Part 1
Introduction

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Research on Wildlife in Old-Growth Forests: Setting the Stage

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Scientifically based forest management proceeds, at best, on the basis of available information. Such information is generally archived in scientific journals, however, and is often neither readily available nor useful to forest managers. Thousands of such pieces of information germane to forest management reside in untold numbers of largely unread journals and transactions of symposia, in researchers' files, and in the minds of knowledgeable individuals. This is especially true for information on the relationships between wildlife and their habitats. In the forms I have listed, that knowledge is not useful in guiding managers of National Forests in meeting the legal mandate to "maintain viable populations of all native and desirable non-native plant and animal species well-distributed throughout" the managed forest.

Some 15 years ago, ad hoc groups of natural resource management professionals began to gather and synthesize existing information on wildlife habitat relationships for use in forest management. Those early work groups published a series of compendia-first for the Blue Mountains in Oregon and Washington (Thomas 1979) and the Southwest (Patton 1978), and then for the Sierra Nevada of California (Vemer and Boss 1980), New England (DeGraaf and Rudis 1986), Colorado (Hoover and Wills 1984), and Oregon and Washington west of the Cascade crest (Brown 1985). The ideas and approaches presented in these documents evolved into the Forest Service's Fish and Wildlife Habitat Relationships Program, whose mission is to encourage the development and updating of synthesis documents describing wildlife habitat relationships in forested ecosystems across the United States. Similar efforts are underway in Canada.

Examination of these documents quickly reveals gray areas where information is contradictory or absent or where authors relied on their judgment to formulate working hypotheses to fill gaps in published data. Research can then be directed to the information needs that are most germane to the resolution of conflicts inherent in multiple-use forest management. The allocation of resources for large-scale research programs, however, will occur only where such conflicts result in significant social, economic, and political impacts.

Nearly all the documents listed previously put forth the hypothesis that the forest state that exists at, or approaching, the culmination of forest succession-old growth-is a significantly different habitat for wildlife than earlier, more structurally simple states. Some wildlife species were hypothesized to find their preferred or only habitats in old growth, and species diversity was expected to be higher there. These hypotheses were formed from observation and experience, some research results, and the assumption that, because most forest stands were in the old-growth state in historic times, some species of wildlife have evolved largely in old growth.

These hypotheses were used in the Forest Service's ongoing land-use planning. Immediate and intense controversy over the amount of old-growth forests to be preserved ensued and is currently increasing. When Forest Plans called for retaining old growth to meet the needs of wildlife, sometimes the amount of timber that could be offered for safe declined. Conversely, those interested in preserving old growth, for whatever reason, pushed vigorously to achieve their goal; concern for wildlife was foremost among the arguments presented.

The controversy became most pronounced in western Oregon and Washington, where significant amounts of old growth containing very old and very large trees, particularly Douglas-fir, still exist. Such stands have high economic value per tree and per acre. Coupled with the potential economic values of those stands were the social and political consequences of jobs retained or lost and issues of community stability associated with the annual timber harvest anticipated under various management alternatives.

The inevitability of these conflicts was obvious to some, even a decade ago. Examination of how the law evolved through the Multiple Use-Sustained Yield Act of 1960, the Endangered Species Act of 1973, the Forest and Rangeland Renewable Resources Planning Act of 1974, and the National Forest Management Act of 1976 reveals an increasing emphasis on the multiple-use philosophy in National Forest management (Thomas 1979; U.S. Department of Agriculture, Forest Service 1983). These changes strongly emphasized the need to recognize the importance of water, wildlife, recreation, and forage, in addition to wood production. This emphasis inevitably led to increasing debate over how, and in what quality and quantity, old growth would be retained as part of the managed forest.

Maintaining biological diversity, as an overriding goal for Federal land management, has played an important role in the evolution of Iaw and thought about how land is to be managed. This evolving concern encompasses retaining the diversity of plant and animal life, forest structure, human experience related to the forest in its many forms, and an expansion of management concerns from the immediate and the site-specific to long-term considerations of changing landscapes over time. These concerns seem likely to become embodied in law and regulation.

These changes in laws and regulations strongly influence management philosophy for the National Forest. New words and concerns reach the ear of natural resource management professionals and the scientific community with increasing frequency--biodiversity, landscape ecology, conservation biology, environmental ethics, and new perspectives in forestry. Public forest managers are becoming convinced that maintaining biological diversity should be the overriding land-use management objective. Whether or not this momentum will force adjustments in how natural resource management is conducted after it becomes clear that meeting such a mandate is very difficult, lies in the future-perhaps the near future. The increasing political uproar in the Pacific Northwest over old-growth management will not be easily resolved. And the resolution of this conflict, whatever it is, will likely not be popular-not with the timber industry and not with environmentalists.

Those who foresaw threats to preserving biodiversity in managed landscapes conducted small, but now significant, research efforts on the interactions between wildlife and old-growth habitat. Among these efforts were studies on the habitat associations of northern spotted owls in Oregon conducted by an Oregon State University graduate student with modest Forest Service funding; these studies marked the beginning of the spotted owl issue. The total expenditure for those early studies was certainly much less than the cost of publishing this volume.

The northern spotted owl was found to be associated primarily with the forest structure that is most common in old growth in the Douglas-fir region. This observed association with a habitat that was being systematically diminished and fragmented would eventually lead to listing of the owl as threatened by the U.S. Fish and Wildlife Service. As a result, much subsequent research and management attention has focused on the northern spotted owl. The consequences of such initial small-scale studies reverberate today in many scientific and political debates. This research, together with the evolution in law concerning forest management over the past two decades, set the stage for the research reported in this book.

By 1978, a well-funded, broad-scale research effort was clearly needed to evaluate the hypothesis that old growth is a significantly different wildlife habitat than younger forests. A Forest Service Research and Development Program was instituted in 1982 at the Pacific Northwest Research Station in Olympia, Washington, to address these issues. Technical experts were brought together to formulate the research approach. Until then, public attention and the emphasis of research was focused on the northern spotted owl. The teams that had gathered information on wildlife habitat relationships in Douglas-fir forests (Brown 1985), however, had identified other wildlife species that were likely to have primary habitats in old-growth forests.

Advice came from consultants to put the emphasis on studies of wildlife species identified as likely to be closely associated with old growth. Such studies would be relatively straightforward (as compared to studies of plant and animal communities) and easier for promoters of the research to understand and support. Furthermore, this approach was best suited to satisfying forest managers' demands for information to use in response to requirements arising from the Endangered Species Act of 1973. This research approach would undoubtedly meet with strong support from those actively involved in the developing old-growth management issue.

The research alternative was to emphasize community studies. Compared to studies on selected species thought to be closely associated with old growth, community studies would be more technically complex, difficult to understand by the concerned public, expensive to conduct, and hard to explain. And, in the end, they would require innovative syntheses of the results from separate studies conducted across a spectrum of environmental gradients. Though not as politically expedient, the community approach seemed best from a scientific standpoint. The community approach would not, however, satisfy the demands for immediate answers to questions about the habitat relationships of key species, such as management indicator species. These species would loom larger still in the press as resource conflicts intensified and management plans were appealed. Furthermore, the temptation to simplify this extremely complex biopolitical issue as one of spotted owls (or some other species) versus jobs, profits, or some other criteria, would be great.

To their credit, Leonard Ruggiero, the research program manager, and Andrew Carey, the research coordinator, put primary emphasis on questions of old-growth community ecology. Attention was focused on fundamental questions concerning the form and function of the old-growth ecosystem to produce answers that would satisfy demands of the moment, but would also be germane to the larger questions that would arise as the debate continued.

This volume reports the results of those community studies. These studies were designed to provide answers to a number of questions. Foremost among these was, is Douglas-fir old growth significantly different as wildlife habitat from other stages of forest development? Corollary questions are, If significant differences exist, what are they? How pronounced are the differences? How might these differences be preserved or modified most effectively and efficiently through forest management? To provide these answers is no small shore. Questions about the uniqueness of old growth as wildlife habitat will change over time, beyond current emphases on individual species to the larger and more significant issues of community stability, aesthetic values, and maintaining biodiversity.

The legal and conceptual tools provided by the Endangered Species Act of 1973 and the National Forest Management Act of 1976, coupled with an emphasis on managing indicator species in Forest Service planning, have led to a situation where the welfare of a single species drives the debate on the premier natural resource allocation issue of this quarter-century in the United States. This, perhaps inevitable, course has led to an unfortunate trivialization of a much larger and more significant issue-preserving and perpetuating significant amounts of unique ecosystems in such a fashion that they function as they evolved. In this approach lies the only real chance for maintaining biodiversity.

The political strategies of various factions in the old-growth allocation controversy have produced a situation where economics, social concerns, and biology have become so inextricably tangled that knowing where science and economic analyses end and politics begins is increasingly difficult. The initial emphasis on understanding the habitat relationships of spotted owls, and of ensuring their survival, was a logical, probably inevitable, outcome given the state of knowledge on the ecology of old growth and the desire and necessity to meet requirements of law and regulation within reasonable time frames for the drafting of National Forest Plans.

I am not saying that research and management activities directed at individual species will cease-nor should they. In fact, the old-growth issue has become a crucial regional and national issue with the recent listing of the spotted owl by the Fish and Wildlife Service. The chaos, conflict, and intense political activity that have emerged, however, will eventually lead to societal consideration of much larger and more complex questions about the form and function of entire ecosystems in a rapidly changing world. The political implications of this debate will extend far beyond the borders of the Pacific Northwest or of the United States. How our country resolves this conflict will strongly influence less-affluent nations as they struggle with resource allocations. This debate will not take place in isolation. Rather, it will occur in the context of emerging concerns about global climate change and the loss and fragmentation of forest ecosystems throughout the world.

The information presented in this volume will be quickly applied in the management arena and will come to bear-technically and politically-on forest management. Such research represents incremental steps toward truth, appreciation, and understanding. All concerned with the old-growth management issue should welcome closer and closer approximations of truth.

Wildlife Habitat Relationships in Unmanaged Douglas-Fir Forests: A Program of Research

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The research reported in this book is the result of a single Forest Service research initiative called the Old-Growth Forest Wildlife Habitat Research and Development Program (Ruggiero and Carey 1984). The Program focused on the Douglas-fir forests of western Oregon, western Washington, and northern California. The Old-Growth Program initially included Region 5 and Region 6 of the National Forest System and the Pacific Southwest and Pacific Northwest Research Stations; the Bureau of Land Management was an early cooperator and supporter. The Program-headquartered in Olympia, Washington--proceeded under the aegis of the Pacific Northwest Research Station.

Many activities led to the Old-Growth Program. Biologists like Eric Forsman, Jeny Franklin, Thomas Hanley, Glenn Juday, William Mannan, Chris Maser, Charles Meslow, John Shoen, James Trappe, and others had been studying the ecology of old-growth Douglas-fir forests at least since the early 1970s. Early old-growth studies conducted in California by Martin Raphael and Bruce Marcot were the first to have a major focus on wildlife communities, and these efforts provided valuable information for the design of future studies. Insights offered by all of these people led to growing concerns that old growth was a dwindling and poorly understood resource that could be crucial to long-term forest productivity and to the survival of numerous plant and animal species.

A great deal of public interest was generated by these and related issues during the mid-1970s through the early 1980s. And all this led to major changes in the way land managers and the public thought about old-growth forests. For example, the notion that late-successional forests were “biological deserts” was being effectively challenged; the spotted owl had emerged as an example of close interrelationships between wildlife and late-successional forests; and Jack Thomas’ book (1979) about wildlife habitat in Oregon’s Blue Mountains had challenged the conventional wisdom that good timber management is good wildlife management.

By 1981, concerns about managing old-growth forests in the Pacific Northwest were running high. A series of public meetings confirmed a great deal of interest in old-growth issues. In response, the Forest Service chartered the Old-Growth Program-the first step towards initiating the research reported in this book.

The Old-Growth Program objectives were to (1) define old-growth Douglas-fir forests, (2) identify wildlife species closely associated with these forests, and (3) determine the biological requirements and ecological relationships of closely associated species. The intent was to do research that would provide forest managers and decisionmakers with some of the tools they need to maintain viable wildlife populations on lands of the National Forest system. This problem was, and still is, important for land managers because the National Forest Management Act of 1976 and related regulations contained clear mandates to maintain or enhance biological diversity and to maintain viable populations of all native vertebrates. Learning more about wildlife habitat relationships in old-growth forests was thus extremely important, especially in the Pacific Northwest where the remaining Douglas-fir old growth had very high economic and social value.

My first objective as program manager was to complete a plan called the Program Direction Document. This plan benefited from the contributions of an early ad hoc advisory group comprised of John Faaborg, Jerry Franklin, Martin Raphael, Hal Salwasser Fred Samson, Mark Shaffer, and Jared Vemer. The plan indicated forest fragmentation as a key consideration in Program research. The plan also recognized the necessity for studying vertebrate communities (patterns of vertebrate abundance) in all stages of forest development. A detailed account of the experimental design is presented by Carey and Spies elsewhere in this volume. For my purposes here, simply note that the research plan we went on to develop called for a very ambitious, highly integrated, cooperative research effort.

The Program's charter limited our planning horizon to 5 years and, for that period, the funding needed to implement the plan was estimated to be $10 million. We actually ended up with around $2 million as the basis for all the studies being reported here. This funding shortfall resulted in some significant problems. For example, we were not able to conduct the forest fragmentation studies we had planned, and both the geographic scope and duration of our community studies were greatly reduced.

The Old-Growth Program staff managed and coordinated the research effort; others did most of the actual data collection and analysis. We soon learned about the difficulties of coordinating and integrating the efforts of a team of scientists from three major universities, three Forest Service laboratories, and two units of the Fish and Wildlife Service.

Several important practical constraints influenced the scope and conduct of Program studies. For example, in spite of requests to be included from Alaska, eastern Oregon, and eastern Washington, we were forced to limit the geographic scope of our studies. In addition, the relatively small sizes and young ages of existing managed stands led us to conduct most of our sampling in naturally regenerated, unmanaged stands. Thus, comparisons of young, mature, and old-growth forests would be complicated by the residual components of old growth (such as large trees, snags, and logs) that carry over to the new, younger stands after a catastrophic disturbance like fire. Many authors will discuss in detail how this situation affected study results and also how it generated important insights about the influences of this natural structural complexity on patterns of vertebrate abundance.

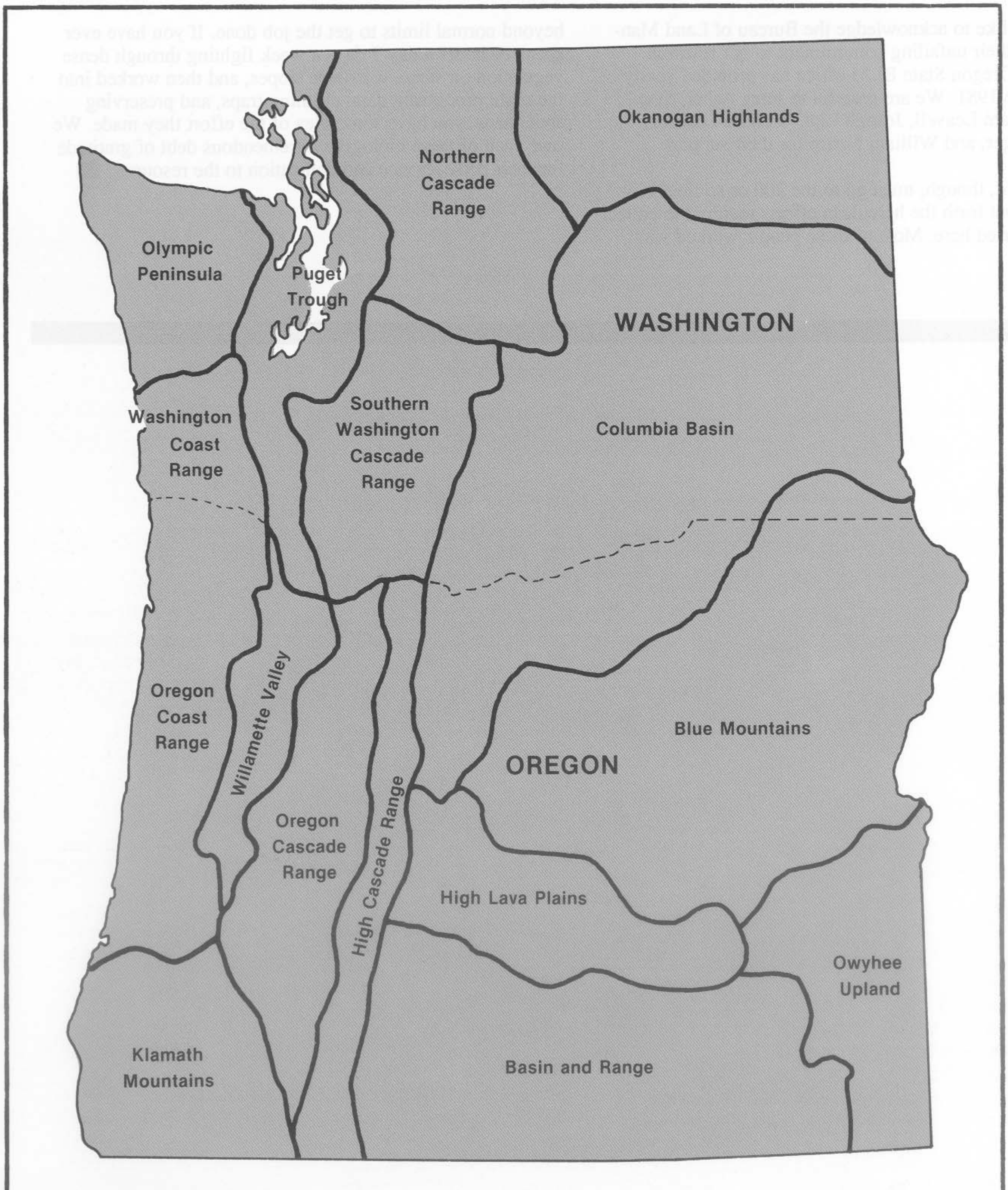
In addition to the practical constraints on geographic scope and kinds of stands sampled, we were also constrained by available funding to study either vertebrate communities or a limited number of high-visibility species that were thought at that time to be closely associated with old growth. We could not do both. Because relatively little wildlife research had actually been done in the geographic area of concern, we decided to emphasize the community approach.

The decision to emphasize communities involved a major tradeoff because several large, highly mobile species would not be well represented in our community sampling. In addition, we were trading the opportunity to learn a great deal about the ecology of a few species for the opportunity to learn about the patterns of abundance of many species. Our original intent did not include these compromises; we had planned to begin the more intensive species-specific studies after the first 2 years of the community studies. These intensive studies would have further defined the mechanisms and the nature of observed habitat associations while producing the information needed for more precise management recommendations. The need for intensive studies of certain species or species groups is now more acute than ever.

I would like to acknowledge that our Program efforts benefited from the scientific advice of a Technical Committee and the guidance of an Executive Committee. The Technical Committee was comprised of John Faaborg, Jerry Franklin, Chris Maser, Richard Pederson, James Rochelle, Fred Samson, Mark Shaffer, Jack Thomas, Robert Vincent, and Bruce Wilcox. The Executive Committee included representatives from State and Federal land management agencies, environmental groups, and the timber industry.

I would also like to acknowledge the Bureau of Land Management for their unfailing commitment to our research efforts. The Oregon State BLM office has provided yearly funding since 1981. We are grateful to Jerry Asher, Stan Butzer, William Leave, Joseph Lint, William Luscher, Robert Metzget, and William Neitro for their support.

The real credit, though, must go to the 200 or so field biologists who put forth the herculean efforts required to collect the data reported here. Most of these people worked way beyond normal limits to get the job done. If you have ever spent 10 hours a day 7 days a week fighting through dense vegetation on steep, west-side slopes, and then worked into the night processing data, cleaning traps, and preserving specimens, you have some idea of the effort they made. We owe each of these biologists a tremendous debt of gratitude for their perseverance and dedication to the resource.



Physiographic provinces in Oregon and Washington (modified from Franklin and Dyrness 1973).

Sampling Design of the Old-Growth Forest Wildlife Habitat Program

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Introduction

The Old-Growth Forest Wildlife Habitat Program (the Program) was chartered in 1981, with four objectives:

- To identify animal and plant species that are dependent upon or find optimum habitat in old-growth forest stands;
- To define, classify, and inventory old-growth forest ecosystems;
- To determine the biological requirements and ecological relationships of species that are found only in old growth or find optimum habitat there; and,
- To evaluate old-growth management alternatives and determine economic aspects of old-growth forest ecosystems.

The first step taken to achieve these goals was to implement studies of wildlife and plant communities in different-aged Douglas-fir forests. A research plan was developed in 1982. The purpose of this paper is to describe in detail the research that was planned and discuss some of the major problems encountered in its implementation. Although several aspects, of the research were not conducted because of budget constraints, we include a detailed description of the original plan for use by others in future studies. Details of the sampling designs and analytical approaches used for the various communities studied in each province are described in the individual papers that follow.

Providing the basis for the Program approach were the sampling and statistical considerations discussed in Capen (1981) Cochran and others (1954), Eberhardt (1976), Gauch (1982), Green (1979), Pielou (1977), Ralph and Scott (1981), Scott (1982), and Snyder (1978); ecological descriptions provided by Franklin and Dyrness (1973), Franklin and others (1981) and Lang (1980); the expertise of the Program staff and technical committee; and review comments on draft proposals.

The Program charter called for accelerated research and development that would be applicable to a large geographic area. All research endeavors are constrained by time, money, and personnel, however, and we recognized that the plan would have to change as new information developed, constraints changed, or research objectives altered.

Scope of the Research

The biogeographic scope of the Program was the Western Hemlock Zone, lower elevations of the Pacific Silver Fir Zone, the Mixed-Conifer Zone, and the Mixed-Evergreen Zone (Franklin and Dymess 1973) in Washington, Oregon, and northern California where Douglas-fir is the dominant tree species in seral stages of forest development through subclimax. These regions span 8 degrees of latitude and encompass at least eight physiographic provinces (see frontispiece). Because the structure and composition of Douglas-fir plant communities vary among these physiographic provinces, the sampling plan included geographic stratification. These communities may also vary markedly along moisture and temperature gradients within provinces. Consequently, these gradients were also included in the sampling plan.

The sampling plan for each geographic replicate was to include both managed and unmanaged stands, but we found that managed stands were few, and often either too small or too young to be included. Although the program focused on the uniqueness of old-growth Douglas-fir communities, we also had to study biotic communities found in earlier stages of forest development for comparison. If our research was to provide new information relevant to forest management, we needed to assess the potential effects of management on the structure and composition of seral communities. Including the entire sere of forest development in sampling plans was impractical, but we could include at least those stages that would be expected to constitute the oldest managed stages-stands that are regarded by foresters as the last stage before harvest. We planned to describe all earlier stages through a review of the literature to ensure that community patterns in old-growth Douglas-fir were viewed in the full context of forest development.

We also planned to conduct an old-growth inventory independently of (hut concurrent with) the plant community studies. Funding constraints, however, prevented us from conducting the inventory.

Pilot Studies

We planned experimental sampling with various methodologies both to ensure that target populations would be adequately sampled with our methods, and to assess the natural variability within our study areas in order to determine the sampling intensity required to ensure statistically reliable sample sizes. These pilot studies would also enable us to evaluate the experimental design to ensure that the stratification and the gradients (and treatments) identified in the sampling plan were sufficient to meet the study's objectives. Pilot studies were to be performed before a final sampling plan was developed and implemented.

Vegetation pilot studies were not needed. A number of vegetation studies, including preliminary classifications of Douglas-fir communities, had been conducted throughout the region (see Franklin and Dymess 1973). Previous vertebrate community studies sponsored by the Pacific Southwest Region of the Forest Service and conducted by M.G. Raphael and R.H. Barrett at the University of California at Berkeley and B.G. Marcot at Oregon State University provided the Program with a substantial amount of information on sampling birds and forest-floor vertebrates (see Raphael and Barrett 1981, Raphael and Rosenberg 1983, Raphael and Marcot 1986). Little information, however, was available on sampling bats, arboreal mammals, fossorial mammals, raptorial birds, or aquatic amphibians. Although we fully recognized the ecological and economic importance of invertebrate communities, we had insufficient resources to describe these communities adequately.

Sampling Considerations

General questions can be answered with descriptive statistics. When the objective is to test specific hypotheses, however, statistical considerations become more important, and greater constraints are put on the sampling plan.

We planned studies at the community scale to answer the following general questions: Do old-growth stands represent a unique forest ecosystem? Do old-growth stands contain distinct fauna1 associations? Do certain species find optimal environments in old-growth stands? Are any species found only in old-growth stands? How do we classify old growth for inventory purposes? Answers to more specific questions were also sought: What changes take place in a developing Douglas-fir forest community after trees become dominant? How do management activities affect these changes? Do these changes differ significantly among physiographic provinces? Do these changes differ significantly within provinces because of topographic position, site quality, or position on a temperature or moisture gradient? Do the effects of management activities change with province, or within province with site?

Previous work on the plant communities in this region (Franklin and Dymess 1973) suggested that we stratify our sampling by physiographic provinces. Five provinces were originally planned to be sampled: the Northern Cascade Range, Southern Washington Cascade Range, Oregon Cascade Range, Oregon Coast Range, and Klamath Mountains in southern Oregon and northern California (see frontispiece).

The best possible approach would have been to complete an inventory of all late-seral Douglas-fir stands in each physiographic province before choosing stands for study. We could then have randomly selected stands in each stratum, accurately estimated the variability within and among stands, and used rigorous statistical tests of hypotheses about the similarity of gradients, community structure, and community composition in different forest types. In addition, sampling using quantitative methods would have resulted in reliable and generalizable models of forest development and environmental gradients. Unfortunately, this approach would have poorly met the needs of a research program that was constrained in both time and resources. Although a departure from this approach entailed risks of incomplete information and consequent failure of classifications or predictions, the need to produce timely and reliable information eventually took precedence.

We chose to describe and classify late-seral stages of Douglas-fir communities in these five provinces by preferentially (see Gauch 1982) sampling sites that represented the full range of variation occurring along age, moisture, and temperature gradients. Although the sites would not be random samples, the chance of not encompassing the ranges of natural variation would be less than for random sampling with the same number of samples. Good descriptions of community patterns would be obtained if no unknown biases influenced the selection of study sites. Because practically all statistical tests are based on random samples, however, tests for differences among strata or among sites (stands) could only be used heuristically. Likewise, classifications derived from preferentially sampled stands would represent potential communities-they could not be presumed to be applicable to all stands.

Plant Community Studies

Sampling

We planned to select a series of homogeneous sites that represented the full range of variation occurring along seral and moisture-temperature gradients. Replicate sites would be chosen. We planned to calculate the number of replicates (and sample sizes within replicates) required using measures of dispersion estimated in previous studies (see Franklin and Dymess 1973). We also planned to include riparian areas, as well as managed stands.

We planned to study both the structure and composition of the plant communities. Different sizes, shapes, and numbers of sampling units were to be used in sampling plant taxa. For example, Gauch (1982) recommended quadrats of 0.1 to 0.4 m^2 for epiphytes, 1 to 4 m^2 for mosses, and 200 to 800 m^2 for trees. In addition to commonly measured compositional elements, special attention would be paid to cryptogams, particularly lichens and fungi. Sampling hypogeous fungi would be attempted. The use of modified life-form categories would be considered for describing some aspects of stand structure and as part of the classification system. Structural elements of wildlife habitat that would be quantified included crown structure, snag and log abundance (by both size- and decay-classes), litter depth and humus development, vertical layering of the vegetation, and diameter-class distributions. A substantial effort would be made to ensure that data was collected in such a way that the results of the study would be compatible with information systems used by the National Forest system.

Analysis

Gradient analyses would be used for both stand-by-structure data and stand-by-species data. Direct gradient analysis would help to identify nonlinear responses to gradients and aid in interpreting more sophisticated analyses. In addition, direct gradient analysis would provide heuristic illustrations of community patterns and help to identify “potential” communities associated with major segments of gradients.

Ordination (for example, detrended correspondence analysis and nonmetric multidimensional scaling) of site-by-species and site-by-structure matrices of appropriately transformed and standarized data was planned to determine the major components of variation in the data resulting from complex gradients. Classification algorithms were then to be used to identify more objectively defined “potential” communities than is possible with direct gradient analyses. After the data were analyzed within strata, we planned similar analyses among strata to determine if regional gradients exist.

Products-The plant community study was to produce:

- A definition of old growth;
- A classification of late-seral Douglas-fir communities;
- A classification algorithm that could be tested on a new set of randomly selected late-seral Douglas-fir stands;
- Heuristic descriptions of forest development;
- Heuristic descriptions of the effects of major environmental gradients;
- Quantification of community patterns along complex gradients;
- Identification of “potential” communities associated with parts of complex gradients;
- Qualification (possibly quantification) of plant species’ responses to gradients, including
  - -Taxa closely associated with old growth,
  - -Correlations (negative and positive) between certain species and certain environmental variables, and
  - -Correlations (negative and positive) between species; and

Research hypotheses on:

- The effects of management on community structure and composition, and
- The effects of management on certain plant groups.

Vertebrate Community Studies

Sampling

Sampling vertebrate populations is much more complex than sampling terrestrial plant populations, in part because of the mobility of vertebrates and the tendency of their populations to vary in size both among seasons and among years. One visit per sampling unit is often adequate for many purposes in vegetation sampling, such as estimating the density, size, and species composition of trees. In contrast, 8 to 10 visits per site in each of four seasons for at least 3 years would be necessary to adequately estimate the species composition and population density of a bird guild characteristic of that particular site. In addition, a variety of sampling techniques are required to sample different vertebrate populations, and quantitative techniques are lacking for many key species, such as marbled murrelets, Vaux's swifts, and red tree voles.

We decided the best approach to selecting stands for vertebrate community studies would be to subsample the stands preferentially chosen for plant studies. This was to be accomplished by randomly choosing three replicates of at least 15 stands, with each replicate representing the full range of variation in late-seral stages. The total number of stands (45) was consistent with the work done by Raphael and Barrett (1981), which suggested that 45 stands was a suitable number for a team consisting of a field crew of four and total technical support of less than 10 people. We recognized that statistical tests could be applied with this sampling plan, but that samples would be drawn from preferentially chosen stands, not from all existing stands. The skill with which the preferential sampling was conducted was an essential element of many aspects of the Program. Our approach assumed that sample sizes for plant studies would greatly exceed 45 per stratum. Gauch (1982) suggested that a minimum of 50 to 60 stands per plant community type are necessary in areas with high environmental variation, whereas 50 to 100 homogeneous stands are necessary in substantially disturbed landscapes.

The ordination of stands along environmental gradients resulting from the plant study would provide a template for measuring the habitats of the vertebrates. Vertebrate ecologists were to examine gradients within the communities sampled to quantify vertebrate niches. These studies would provide descriptions of the structure and composition of the vertebrate communities and of the habitat relationships of vertebrate species: Environmental variables that are predictors (discriminating variables) of potential vertebrate communities associated with late-seral Douglas-fir stands could then be determined.

Study Establishment

The boundaries of stands chosen for study were to be drawn on topographic maps. A 50-m "no sampling" zone would be located within the periphery of the stand. Slope, aspect, and the location of riparian zones was to be noted. An initial transect line oriented to the elevational gradient was to be randomly located within the stand. Subsequent transect lines would then be located at 200-m intervals parallel to the initial line. The starting point of each line was to be located at a random distance of less than 50 m from the no sampling zone. These transects would serve as reference lines for locating sampling points, plots, lines, and grids. Lines along the elevational gradient would provide the basis for describing the stand, whereas lines perpendicular to riparian zones would be used to study riparian effects. Sample shapes, sizes, and numbers were to vary with the sampling technique used, the homogeneity of the area (as defined by the mobility of the species sampled), and the life history traits of the target species. All samples were to be replicated over time (some by weeks, seasons, and years; some just by years).

Analysis

Procedures similar to those outlined in the plant community data analysis section were to be followed. In addition, because we recognized that the reliability of density estimates will differ greatly among species, abundance values were to be standardized over all stands. The year-to-year dynamics of each species' status (its abundance and role in the various stands) were to be examined and interpreted before further analyses were completed. If analyses warranted, null model simulations were to be used to examine associations among species and to address questions of species' dependencies on old growth.

Even though only stands $\geq$ 40 ha were to be sampled, they would be "large" to some species, such as amphibians and small mammals, but "small" to other species, such as carnivores and raptors. Consequently, the effects of stand size would also be considered. For example, cluster analysis was to be used to classify groups of stands on the basis of species assemblages (vertebrate community composition). Multivariate analyses would then be used to separate the stands in a multidimensional "environmental" space. The magnitude of the contribution of each species to the community classification was to be determined by examining the ratio of the among-community variance to the within-community variance of the species' log-transformed or standardized abundance (similar to an F-test). Multivariate analysis of variance and multivariate analysis of covariance would then have to be used to determine if stand size provided a significant degree of separation and, if it did, whether other environmental variables also contributed significantly to the separation of clusters.

Within-stand analyses were to be used to compare patterns of species abundance within stands to patterns among stands. Each stand was expected to contain some portion of the gradients operating across all stands. Comparison of species' abundances across each gradient with the portion of the gradient occurring within each stand was to be used to explain community patterns and provide descriptions of each species' adaptability to gradients of limited scope. If certain species were absent from small stands but present in large stands, this approach was to be used to formulate hypotheses about mechanisms underlying the effect of stand size on community composition. Furthermore, potential competitive interactions could be explored by contrasting the portions of gradients occupied by a species in the presence of another species to the portions of gradients occupied in the absence of that species.

We planned to contrast classifications of stands based on vertebrate community composition to classifications based on plant community structure, composition, or both. If community classification based on plant data is to be used for management purposes, it is crucial to understand how these plant communities are related to the vertebrate communities.

Products-The vertebrate community study was to produce:

- A list of species closely associated with old growth;
- A classification of vertebrate communities found in late-seral Douglas-fir communities;
- A classification algorithm for "potential" communities that could be tested on a set of randomly selected late-seral Douglas-fir stands;
- Heuristic descriptions of species' responses to forest development;
- Heuristic descriptions of species' responses to major environmental gradients;
- Quantification of vertebrate community patterns along complex gradients;
- Descriptions of species' responses to extensive complex gradients (species' habitats);
- Descriptions of species' responses to intracommunity factors (species' niches);
- Predictions of the effects of large-scale management activities on vertebrate community structure and composition;
- Descriptions of species' responses to management activities;
- A comparison of plant community classifications to vertebrate community classifications;
- A description of the role of riparian zones in late-seral vertebrate communities;
- A measure of the effect of stand size on community composition;
- A list of key species, environmental variables, and gradients for late-seral Douglas-fir stands; and

Research hypotheses on:

The effects of stand size,
The effects of competition, and
The effects of predator-prey relationships.

Insular Ecology Study

The fragmentation of old-growth Douglas-fir forests may result in substantial changes in the wildlife and plant communities occurring in those forests. Both community and species-specific studies are necessary to assess the effects of forest fragmentation and to provide guidelines for mitigating them. The impact of fragmentation largely depends on the sizes and patterns of abundance of the resulting old-growth stands. The smaller the stand and the more disparate the environment surrounding the stand (the stand context), the greater the pressure would be from early-seral species on old-growth species. If an old-growth stand was only marginally capable of supporting populations of species that require old growth for population persistence, and if it was not near (relative to the dispersal abilities of those species) other old-growth stands, these populations would eventually become extinct. Additional causes of the species/area effect are unknown, but presumably could operate in these situations. Finally, at some lower size limit, the stand would begin to lose its old-growth characteristics because of environmental influences alone, such as successive loss of trees at the periphery from blowdown and drier microclimates within the stand from edge effects.

The species/area relationship in sampling makes the problem of studying the effect of stand size and stand context difficult. For example, if IO-ha plots were randomly sampled in an extensive old-growth forest, we would not expect to find many plots containing all the key species representing that forest's community. Indeed, the average composition of species on the 10-ha plots would probably differ from that of a random sample of 20-ha plots, even if the total areas sampled were equal. Thus equal-sized plots were to be compared among stands of different sizes.

To study fragmentation, we planned to use a sample plot size between 1 and 10 ha. Such a small plot provides a high probability that any particular species would not be detected, so many plots were to be randomly sampled to estimate the probability of a particular species being present. Plots were to be located within randomly selected stands that were 0 to 10,20 to 40, and 80 to 160 ha. The effects of stand size at the large end of the scale would also be evaluated in the vertebrate community studies.

The stands thus chosen were to be cross-classified according to stand context, "potential" old-growth community classification (from the vegetation study), and the presence or absence of species associated with old growth. The resulting data would be placed into a contingency table conditioned on stand size. Discrete multivariate analysis (log-linear analysis) was to be used to test for independence between and among the categories. A table of expected cell frequencies was to be used to estimate the probability that a stand of a particular size, context, and vegetation class would have none, some, or most old-growth species. The magnitude and direction of interactions were to be reported in the tables of the ratios of the log-linear parameter estimates to their standard errors. An important feature of this approach is that the effects of fragmentation (size, context, and class) are as likely to be multiplicative as linear, and whereas this presents problems in analysis of variance designs, it does not in log-linear model analyses.

Species-Specific Studies

The insular ecology study was to examine the general effects of old-growth forest fragmentation on wildlife and plant communities. Certain species deemed to be sensitive to the loss or alteration of old-growth habitats were also to be studied in detail to identify management prescriptions that might be applied to ensure viable populations. Several species had been identified as sensitive to the loss of extensive areas of old growth, the foremost being the spotted owl. The Program initiated two studies on the spotted owl and cooperated with the State of Washington on a third; the results of these studies will be published elsewhere. Similar projects on other species were to be initiated as needs became apparent.

We planned species-specific studies to identify key elements of the species' habitat, quantify its responses to both inter- and intra-community dynamics, including competitive and predator-prey relationships, and examine aspects of its population biology, with emphases on population dynamics, dispersal behavior, and minimum area requirements. These studies were to be designed to result in specific management guidelines that would ensure species viability.

Other Research

The Program charter also called for determining economic aspects of old-growth forest ecosystems, evaluating management alternatives, evaluating silvicultural options (including cost/benefit analyses), and determining the role of old growth in biological diversity. Because of funding constraints, however, research planning focused primarily on wildlife and plant community studies.

Because of the interweaving of our research approach, the results of these studies were to be integrated. The results would be synthesized to produce management recommendations and data bases that would be available to the National Forest system, cooperating groups such as the Bureau of Land Management, and other potential users of the information. The goal of synthesizing Program results was to be met by several methods, including convening a symposium for the presentation of Program results.

Implementation

Study Site Selection and Sampling Design for Community Studies

The design chosen for studies of terrestrial ecosystems was labeled a "T-matrix." The result was a five-cell matrix (three cells in old growth, one in mature, and one in young) with nine stands per cell per province (fig. 1).

The complex moisture-temperature gradient prevalent in the Pacific Northwest was studied only in old growth—equal numbers of stands were chosen for provisional categories of "wet old growth," "mesic old growth," and "dry old growth." The age gradient was studied only in mesic stands, with equal numbers of stands chosen in the provisional categories of "mesic young" and "mesic mature."

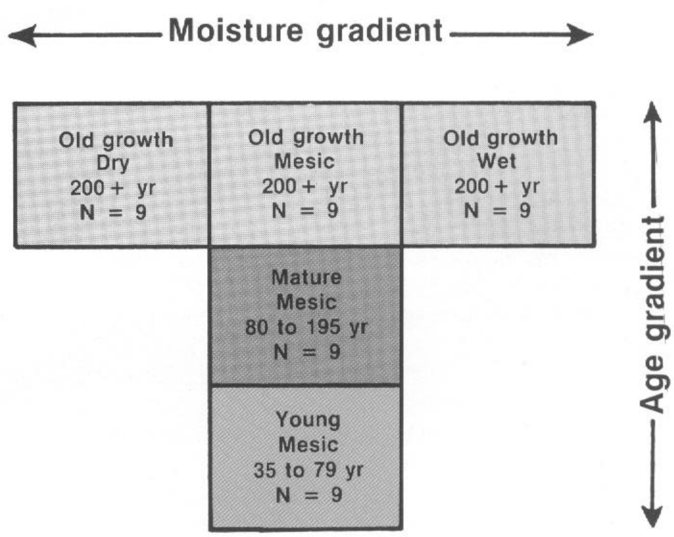

Figure 1—T-matrix sampling design used to select study sites in each province.

The general concept of using this T-matrix design to structure sampling and data analyses was fundarnentally sound; however, implementing it in a strict balanced ANOVA-type design was unrealistic. Although the study was stratified into physiographic provinces, the provinces (especially the Oregon Cascade Range) were so large that within-province variation made it difficult to develop a single province-wide classification. For example, a dry old-growth site in the northern Oregon Cascades was typically quite different from a dry old-growth site in the southern portion of the province. Objectively classifying the moisture-status of a 40-ha stand relative to other stands in the province based on an hour or two of field inspection was impossible. A major variable that could not be controlled well in stand selection was elevation. Although the age- and moisture-classes typically had similar mean elevations, considerable elevational variation occurred within each class. Because elevation represents a complex temperature-moisture gradient and could compensate for other factors (such as slope, aspect, and soil depth) that determine moisture condition, the simple one-way classification of stands into moisture-classes should be used cautiously.

Another difficulty in meeting study requirements during stand selection was caused by the restrictive nature of the stand selection criteria. In general, only a subset of the selection criteria could be satisfactorly met in any given stand. Finding stands that were over 40 ha; could be walked to from a vehicle in less than 30 minutes; were free from previous management activity; had no management activities planned during the 3-yr sampling period; were not close to large, noisy streams where bird calls could not be heard; were accessible from roads that were free of snow in the spring; and met age- and moisture-class requirements was generally not possible. As a result, logistic criteria often outweighed criteria formed by the research questions. Some stands had to be selected that were not optimal in terms of stand structure, homogeneity, freedom from past human activity, or site moisture conditions. The major effect of this problem was an unbalanced design in terms of the five age-moisture classes. These problems did not appear to seriously bias the range of age and moisture conditions sampled, however.

Locating large stands that fit only within one plant association or moisture-class was often not possible. Most plant community classifications in the region have been based on 500-m^2 plots rather than entire stands. At the time of stand selection, little information was available about the spatial properties of regional plant associations at larger scales. For example, during stand selection, very dry and very wet sites were often found to be small in extent and typically embedded within a matrix of wetter or drier conditions. The large size of the sampling area (relative to the scale of the plant associations) required the somewhat subjective approach of considering topographic position and coarse-scale physiographic features in conjunction with vegetation to select large areas that fell into one of three moisture-classes-wet, mesic (or moderate), and dry.

The sample size problem was generally not as severe for the three age-classes-old growth, mature, and young. Disturbed forests in the southern areas, parts of the Oregon Coast Range, and dry sites in general often contained a greater mix of age-classes than desired, however. In areas where the landscape was more of a natural mosaic of age-classes, stands were located in areas where aerial photographs and ground truthing indicated that one age-class was predominant and contrasts between age-classes were minimal. Although the “search image” for study stands was for uniform age-classes and structural patches, some mixed age-classes were included in the sample if they were typical of the landscape or site moisture conditions.

Despite some difficulties in implementing the sampling design, the stand selection process was considered to be generally successful in meeting Program goals. A wide range of old-growth stands, on different sites, with different structures and stand histories was sampled. Although more variability was encountered in site conditions of mesic young and mesic mature stands than originally intended, measures of site and environment (understory vegetation) indicated that no major differences exist along the age gradient of stands that would invalidate comparisons based on age-related characteristics.

The T-matrix concept provided a framework for stand selection and data analysis but was not considered a prescription for strict application of ANOVA models in statistical hypothesis testing. The stand selection and ecological survey was well suited to gradient analyses and regression approaches in an exploratory sense. The use of age- and moisture-classes to investigate ecological relationships should be viewed as a coarse-scale gradient analysis rather than an analysis of replicates of discrete forest types. Although classifications into broad types were useful for simplifying the results and transferring them to managers who often have to deal with simplified forest response units, gradient and regression analyses were most useful for understanding the details of successional relationships.

Pilot Studies of Vertebrates

Pilot studies of vertebrate sampling methods were conducted in 1983 on the Wind River Experimental Forest in the Southern Washington Cascade Range and on the H. J. Andrews Experimental Forest in the Oregon Cascade Range.

Various techniques were evaluated for sampling different segments of the vertebrate communities. Sampling protocols (on file at the Forestry Sciences Laboratory in Olympia, Washington) were developed for aquatic amphibians (stream surveys), terrestrial amphibians (time-constrained searches of the forest floor and pitfall traps), forest-floor small mammals (snap-trapping and pitfalls), squirrels (tracking stations), bats (ultrasonic recording of echolocation calls), and small, diurnal forest birds (point counts and foraging observations). We were unable to develop practical methods for conducting extensive surveys of raptors or medium- to large-sized mammals. Reptiles proved to be rare in the forests, and we did not study them. Evaluations of these and other techniques are being published elsewhere (Carey and Ruggiero, in press).

Plant Community Studies

The scale of community and age-class patterns posed sampling problems for vegetation studies that could not be adequately addressed within the research schedule because we did not conduct vegetation pilot studies. For example, although sampling design of the vegetation studies appeared to be adequate for the overstory tree component (five O.l-ha plots 100 to 150 m apart per stand), how well this design would sample low-density structures such as large snags was not known. During the first field season, some sampling tests were undertaken, and minor modifications were made to vegetation sampling during the next and final field season, such as doubling the plot size for large snags.

Conducting a detailed community survey of mosses and lichens was not possible. Common species were identified but many less-common species required more time and taxonomic skill than was available in this rather extensive survey. In addition, many mosses and lichens inhabit tree canopies and could not be adequately sampled. Foliose canopy lichens, such as *Lobaria* spp., that had fallen to the forest floor were tallied in ground cover vegetation surveys, however. Hypogeous fungi were not sampled during the plant community study because of the seasonality of the fungi and the effort required to identify genera and species in a large survey.

Vertebrate Community Studies

Because of funding constraints, the Northern Cascade Range province was not sampled. The community studies were implemented as planned in the remaining four provinces with only a few exceptions. Because of both funding and logistical constraints only one replicate of the study design (15 stands) was sampled in the second year in the Oregon Cascade Range, and bat communities were studied only in the southern Washington Cascade Range and Oregon Coast Range.

In addition, gathering observations of foraging birds required much more time than expected. As a result, these data were only recorded incidentally, which resulted in insufficient data for analysis. Similarly, because relatively little data was collected on squirrels from tracking stations, these results are also not reported here.

Vertebrate community studies were implemented in the Southern Washington Cascade Range, Oregon Cascade Range, and Klamath Mountains and, in part, the Oregon Coast Range in 1984. Studies were continued in the Southern Washington Cascade Range, Oregon Cascade Range, and the Klamath Mountains, and fully implemented in the Oregon Coast Range in 1985. Community studies ended in 1985 in the Southern Washington Cascade Range, Oregon Cascade Range, and Klamath Mountains, and in 1986 in the Oregon Coast Range.

Insular Ecology Study

This study was not conducted because of funding constraints.

Species-Specific Studies

Major research efforts were initiated on the marten and on arboreal rodents that are important prey species of spotted owls. Brief descriptions of these studies are provided by Biswell and Carey, Biswell and others, Center and others, Corn and Witt, Gillesberg and Carey, and Jones and others in the Poster Abstracts section of this volume. Ma’or findings of these studies will be reported elsewhere.

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