaps in the canopy may provide a better environment for foraging than do young forests. Testing this hypothesis in field studies would be difficult, but Forsman and others (1984) observed foraging behavior and documented that spotted owls select old growth for foraging. Their study lends support to the hypothesis. Gutiérrez and others (1984) reported that they had unpublished data to support the hypothesis also. Some of these data include observations of spotted owls using perches in riparian corridors and in the edges of old-growth and mature forest to search for prey in clearcuttings and brushfields.5/

Predation hypothesis.--Great horned owls (*Bubo virpinanus*) will prey upon juvenile spotted owls (Forsman and others 1984, Gutiérrez and others 1985, Miller and Meslow 1985); thus it is hypothesized that spotted owls use old growth or avoid open areas) to avoid predation by great horned owls. The evidence for this hypothesis is anecdotal as there is no evidence of intensive predation on adult spotted owls or that predation on juveniles is anything but opportunistic. It is generally accepted however, that dispersing juveniles of most species are especially vulnerable to predation. The apparent reluctance of both juveniles and adults to cross large open spaces like large bodies of water may reflect this vulnerability. Extensive forest fragmentation could affect the ability of juveniles to disperse successfully.

Another interspecific interaction may become important. Barred owls (Strix varia) are extending their range and are now found in western Washington, Oregon, and California. The barred owl is very much like the spotted owl, except it seems to be more versatile. The barred owl may become a serious competitor of the spotted owl Gutiérrez and others 1984, Taylor and Forsman 1976). Harriet Allen6/ has been recording sightings of barred owls and monitoring adjacent pairs of barred owls and spotted owls to determine how they interact.

Adaptation hypothesis.--The adaptation hypothesis states that spotted owls are behaviorally and physiologically adapted to old-growth forests simply because old growth has been the dominant, stable feature of the landscape for many generations of spotted owls. This hypothesis would be impossible to test. There is some evidence that spotted owls do exhibit behaviors such as site tenacity (Forsman and others 1984). Old growth may be a "niche gestalt" (James 1971) for dispersing juvenile--in other words, dispersing juveniles seek areas of a certain structure that are not occupied by adult owls and settle in such areas as a response to the structure. This response could be innate or it could reflect the owl's fledging environment.

Summary of determinants of habitat.--The various hypotheses and the supporting evidence provide a description of spotted owl life requirements that eliminate the need for terms like old-growth, mature, and young forests. It is clear that spotted owls need stands: (1) that are multi-layered with an understory (often containing

---

5/ Unpublished adminstrative study report, "Winter Ecology of Radio-Tagged Spotted Owls on Six Rivers National Forest, HuM ldt Co., CA," by Chuck Sisco, Humboldt State University, Arcata. CL 95521.

6/Personal communication, Harriet Allen. Washington Department of Game, 6OC North Capitol Way, Olympia, WA 98504.

hardwoods), a midstory, and an overstory; (2) that contain large (39 to 67 inches in d.b.h.) trees that contain cavities, depressions in broken tops, or platforms of large branches and organic debris at least 33 feet above the ground; and (3) that concomitantly support abundant populations of small mammals, particularly flying squirrels or woodrats. Large, fallen, decayed trees contribute to the abundance of small mammals (Maser and Trappe 1984) and streams and seeps would further raise the quality of the stand for spotted owls. Many will equate such stands with old growth as described by Franklin and others (1981) and Franklin and Spies (1984). Franklin and others (1981) suggested that old-growth stands should be maintained in blocks of 296 to 494 acres to maintain their ecological characteristics. And that 494 to 988 acres of old growth are needed to influence the character of a third-order stream drainage. Empirical data (Forsman and others 1984, Gutiérrez and others 1984) indicate that 2,470 acres will make 7.7 square miles suitable for one pair of spotted owls. The greater the proportion of the landscape in multilayered and closed-canopy stands, the greater the number of pairs of spotted owls that can be maintained.

Managing for Viable Populations

Federal regulations direct the Forest Service to maintain viable populations of indigenous wildlife. The regulations state that a viable population is "one which has the estimated numbers and distribution of reproductive individuals to insure its continued existence is well distributed in the planning area" (MacCleery 1982). Habitat must be managed not only to maintain this minimum number but also to ensure interaction among the individuals. The key phrases in the regulations are "continued existence," "well distributed," "interact with others," and "habitat must be provided."

Continued existence of spotted owls.--Federal and State agencies plan to maintain 800-1,000 units of habitat suitable for pairs of spotted owls in northern California, Oregon, and Washington to ensure the continued existence of spotted owls. The Pacific Northwest Region of the Forest Service plans to maintain 530 of these SOMUs (Lee 1985). The adaptive management approach to managing for viable populations that is used by the Pacific Northwest Region is summarized by Salwasser and others (1984).

Two classes of factors work against the continued existence of wild populations: systematic factors are continuing or recurring events; stochastic factors are unpredictable or random changes in a species' demography, environment, or genetics and natural catastrophes (Shaffer 1981, 1985).

Systematic factors include expanding human populations, land use changes, and timber harvests. The migration of spotted owls between midelevation federal lands and low-elevation private lands in the Sierra Nevada subjects the owls to land use changes brought about by expanding human populations. Although the development is on private land, owl populations on federal lands are affected (Laymon 1985). Systematic harvests of timber have reduced the amount of spotted owl habitat; continuing harvests in the Coast Range are jeopardizing the continued existence of spotted owls there (Carleson and Haight 1985). Land exchanges among Federal agencies and private landowners and timber harvest on private land affect spotted owls and management of spotted owl habitat on federal lands in Oregon and Washington (Ruediger 1985). Past systematic timber harvest, including timber harvests on Federal land, has jeopardized the spotted owl population of the Olympic Peninsula (Beckstead 1985, Juelson 1985). Forsman and others (1982) conclude that if the trends in timber harvest continue, spotted owls will become rare in the Pacific Northwest.

Demographic stochasticity refers to chance events in survival and reproductive success. Spotted owlssuffer accidents, are preyed on occasionally, and are variable in producing young from year to year (Barrows 1985, Forsman and others 1984; Gutiérrez 1985; Gutiérrez and others 1984, 1985; Miller and Meslow 1985). The survival of juveniles from hatching, through fledging and dispersal, to establishing a territory and acquiring a mate is subject to so many chance events that it is rare (Allen and Brewer 1985, Gutiérrez and others 1985, Miller and Meslow 1985). The structure of a population (sex ratio, age structure, proportion of adults that breed) may reflect many random events.

Environmental stochasticity includes temporal variation in weather, in the owls' habitat, and in the species populations the owls interact with--prey, competitors, and parasites. Ongoing studies by the Old-Growth Forest Wildlife Habitat Program (Forest Service) are documenting marked annual variation in the population sizes and reproduction of the small mammals that serve as prey for spotted ow1s. 7/ Juvenile spotted owls are sometimes killed by great horned owls or other raptors (Forsman and others 1984, Gutiérrez and others 1985, Miller and Meslow 1985). The probability of an owl being preyed on is partially a function of the pattern of abundance of its potential predators, which in turn is a function of systematic and stochastic factors that affect the predators' populations and is due partially to chance. A potential competitor of the spotted owl, the barred owl, is expanding its population in the Pacific Northwest and may usurp some of the habitat maintained for spotted owls (Taylor and Forsman 1976, also see footnote 6). Present interactions between the two species are rare and by chance; in the future, barred owls could bring systematic pressure to bear on spotted owls. Juvenile owls leave the nest before they can fly probably because of increasing numbers of parasites in the nest (Forsman and others 1984). Leaving the nest at an early age increases the susceptibility of young owls to accidents and

---

7/Unpublished data on file. Forestry Sciences Laboratory, 3625 - 93d Avenue SW, Olympia, WA 98502.

predation. Ruediger (1985) documents how unpredictable changes in habitat, such as destruction by high winds or by small wild fires, have affected the carrying capacity of the Gifford Pinchot National Forest for spotted owls.

There are no data on the genetics of spotted owls, but Barrowclough and Coats (1985) discuss spotted owl demography in the light of current genetics theory. They illustrate how chance genetic events can be of great importance when populations are small. They also point out the differences between effective population size and total population size. Effective populations (from a demographic-genetic standpoint) are much smaller than total populations.

Natural catastrophes play an important role in forest ecosystems in the Pacific Northwest. The nature and distribution of old-growth forests are results of catastrophic fires that occurred 200-1,200 years ago (Franklin and Dyrness 1973). Large areas of spotted owl habitat in the Cascade Range of southern Washington were destroyed in the early 1980's by the volcanic eruption of Mount St. Helens (Ruediger 1985). There is an interplay between systematic and stochastic factors. Systematic factors may depress population levels. At low population sizes, stochastic factors are of great importance. In at least two areas (the Coast Range in Oregon and the Olympic Peninsula in Washington) systematic factors have reduced spotted owl populations to the level where stochastic events may determine whether or not the populations persist. Indeed spotted owls have already been essentially eliminated from the Coast Range in northern Oregon and southern Washington. In other areas (northern California and the Cascade Range in Oregon and Washington) systematic factors continue to deplete spotted owl habitat and are probably a greater influence on spotted owl populations than are stochastic events. Barrowclough and Coats (1985) suggest that the 800-1,000 SOMUs (habitat for one pair) planned for the Pacific Northwest will be adequate to minimize stochastic demographic and genetic effects in a "best case,, implementation scenario. Shaffer (1985) concludes that more than 1,000 SOMUs must be provided to maintain the 1,000 pairs of adult owls that he feels are necessary to minimize stochastic environmental effects. Ensuring 1,000 pairs requires more than 1,000 SOMUs because not all SOMUs will be occupied by pairs all the time.

Distribution.--Forest Service guidelines for spotted owl management incorporate requirements for distribution and interaction. 8/ Spotted owl management areas (SOMAs) are to provide habitat for three or more pairs of spotted owls and are to be 12 miles or less apart. Single-pair SOMAs (equivalent to a SOMU) are to be established only to improve the distribution of SOMUs and must be 6 miles or less from other SOMUs. Implementation of the guidelines for distribution and interaction has required more SOMAs than were thought necessary for continued existence from the standpoint of population size (Beckstead 1985, Carrier 1985, Lee 1985. Ruediger 1985). These guidelines still seem reasonable in the light of additional information on spotted owl dispersal Gutiérrez and others 1985, Miller and Meslow 1985). It is difficult however, to meet the guidelines in the Coast Range (Carleson and Haight 1985) and on the Olympic Peninsula (Beckstead 1985). The guidelines do not (and cannot) ensure interaction among all spotted owl populations. The population on the Olympic Peninsula seems to be isolated from all others by Puget Sound, extensive human development in the Puget Trough, and large areas of unsuitable habitat in the Chehalis Valley and southward. The populations in the Cascade Range in Washington may be isolated from those in the Cascade Range in Oregon by the Columbia River. Similarly, the Willamette Valley may separate Coast Range populations from Cascade Range populations in Oregon. And the guidelines do not account for stochastic environmental events, catastrophes, or chance demographic events that result in unoccupied SOMAs. The guidelines assume that SOMAs will persist indefinitely and will be occupied routinely.

Habitat.--Simply defined, habitat is the area occupied by one or more individuals of a species. The Pacific Northwest Region management guidelines (see footnote 8) define the requirements of a reproducing pair of spotted owls as 300 acres of old growth in a core area around a nest and an additional 700 acres of old growth in patches larger than 30 acres within 1.5 miles of the nest. If there is not 1,000 acres of old growth within 1.5 miles of the nest, then the oldest stands available may be substituted for the lacking old growth.

It has not been possible to locate SOMUs on the basis of actual nesting sites and home ranges; SOMUs and SOMAs have been established using crude surveys for spotted owls and old growth and to minimize land-use conflicts (Beckstead 1985, Ruediger 1985). To be effective, SOMAs must contain pairs of adult owls that fledge young from time to time. It is not safe to assume that all l,OOO-acre areas of old growth (or a mixture of old-growth and mature forest) will contain a reproductively active pair of spotted owls. In general, old growth is habitat for spotted owls. But in specific instances, to be habitat the forest must contain nesting, roosting, and foraging-sites, a sufficient abundance of prey, a suitable microclimate, and spotted owls to be habitat. The l,OOO-acre guideline is based on the smallest area of old growth known to support a pair of spotted owls in a heavily fragmented forest for a 4-month period; the average acreage of old growth per pair in that forest during the 4 months was over 2,000 acres (Forsman and Meslow 1985). Thus one would expect, and experience has shown, that many apparently suitable areas (as defined by the guidelines) do not contain spotted owls (Beckstead 1985, Ruediger 1985). Therefore the size and character of SOMAs must be ultimately

---

8/Unpublished administrative document, 1983. "Regional Guidelines for Incorporating Minimum Management Requirements in Forest Planning,, Jeff M. Sirmon. Pacific Northwest Region, USDA Forest Service, 319 S.W. Pine Street, Portland, OR 97208.

determined by verification procedures and monitoring (see Carey and Ruggiero 1985). One approach would be to designate more than 1,000 acres of old growth per pair until occupancy of the SOMAs has been verified and monitoring has shown that pairs are reproducing and that most spotted owl pairs can exist and fledge young with 1,000 acres of old growth.

Summary of managing for viable populations.--The accumulated information relevant to ensuring viable populations of spotted owls in the Pacific Northwest includes the following findings and conclusions:

1. The existing guidelines for the network distribution of SOMA's still seem reasonable in view of recent research on dispersing owls.

2. Original studies showed that the average amount of old growth in the ranges of owl pairs is around 2,200 acres. Subsequent studies corroborated that work.

3. Distributional guidelines require a network of 800-1,000 spotted owl management units. A demographic analysis concentrating on genetics concludes that 1,000 pairs of owls would be adequate for ensuring continued existence throughout the existing range only in a "best case,, scenario. And a viable population analysis considering systematic and stochastic factors conclude that more than 1,000 management units would be necessary to maintain 1,000 pairs of owls. The viable population analysis is corroborated by case histories of implementation of spotted owl management plans and the preliminary results of a monitoring program for spotted owls.

4. Monitoring can be used to determine occupancy rates and rates of loss of habitat. The results of monitoring could be used to determine how many management areas would have to be set aside to ensure that a minimum of 1,000 pairs of spotted owls would be maintained and what margin of safety (additional management units) would be necessary to offset loss of management units to unforeseen events.

5. Management for viable populations of spotted owls will be effective only if there is close collaboration among land management agencies to implement a common management scheme. That situation does not exist today. State and Federal agencies have not adopted the same guidelines. The Forest Service, which manages the majority of the remaining suitable habitat, is carrying the primary burden of owl management. Also, the National Park Service, because of its mission to maintain natural environments, is protecting the spotted owl habitat on its lands.

FORTHCOMING INFORMATION

A review of ongoing research and monitoring Gutiérrez and Carey 1985) reveals that a significant amount of new information is being gathered on spotted owls. Research on the seasonal movements of spotted owls in the Sierra Nevada is continuing. State wildlife agencies are compiling inventories of actively used spotted owl territories in California and Oregon and estimates of the statewide population in Washington. Habitat use by adult owls is being described in California and Washington. Breeding, reproductive attainment, and dispersal of juvenile owls is being studied in California, Oregon, and Washington. Information on the food habits of spotted owls is being accumulated throughout the Pacific Northwest. SOMA occupancy rates and spotted owl home ranges are being determined in Washington. The Bureau of Land Management is planning a monitoring study in Oregon that also will determine occupancy rates and reproductive attainment.9/ In California, the Bureau of Land Management is determining the effect of timber harvesting on nearby spotted owls.10/

THE STATE OF WILDLIFE SCIENCE

Wildlife managers and researchers are addressing the problem of ensuring the continued existence of regional populations of species that are jeopardized by the accumulating impacts of human activities (see Lehmkuhl 1984 and Shaffer 1981). But theory and management concepts are still poorly developed. And case histories and empirical data are lacking. Theoretical constructs for defining dependencies of species on particular types of environments or elements of the landscape are not yet supported by successful application to real situations (Carey 1981, 1984; Crowley 1978; Van Home 1983). Theories for determining the patterns of abundance (numbers, sizes, spatial distributions) of suitable environments that will maintain sufficient numbers of individuals for the species to persist despite systematic pressures and stochastic demographic, genetic, and environmental events are just being developed. Concepts for determining minimum viable populations have been proposed (Lehmkuhl 1984, Salwasser and others in press, Shaffer 1981) but not tested.

Many authors have addressed the general aspects of population genetics as related to conservation (see Schonewald-Cox and others 1983 and Soulé and Wilcox 1980 for examples), but very little is known about the role genetic events play in wild populations. For this paper, I applied concepts of dependency to the problem of ensuring the continued existence of spotted owls in the Pacific Northwest. Shaffer (1985) applies the concept of minimum viable populations to spotted owl management. Barrowclough and Coats (1985)

9/Unpublished draft plan, 1984, "Northern Spotted Owl Management Plan,, by the U. S. Department of the Interior, Bureau of Land Management, Oregon State Office, 825 NE Multnomah Street, Portland, OR 97232.

10/Personal communication, C. J. Ralph, Redwood Sciences Laboratory, 1700 Bayview Drive, Arcata, CA 95521.

examine spotted owl management from a population genetics standpoint. It is evident from these three papers that long-term, empirical, demographic studies will be necessary if there are to be definitive answers to questions about the viability of spotted owl populations. But the need for further development of theory and concepts is also evident.

INFORMATION NEEDS

Three types of studies are needed to refine spotted owl management: monitoring studies, demographic studies, and region-specific studies.

Monitoring Studies

The most immediate need for information is to determine how well the present management is working. Are owls using spotted owl management areas? Are the owls in SOMAs routinely producing young? What happens when the old growth in a SOMA is gradually reduced to the l,OOO-acre-per-pair standard? How long does it take a vacated SOMU to be recolonized? A monitoring program to answer some of these and related questions for the SOMAs in Washington is described by Carey and Ruggiero (1985).

Demographic Studies

A major gap in the knowledge of spotted owl biology is spotted owl demography. What are the life expectancies of owls? At what age do owls first mate to produce young? What are the age structures of various populations? What are common rates of reproductive attainment? What are the rates of recolonization of vacated territories? What are common effective population sizes? What is the genetic diversity of the various populations in the Pacific Northwest? Is there regular exchange of genetic material among the various populations in the Pacific Northwest? How are demographic parameters affected by forest fragmentation and increased isolation of breeding pairs?

Estimates of demographic parameters can only be gained through long-term (10 years or more) studies of large numbers of owl territories (say 45-100) in each of the six major geographic areas of the Pacific Northwest. To be effective, both adult and juvenile owls would have to be banded in the study areas. During capture of the owls blood samples could be taken for genetic studies. Genetics could, thus, be a part of the study of demography. Because of the large-scale nature of the studies, they would have to be cooperative in nature. Demographic studies could capitalize on monitoring studies but it is unlikely that monitoring studies would be conducted for long enough periods to substitute for demographic studies. Demographic studies are expensive and would not provide managers with definitive information in just a few years. The information from the demographic studies would be most appropriate for building population models and for contributing to theories about minimum viable populations. The empirical data, models, and theories could then be related to management.

Region-Specific Studies

Most work on northern spotted owls has been conducted in Oregon and northern California. Information on habitat use that is specific to the Olympic Peninsula and Cascade Range in Washington should also be developed. Ongoing research (Allen and Brewer 1985) and a SOMA monitoring program (Carey and Ruggiero 1985), if continued, will provide the necessary regional information. Research on California spotted owls in the Sierra Nevada must continue if reasonable management recommendations are to be made for the apparently migratory populations there.

CONCLUSION

When the results of recent and ongoing studies are published, the information on the habitat requirements of northern spotted owls should be sufficient for management purposes. More definitive information on what constitutes the size of a viable population of northern spotted owls, however, will be available in the future once a theoretical framework for defining viability is developed. But it seems likely that no fewer than 1,000 pairs of adults will be required. Recent studies of juvenile dispersal suggest the present guidelines for distributing SOMAs should be maintained. It is unlikely that more definitive information on distribution of SOMAs can be gained through dispersal studies. The major information gap is how well present management is working. Monitoring will be essential for effective spotted owl management.

Long-term studies of spotted owls will allow development of models of viable populations. The data from these studies will however, be of limited use to managers because most decisions on the retention of old-growth and mature forests will be made before the results of such studies will be known.

Other studies will be useful. Studies on how to silviculturally create old growth or how to speed forest development will provide the information needed to replace old growth as it ages into climax forest. Studies of interactions between spotted owls and barred owls could add another dimension to the concept of viability. As with most wildlife, there are numerous aspects of biology that could be studied but that have no apparent, immediate management application. Such basic knowledge enhances management in the long term.

ACKNOWLEDGMENTS

I thank L. Brewer, G. Cooper, H. Black, Jr., H. Salwasser, K. Horn, B. Marcot. E. Forsman. R. Gutiérrez, L. Ruggiero, E. Meslow, and G. Miller for their careful reviews of an earlier draft of this paper.

LITERATURE CITED

Allen, Harriet; Brewer, Larry W. A review of current northern spotted owl (Strix occidentalis caurina) research in Washington State. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwes . Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 55-57.

Barrowclough. George F.; Coats, Sadie L. The demography and population genetics of owls, with special reference to the conservation of the spotted owl (Strix occidentalis). In: Gutiérrez Ralph J.; Carey, Andrew B.. tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 74-85.

Barrows, Cameron W. Roost selection by spotted owls: an adaptation to heat stress. Condor. 83: 302-309; 1981.

Barrows, Cameron W. Breeding success relative to fluctuations in diet for spotted owls in California. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 50-54.

Barrows. Cameron; Barrows, Katherine. Roost characteristics and behavioral thermoregulation in the spotted owl. Western Birds. 9: 1-8; 1978.

Beckstead, Maureen. Olympic National Forest spotted owl habitat management: translating evolving management guidelines into actions. In: Gutiérrez. Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 14-20.

Bent, Arthur Cleveland. Life histories of North American birds of prey. Part 2. U.S. National Museum Bulletin 170. Washington, DC: Smithsonian Institution; 1938. 482 p.

Campbell, R. Wayne; Forsman, Eric D.; Van Der Raay, Brigitta M. An annotated bibliography of literature on the spotted owl (an old-growth dependent species). Victoria, Canada: British Columbia Provincial Museum; in press. 586 references.

Carey, Andrew B. Multivariate analysis of niche, habitat, and ecotope. In: Capen, David E.. ed. The use of multivariate statistics in studies of wildlife habitat. Proceedings of a workshop; 1980 April 23-25; Burlington, VT. Gen. Tech. Rep. RM-87. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station; 1981: 104-113.

Carey, Andrew B. A critical look at the issue of species-habitat dependency. In: Proceedings of the convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 346-351.

Carey, Andrew B.; Ruggiero, Leonard F. Spotted owl management: meeting NFMA requirements through monitoring. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 34-38.

Carleson, Richard D.; Haight, William I. Status of spotted owl management in Oregon as perceived by Oregon Department of Fish and Wildlife. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service. Pacific Northwest Forest and Range Experiment Station; 1985: 27-30.

Carrier, W. Dean. Planning and managing for the spotted owl in the National Forests, Pacific Southwest Region. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 2-4.

Crowley, P.H. Effective size and the persistence of ecosystems. Oecologia. 35: 185-195; 1978.
Erckman, W. James. A preliminary study of spotted owls on Mt. Baker. Seattle, WA: Seattle City Light Environmental Affairs Division; 1982. 29 p.

Forsman, Eric D.; Horn, Kirk M.; Neitro, William A. Spotted owl research and management in the Pacific Northwest. In: Transactions, 47th North American wildlife and natural resources conference; 1982 March 29-31; Portland, OR. Washington, DC: Wildlife Management Institute; 1982: 323-331.

Forsman, Eric D.; Meslow, E. Charles. Old-growth forest retention for spotted owls--how much do they need? In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 58-59.

Forsman. Eric D.; Meslow. E. Charles; Strub, Manic J. Spotted owl abundance in young versus old-growth forests, Oregon. The Wildlife Society Bulletin 5(2): 43-47; 1977.

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Distribution and biology of the spotted owl in Oregon. Wildlife Monograph No. 87. Washington, DC: The Wildlife Society; 1984. 64 p. Supplement to Journal of Wildlife Management. 48(2): 1984 April.

Franklin,. Jerry F.; Cromack, Kermit, Jr.; Denison, William [and others]. Ecological characteristics of old-growth Douglas-fir forests. Gen. Tech. Rep. PNW-118. Portland, OR: U.S. Department of Agriculture, Forest **Service**, Pacific Northwest Forest and Range Experiment Station; 1981. 48 p.

Franklin, Jerry F.; Dyrness, C.T. Natural vegetation of Oregon and Washington. Gen. Tech. Rep. PNW-8. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1973. 417 p.

Franklin, Jerry F.; Spies, Thomas A. Characteristics of old-growth Douglas-fir forests. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 328-334.

Garcia, Ernest R. A survey of the spotted owl in southwestern Washington. In: Schaeffer, P.P.; Ehlers. S.H., eds. Proceedings of the National Audubon Society's symposium on owls of the West, their ecology and conservation. Tiburon, CA: National Audubon Society Western Education Center; 1979: 18-28.

Gould, Gordon I.. Jr. Distribution of the spotted owl in California. Western Birds. 8: 131-146, 1977.

Gould, Gordon I., Jr. Management of spotted owls by California Department of Fish and Game. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 21-26.

Gutiérrez R.J. An overview of recent research on the spotted owl. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 39-49.

Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland. OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 119 p.

Gutiérrez, R.J.; Franklin, Alan B.; LaHaye, William [and others]. Juvenile spotted owl dispersal in northwestern California: preliminary results. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 60-65.

Gutiérrez R.J.; Solis, David Munoz; Sisco, Charles. Habitat ecology of the spotted owl in northwestern California: implications for management. In: Proceedings of the convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters; 1984: 368-373.

Heinrichs, Jay. The winged snail darter. Journal of Forestry. 81(4): 212-214, 262; 1983.

Howie, Richard. The spotted owl in British Columbia. In: State-Smith, R.; Johns, Li; Joslin, P., eds. Threatened and endangered species and habitats *in* British Columbia and the Yukon. Victoria, B.C.: British Columbia Ministry of Environment; 1980: 96-105.

James, Frances C. Ordinations of habitat relationships among breeding birds. The Wilson Bulletin. 83(3): 215-236; 1971.

Juelson, Tom. Managing northern spotted owls in Washington: the position of the Washington Department of Game. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 31-33.

Kerrick, Michael A.; Johnson, Kathy; Pedersen, Richard J. What information is necessary for planning the management of old-growth forest for wildlife? In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters; 1984: 383-386.

La Follette, Cameron. Analysis of the Oregon interagency spotted owl management plan. Forestry Res. Pap. 6. Eugene. OR: Cascade Holistic Economic Consultants; 1979. 32 p.

Laymon, Stephen A. General habitats and movements of spotted owls in the Sierra Nevada. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 66-67.

Lee, Philip L. History and current status of spotted owl (Strix occidentalis) habitat management in the Pacific Northwest Region, Forest Service, USDA. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management **of** the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 5-9.

Lehmkuhl, John F. Determining size and dispersion of minimum viable populations for land management planning and species conservation. Environmental Management. 8(2): 167-176; 1984.

MacCleery, Douglas W. National Forest System land and resource management planning. Federal Register (Rules and Regulations). 47(190): 43026-43052; 1982.

Marcot, Bruce G.; Gardetto, Jeffrey. Status of the spotted owl in Six Rivers National Forest, California. Western Birds. 11: 79-87; 1980.

Marshall, Joe T., Jr. Food and habitat of the spotted owl. Condor. 66-67; 1942.

Maser, Chris; Trappe, James M., tech. eds. The seen and unseen world of the fallen tree. Gen. Tech. Rep. PNW-164. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1984. 56 p.

Meslow, E. Charles; Maser, Chris; Verner, Jared. Old-growth forests as wildlife habitat. In: Transactions, 46th North American wildlife and natural resources conference; 1981 March 21-25; Washington, DC. Washington, DC: Wildlife Management Institute; 1981: 329-335.

Miller, Gary S.; Meslow, E. Charles. Dispersal data for juvenile spotted owls: the problem of small sample size. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 69-73.

Postovit, Howard R. A survey of the spotted owl in northwestern Washington. Washington, DC: National Forest Products Association; 1979. 15 p.

Raphael, Martin G.; Barrett, Reginald H. Diversity and abundance of wildlife in late successional Douglas-fir forests. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 352-360.

Ruediger, William C. Implementing a spotted owl management plan: the Gifford Pinchot National Forest experience. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland. OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 10-13.

Ruggiero, Leonard F.; Carey, Andrew B. A programmatic approach to the study of old-growth forest-wildlife relationships. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 340-345.

Salwasser, Hal. Preface: challenges for wildlife and fish--the old-growth ecosystem in managed forests. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 319.

Salwasser. Hal; Mealey, Stephen P.; Johnson, Kathy. Wildlife population viability--a question of risk. In: Transactions, 47th North American wildlife and natural resources conference; 1984 March 27; Boston, MA. Washington, DC: Wildlife Management Institute, 1984: 421-439.

Schonewald-Cox. Christine M.; Chambers, Steven M.; MacBryde, Bruce; Thomas, W. Lawrence, eds. Genetics and conservation: a reference for managing wild animal and plant populations. Menlo Park, CA: The Benjamin/Cummings Publishing Company, Inc.; 1983. 722 p.

Shaffer, Mark L. Minimum population sizes for species conservation. Bioscience. 31: 131-134; 1981.

Shaffer, Mark L. The metapopulation and species conservation: the special case of the northern spotted owl. In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 86-99.

Sirmon, Jeff M. Regional, political and economic issues in managing old-growth forest on National Forest land. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 325-327.

Soulé, Michael E.; Wilcox, Bruce A., eds. Conservation biology. Sunderland, MA: Sinauer Associates, Inc.; 1980. 395 p.

Taylor, Avery L.; Forsman, Eric D. Recent range extensions of the barred owl in western North America, including the first records for Oregon. Condor. 78: 560-561; 1976.

Teeguarden, Dennis E. National policy, tradeoffs, and issues in managing old-growth forests for multiple benefits. In: Proceedings of the annual convention of the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 320-324.

U.S. Department of Agriculture. The principal laws relating to Forest Service activities. Agric. Handb. 453. Washington, DC: U.S. Government Printing Office, Superintendent of Documents; 1983. 591 p.

U.S. Department of the Interior, Fish and Wildlife Service. The northern spotted owl: a status review. Portland, OR: U.S. Department of the Interior, Fish and Wildlife Service Regional Office; 1982. 29 p.

Van Horne, B. Density as a misleading indicator of habitat quality. Journal of Wildlife Management. 47(4): 893-901; 1983.

Zarn, Mark. Habitat management series for unique or endangered species: Report No. 10: spotted owl (Strix occidentalis). Tech. Note T-N-242. Denver, CO: U.S. Department of the Interior, Bureau of Land Management, Denver Service Center; 1974. 22 p.

INFORMATION AND RESEARCH NEEDS FOR SPOTTED OWL MANAGEMENT

R. J. Gutiérrez

ABSTRACT: The information and research needs for spotted owl management are presented. The following priority list for research is given with the understanding that research needs may vary among USDA Forest Service regions and that many research topics could effectively be coordinated or conducted together. Research and information are needed on: (1) population dynamics, (2) major prey ecology, (3) habitat requirements, (4) juvenile dispersal, (5) effects of habitat modification on spotted owls, (6) inventory and monitoring, and (7) owl genetics.

The National Forest Management Act of 1976 (U.S. Laws, Statutes, etc. 1976) requires the USDA Forest Service to develop Land Management Plans (LMPs) for each National Forest. These plans will contain spotted owl (Strix occidentalis), management plans (SOMPs). The Forest Service is funding several studies to provide-information on the basic ecology of the northern spotted owl (S. o. caurina) to help formulate SOMPs within the general LMPs. Because these LMPs will be completed within 1-2 years and then be subject to review and revision in 5-10 years, it is important that research continues on the northern spotted owl. In this paper I suggest areas of spotted owl research that will provide much of the information needed to adequately review and revise the Forest Service's SOMPS.

I believe that there are some areas of spotted owl ecology that need immediate research attention. I present in this paper a list of research needs that is the result of my personal experience with spotted owls, the suggestions of this symposium's participants, and suggestions from other spotted owl research biologists. In addition, my list is strongly influenced by discussions with Cameron Barrows, Eric Forsman, Gordon Gould, Stephen Laymon, Charles Sisco, and David Solis during an informal spotted owl workshop at Arcata, California, April 6-7, 1983. The responsibility for developing the following list, however, is my own.

SPOTTED OWL RESEARCH NEEDS

The following suggested areas of spotted owl research are listed in my priority order. Clearly, several different research investigations may continue concurrently. It is my intention only to suggest areas of research that will provide critically lacking information on the spotted owl. I further encourage all research on the spotted owl to continue and to be shared among all interested persons.

1. Demography: Only the work of Forsman and others (1984) presents any substantive data on population biology. Yet it is clear from Barrowclough and Coats (1985) that demographic studies should be considered a top priority. Such information as age at first reproduction, life span, reproductive potential, and adult and juvenile survivorship will be needed to construct models sufficient to predict effective population size. This information will also be critical for evaluating the impact of environmental change on the species (Shaffer 1985).

R. J. Gutiérrez is an associate professor of wildlife management and chairman of the Department of Wildlife Management, Humboldt State University, Arcata, Calif.

To my knowledge the only study currently in progress on demography is in northwestern California[1]. Spotted owl monitoring in the National Forests of Washington State will also be a source of demographic data by observing changes in occupied territories (Allen and Brewer 1985, Carey and Ruggiero 1985). I suggest that most of these studies be replicated to assess geographic variation within northern spotted owl populations and among other spotted owl subspecies. It is apparent from other studies that there is geographic variation within aspects (for example, food habits) of their natural history (Gutiérrez 1985).

2. Major prey ecology: The ecology of the major prey of the spotted owl is not well understood yet prey relationships may be a major reason for the birds dependence on large areas of old growth (Gutiérrez 1985). Barrows (1985) also points out the potential relationship between owl breeding success and the proportion of large prey in their diet. Thus, it seems that both the flying squirrel (Glaucomys sabrinus) and wood rat (Neotoma sp.) warrant investigation.

Several studies are assessing the status of these animals in old growth (Raphael and Barrett 1984, Ruggiero and Carey 1984). These studies are not designed, however, to provide the most needed information on these animal's population dynamics, distribution, density, and geographic variation in abundance and reproductive success within known spotted owl territories. The study of spotted owl prey could be effectively coordinated with owl demographic studies. This could be accomplished through monitoring prey populations within known spotted owl territories. Southern (1970) successfully used this study design with tawny owls (Strix aluco).

Throughout this discussion I will not predict the cost or the time required to conduct these studies. The cost and time necessary to effect these studies will depend on the logistical constraints of terrain, the level of statistical precision required, and the type of research investigation (that is, population dynamics vs. habitat analysis).

Funding considerations and decisions should be made using advice from people who know the terrain and the logistical problems of sampling within a particular area.

3. Habitat requirements: The specific characteristics of habitat used by and available to spotted owls are not identified for all major areas of the owl's range. Solis (1983) provides data for northwestern California. Laymon (1985) will provide specific habitat characteristics for the northern Sierra Nevada. Yet data from mesic Oregon and Washington, arid Washington, and the disjunct populations of S. o. caurina in Mendocino, Napa, and Marin Counties of California are not available. In addition, the relationship among home range size, habitat dispersion, habitat quality and reproduction is not well understood.

Habitat models are as yet lacking for the spotted owl. A U.S. Department of the Interior, Fish and Wildlife Service, Habitat Evaluation Procedure type Habitat Suitability Index Model is being developed by Salwasser and Laymon (in press). In addition a model for predicting suitable nesting habitat is being developed by LaHaye.[2]

One aspect of habitat research that is very important (when trying to predict the impact of management scenarios) is quantifying the total available habitat for spotted owls. There are no published accounts that have assessed the total amount, patch size, or distribution of suitable spotted owl habitat in the Pacific Northwest. Remote sensing technology does exist for conducting such a study.

4. Juvenile dispersal: The pattern of juvenile dispersal and the success of owl dispersers are still important questions to resolve. Dispersal studies, however, are expensive research considering the resultant data. At this time I feel it is important that the study of Miller and Meslow (1985) continue for its final year. Barrowclough and Coats (1985) point out the importance of juvenile dispersal for estimating effective population size.

In addition to the study of Miller and Meslow (1985), Laymon (1985) is completing a limited study of juvenile dispersal in the Sierra Nevada in California. His studies will provide useful comparative dispersal data.

5. Effects of habitat modification on spotted owls: Much timber harvesting is occurring in known spotted owl habitat. There is ample opportunity to study the impact of timber harvesting on spotted owl reproductive, foraging, and habitat use in National Forests. Knudsen-Vandenberg Funds can be used for monitoring wildlife affected by a specific timber harvest. Within a region of the Forest Service or the Bureau of Land Management a sufficient owl sample size could be gained through regional cooperation and planning to study the impact of logging on resident owls.

Controlled experiments on the effects of timber harvesting will be more difficult to execute given the nature of commercial timber harvesting in the Pacific Northwest and the number of owl sites needed to gain a high level of statistical precision. Thus far, only anecdotal data has been gathered on the effects of timber

---

1/Study in progress, Alan Franklin and others, Wildlife Management Department, Humboldt State University, Arcata, Calif.

2/Study in progress, William LaHaye, Wildlife Management Department, Humboldt State University, Arcata, Calif.

harvesting on owls3/ (for example, Forsman and others 1984, Solis 1983).

6. Inventory and monitoring: The Forest Service, Bureau of Land Management, and various State wildlife agencies have all conducted some spotted owl inventories. The efficiency of these efforts, however, has never been assessed. I believe owl populations were probably underestimated. Inventory was done through calling surveys, and response rates during these surveys may have been affected by time of day or year, by temperature, by reproductive condition of the owl, by territorial status of the bird, by individual variation in owl response rates, and by the number of calling episodes within an area. If spotted owl numbers have been underestimated, then the magnitude of the impact on regional populations of owls would be greater than previously anticipated by spotted owl management schemes.

Monitoring of spotted owl territory occupancy rates should be addressed to predict the effectiveness of the spotted owl management plans of the Forest Service and Bureau of Land Management (Carey and Ruggiero 1985). Allen and Brewer (1985) are currently monitoring spotted owl territories in Washington. Some of these monitoring studies could be conducted in concert with studies of population dynamics.

7. Owl genetics: Genetic variability in spotted owls or between spotted owl demes has never been investigated. This information may be important for constructing models of population viability and determining genetic relationships among spotted owl populations. These investigations could be conducted as part of larger studies (Barrowclough and Coats 1985). Regional coordination would be helpful.

ADDITIONAL SPOTTED OWL RESEARCH PROGRAMS

In this section I will mention several notable research programs that have not drawn the same attention as the Oregon and Northwestern California studies. I mention these to facilitate communication among persons interested in spotted owls. The first is the long-term investigation of Cameron Barrows at the North Coast Preserve, Branscomb, California. Barrows is continuing his prey studies presented elsewhere in this symposium (Barrows 1985) and is monitoring the long-term reproductive effort of a few selected pairs of spotted owls. Another research effort is being conducted in Washington by Harriet Allen and Larry Brewer of the Washington Department of Game. Additional studies by Allen and Brewer (1985) and Barrows (1985) are discussed above or elsewhere in this symposium (Allen and Brewer 1985, Barrows 1985). Allen and Brewer are also investigating a very important aspect of spotted owl biology: competition and interaction between spotted owls-and barred owls (Strix varia). In addition. the Pacific Northwest Region (USDA Forest Service) is monitoring the implementation of their spotted owl management plan. This latter investigation is headed by Bruce Marcot. Efforts are being made to design, to implement, and to coordinate monitoring of spotted owl management on Federal lands in the Pacific Northwest through a Federal interagency committee under the auspices of the USDA Forest Service's Old-Growth Wildlife Habitat Program.4/

This brief outline of research needs and research in progress has been presented to encourage spotted owl research in areas for which management agencies have specific information needs. The Old-Growth Wildlife Habitat Program of the USDA Forest Service, Pacific Northwest Range and Experiment Station, Olympia, Washington, has been serving as a clearing-house for west coast spotted owl studies. Investigators are encouraged to coordinate their efforts with that program.

LITERATURE CITED

Allen, Harriet; Brewer, Larry W. A review of current northern spotted owl (Strix occidentalis caurina) research in Washington State. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 55-57.

Barrowclough, George F.; Coats, Sadie, The demography and population genetics of owls, with special reference to the conservation of the spotted owl (Strix occidentalis). In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 74-85.

Barrows, Cameron W. Breeding success relative to fluctuations in diet for spotted owls in California. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 50-54.

Carey, Andrew B.; Ruggiero, Leonard F. Spotted owl management: meeting NFMA requirements through monitoring. In: Gutiérrez, Ralph J.;

3/Unpublished data on file with R. J. Gutiérrez, Wildlife Management Department, Humboldt State University, Arcata, Calif.

4/Personal communication, A.B. Carey, Pacific Northwest Forest and Range Experiment Station, 3625 93d Ave., S.W., Olympia, WA 98502.

Carey, Andrew B., tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 34-38.

Forsman, Eric D.; Meslow, E. Charles; Wight, Howard M. Distribution and biology of the spotted owl in Oregon. Wildl. Monogr. 87. Washington, DC: The Wildlife Society; 1984. 64 p. Supplement to Journal of Wildlife Management. 48(2): 1984 April.

Gutiérrez, R.J. An overview of recent research on the spotted owl. In:Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 39-49.

Layman, Stephen A. General habitats and movements spotted owls in the Sierra Nevada. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech, eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 66-68.

Miller, Gary S.; Meslow, E. Charles. Dispersal data for juvenile spotted owls: the problem of small sample size. In: Gutiérrez, Ralph J.; Carey, Andrew B., tech eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 69-73.

Raphael, Martin G.; Barrett, Reginald H. Diversity and abundance of wildlife in late successional Douglas-fir forests: In: Proceedings, annual convention of the Society of American Foresters, 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 352-360.

Ruggiero, Leonard F.; Carey, Andrew B. A programmatic approach to the study of old-growth forest-wildlife relationships. In: Proceedings, annual convention of-the Society of American Foresters; 1983 October 16-20; Portland, OR. Bethesda, MD: Society of American Foresters, 1984: 340-345.

Salwasser, Hal; Laymon, Stephen A. Habitat suitability model for the spotted owl. FWS/OBS-85/-, Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service; [in press].

Shaffer, Mark L. The metapopulation and species conservation: the special ‘case of the northern spotted owl. -In: Gutiérrez Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Depart‘-ment of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; 1985: 86-99.

Solis, David M. Summer habitat ecology of spotted owls in northwestern California. Arcata, CA: Humboldt State University; 1983. 168 p. M.S. thesis.

Southern, H.N. The natural control of a population of tawny owls (Strix aluco). Journal of Zoology. London, 162: 197-285; 1970.

U.S. Laws, Statutes; etc.; Public Law 94-588. National Forest Management Act of 1976. Act of Oct. 22, 1976. 16 U.S.C. 1600 (1976).

ENGLISH AND METRIC EQUIVALENTS

Metric	English
1 inch = 25 millimeters	1 millimeter = 0.039 inch
1 inch = 2.5 centimeters	1 centimeter = 0.39 inch
1 foot = 30.5 centimeters	1 meter = 39.37 inches or 3.28 feet
1 mile = 1.6 kilometers	1 kilometer - 0.62 mile
1 ounce = 28 grams	1 gram = 0.0353 ounce
1 pound = 453.6 grams	1 kilogram = 2.2045 pounds
1 ton = 0.907 metric ton	1 metric ton = 1.02 tons
1 acre = 0.40 hectare	1 hectare = 2.47 acres
$^{o}F = (9/5\ ^{o}C) + 32$	$^{o}C = (^{o}F - 32)/1.8$

Gutiérrez, Ralph J.; Carey, Andrew B., tech. eds. Ecology and management of the spotted owl in the Pacific Northwest. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station; **1985.** 119 p.

The spotted owl is at the center of the old-growth forest and wildlife habitat management controversy in the Pacific Northwest. There is confusion about USDA Forest Service management activities, the present state of knowledge of spotted owl biology, and what further research is needed to provide managers with the tools to ensure viable populations as mandated by the National Forest Management Act. This proceedings documents current and past management activities, current knowledge, and research needs.

Keywords: Owls (spotted), wildlife habitat management, research needs.

The **Forest Service** of the U.S. Department of Agriculture is dedicated to the principle of multiple use management of the Nation's forest resources for sustained yields of wood, water, forage, wildlife, and recreation. Through forestry research, cooperation with the States and private forest owners, and management of the National Forests and National Grasslands, it strives — as directed by Congress — to provide increasingly greater service to a growing Nation.

The U.S. Department of Agriculture is an Equal Opportunity Employer. Applicants for all Department programs will be given equal consideration without regard to age, race, color, sex, religion, or national origin.

Pacific Northwest Forest and Range
Experiment Station
319 S.W. Pine St.
P.O. Box 3890
Portland, Oregon 97208