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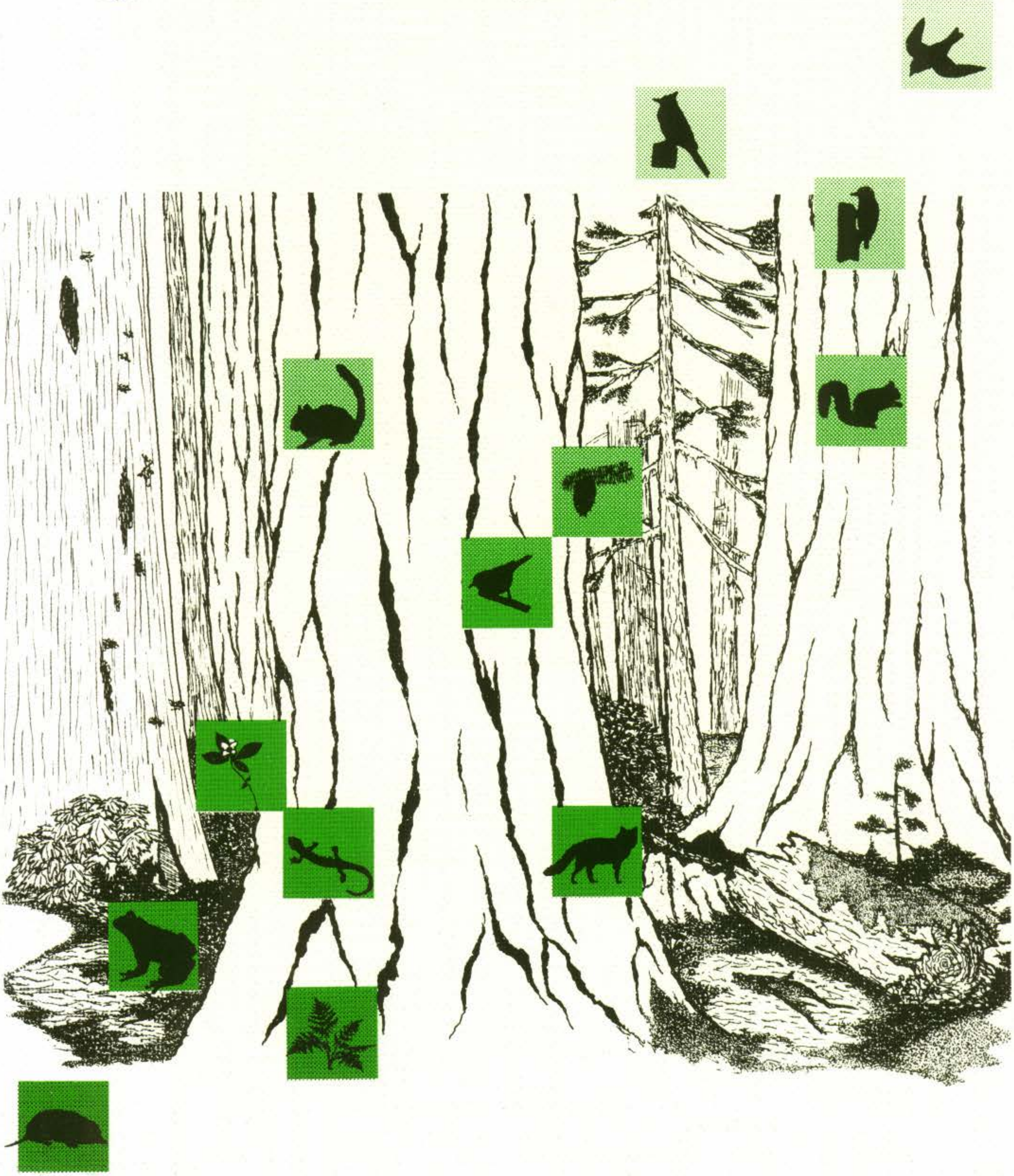
Wildlife and Vegetation of Unmanaged Douglas-Fir Forests



WILDLIFE AND VEGETATION OF UNMANAGED DOUGLAS-FIR FORESTS

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Preface

Old-growth Douglas-fir forests in the Pacific Northwest-and their most celebrated inhabitant, the northern spotted owl-have engendered an acrimonious controversy that has been raging for over a decade. Should ancient forests be protected for their aesthetic appeal and because they provide a broad range of ecological values, including the most amenable environment for some plants and animals? Or, should they be harvested because the revenue they provide affects the economic stability of the entire region? These questions encapsulate one of the most heated and socially significant conservation and natural resource management debates of this century. This book is an outcome of that debate, and represents the major findings of the USDA Forest Service's Old-Growth Forest Wildlife Habitat Research and Development Program.

This research program began long before the term "ancient forest" added an emotional dimension to the controversy. When this research began in 1983, these forests were simply "old growth," and the debate was about whether old growth was a unique stage of Douglas-fir/western hemlock forest development that provided critical habitat for a broad array of associated species. Some people believed that upwards of 125 species were "dependent" on old growth for their survival; others maintained that although some animals might prefer old growth, none really needed it. The first of these arguments is probably an overstatement and the second is ecologically naive.

Program research has provided new insights about how nature regenerates forested ecosystems in a way that maintains aspects of the structural complexity of old-growth forests in the new stand. These insights have changed the way old growth is perceived, and they have forever changed resource management in the Pacific Northwest through such concepts as "new forestry" and "new perspectives (in forestry)," and a clearer understanding of the ecological value of unmanaged forests in all stages of development. Land management policies, politics, and prescriptions have all been influenced in ways that were not predictable at the outset.

Much has been learned from this research about the effects of spatial variation (for example, different physiographic provinces and different elevation zones) and temporal variation (for example, differences among winters) on patterns of species abundance. Perhaps most of all, we understand clearly now that very complex issues are involved in determining the kinds, amounts, and arrangements of environments necessary to ensure the viability of plant and animal populations.

The fundamentals of population persistence and of maintaining biological diversity in managed landscapes are just beginning to be understood. Although the findings presented here are most pertinent to Douglas-fir forests in the Pacific Northwest, many of the ecological insights contained in these papers have more general applicability. We hope that this book will be an important resource for managers and researchers working in any forested ecosystem. We also hope the book will stimulate new studies to build on the information presented here.

To improve the readability of these papers, only common names for vertebrates, trees, and shrubs are used in the book. A list of the scientific names of all species mentioned is included in Appendix A at the end of the book. The papers contained in this volume were originally presented at a symposium entitled, “Old-Growth Douglas-Fir Forests: Wildlife Communities and Habitat Relationships,” held in Portland, Oregon, on March 29-31, 1989. Manuscripts prepared from these presentations, however, have been reviewed by at least two technical experts. Consequently, many of the papers have undergone extensive revision, and certain aspects may differ substantially from presentations given at the symposium. Abstracts of poster presentations from the symposium are included in Appendix B.

We thank Julianne Bulgrin for her help in preparing maps and figures and Janet Jones for compiling and editing the References and assisting with desktop publishing. We would especially like to acknowledge Sharon Kuhnau for the inestimable administrative and moral support she provided during the entire tenure of the Old-Growth Forest Wildlife Habitat Program

Leonard F. Ruggiero
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Introduction

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

Jack Ward Thomas

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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

Leonard F. Ruggiero

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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.

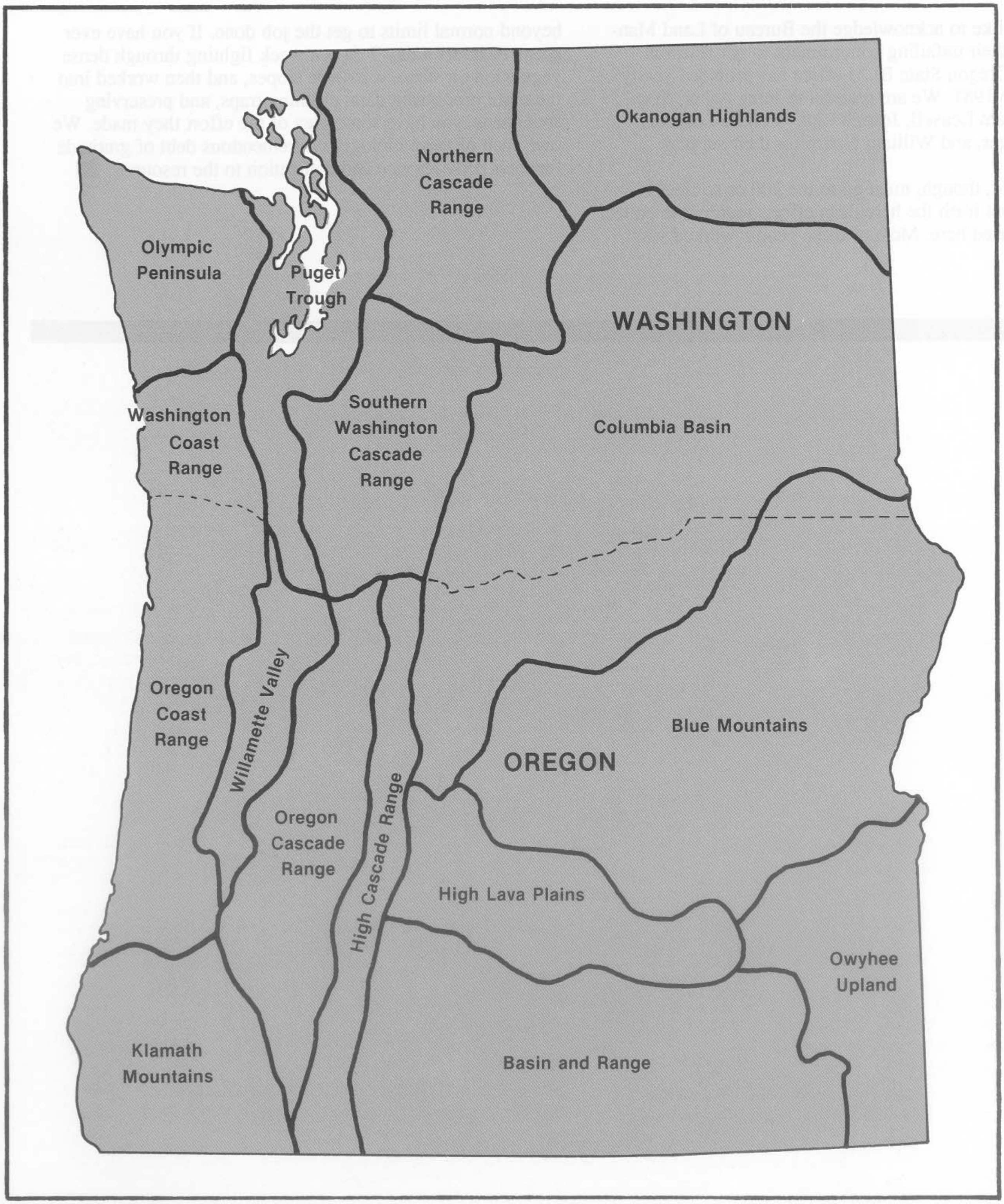
In addition to the practical constraints on geographic scope and kinds of stands sampled, we were also constrained by available funding to study either vertebrate communities or a limited number of high-visibility species that were thought at that time to be closely associated with old growth. We could 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

Andrew B. Carey and Thomas A. Spies

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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."

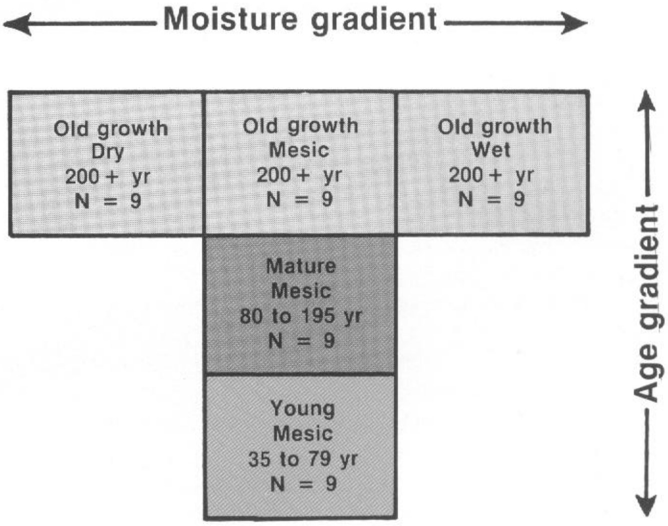

Figure 1—T-matrix sampling design used to select study sites in each province.

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.

Continue

Part 2

The Environmental Setting

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Climate Change and the Origin of Old-Growth Douglas-Fir Forests in the Puget Sound Lowland

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Abstract

The vegetation and climate history of the Pacific Northwest is best understood from fossil pollen records and climatic simulations by general circulation models of the Earth's atmosphere. Paleoclimatic simulations by these models provide a physical explanation of the climate associated with past vegetation changes. During the maximum of the North American continental glaciation (30,000 to 18,000 years Before Present (years BP)), the Pacific Northwest experienced dry-cold easterly airflows from a strong high-pressure system centered above the massive continental ice sheet. Vegetation west of the Cascade Range consisted of open forest-tundra parklands with lodgepole pine, Engelmann spruce, and mountain hemlock interspersed with tundra communities. By about 10,000 years BP, the continental ice sheet had collapsed, and summer insolation increased because of changes in the Earth's orbital features. These changes brought warm-dry summers to the Pacific Northwest, and pollen records in the southern Puget Lowland indicate a predominance of Douglas-fir, oak, alder, and prairie herbs. Fires became more frequent, as lake sediments show a marked increase in charcoal concentrations. The closest modern analog to this vegetation may be the oak savannas and Douglas-fir forests of the Willamette Valley. By 6,000 years BP, modern climatic conditions were established, and pollen records in this region show decreases in Douglas-fir, alder, oak, and grass pollen and increases in western redcedar and western hemlock pollen. Charcoal concentrations in sediments decrease rapidly at this time.

Pollen evidence indicates, therefore, that the modern forest composition of the Puget Lowland was established about 6,000 years BP. Although structural properties of these forests cannot be inferred from the pollen record, both the structure and composition of old-growth Douglas-fir forests can reasonably be assumed to have first established at this time. No compelling evidence in pollen data and paleoclimatic simulations suggests that this forest type existed elsewhere before 6,000 years BP. Old-growth Douglas-fir forests thus developed relatively recently on an evolutionary time scale and probably do not represent a coevolved complex of species bound together by tightly linked and balanced interactions.

Introduction

Pacific Northwestern forests have changed profoundly over the past 30,000 years in response to climate variations driven by changes in large-scale controls of the Earth's climate system (such as solar radiation, sea surface temperature, extent of land and sea ice, and atmospheric trace gases and particulates) (Barnosky and others 1987). Both fossil pollen records of past vegetation and physical models of global atmospheric circulation clearly show that climate variations follow unique paths as new combinations of boundary conditions establish and disappear with varying periodicities (COHMAP members 1988, Huntley and Webb 1989). As a result, the climate history of the Pacific Northwest, as in other regions of the world, should not be viewed as a simple sequence of latitudinal or elevational displacements of modern climatic zones.

Plants have, therefore, not been able to escape climatic change by migrating within zones of climate that are simply displaced in space. Species continually face new conditions and must adjust to them by evolutionary, ecological, or phenotypic mechanisms (Brubaker 1986). Genetic change in long-lived species such as Northwestern conifers is probably too slow to keep pace with rates of climatic change (Bartlein and Prentice 1989). Thus, these species are probably not perfectly adapted to current climates and should retain some “memory” of past conditions in their current genetic make-up. The short-term responses of Pacific Northwest conifers to climatic change primarily involve ecological mechanisms (for example, altered reproduction and establishment rates) and physiological adjustments (for example, drought avoidance or tolerance mechanisms) that affect tree establishment and survival.

Pollen preserved in lake and bog sediments have provided most of the empirical evidence of past vegetation and climate in the Pacific Northwest (see Baker 1983, Bamosky and others 1987, Heusser 1986). Pollen data accurately reveal the general composition of regional forests but are less precise for reconstructing fine-scale forest features such as the composition and structure of individual stands. Stand conditions are generally inferred from knowledge of stand characteristics in modern forest zones thought to be similar to ancient forests. Plant macrofossils (such as leaves, seeds, and cones), which are often present in such sediments, have been invaluable for confirming and refining interpretations of pollen records (for example, Cwynar 1987, Dunwiddie 1986).

Fossil pollen records in the Puget Sound region indicate that Western Hemlock Zone forests (Franklin and Dyrness 1973) first established about 6,000 years ago. By inference, old-growth Douglas-fir forests date from this time. Because no evidence has been found that Douglas-fir forests existed as a zonal forest type elsewhere in the Pacific Northwest before this time, this forest association is young on an evolutionary time-scale and may not represent highly coevolved species-interactions.

In this paper, I will discuss forest and climate change in the lowlands west of the Cascade Range over about the past 30,000 years, with emphasis on the Holocene (the present interglacial, from 10,000 years ago to the present) because pollen and plant macrofossil records are most abundant and old-growth Douglas-fir forests first became dominant during this period.

Sources of Paleoenvironmental Information

Pollen and Plant Macrofossils

Pollen and macroscopic plant parts are well preserved in anaerobic lake and bog sediments. Pollen is much more abundant than plant macrofossils because pollen (particularly of trees) is often produced in large amounts and widely dispersed by the wind. Owing to its ubiquitous occurrence, pollen has been the most important source of information about past vegetation in the Pacific Northwest (Baker 1983, Bamosky and others 1987, Heusser 1986). Pollen data have been supplemented in several studies by plant macrofossils, however, to increase the taxonomic and spatial resolution of vegetation reconstructions (Bamosky 1981, 1985, Cwynar 1987). Plant macrofossils provide finer taxonomic information than pollen because seeds and leaves typically can be identified to species, but pollen is generally identified to the genus for trees and shrubs and only to family for some important herbs (such as grasses and sedges) (Birks and Birks 1980). Macrofossils also reveal the local occurrence of plants near the collecting site because leaves and seeds fall close to the parent plant. Pollen, on the other hand, is often carried several kilometers before falling to the ground and, therefore, reveals the general composition of regional vegetation.

Fossil pollen data are interpreted primarily by making comparisons between modern and fossil pollen assemblages (Birks and Birks 1980). Researchers look for pollen assemblages in modern sediments that match those found in fossil sediments. If a close match is found, the modern vegetation is considered to be a good analog for past vegetation. Fine features of the vegetation, such as stand structures or local variation in stand composition, are inferred to have been the same as in the modern vegetation.

Radiocarbon dates or well-dated volcanic ash layers establish the timing of past vegetation change. Ash from the eruption of Mt. Mazama (about 6800 years BP, S. Porter, pers. comm.) forms a well-defined layer in lakes and bogs throughout the Pacific Northwest and provides an important time marker in Holocene sediments of the region.

Because lakes are formed primarily by the action of glaciers (such as glacial scouring and kettle formation), the spatial coverage of lake pollen records in the Pacific Northwest is related to the limits of continental and alpine glaciation (for example, see Barnosky and others 1987). Although alpine glaciers covered most of the Olympic Mountains and the Cascade Range, only one study (Dunwiddie 1986) has been done at high elevation, and the vegetation history in most of these mountains remains unknown. Continental glaciers

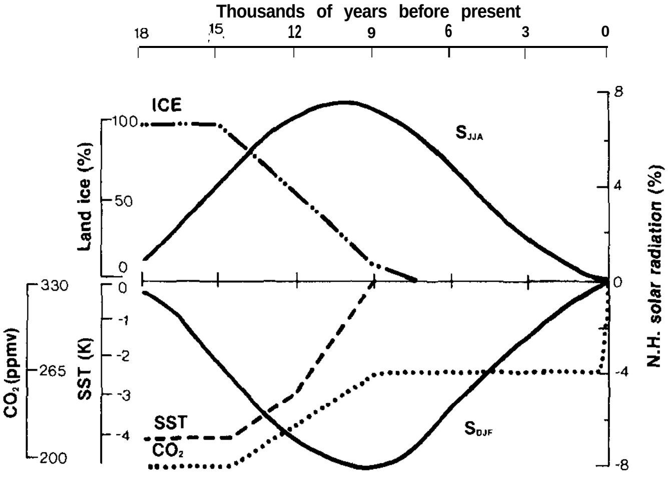

Figure 1-Major changes in external and internal boundary conditions of the Earth's climate system since 18.000 years BP (after Kutzbach and Guetter 1986). S_{JJA}, SDJF: Northern Hemispheric solar radiation in June-August and December-February, respectively, as Percentage difference from present. Land ice as percentage of present. SST: global mean sea surface temperature as departure from the present. CO_2 as concentration in parts per million.

extended as far south as the central Puget Lowlands in Washington (Waitt and Thorson 1986). Consequently, lowland pollen records are relatively abundant from central Washington to southern British Columbia but are scarce in southern Washington and Oregon. Several excellent reviews of the vegetation history of the Pacific Northwest have recently been published (Baker 1983, Bamosky and others 1987, Heusser 1986).

Paleoclimatic Simulations by General Circulation Models

Over the past two decades, physical models of atmospheric circulation have been developed to examine the interactions of the major external and internal controls of global climate (for example, Hansen and others 1984, Kutzbach and Guetter 1986, Schlesinger and Zhao 1988, Whetherald and Manabe 1988). These models represent the current understanding of Earth's climate system and are being used to assess the characteristics of past and potential changes. The Community Climate Model (CCM) of the National Center for Atmospheric essearch (NCAR) (Kutzbach and Guetter 1986) has been used to examine the ability of one model to reconstruct past climate change as recorded by fossil data (COHMAP members 1988). The major boundary conditions of this model are seasonal solar radiation, sea surface temperature, atmospheric aerosol and carbon dioxide concentrations, and the volumes of land and sea ice (fig. 1). The degree of agreement between paleoclimatic simulations and empirical evidence of past climate measures the success of the model. The model has been tested with paleovegetation and lake-level records from North America, Europe, and tropics of Africa and Asia. In general, the agreement has been good, and the model is presently considered to be a reasonable mechanistic explanation of the climatic variations that drove past vegetation change. The comparison of these simulations with vegetation history in the Pacific Northwest is described in greater detail in Bamosky and others (1987) and COHMAP members (1988).

Definition of Old-Growth Douglas-Fir Forests and Their Identification in the Fossil Pollen Record

Old-growth Douglas-fir forests of the Western Hemlock Zone (Franklin and Dymess 1973) are defined by a combination of compositional and structural characteristics (Old-Growth Definition Task Group 1986). Old-growth forests generally may be identified by the presence of two or more tree species with large diameters (typically Douglas-fir plus one or more shade-tolerant associates, such as western hemlock or western redcedar); a wide range of sizes and ages and a deep, multilayered canopy; and substantial woody debris in the form of logs and standing snags.

Because pollen records reveal the compositional aspects of the vegetation, they indicate whether tree species that currently characterize old-growth stands were common in the past. They cannot, however, provide definitive evidence that those trees grew together in the same stands, or that past stands had the structural characteristics of modem old-growth forests. In this paper, I assume that structural characteristics follow compositional characteristics, and thus that old-growth Douglas-fir stands were first established in the Pacific Northwest when fossil pollen assemblages first matched pre-settlement pollen percentages of the modern Western Hemlock Zone. Because of the poor resolution of pollen data, the terms "old-growth Douglas-fir forests" and "Western Hemlock Zone forests" are used interchangeably in this paper.

Full- and Late-Glacial Vegetation and Climate (30,000 to 10,000 years BP)

The last ice age in the Pacific Northwest culminated in the Fraser Glaciation about 25,000 to 10,000 years BP (Waitt and Thorson 1983). Mountain glaciers covered the Cascade Range and Olympic Mountains from 29,000 to 22,000 years BP (Porter and others 1983), but lowland areas remained ice free until about 18,000 years BP, when ice advanced from southern British Columbia into the coastal Olympic Peninsula and the Puget Lowland (Waitt and Thorson 1983). These ice lobes coalesced and reached their maximum extent in the southern Puget Lowland south of Olympia, Washington. Lowland ice began to retreat about 15,000 years BP.

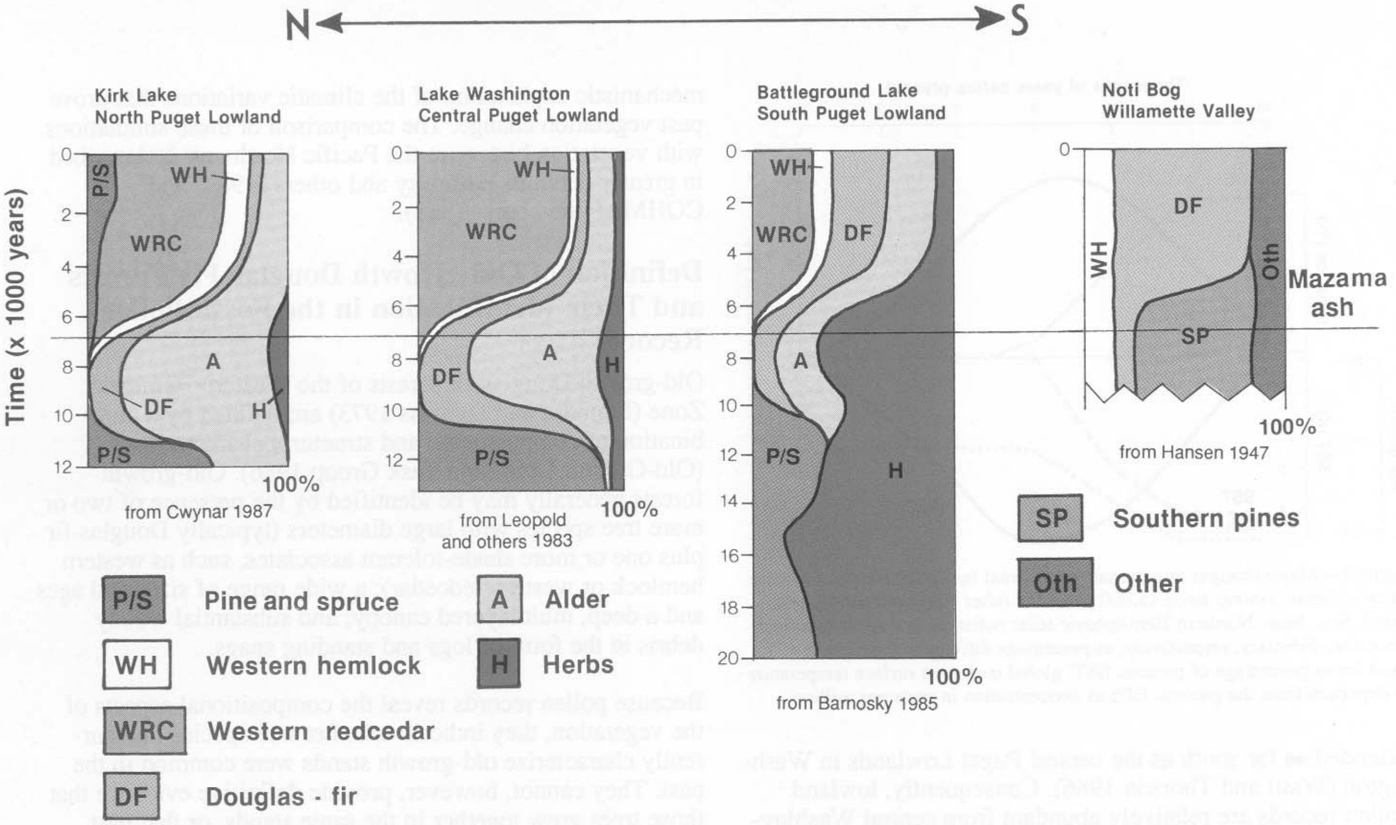

Figure 2—Schematic summary pollen diagrams from selected sites in the Puget Lowland and Willamette Valley. Each panel summarizes the percentage changes of major pollen taxa over time. Sources of data are indicated at the base of each panel.

Full-glacial vegetation (about 30,000 to 20,000 years BP) is recorded by several pollen diagrams south of the ice margin in the Olympia Peninsula and southern Puget Lowland (see Barnosky and others 1987). Unfortunately, no full-glacial pollen records are available for Oregon, so the vegetation south of the Columbia River during this period is unknown. Before 17,000 years BP, pollen assemblages of the southern Puget Lowland were dominated by grass, sedge, and sagebrush, but also showed moderate amounts of mountain hemlock, spruce, and pine (fig. 2) (Barnosky 1985). Needle fragments of Engelmann spruce and lodgepole pine have been found in sediments of this age (Barnosky 1981, Barnosky 1985). The abundance of both herb and tree pollen suggests that a parkland vegetation of tundra interspersed with trees covered the lowland landscapes. The presence of conifer needles indicates that trees survived in protected areas around lake basins. The full-glacial vegetation of the southern Puget Lowland may have resembled modern treeline associations in the Rocky Mountains of Idaho and southern Alberta (Barnosky and others 1987).

Climatic warming at the end of the last glaciation initiated a series of rapid vegetation changes (Barnosky and others 1987). Pine pollen (presumably lodgepole pine) increased between about 17,000 and 15,000 years BP. At one site, the increase in pine was associated with macrofossils of Douglas-fir and Sitka spruce. Tundra communities must have been rapidly invaded by trees because herb pollen declined sharply during this period. Between 15,000 and 12,000 years BP, Sitka and Engelmann spruce, lodgepole pine, mountain hemlock, and true fir (species unknown) were the most important conifers in the southern Puget Lowlands. From 12,000 to 10,000 years BP, western and mountain hemlock, Douglas-fir, Sitka spruce, grand fir, red alder, and Sitka alder characterized the regional vegetation. These late-glacial pollen records reveal interesting mixtures of montane and lowland tree species with both dry and mesic site requirements (Barnosky and others 1987). Under late-glacial climates, local substrate and topographic variations may have caused strong moisture and temperature gradients, resulting in a complex mosaic of differing forest types. Regardless of the cause, similar assemblages of species are rare on the modern landscape. Furthermore, no evidence exists that old-growth Douglas-fir forests were present south of the ice sheet in western Washington during late-glacial times.

Climate simulations for the full-glacial period (represented by 18,000 years BP) show that atmospheric circulation over North America was strongly influenced by the large Laurentide ice sheet that covered much of the continent (Kutzbach and Guetter 1986, COHMAP members 1988. See fig. 3). Air descended from the upper atmosphere above the ice sheet

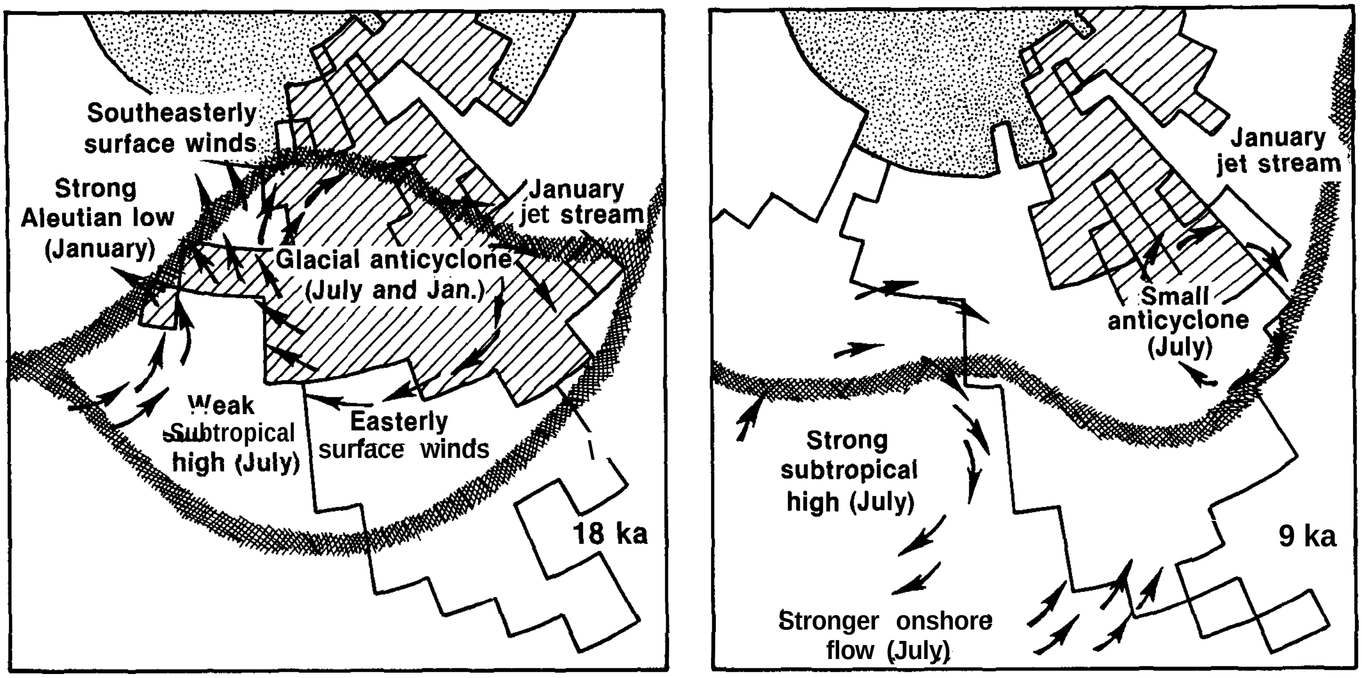

Figure 3-Paleocliiatic conditions for the Pacific Northwest as simulated by the NCAR CCM model for 18,000 and 9,000 years BP (after Bamosky and others 1987).

causing a strong high-pressure system, "the glacial anticyclone," centered over the ice cap. Anticyclonic circulation brought prevailing easterly airflows across the Pacific Northwest, particularly in winter. Because of cold-dry airflow from the mid-continent ice cap, simulated temperatures, precipitation, and precipitation-minus-evaporation for 18,000 years BP were substantially lower than at present. These simulations agree with fossil pollen and macrofossil records that show tundra and xeric treeline species such as Engelmann spruce in the Puget Lowland during the full-glacial period.

Interglacial Vegetation and Climate (10,000 Years BP to Present)

The present interglacial is called the Holocene. By convention, it is defined as the period from 10,000 years BP to the present. By 10,000 years BP, lowland glaciers had receded from the Puget Lowland into southern British Columbia, and alpine glaciers were restricted to very high elevations in the Cascade Range and Olympic Mountains (Burke and Birkeland 1982, Thorson 1980).

Early Holocene (10,000 to 6,000 years BP)

Tree species indicative of cold climates had disappeared from the Puget Lowland by the beginning of the Holocene. Rapid changes in pollen and macrofossils suggest the onset of substantially warmer and drier climate than at present. Between about 10,000 and 6,000 years BP, pollen diagrams from southern British Columbia to the central Puget Lowland showed maximum percentages of Douglas-fir, red alder, grass, and prairie herbs (Barnosky 1981, Leopold and others 1982, Mathewes and Rouse 1975, Tsukada 1982, Tsukada and others 1981). Pollen diagrams from the southern Puget Lowland show less Douglas-fir and alder but more grass and oak pollen (Bamosky 1985), suggesting a north-south vegetation gradient with a higher frequency of open, xeric communities in southern areas. Pollen of mesic tree species, such as western redcedar and western hemlock, was rare throughout the region. In addition, charcoal concentrations increased dramatically and spores of bracken fern became abundant in sediments.

Old-growth Douglas-fir forests were not important at the regional scale during the early Holocene because pollen assemblages of this period differed substantially from presettlement pollen spectra in modem forests in the Western Hemlock Zone (Barnosky 1981, Heusser 1977, 1986). The general importance of oak and grass pollen and the scarcity of mesic taxa in early Holocene pollen assemblagessuggest that ancient vegetation may have been similar to modem oak savanna and Douglas-fir woodlands in the southern Willamette Valley of Oregon (Bamosky and others 1987). This hypothesis must be tested with modem pollen data from Oregon, however.

The most compelling climatic interpretation of the fossil pollen data is that warm-dry climates dominated the Puget Lowland during the early Holocene. Summer droughts were probably more severe and fires more frequent than today. Grassy areas, oak savannas, Douglas-fir woodlands, and riparian alder stands probably characterized the regional vegetation, with strong north-south gradients in the predominant community types. Southern areas may have been characterized by extensive grasslands and oak savannas, and northern areas by a shifting mosaic of dry Douglas-fir forests in early successional stages. This vegetation gradient was probably maintained by interactions of climate and fire.

Summer droughts were probably most severe in the southern Puget Lowland, resulting in discontinuous tree cover and sparse, dry fuels. These conditions would have favored frequent low-intensity fires, which can maintain savannas and grasslands effectively. Oregon white oak was probably common because it readily resprouts after fire. The thick bark of mature Douglas-fir probably allowed old trees to survive fire at scattered locations. The establishment of Douglas-fir would have been difficult, however, because of the sensitivity of young trees to even low-intensity fires (Agee, this volume). The distribution of parent materials (coarse outwash, till, pro-glacial lake sediments) may have controlled major spatial patterns of plant communities in the southern Lowland. In particular, extensive areas of coarse outwash were deposited south of the lowland ice sheet during late-glacial times (Thorson 1980). The soils of these areas were undoubtedly exceedingly droughty during the early Holocene and probably supported only grassland vegetation. Woodlands and savannas probably occupied finer textured soils in the region. Small modem prairies south of Olympia, Washington, may be remnants of extensive early Holocene grasslands. Prairies also may have been maintained in part by fires set by Native Americans who were present in the Northwest during the early Holocene.

The greater abundance of tree pollen in sediment records from the central and northern Puget Lowland (fig. 2) suggests that these areas were more heavily forested. The northern forests may have experienced fires of variable intensity (Agee, this volume) that were less frequent than in the savannas and grasslands to the south. Fire effects would have varied depending on tire intensity. Low-intensity fires would have removed understory plants but caused little tree mortality. Moderate fires would have killed some trees and opened growing space within stands, but intense fires would have killed most of the trees in a stand, thereby reinitiating succession. This type of variable fire regime characterizes dry Douglas-fir forests of southwestern Oregon and results in patchy mosaics of young and old stands of various tree densities. These forests may be reasonable modem analogs to those growing in the northern Puget Lowland during the early Holocene.

Pollen diagrams from coastal areas of the Olympic Peninsula also show maximum values of Douglas-fir and alder pollen in the early Holocene, but western hemlock pollen was more common than in the Puget Lowland (Bamosky and others 1987, Heusser 1986). Oak and grass pollens were rare in these diagrams. Apparently, maritime influences caused more mesic densely forested vegetation along the Pacific coast than farther inland. Coastal diagrams are nevertheless consistent with records from the Puget Lowlands, in that they show forest types with drier affinities in the early than in the mid- to late-Holocene.

The only pollen records from Oregon were published nearly 50 years ago by Hansen (1947), who pioneered palynological research in the Pacific Northwest. Hansen worked before techniques such as radiocarbon dating and fine taxonomic discrimination of pollen were developed. His diagrams, therefore, provide only very general descriptions of past vegetation. Nevertheless, they remain invaluable to current understanding of the forest history of the Pacific Northwest.

Hansen (1947), fortunately, identified the Mazama ash layer at several sites. It is now dated and can be used as a basis for comparing early- and late-Holocene pollen assemblages. High pine-pollen percentages are a striking feature of early-Holocene pollen diagrams from the central Willamette Valley. Although the pine species comprising this peak are not known, the conclusion seems reasonable that they were species currently more abundant to the south (such as ponderosa pine, Jeffrey pine, sugar pine, knobcone pine) rather than lodgepole pine, which typically characterizes full- and late-glacial pollen assemblages in the Northwest. This interpretation implies warmer-drier climates during the early-Holocene than at present and is thus consistent with interpretations of pollen records farther north. Regardless of their climatic significance, early-Holocene assemblages in western Oregon do not match mid- to late-Holocene spectra from the same area or from sites in Washington and southern British Columbia. One must conclude, therefore, that old-growth Douglas-fir forests were not common in Oregon during the first half of the present interglacial period.

Climate simulations for the early-Holocene are represented by the model for 9,000 years BP, when summer insolation at 40^0 N. latitude was 8 percent greater than present, the Laurentide ice sheet was greatly reduced, and the influence of the glacial anticyclone had essentially disappeared (COHMAP members 1988, Kutzbach and Guetter 1986). The simulated July temperature was higher, and precipitation-minus-evaporation was Iower than at present,,because of increased insolation. At 9,000 years BP the Earth was closest to the sun during the summer and the tilt of the Earth’s axis was more extreme than at present, both of which increased the intensity of solar radiation, Paleoclimatic simulations, therefore, agree with pollen data for warmer and more xeric forest associations during the early-Holocene.

Mid- to Late-Holocene (6,000 years BP to Present)

Holocene pollen records from the Pacific Northwest generally show the establishment of modem forest composition about 6,000 years BP (Baker 1983, Bamosky and others 1987, Heusser 1986. See fig. 2). Pollen of western hemlock and western redcedar increased, and pollen of Douglas-fir, grass, and alder decreased about that time at sites from the central Puget Lowland to southern British Columbia. Pollen changes were similar in the southern Lowland, except that Douglas-fir pollen increased during the mid-Holocene. The changes in both areas suggest a shift to more mesic forest communities and thus a trend toward a cooler and moister climate. This interpretation is supported by decreases in charcoal and bracken fern spores at about 6,000 years BP. Fire frequencies certainly decreased, favoring the expansion of fire-sensitive species such as western hemlock and western redcedar, and most parts of the region became densely forested by communities that were similar to those of the present.

Pollen changes in other parts of western Washington and Oregon also suggest a more mesic condition in the mid- and late-Holocene. For example, on the Olympic Peninsula, Douglas-fir and alder pollen decreased, while western hemlock and western redcedar pollen (not identified in some diagrams) increased (Bamosky and others 1987, Heusser 1977, 1986). In the Willamette valley, pine pollen decreased and Douglas-fir pollen increased in the mid-Holocene (Hansen 1947).

Although pollen data do not provide evidence of the structural features of the forests of about 6,000 years BP, the simplest interpretation of these data is that old-growth stand characteristics developed with the shift to modem forest composition. Structural changes may have lagged somewhat behind compositional changes, however, because features such as large woody debris and standing snags require time to develop. The length of time would have varied depending on forest type. For example, only a few hundred years would have been required for old-growth Douglas-fir stands to develop, but possibly more than a thousand years were needed for old-growth structures to develop in western redcedar stands. Northwest Indian cultures that depended on wood from massive western redcedars developed 2.000 to 3,000 years after the expansion of western redcedar on the Olympic Peninsula and Vancouver Island (Hebda and Mathewes 1984), suggesting that the establishment of old-growth conditions lagged considerably behind the first increase in western redcedar in these areas.

Pollen records from the Pacific Northwest provide convincing evidence for a climatic cooling and an increase in moisture during the second half of the Holocene. This interpretation is supported by geologic evidence showing the expansion of mountain glaciers (Burke and Birkeland 1983) and by paleoclimatic simulations. Models for 6,000 years BP are based on climatic boundary conditions similar to the present (COHMAP members 1988, Kutzbach and Guetter 1986). Summer insolation was slightly greater than today, but other boundary conditions were at modem values. By 6,000 years BP, simulations for the Northwest show the summer precipitation increased and summer temperature decreased by comparison with 9,000 years BP and thus they corroborate the climatic interpretation of the pollen dam.

Discussion

No pollen evidence indicates that old-growth Douglas-fir stands were an important component of Pacific Northwestern forests before 6,000 years BP. Additional data are needed to confirm this statement, however, because the vegetation history of western Oregon is very poorly documented. The lack of data from Oregon is a particular problem for interpreting forest composition during full-glacial times. Douglas fir forests did not exist south of the ice sheet in western Washington, but no data exist to assess whether such forests occurred farther south. Circumstantial evidence from climatic simulations suggests that western Oregon was too cold and dry for the large-scale survival of Douglas-fir forests, and pollen records from northern California indicate xeric pine and possibly juniper woodlands during this period (Adams 1986). Thus, for old-growth Douglas-fin forests to have survived full-glacial conditions as an important forest type in the Pacific Northwest is unlikely.

A sufficient number of well-dated pollen diagrams are available from western Washington and southern British Columbia to conclude that old-growth Douglas-fir forests were rare or absent during the early-Holocene. Even the less-detailed and undated diagrams from western Oregon provide convincing evidence that old-growth forests did not exist south of the Puget Lowland in the early-Holocene. Even if Douglas-fir forests occupied western Oregon during full-glacial times, they must have disappeared as a zonal forest type during the warm, dry climates of the early-Holocene and then reassembled about 6,000 years BP.

During the early-Holocene, mesic late-successional conifers such as western hemlock and western redcedar may have formed small populations in moist topographic depressions or in stable riparian sites. These fire-sensitive species would have been relatively protected from fire in such environments. Both species presently occur in similar settings in warm, dry summer climates east of the Cascade Range (Franklin and Dymess 1973). At the onset of the cooler, wetter climate of the mid-Holocene, such populations would have provided seeds for the rapid colonization of upland areas. With this expansion, modern zonal forests were established.

As in other parts of the world, the interpretation of forest history in the Pacific Northwest is limited by the coarse spatial resolution of pollen data. Extensive old-growth forests typical of the modern Western Hemlock Zone were clearly absent from western Washington before the mid-Holocene, but pollen data cannot evaluate the possibility that local old-growth stands occurred at restricted, scattered locations. Future research should address this question by examining pollen and macrofossil records from small collecting basins because such sites could provide records of local stand composition (Dunwiddie 1986).

Conclusion

Modern forests in the Western Hemlock Zone were established in western Washington about 6,000 years ago. These forests did not migrate into the region as intact communities from the south. Instead, dominant tree species of this forest zone had differing late-glacial and early-Holocene histories and responded individually to climate change.

Because climate is driven by a complex set of boundary conditions that do not change in unison, new conditions constantly arise and disappear on time scales of several thousand years. Over these broad time scales, tree species continuously reassemble in different combinations that follow the rhythm of changing climate.

Fire History of-Douglas-Fir Forests in the Pacific Northwest

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Abstract

The fire history of Pacific Northwest Douglas-fir forests is varied and complex because Douglas-fir exists in a variety of forest types over a wide range of environments. Douglas-fir has been dominant over this region because of disturbance by fire and the species' adaptations to fire. Human-caused fires have been locally important, but lightning appears to be most significant in explaining fire history. A lightning fire model based on climate suggests a strong north-south gradient in lightning ignitions. The western Olympic Mountains have a very low probability of ignition by lightning; the southern Washington Cascades have twice as much; the western Oregon Cascades have another 60 percent more; and the Siskiyou Mountains have twice, again as much. Our knowledge of fire return intervals based on forest age-class data shows a parallel history, ranging from fire return intervals over several centuries in the Olympics to several decades in the Siskiyous. Most Olympic forests have developed as first-generation stands after historic fires; Siskiyou forests are usually multi-aged stands that have experienced several fires. Almost all of the old-growth Douglas-fir resource is a product of fire: it not only has created and maintained such stands but has destroyed them as well. In the short term, management strategies to perpetuate old growth can focus on protection against fire. In the long term, we will be forced to recognize a more dynamic management strategy, sensitive not only to historic fire regimes, but also to those expected with future climatic change.

Introduction

The fire history of Douglas-fir forests is varied and complex because Douglas-fir exists in a variety of forest types with a wide range of environmental conditions and associated species. Classical Pacific Northwest Douglas-fir forest is characterized by those low- to mid-elevation forestswest of the crest of the Cascade Range extending into the coastal and Klamath Mountain regions of California. This area is commonly known as the Douglas-fir region, and is the area to which this paper is applicable.

Although the region has been named after Douglas-fir because of the dominance of this one tree species over a wide area, Douglas-fir is a late-successional or climax species over only a small portion of the area for which it is named. Its dominance at the time of European settlement was largely due to disturbance, primarily by fire, for many centuries before such settlement. Pollen records establish that Douglas-fir dominance in past millenia often coincided with charcoal peaks in the pollen profile (Brubaker, this volume).

Such disturbance by fire was neither a unique event nor one easily characterized. Fire can occur at various frequencies, intensities, and extents. Severity, defined as the effect on the tree or the stand, varied because of these factors as well as because of the age and composition of the stands. These variables, although initially introducing a great deal of confusion, can be used to order our knowledge of the ecological effects of fire in Douglas-fir forests. In particular, they can be used to understand how old-growth Douglas-fir forests across this wide region have been created, maintained, and destroyed by this powerful agent of disturbance.

Disturbance as an Ecological Factor

The role of disturbance in ecosystems can be characterized by describing the type of disturbance and its frequency, magnitude, extent, and variability (Pickett and White 1985, White 1979). Moving from this simplistic characterization to the field application, however, is often quite difficult because of the problems associated with separating these various factors and the lack of independence between them. For Douglas-fir, which can live 750 to 1000 years or more, a millenium of history may have to be unravelled to understand the evolution of present species composition, structure, and pattern.

Many disturbances in addition to fire may also be important in stand history. Wind can cause catastrophic damage to stands (Franklin and Forman 1987, Ruth and Yoder 1953). Disease and insects can create locally patchy stands (DeBell and Franklin 1987, Russell and others 1986). Landscape-wide, however, fire appears to be the primary large-scale disturbance factor. Across the region, one estimate of average fire return interval is 230 years (Fahnestock and Agee 1983), about one-fifth the potential longevity of an individual tree (Franklin and Dymess 1973). Fire, therefore, is likely to disturb this "average" stand long before Douglas-fir disappears from the stand, even where Douglas-fir is an early seral species.

Relative Adaptations to Fire

Douglas-fir has long been characterized as a species adapted to fire (Flint 1925, Starker 1934). Its ability relative to other species to adapt to the presence of fire is critical to understanding the ecological impacts of fire. The fire strategy (for example, Rowe 1981, Wright and Bailey 1982) of major tree species of the Douglas-fir region is summarized in table 1. The relative success of Douglas-fir compared to its competitors depends on which other "players" are part of the stand. Where western hemlock and western redcedar are the only other species in a mature stand and a fire kills all the trees but does not consume all the organic mat (which would encourage the invader red alder along with Douglas-fir), Douglas-fir is likely to be a dominant in the new stand. Douglas-fir is also likely to be a dominant after fire in a mature stand where Pacific madrone and tanoak are understory species. In a mature state in the presence of a moderate fire, Douglas-fir generally exhibits a "resister" strategy; and madrone and tanoak are "endurers" that are top-killed and will have to resprout from the ground. If a young stand with the same species mix is burned again in 20 years, however, Douglas-fir as a small tree will not be fire tolerant, and as an "avoider" will be killed, leaving the madrone and tanoak to resprout again and dominate the post-fire stand.

Table 1-Relative adaptations to fire of major species in the Douglas-fir region

	Life-history strategy[a] to fire when:		
Species	Young/small	Intermediate	Old/large
Douglas-fir	Avoider	Resister	Resister
Western hemlock	Avoider	Avoider	Avoider
Western redcedar	Avoider	Avoider	Avoider
Red alder	Invader	Avoider	Avoider
Black cottonwood	Invader	Endurer	Endurer
White/grand fir	Avoider	Avoider	Resister
Sugar pine	Avoider	Avoider	Resister
Knobcone pine	Invader	Evader	Evader
Pacific madrone	Invader	Endurer	Endurer
Tanoak	Invader	Endurer	Endurer
Ponderosa pine	Invader	Resister	Resister
Pacific silver fir	Avoider	Avoider	Avoider

[a] Invaders = highly dispersive pioneers, rapid early growth; evaders = species with long-lived progagules stored in soil or canopy; avoiders = fire-sensitive individuals, even to low-intensity surface fires; resisters = able to resist fires of low to moderate severity; and endurers = resprouting species.

This system (table 1) treats the species as a variable, but it assumes that fire is something of a constant. As the examples above illustrate, the frequency of fire can create different ecological effects, as can different fire intensities. Over the region, fire frequency, intensity, and extent vary considerably, which helps to explain the myriad ecological effects of fire.

Regional Fire Patterns

Ignition Patterns

Ignitions by humans-Ignitions by humans are known to have been important in certain forest and grassland types of the Pacific Northwest. The dry Douglas-fir and ponderosa pine forests of the eastern Cascades may have been burned frequently by Native Americans (Barrett and Amo 1982). West of the Cascades, however, the role of aboriginal burning is much less clear for Douglas-fir forests. Burning by Native Americans was a common practice in the Willamette Valley grasslands and oak woodlands (Boyd 1986), and they apparently burned the valley bottoms of at least some of the major tributaries of the Willamette River (Teensma 1987). Norton (1979) and White (1980) make a strong case for aboriginal ignitions in prairies adjacent to the relatively dry Puget Lowland Douglas-fir forests. Botanical (Habeck 1961, Kertis 1986, Thilenius 1968) and pedological (Ugolini and Schlicte 1973) evidence suggest that prairie-forest ecotones frequently burned and that forest area has expanded over the last century at the expense of prairie. Outside of these dry lowland prairie and woodland areas, little convincing evidence exists that aboriginal ignitions were a significant ignition source, although future investigations may shed more light on the debate.

Some of the earliest evidence for Native American fire-setting in the Douglas-fir region was collated by Morris (1934), who first documented the accounts of large historical fires in the Pacific Northwest. Although Native Americans are implicated in anecdotal accounts as the source of several large fires, the evidence is not overwhelming that they ignited many fires in upland forests. The coastal Oregon Native Americans were the victims of some of these fires, having been driven to the waters of the Pacific Ocean to survive (Morris 1934). The source of these fires is never clearly identified or placed in a cultural context. Legends tell of two other fires, both in Washington, that occurred in prehistoric times. The Quinault tribe has a legend of a great fire that swept down from the Olympic Mountains perhaps 500 years ago, pushing the people into the sea, but the ignition source is not identified (Anon. 1983). In an area roughly bounded by Mount St. Helens, Mount Rainier, and Centralia, a 500 000-ha fire is rumored to have occurred about 1800. This so-called "Big Fire" was supposedly set by the Cowlitz tribe against the Nisqually tribe, or was set by the Nisqually tribe as a means of generating rain during a drought (Clevinger 1951). The existence of two stories about the same fire make both suspect; alternatively, either or both could be true. At present, the case for widespread aboriginal fires throughout the Douglas-fir region is not convincing.

Lightning ignitions—The variability in regional lightning ignition patterns is illustrated by the application of a fire-cycle model based on climate. The Olympic fire-cycle model (Agee and Flewelling 1983) generates both significant fire ignitions and sizes based on climatic parameters of the site. For this application, only the ignition portion of the model is presented because the size (and fire-cycle) portion of the model is based on historic relations between fire size and climate not available regionally. The ignition portion of the model presents the expected ignitions exceeding 1 ha within a 175 000-ha area over a given period.

The model requires four inputs, each used by the model in one of twelve 10-day periods during the fire season: probabilities of long-term drought, a rain exceeding 0.25 cm, occurrence of a thunderstorm, and an east wind. The model was applied to four regional locations: the western Olympic Mountains, the Wind River area in southern Washington, the McKenzie River area in the central Oregon Cascade Range, and the eastern area of the Siskiyou Mountains (Jacksonville-Kerby) (fig. 1). The probability of long-term drought, defined as below-average annual precipitation, was set at 0.5, with additional cumulative years of drought at lower probabilities defined similarly to the Olympic model. Short-term drought was defined as 1 minus the probability of significant precipitation during 10-day summer periods and was gathered for each area based on records from nearby stations (Munger 1925). Thunderstorm probability was determined from Pickford and others (1980) for the Olympics and from Morris (1932) for the other sites.

Figure 1—Location of the sites used to simulate lightning ignitions in the fire-cycle model.

As for any stochastic model, long-term expected averages are best calculated using many model repetitions; here, each simulation is based on averages from a 10,000-year run of the model. This represents not the Late-Quaternary period, but only a long-term average (or expected value) of the effects of 20th-century weather on ignition patterns. The results should be interpreted as relative rather than absolute values, although the model predicted well the proportional seasonal distribution of Olympic fires (fig. 2).

The probability of ignitions exceeding 1 ha increases as location shifts east and south from the western Olympics (fig. 3). The Wind River area has twice as many ignitions as the western Olympics, McKenzie River has about 60 percent more than Wind River, and the Siskiyou Mountain area has more than twice the number of ignitions as McKenzie River.

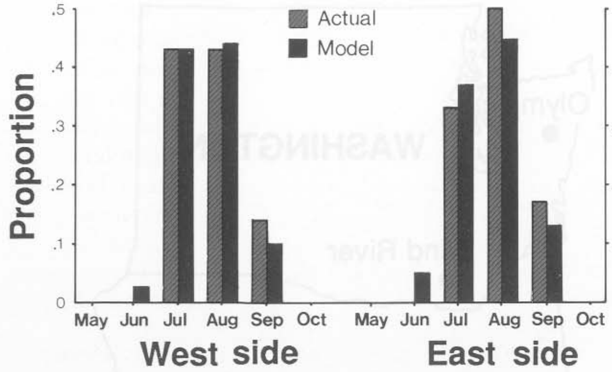

Figure 2—Seasonal distribution of simulated and actual (20th century) lightning ignitions for the western and eastern Olympics (from Agee and Flewelling 1983).

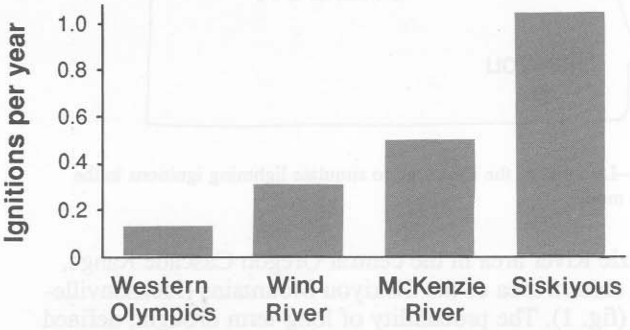

Figure 3—Simulated lightning ignitions for the locations shown in figure 1, from the fire-cycle model. Ignitions are simulated for a 175 000-ha area at each site. The figures should be interpreted as relative numbers between sites, rather than an absolute estimate at any one site.

The differences are largely due to increased frequency of lightning and decreasing summer precipitation patterns from northern Washington to southern Oregon. In each area, July and August are the months of greatest ignition activity, but September in the two southerly areas contains a higher proportion of total ignitions than in the two northerly areas. The model, which was initially designed for the Olympic Mountains, does not include October ignitions, which would likely increase the total ignitions for the southerly stations even more.

The patterns of ignition clearly support the hypothesis of higher fire activity towards the southern end of the Douglas-fir region. Ignition, however, is but one of the factors influencing fire activity; spread is another significant component.

Spread Patterns

We have little, if any, regional data on which to compare regional patterns of fire spread. Modern fire suppression activities have largely prevented fires from burning free in the forest, as they once did. The pattern of fire spread in the Olympic Mountains is typically a period of relatively rapid spread during periods of east wind until the onset of significant precipitation. Although longer droughts and longer burning fires have likely occurred in the past, the typical fire of this century has burned for a few days before being naturally suppressed by onshore marine airflow and precipitation.

In the southern Douglas-fir region, fires most likely spread over periods of weeks to months. Morris (1934) quotes the Jacksonville Sentinel in September 1864: "...during the past few weeks...the fire [in the Siskiyous] has been raging with increasing fury." During the large wildfires of 1987, so many lightning-caused fires started that control actions were ineffective in stopping them. The fires, which started August 30, burned into November, with 39 fires burning over 75 000 ha. This event has been superceded twice in the recorded history (since 1907) of the Siskiyou National Forest (Atzet and others 1988, Helgerson 1988), however, suggesting that 1988 was an unusual but not unprecedented year. Similar examples of long-burning fires in different forest types can be found in areas with prescribed natural fire plans: red fir forests of Crater Lake and in the southern Sierra have sustained fires for several months (Kilgore 1971; F. Van Horn, pers. comm.).

In a relative sense, then, the spread patterns of fires across the Douglas-fir region probably mimic the ignition patterns. Although no long-term records are available for any area of the region, the lower probability of precipitation towards the south probably allows fires to die down but not be extinguished during periods of low winds or moderate weather, and remain capable of renewed spread under patterns of windy or warmer weather.

Fire Return Intervals

Regional fire patterns can also be deduced from records of vegetation. Fire scars on living trees are one source of fire presence in the past. Age-classes of trees that either resist or endure fire or invade after fire are another source of information about fire history (Agee, in press). The mosaic of even-aged and multi-aged stands across the landscape can provide clues about fire severity as well as fire presence.

A regional average fire return interval for forests where Douglas-fir is a dominant in the stand has been estimated at 230 years, based on an analysis of forest survey records from the 1930s (Fahnestock and Agee 1983). Considerable spatial variability is included in this estimate, as suggested by results of the fire-cycle model. Significant temporal variability is also characteristic of these fire return intervals, so that the 230-year average is of limited utility as a parameter of fire frequency across the region.

The notion of a "fire cycle," or a return interval of regular frequency, is not as meaningful as in drier forest types, where with some measure of variability a roughly cyclic occurrence of fire can be assumed (compare mixed-conifer forest, as in McNeil and Zobel 1980). Rarely in a Douglas-fir stand is the fire record long enough or regular enough to infer a cyclic pattern of fire, particularly in the presence of climatic shifts that would alter any cycle in operation. Different patterns of historic fire have clearly affected the Douglas-fir forests of the region, however.

Moist Douglas-fir forests—In the moist Douglas-fir forests of the Coast Range of Oregon, the Washington Cascade Range, and the Olympics, most forests are first-generation post-fire forests less than 750 years old. This pattern would suggest a fire return interval somewhat less than 750 years. The fire-cycle model of Agee and Flewelling (1983) could not reproduce a natural fire rotation (essentially a fire cycle) of less than 3500 years using 20th-century climate patterns, and even with significant alteration in climate input to the model, fire return intervals could only be brought down to about 900 years. They suggested that perhaps much larger than average events may have occurred in the past (also suggested by Henderson and Peter (1981) for the southeastern Olympics) as a result of short-term but very extreme changes in two or more of the climate parameters that drive the model.

Our knowledge of the dates of old-growth forest establishment is so weak as to preclude firm hypotheses about disturbance pulses of the past. The forests around Mount Rainier appear to have had a major fire about 750 years ago (Hemstrom and Franklin 1982), and similar-aged stands have been identified in the southern and western Olympics (Agee, pers. obs.). A series of about 650-year-old or 450- to 500-year-old fires—or both—are apparent from the data of Henderson and Peter (1981) in the southern Olympics, Franklin and Hemstrom (1981) and Yamaguchi (1986) in the southern Washington Cascade Range, and Huff (1984) in the western Olympics. Although the forest age-class data are sparse, these are also times of sunspot minima identified by Stuiver and Quay (1980), using tree-ring analysis of carbon-14 activity. If large fires are associated with these periods of general global cooling, they may represent periods where altered synoptic weather patterns, particularly during the growing season, contained higher frequency of lightning and foehn (east) wind patterns.

In moist Douglas-fir forests, long early seral tree recruitment (for example, 75-100 years for Douglas-fir) has been documented after disturbance by fire (Franklin and Hemstrom 1981). This pattern is not characteristic of all prehistoric fires. For example, Huff (1984) shows a 60-year recruitment interval for a fire in about 1465 in the western Olympics, and Yamaguchi (1986) shows that about 95 percent of Douglas-fir was recruited within 40 years after a fire in about 1300 near Mount St. Helens. Even on these sites, however, the regeneration period is decades long and probably represents some regeneration from trees that initially colonized the burn and grew large enough to produce viable seed to help completely restock the stand. Lack of seed source, brush competition, and reburns—or a combination of these factors—have been identified as delaying regeneration on such sites (Franklin and Hemstrom 1981). Patterns of reburns on the Tillamook fire of 1933 at 6-year intervals (1939, 1945, 1951; Pyne 1982), at Mount Rainier in the late 19th century, and at the southern Washington Yacolt burn of 1902 (A. Gray, unpubl. data) are evidence these sites will reburn. High surface fire potential during early succession in Douglas-fir forest was identified by Isaac (1940) as a "vicious cycle" of positive feedback, encouraging rhizomatous bracken fern; this pattern was quantified by Agee and Huff (1987, fig. 4). Given sufficient sources for reignition (the original Yacolt and Tillamook burns and all reburns are thought to have been human-ignited), the reburn hypothesis is likely to be true in certain areas. Whether reburns were a common event before European settlement in the moist portion of the Douglas-fir region is not clear, however.

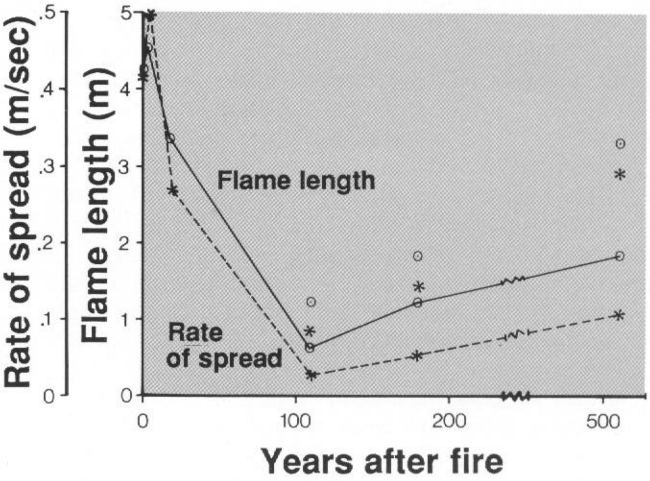

Figure 4—Rate of spread and flame length by stand age for a sere in the western Olympic Mountains. Wind speed is 268 m per minute, and dead fuel moisture contents are 6, 7, and 8 percent for 1-hour, 10-hour, and 100-hour timelag fuels at stand ages 1, 3, and 19. Connected points represent microclimate buffering at stand ages 110, 180, and 515: wind speed is reduced to 134 m per minute and fuel moisture increases to 10, 11, and 12 percent. Unconnected points at these ages represent constant microclimate across all sites.

After disturbance and over time, potential surface-fire behavior declines, particularly after crown closure, and then gradually increases in the old-growth seral stage (Agee and Huff 1987). Reburns in roughly 100-year-old stands during the late 1400's suggested by Henderson and Peter (1981) suggest that independent crown-fire behavior in these thick-canopied stands may be an additional significant type of fire. Our present state of knowledge is insufficient to tell.

Mesic-to-dry Douglas-fir forest—For many years, the pattern of stand-replacement fire summarized above was a paradigm for the Douglas-fir region. Recent work, particularly in the Oregon Cascades, suggests a higher fire frequency, and different ecological role, for fire in mesic-to-dry Douglas-fir forest, reinforcing the output of the fire-cycle model (fig. 3). A site in the western Oregon Cascades (Stewart 1986) near the H.J. Andrews Experimental Forest regenerated after a stand-replacement fire in about 1530, but it has had three partial-mortality fires since then, in about 1660, about 1860, and about 1890. Some of these fires were in the settlement period and probably reflect human-caused fires, but the partial mortality associated with them is significant. Over a broader area several kilometers to the southeast, encompassing similar forest types, Morrison and Swanson (1990) suggest a natural fire rotation of 95 to 145 years over the last five centuries, well below that of the moist Douglas-fir forests of Washington. The patchiness of at least some of the fires is illustrated by a fire-severity map from Morrison and Swanson (1990; fig. 5A). A similar fire regime was noted by Means (1982) on dry sites in the western Oregon Cascades and by Agee and Dunwiddie (1984) for dry Douglas-fir forests in Washington's San Juan Islands (fig. 5B). Another fire-frequency analysis was completed by Teensma (1986), near the area studied by Morrison and Swanson. Using conservative methods that did not recognize underburns with no resulting regeneration or substantial fire scarring of trees, Teensma estimated a natural fire rotation of 100 years over the last five centuries. If fires of moderate severity are removed from the analysis, a stand-replacement mean fire return interval is 130 to 150 years, suggesting that intense fires are a significant part of the natural fire regime in this area, but that fires of lower severity also occur. Other stands 500 years old or older exist without much evidence of recurrent fire.

These studies strongly indicate that a variable fire regime with much higher frequency than found in the typical, moist, Washington Douglas-fir forest occurs in the central Oregon Cascades, and in other mesic-to-dry Douglas-fir forests.

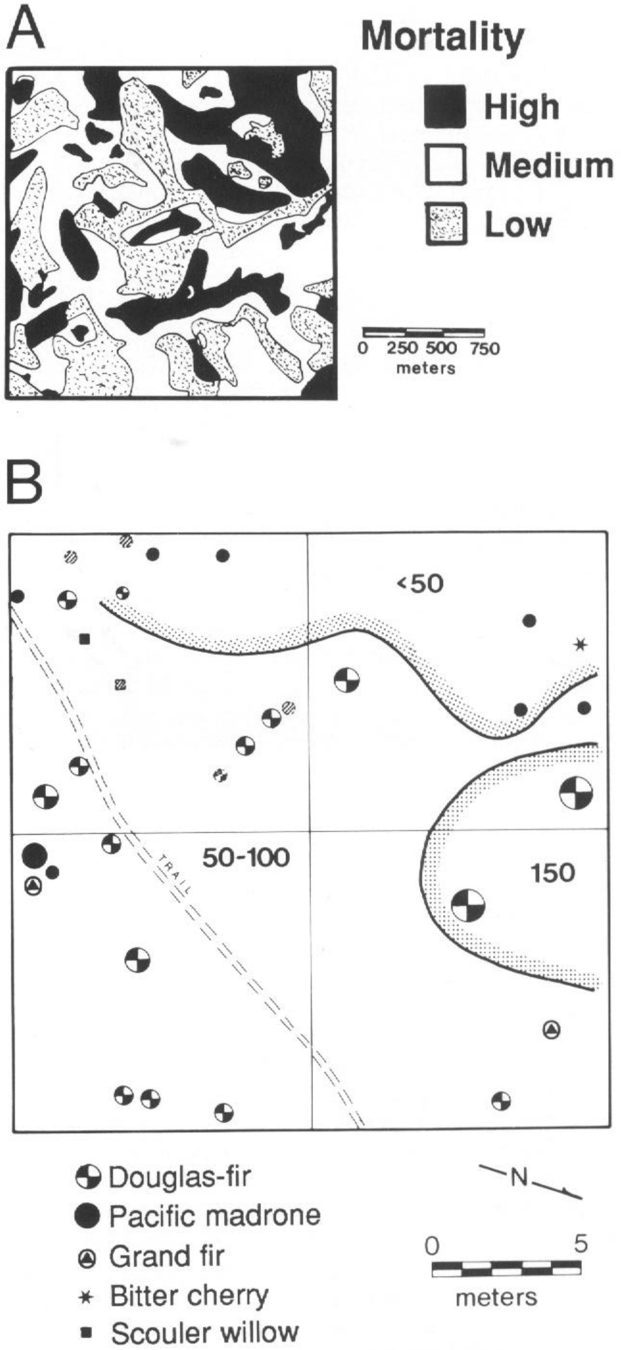

Figure 5—**A.** Reconstructed fire severity for a site in the central western Cascades, redrafted from data of Morrison and Swanson (1990). More area in this particular fire burned with moderate-to-low severity than high severity, but high-severity fire remains an important disturbance process in the mesic-to-dry portion of Douglas-fir forests. **B.** Stem map of an intensive plot on Yellow Island in the San Juan Islands (from Agee and Dunwiddie 1984). Three age-classes (<50, 50-100, and 150 years) are distinct. Relative diameter of stems is shown by the size of the symbol: smallest symbols are 0 to 20 cm, and largest symbols are >100 cm. Dead stems are shown by parallel lines within symbols.

Figure 6—**A.** The south-facing slope of Kinney Creek, near the Applegate River in southwest Oregon, photographed in 1917 (Hofmann 1917). The numbers correspond to fire dates of: 1 = 1915; 2 = 1914; 3 = 1910; 4 = 1897; 5 = 1886; 6 = 1854. **B.** The same landscape photographed in 1988. **C.** A fire-scarred Douglas-fir in a clearcut just north of the ridgeline (see arrow in B); each of the white marks identifies a distinct fire scar.

Very dry Douglas-fir forests—The Douglas-fir forests of the central-to-eastern Siskiyou Mountains are among the driest forest types in which Douglas-fir is a dominant and where old-growth Douglas-fir is recognized (Old-Growth Definition Task Group 1986). The complex geology, land-use history, steep environmental gradients, and variable fire history of this area have prevented generalizations about fire history and its ecological effects. Native Americans may have significantly affected these drier Douglas-fir forests, but their effect is largely unknown. Miners, settlers, and trappers altered the patterns of burning in the 19th century, and fire suppression has altered burn patterns in the 20th century (Atzet and Wheeler 1982, Atzet and others 1988). From the coastal forests of southwest Oregon and inland to the crest of the Coast Range, fire frequency decreases from perhaps between 90 and 150 years to about 50 years. Frequencies averaging 20 years have been found in the eastern Siskiyou Mountains (Atzet and others 1988) in the area where fire ignitions were simulated by the fire-cycle model.

An example of frequent fires in the eastern Siskiyous is shown by the Kinney Ridge landscape west of the Applegate River, originally photographed by Hofmann (1917) (fig. 6A) and rephotographed in 1988 (fig. 6B). In the area shown by the arrow in figure 6A, fire scars on stumps in a recent clearcut (fig. 6C) in old-growth Douglas-fir indicated a fire return interval of about 18 years between 1740 and 1860, although most of the fires indicated by Hofmann (1917) on the photograph after 1860 are not recorded in the sampled scars on the north (left) side of the ridgeline.

Species Composition and Structural Effects of Fire

Old-growth Douglas-fir forests are biologically defined on the basis of species composition and structural characteristics (Old-Growth Definition Task Group 1986). Among these characteristics are criteria for size, density, and age of Douglas-fir; generally multilayered canopies; snags; and logs. The interim minimum standards are slightly different between the major plant series (western hemlock, Pacific silver fir, Douglas-fir, tanoak, white fir) where old-growth Douglas-fir exists. Given that the fire regimes are probably different between these plant series, it is not intuitively obvious how apparently similar species composition and structural characteristics developed.

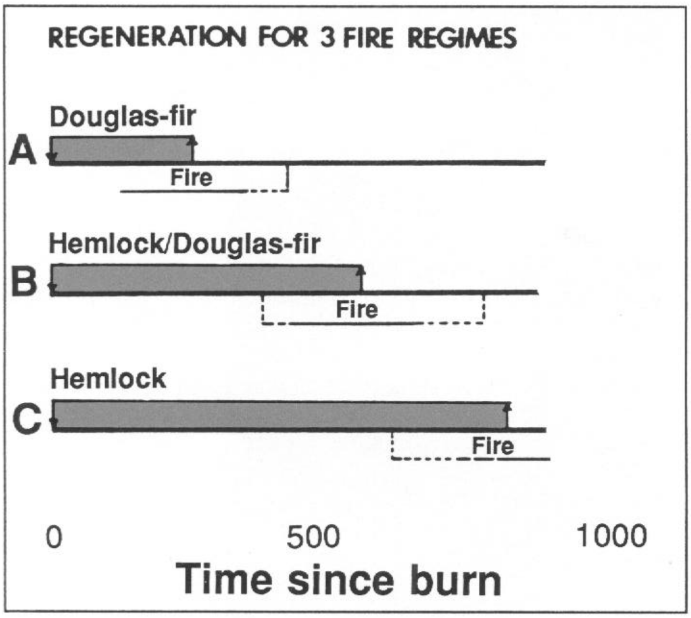

Figure 7—Species responses to changes in fire frequency (from Huff 1984). These fire regimes represent fire return intervals of about 100+ years (A) to about 1000+ years (C). The solid-to-dashed lines underneath each thick line represent the average range of fire return intervals, and the paths denoted by the arrows above the thick line represent occurrence of a fire, along with the species likely to dominate after disturbance.

Huff (1984) has summarized the species response to disturbance regimes for a range of wet-to-dry Douglas-fir forests (fig. 7). If fire is absent for 700 to 1000 years on wet sites, Douglas-fir will drop out of the stand, and western hemlock or Pacific silver fir will be the primary seed source for postfire regeneration (fig. 7C). On sites with fire return intervals in the 300- to 600-year range—well within the longevity of individual Douglas-fir—mixed dominance of Douglas-fir and western hemlock or Pacific silver fir will result from a typically severe stand-replacement fire (fig. 7B). A stand-development sequence will occur as illustrated in figure 8 (modified from Huff 1984). At age 200+, the characteristics of old growth are usually present. The Douglas-fir component, having developed after the previous centuries-old fire, provides the live-tree criterion, and those large Douglas-fir and western hemlock begin to supply the large-log component.

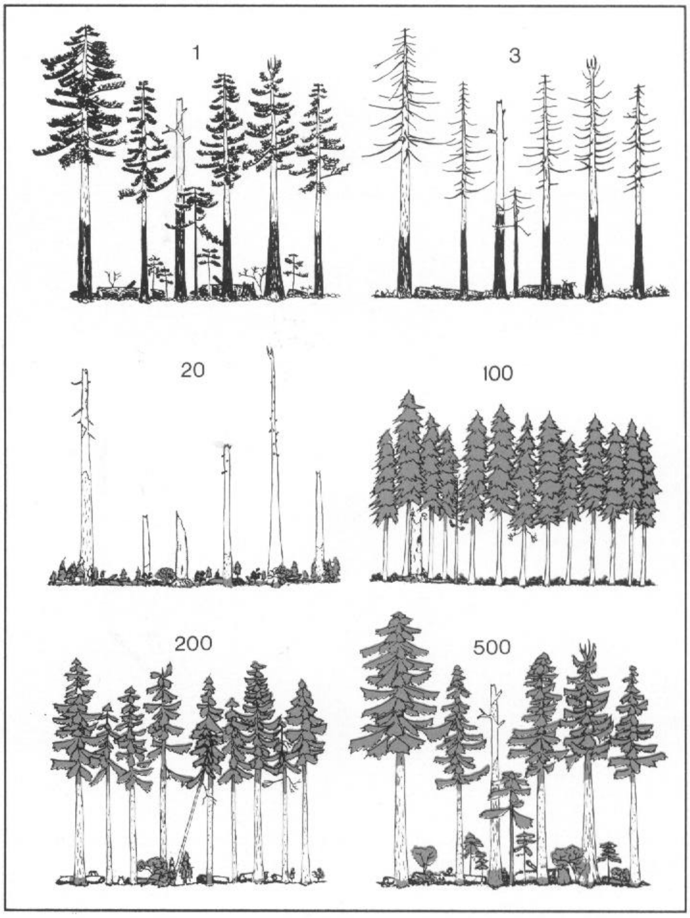

Figure 8—Stand-development sequence for wet Douglas-fir forests, illustrating the creation of old-growth character. Fire return interval is 500 years or more, and the old-growth character is found after about 200 years. Even after 500 years, the old-growth character remains a function of the previous disturbance that initiated the Douglas-fir.

When fire return intervals are reduced to 30 to 70 years in drier and warmer environments, western hemlock may not even be present on the site (fig. 7A), and a stand-development sequence similar to that shown in figure 9 may occur. Beginning after a stand-replacement fire, the Douglas-fir regenerating on the site may survive several moderate-severity fires that thin the Douglas-fir ("resisters"), remove the understory white or grand fir ("avoiders"), and topkill the associated hardwoods, such as madrone and tanoak ("endurers"). Several reoccurrences of such fires will create a stand with several age-classes of Douglas-fir (some of which are large), and an age-class of Douglas-fir and hardwoods representing regeneration after the last disturbance. Understory-tolerant conifers of other species will also be represented in this most-recent regeneration. Large logs are provided by residual Douglas-fir or sugar pine that have died from insect, disease, or the last fire, or have blown over. At age 250+, the structure of this stand may meet the old-growth criteria, having developed in a very different way than the wet-site Douglas-fir stand. Such stands will usually be intermixed with others that have experienced a stand-replacement event during one of the intermediate fires, so that the landscape is more patchy than in the wetter Douglas-fir forests.

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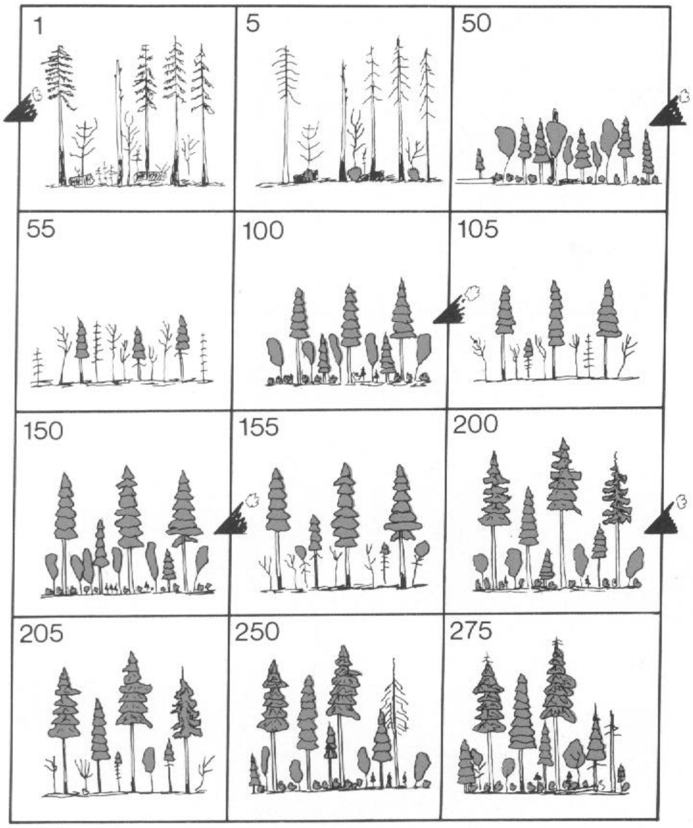

Figure 9—Stand development sequence for dry Douglas-fir forest. Fire return interval is about 50 years. Old-growth character is found in those stands that burn with low-to-moderate severity over several fires, allowing the development of large residual Douglas-fir. The minimum criteria for old growth are met through a much different developmental sequence than shown for wet-site Douglas-fir forest in figure 8.

Discussion

The historic role of fire in Pacific Northwest forests is critical in understanding how these Douglas-fir forests developed, and to what extent they provide habitat for wildlife. The extent to which such patterns and processes provide a blueprint for future management is less clear. No areas are large enough to allow totally free-ranging fire; few areas have management objectives that will allow prescribed natural fire (lightning ignitions allowed to burn under certain conditions in certain zones). Logging followed by slash burning has sometimes been called a mimic of natural process (Agee 1989). Although some aspects (for example, smoke production; Fahnestock and Agee 1983) may be similar, the functional result in the past has been quite different: no snags are left (shade, woodpeckers) and much more soil disturbance is present after logging, which may redirect postdisturbance plant succession (Scott 1980).

Historic fire patterns have several implications for remaining old-growth forests. Today's old growth tends to be fragmented—that is, broken into small units—as a result of harvest. Based on historic patterns of fire, increased fragmentation compared to natural conditions should be more significant to the north, which apparently had larger blocks of single-aged stands. The increasingly smaller size of old-growth stands will create a drier, windier microclimate along stand edges, accelerating both windthrow and potential fire behavior. Slash burns may increase the risk of fire escape to neighboring stands (Agee 1989). Such units will also be easier to reach and protect from fire, however, if that is the appropriate management strategy.

To suggest that fire is an appropriate process in the preservation of old-growth forest seems paradoxical. Yet it is apparent that almost all of our Douglas-fir old-growth forest resource consists of first- or multi-generation forests born of fire. Fire is responsible for their destruction; yet it is also responsible for their creation and maintenance. Without fire, the old-growth forests of the Pacific Northwest would have significantly different species composition and structure, and would likely function quite differently as wildlife habitat.

In the short term, management plans to perpetuate old-growth forest can ignore fire. So many other disturbances are reducing the area of old growth that short-term management should be oriented to a preservation- rather than a process-oriented approach: preserve what we have without regard to its long-term maintenance. Eventually, we must come to grips with the realization that these living systems will change, even with complete protection from disturbance. The proportion of Douglas-fir will decline, particularly on more mesic sites, with attendant changes in wildlife habitat. In the long run, we will be forced to recognize a more dynamic management strategy, sensitive not only to historic fire regimes, but also to the new fire regimes expected with global climate change. ■

Forest Fragmentation in the Pacific Northwest and its Potential Effects on Wildlife

John F. Lehmkuhl and Leonard F. Ruggiero

Authors

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Abstract

Fragmentation is the creation of a complex mosaic of spatial and successional habitats from formerly contiguous habitat. Loss of habitat and the less obvious phenomenon of habitat-patch isolation are aspects ‘of fragmentation that threaten the viability of wildlife populations, the components of biotic diversity. Fragmentation of forests on Federal lands in the Pacific Northwest is the product of staggered-set clearcutting of late-successional forest. Large-scale block clearcutting on private lands has minimized fragmentation simply by leaving few or no fragments. Less than 20 percent of the original old-growth forest remains, and the fragmentation of remaining old-growth stands may degrade the quality of these areas for plants and wildlife. Analysis of population vulnerability suggests that life-history characteristics, along with biotic and physical environmental factors, influence population structure and individual fitness. These factors determine the risk of local population extinction. We compiled a list of 93 species associated with late-successional Douglas-fir forests in the Northwest and rated the risk for each species of local extinction from fragmentation on a scale of 1 to 10 based on the frequency of occurrence, abundance, and variation in abundance data from the old-growth community studies (this volume), and on body size, vagility, and migratory status information from the literature. Over 80 percent of the listed species had high to moderately high risk scores (7 to 10); risk for these species was a function of the low frequency and abundance associated with three combinations of body size and vagility. Clearcutting in patterns that minimize fragmentation would reduce the impact of isolation and small patch size for 27 species, likely benefit another 20 species, but probably have little impact on 46 species.

Introduction

Forest fragmentation and its effects on biotic diversity have been recognized during the last decade as one of the most pressing problems faced by conservation biologists. Particular attention has been given to the relatively undeveloped and unstudied tropical region (Soul) and Wilcox 1980). Recent planning activities of Federal land-management agencies and issues related to the conservation of old-growth forest ecosystems, however, have brought forest fragmentation to the forefront of domestic conservation biology (Harris 1984, Harris and others 1982, Lehmkuhl 1984, Lumen and Nietro 1980, Meslow and others 1981, Salwasser and Samson 1985).

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Forest fragmentation typically is the creation of a complex spatial and temporal mosaic of forest patches by staggered-set clearcutting, in which small (<20 ha) clearcuts are scattered over the landscape. Aside from the loss of old-growth forest habitats that results from this practice, the remaining forest patches become smaller and more isolated as logging continues. Nowhere is this problem more evident or controversial than in the old-growth forests administered for multiple use by public land-management agencies in the Pacific Northwest (Franklin and Forman 1987, Meslow and others 1981). The problem is made urgent by the planned harvest of 50 percent of the old-growth remaining on National Forest lands in western Oregon and Washington over the next 5 years, at a rate of more than 75,000 ha per year (Marcot and others, this volume; Ohman and others 1988), and by the planned liquidation of old growth remaining on Bureau of Land Management (BLM) lands in southern Oregon over the next 10 to 20 years (Lumen and Nietro 1980).

A substantial literature documents the effects of forest fragmentation on birds in agricultural landscapes of Eastern North America and Europe (for example, Forman and others 1976, Freemark and Merriam 1986, Galli and others 1976, Van Dorp and Opdam 1987, Whitcomb and others 1981). These studies have generally found that the presence or abundance of forest-interior birds declines with decreasing size and increasing isolation of forest patches. A few studies have analyzed changes in the general abundance of forest birds (Raphael and others 1988), and small mammals and amphibians (Raphael 1988c) as the result of logging in Western forests. Little is known, however, about the specific effects of fragmentation caused by clearcutting formerly extensive old-growth forests in Western North America. In contrast to Eastern forests, studies in Western forests (Lehmkuhl and others, this volume; Raphael 1984; Rosenberg and Raphael 1986) have found vertebrate richness or abundance only weakly related to stand size and isolation, although some negative effects were suggested for particular species. Isolation and small-area effects were suggested by Newmark (1987) as the cause of local extinction for 43 percent of the medium and large mammal species in National Parks of the Western United States. A comparison of the western forest situation with that in eastern forests, however, is weak.

Eastern forests have experienced extensive fragmentation (Whitcomb and others 1981), providing relatively static and simple systems with woodlot patches in an agricultural-land matrix. The relatively static dynamics and high contrast between patch and matrix are ideal for studying the effects of habitat patch size and isolation. Western forests managed for timber production, however, are at an early stage of fragmentation with a dynamic and complex pattern that is more difficult to study. Old growth in a managed landscape forms the matrix, rather than the patch as with woodlots (Harris and others 1982, Vemer 1986), until a threshold is reached where cutover forest area exceeds pristine forest area (Franklin and Forman 1987). Boundaries between old growth and cleat-cuts, although initially distinct, are dynamic and become increasingly ambiguous with secondary succession of clearcuts (Rosenberg and Raphael 1986), whereas woodlot boundaries remain distinct and both boundary and habitat matrix are relatively static.

The incipient nature of Western forest fragmentation nevertheless allows us the opportunity to study and manage forest landscapes to prevent or ameliorate the impacts of timber harvesting on wildlife populations. Our goal in this paper is to assess the state of old-growth forest fragmentation in the Pacific Northwest, and the potential effects of that process on wildlife. Our objectives are to briefly describe the loss and fragmentation of old-growth forests in the Pacific Northwest, to review concepts for assessing the effects of forest fragmentation on wildlife population persistence and diversity and describe the characteristics of species vulnerable to extinction, to compile a list of Pacific Northwest species associated with old-growth forests and rate their vulnerability to fragmentation, and to examine timber harvest alternatives that may minimize the effects of fragmentation on wildlife populations. We will primarily discuss the fragmentation of old-growth, or late-successional forests (synonymous in view of problems in defining the old-growth condition; see Marcot and others, this volume), because they are least likely to be present in managed forest landscapes. The discussion will be oriented to public land management, as opposed to private industrial forest land where old growth has been largely eliminated (Harris 1984, Ohman and others 1988, Spies and Franklin 1988) and where wildlife values are incidental (Hicks 1985) to timber production.

Forest Fragmentation in the Pacific Northwest

Two issues are associated with current harvest patterns of old growth: quantitative loss of habitat for associated species, and qualitative loss of habitat resulting from the reduced capacity of remaining patches to support old-growth conditions and wildlife communities. Assessing the quantitative loss of old growth is problematic because estimates of the area of old-growth forest remaining on public lands vary with the definition of the old-growth condition (Marcot and others, this volume). We are not prepared to defend any particular definition, but we present estimates from the literature to provide order-of-magnitude information.

Estimates of old-growth forest remaining in Oregon and Washington range from 1 to 2.5 million ha, representing 10 to 25 percent of a base 10 million ha of commercial forest land. Spies and Franklin (1988) estimated that 1 million ha of old-growth forest (17 percent) remains from the 6 million ha of commercial forest land that occurred before settlement. The Pacific Northwest Region of the USDA Forest Service estimates that remaining old-growth on National Forests in Oregon and Washington are 2.5 million ha (USFS 1988). More in line with Spies and Franklin, Morrison (1988) reinterpreted Regional data with a stricter definition of old-growth and estimated that little more than 1 million ha remains. Northern California appears to have retained a much larger percentage (50 percent or 400 000 ha) of its original 810 000 ha of old-growth forest (Raphael and others 1988) from a base of 1.1 million ha of commercial forest land.

The qualitative loss of old-growth habitat by the creation of many small fragments in formerly contiguous forest is the second issue associated with forest management. The viability of remnant patches as wildlife habitat is a function of myriad edge effects that depend on patch size and isolation. Some research suggests that a fundamental change in microclimate occurs within 160 m of the forest edge, which creates conditions different from the patch interior (Franklin and Forman 1987, Harris 1984). Patches 10 ha are effectively all edge and have lost the essential attributes of the old-growth condition. This, and other edge effects, which we will discuss later in detail, act to reduce the effective size and functional viability of patches for plant and animal communities.

Forty years of staggered-set clearcutting on National Forest (Harris 1984, Spies and Franklin 1988) and BLM lands (Lumen and Nietro 1980, Monthey 1984) has resulted in various stages of fragmentation of the remaining forest. Data on the patch-size distribution of forest fragments are available for only a few areas. Harris (1984) presented data from the Siuslaw National Forest in the Oregon Coast Range indicating that 3 to 6 percent of the forest area remained in old growth, depending on the definition used; 34 percent of the old-growth stands were smaller than 8 ha and 61 percent of the patches were smaller than 16 ha, accounting for 8 and 21 percent of the total old-growth area. If stands less than 8 ha are not functional as old growth and are subtracted from the old-growth area of the Siuslaw National Forest, only 2 percent of the Forest area remains as functional old-growth, even assuming a total area of 6 percent old growth. The isolation of forest fragments with distances up to 7 km (Harris and others 1982) between patches further limits the functioning of old-growth patches as wildlife habitat.

Monthey (1984) reported a similar patch-size distribution for BLM lands in Oregon: about 50 percent of the patches were less than 12 ha, and most were less than 4 (Lehmkuhl and others, this volume) on 48 2025-ha landscapes on National Forest and National Park lands in the southern Washington Cascade Range indicated that about. 31 percent of the area was old growth; 39 percent of the patches were 110 ha, but they represented only 4 percent of the total old-growth area. Excluding study landscapes in Mount Rainier National Park yielded only a slightly larger percentage (5 percent), of old-growth stands 10 ha, which suggests that much of the remaining old-growth in the southern Washington Cascades may still be in large enough patches to be considered functional. Those study landscapes, however, may be biased for relatively high old-growth area because selection of study landscapes was based on the requirement that stands be >40 ha for the original stand-scale studies. The study landscapes may nevertheless represent the general area as indicated by the similar percentages of clearcut area (16 percent) for study landscapes and the Gifford Pinchot National Forest in general (G. Gruelich, unpubl. data).

Assessing Fragmentation Effects on Wildlife

Species Diversity and Population Persistence

Maintaining species diversity is the ultimate goal of current conservation efforts. Species diversity as an operational goal for management, however, is not always desirable (Anderson 1979; Askins and others 1987; Murphy 1989; Raphael, this volume; Van Home 1983; Vemer 1986). Conventional methods for measuring species diversity do not distinguish between species and do not account for their special ecological and management importance. Clearly, we need to be concerned with individual species, while diversity should be a conceptual goal for conserving regional biota (Anderson 1979, Askins and others 1987, Murphy 1989, Noss and Harris 1986, Van Home 1983, Wilcox and Murphy 1985). To manage for species, we must understand the processes affecting the persistence and stability of populations of individual species as components of species richness.

The persistence of a population is primarily a function of its size, with extinction (local or global) invariably preceded by reduced population size (Gilpin and Soul) 1986, Goodman 1987a,b, Newmark 1987, Pimm and others 1988, Soul) and others 1988, Wilcox 1980). The reduction may result from natural or human-caused disturbance; in our case, smaller populations are a consequence of a quantitative or qualitative loss of habitat. In circumstances where population size is reduced below a threshold number for recovery, the subsequent extinction of the reduced population may be deterministic and unavoidable. More often, extinction depends on the interplay of stochastic (random) factors with population and environmental factors (Gilpin and Soul) 1986, Shaffer 1981). Shaffer (198 1) described four primary stochastic forces of extinction:

- Stochastic demographic changes in small populations, such as variation in birth and death rates and sex or age anomalies randomly affect individuals in a manner that increases the variance in reproductive rate and increases the probability of extinction from a chance reproductive failure (Goodman 1987a, Lande 1988);

- Environmental stochasticity, random temporal changes in environmental quality or interspecific interactions, affect individuals equally in a manner that increases variation in abundance and has proportionately large effects on small populations (Goodman 1987a, Lande 1988);

- Catastrophes may occur at random intervals through time and can arguably be called intense, punctuated cases of environmental stochasticity; and

- Genetic stochasticity arises from a reduction in the effective population size with consequential deleterious short-term effects of inbreeding on reproductive success, and long-term losses of genetic variation (heterozygosity) and adaptability to environmental change from genetic drift (Frankel and Soule 1981, Schonewald-Cox and others 1983).

In general, the probability of extinction for small populations is highest from environmental effects, followed by demographic stochasticity, long-term genetic effects, and lastly catastrophes (Gilpin and Soule 1986, Lande 1988). The importance of stochastic extinction forces is largely determined by the interaction between the particular characteristics of a species, the population, and the environment. An appropriate framework for assessing the strength of this interaction is population vulnerability analysis.

Population Vulnerability Analysis

Population vulnerability analysis as proposed by Gilpin and Soule) (1986) has three aspects: the physical and biotic environment of the individual and population; the population phenotype, or the species life history and habitat requirements; and the expression of the first two aspects in population structure and individual fitness.

The environment-Fragmentation affects the environment by reducing the availability and heterogeneity of original habitats. Forest remaining after logging is a subset of the original area, and it usually represents a less heterogeneous array of habitats. The loss of habitat heterogeneity takes two forms (Goodman 1987a): loss of regional heterogeneity reduces the ability of populations to average effects over their geographic range; and loss of resource hot spots, or locations of stable resource availability, eliminates refugia in which populations can persist under periodic severe environmental conditions and from which they can later recolonize formerly occupied areas.

Fragmentation also alters the context and configuration of a stand by exposing remnant forest patches to edge effects. The present connotation of edge effect differs from conventional usage (Leopold 1933), which suggests that more species diversity occurs on the ecotone of two habitat types. Edge effect here means deleterious effects of ecotones on plant and animal populations (Harris 1989, Laudenslayer 1986, Reese and Ratti 1988, Soule) 1986, Yahner 1989). Many forest-edge effects have been detailed in the literature, particularly for eastern U.S. Forests, but each situation has unique problems (Janzen 1986). Some environmental and edge effects are described below.

- Competition between interior and edge species may occur when edge species that colonize the early-successional habitats and forest edges created by logging (Anderson 1979; Askins and others 1987; Lehmkuhl and others, this volume; Rosenberg and Raphael 1986) also use the interior of remaining forest (Kendeigh 1944, Reese and Ratti 1988, Wilcove and others 1986, Yahner 1989). Competition may ultimately reduce the viability of interior species' populations.

- Generalist species occurring in the forest at the time of fragmentation may benefit from environmental changes outside the forest, receiving a cross-boundary subsidy (Janzne 1986). Consequent increases in generalist species' vigor or populations may alter community interactions, and result, for example, in greater competition with other animal species or altered plant-animal interactions (Janzen 1986). Alverson and others (1988) described how a cross-boundary subsidy from abundant early-successional habitat in logged areas of Wisconsin maintains a high white-tailed deer population, which has a major impact on the composition and regeneration of remnant old forest. Elk likewise receive a subsidy from early-successional habitat on recently logged sites (Hett and others 1978, Raedeke and Lehmkuhl 1986) and can markedly depress understory regeneration of hemlock in Pacific Northwest forests (Harmon and Franklin 1983).

- Nest predation and parasitism have been shown to increase in eastern forests along edges up to 600 m inside the patch, which is nearly four times the distance of microclimatic effects in Pacific Northwest forests (Reese and Ratti 1988, Wilcove and others 1986, Yahner 1989). Corvids and small mammalian omnivores are usually implicated as the most serious nest predators (Reese and Ratti 1988).

- The patch boundary may be a unidirectional filter through which animals pass out of the patch and cannot return (Janzen 1986). Game animals, for example, are most vulnerable to hunting mortality when they venture from the cover of forest patches into large open clearcuts.

- Secondary extinctions may result from the elimination of keystone species (Paine 1969, Soule 1986, Wilcove and others 1986) or altered community processes (Terborgh 1988). Gilbert (1980b) and Terborgh (1988) described situations in the tropics where the elimination of top predators could have cascading effects through the community by changing the size or structure of prey populations, which in turn influence plant-community dynamics through seed dispersal and predation. Soul) and others (1988) described a meso-predator release effect on chaparral birds in which the local extinction of a large predator (coyote) allowed small predators (fox and domestic cats) to increase, decimating prey species that formerly persisted with low populations of the small predators. Maser and Maser (1988) suggested that timber harvest practices that preclude viable populations of mycophagous forest-dwelling squirrels may alter fungal spore dispersal and eliminate a critical link in the symbiosis between hypogeous mycorrhizal fungi and coniferous trees which improves tree productivity.

- Edge creep occurs when extrinsic processes act on patch edges to progressively decrease patch area or quality (Soul) 1986). Ground fires along patch edges, for example, may penetrate only a short distance inside the patch, but they initiate a positive feedback loop of increasing fire effects. The growth of herbaceous vegetation responding to increased light and release from shrub competition after a fire may provide abundant fuel for subsequent fires that creep further into the patch and renew the cycle (Janzen 1986). Other examples are firewood cutters who penetrate progressively deeper into a patch to cut snags for wood, and chronic windthrow and subsequent salvage that progressively decreases patch area.

- Microclimatic changes along patch edges alter the conditions for interior plant and animal species and usually result in drier conditions with more available light (Bond 1957, Harris 1984, Ranney and others 1981). The current estimate suggested for the Pacific Northwest is that microclimatic effects extend up to two tree lengths (about 160 m) inside a patch (Franklin and Forman 1987, Harris 1984), which is tentatively supported by ongoing research (T. Spies, pers. comm.). Seral plants become more vigorous or abundant at edges in response to microclimatic changes, leading to greater abundance of seral plants in the seed pool and a higher probability of their establishment in patch interiors or colonization of gap disturbances (Janzen 1986, Ranney and others 1981).

The dynamics of forest habitat and environmental change with fragmentation are poorly understood. Are there thresholds of change in habitat attributes, or are the changes continuous? Franklin and For-man's (1987) simple checkerboard model with 10-ha patches suggests several patterns and thresholds of change: as the forest matrix becomes smaller with an increasing number of Clearcut patches, the edge length peaks at 50 percent cutover, but then the relation reverses and clearcuts become the matrix with forest patches; total area of forest interior habitat declines linearly to zero at 50 percent cutover, assuming that edge microclimatic effects occur within 160 m from the edge; and patch size does not decline until a threshold of 30 percent cutover when forest patch size drops precipitously until the 50 percent cut level, after which patch size remains steady.

Research data from Lehmkuhl and others (this volume) contradict the Franklin and Forman patch-size model, however, indicating that forest patch size declines linearly between 0 and 50 percent cutover. They support Franklin and Forman's (1987) 50 percent edge threshold when late-successional forests become the patches in a clearcut matrix. The threshold for more strictly defined old-growth forest, however, was lower, near 30 percent cutover. Wilcove and others (1986) suggest that patch numbers increase exponentially with time under a steady rate of fragmentation. Burgess and Sharpe (1981) presented data from southern Wisconsin landscapes that indicated mean distance between patches increased exponentially until about 10 percent of the forest remained.

Population phenotype-The life history characteristics of species are probably the most important aspect of the population phenotype for population vulnerability analysis (Margules and others 1982, McCoy 1982, Shaffer and Samson 1985, Simberloff and Abele 1982). The probability that a population will persist with habitat loss, which is one aspect of fragmentation, is largely a function of population density or abundance: the greater the abundance or density, the lower the risk of local extinction (Diamond 1984, Diamond and others 1987, Newmark 1987, Pimm and others 1988, Soul) and others 1988, Terborgh and Winter 1980, Wilcox 1980). Vulnerability to extinction in isolated habitat patches may also increase with large body size (Diamond 1984, Diamond and others 1987, Pimm and others 1988); low fecundity (Pimm and others 1988); specialization on patchy resources (Karr 1982a, Terborgh and Winter 1980); behavioral patterns requiring the formation of large groups and thus concentrated resources, dependence on keystone or link species, or occurrence at the edge of a species' range (Terborgh and Winter 1980); temporal variation in population size (Diamond 1984, Goodman 1987a,b, Karr 1982b); and metabolic rate (Wilcox 1980).

Persistence despite isolation of habitat patches, the second aspect of fragmentation, is a function of the dispersal abilities of the species (for example, Harris 1984, Soule and others 1988, Wilcox 1980). Dispersing individuals may rescue populations dwindling to extinction (Brown and Kodric-Brown 1977), or found new populations where they have become locally extinct. Species with poor dispersal capabilities, especially those with low powers of persistence, have a high risk of extinction in fragmented landscapes.

Population structure-We have discussed the increased probability of stochastic extinction from a reduction in population size brought on by the loss of forest habitat. Fragmentation also breaks the population into small subunits, each with dynamics different from the original contiguous population and each with a greater chance than the whole of local extinction from stochastic factors. Such fragmented populations are metapopulations, in which the subunits are interconnected through patterns of gene flow, extinction, and recolonization (Gill 1978, Lande and Barrowclough 1987, Levins 1970).

Determining the viability of the subpopulations of a metapopulation in fragmented landscapes is difficult. Long-term study is necessary because extinctions may be highly stochastic or observable effects after fragmentation may be delayed until populations reach an equilibrium with the changed availability of resources (Shaffer 1981). A "source-sink' effect may occur, whereby animals dispersing from undisturbed source areas colonize sink habitat patches that would otherwise not support populations (Pulliam 1988, Wiens 1976). Animals may breed in low-quality sink patches but have a negative reproductive rate, while the appearance of a viable population is maintained by immigration (Pulliam 1988). Then, interpatch distances are important determinants of population persistence, and they interact with species mobility and life-history characteristics to determine the rate at which immigration is effective in maintaining population size and genetic diversity.

The dynamics of population response to various amounts of fragmentation are essentially unknown: is population response gradual or continuous, or is the response nonlinear with thresholds? Several models predict response thresholds. Franklin and Forman's (1987) model predicts that forest-interior species richness declines slowly until 30 percent cutover, then rapidly declines to 50 percent cutover in response to rapidly decreasing patch sizes. Total species diversity increases rapidly up to 30 percent forest removal as edge species colonize in response to increasing edge length, but then declines slowly with the loss of interior species and declining edge. Game species, which are mainly edge species, follow a similar trend. A model by McLellan and others (1986) indicates a threshold of population decline at 50 percent habitat loss for species susceptible to fragmentation (low vagility, small populations). A population persists longer when patches of the same habitat are larger and closer. Less susceptible species begin to decline when 75 percent of the habitat is removed.

The Pacific Northwest Vertebrate Community

The forests of the Pacific Northwest support a large and diverse fauna of over 400 species (Brown 1985), of which 58 percent are bird species, 30 percent mammals, 7 percent amphibians, and 5 percent reptiles (Harris 1984). In a review of the literature, Harris (1984) concluded that species diversity declines with elevation, increases with moisture, and increases with the structural diversity associated with increasing stand age, which mainly consists of the vertical structure afforded by large, living trees; dead, standing trees (snags); and logs on land and in streams. Recent, extensive, field studies have shown forest-bird community richness to be positively associated with increasing temperature, which is a negative function of elevation and distance from the ocean (Huff and Raley, this volume). Concurrent studies of small mammal and amphibian communities indicated richness to be primarily a function of zoogeographic barriers to dispersal (mainly the Columbia River and the Willamette Valley) and localized geographic distributions, especially for amphibians (Aubry and others, this volume; Bury and others, this volume a).

Vulnerability Analysis

Assessing the effects of forest fragmentation from timber harvest on wildlife diversity and population viability raises several basic questions: "What species are associated with late-successional forest landscapes?" "What species are at greatest risk as assessed from an examination of the structural and life-history characteristics of species' populations that influence their persistence in forest landscapes altered by timber harvest?" and "What are the options for timber management to manipulate forest stand- and landscape-scale characteristics to minimize the risks of local extinction?"

To answer the first question, we used the list of species associated with late-successional forest from the summary paper of this symposium (Ruggiero and others, this volume). Other species were added from the wildlife-habitat relationships tables in Brown (1985) to include species that use late-successional stages (large sawtimber and old growth) of the temperate coniferous forest and were not sampled by the old-growth community studies (this volume). The list was edited to exclude species taken from Brown that are not found primarily in temperate coniferous forests. We concentrated on species associated with late-successional forest because this is the stage of forest development least likely to be represented in managed forest landscapes of the future. The list of 93 species is not complete (appendix table 2), but reflects current knowledge of habitat relationships. Earlier lists based on literature reviews are similar in the total number of species listed. Harris (1984) proposed late-successional forest as primary habitat for 118 species, with 40 species dependent on old growth. Brown (1985) described 76 species that use old-growth forest as primary breeding habitat and 65 species that use it as primary feeding habitat.

The vulnerability of listed species was assessed by compiling research data and general information about the abundance, life history, and habitat relationships of species, and then determining the risk of local extinction associated with each variable. Field data on the frequency of occurrence, abundance, and coefficient of variation in abundance among stands from the old-growth community studies (Lehmkuhl and others, this volume) were assembled for 64 of 93 listed species. The values of those variables for each species were converted to percentages of the maximum value for species in the same taxon, and then grouped into three classes: 0 to 33 percent, 34 to 66 percent, and >66 percent of maximum. Risks associated with the percentile classes were scored from low (1) to high (3) depending on the variable. Risk scores declined with increasing frequency of occurrence and abundance, but scores increased with increasing variation in abundance. Scores were estimated for 29 species (for which abundance data were not available from the community studies) by examining scores for similar species and consulting the general literature.

Risks associated with the life-history parameters of body size, vagility, and migratory status were similarly rated as low, moderate, or high. Risk scores increased with increasing body size under the premise that small-bodied species have smaller home ranges and higher densities than larger species, and may persist longer in small patches than large species. Risk decreased with increasing vagility because high vagility enables dispersing individuals to rescue failing subpopulations in isolated habitat patches, or to recolonize patches with locally extinct subpopulations. Risk associated with migratory status was scored low (1) for resident species, moderate (2) for short-distance migrants, and high (3) for long-distance migrants. Robbins and others (1989) showed that long-distance migrants were more susceptible to stand-area effects than short-distance migrants or residents. Pimm and others (1988) found migrants to have a higher risk of extinction than residents, probably because of greater migration risk and variability in population size. The intermediate risk we assigned to short-distance migrants is not clearly supported by the literature, but was inferred from the arguments of Pimm and others (1988) concerning migration risk. Ancillary data on the strength of association with late-successional forest, and use of structural and special habitats, were compiled to further assess risk and aid in habitat management.

A cumulative risk rating was calculated for each species as the weighted sum of risk scores for individual variables, by means of the following formula:

> Cumulative risk = 3 * (frequency score + abundance score) + 2 * (body size score + vagility score) + migratory status + variance in abundance.

Weights were assigned to reflect the relative importance of variables that affect persistence in fragmented landscapes. Frequency and abundance were weighted by 3 to account for the primary importance of population size and density. Body size and vagility were weighted by 2 to reflect the lesser, but still vital, importance of body size for persistence in isolated patches, and vagility in the rescue and recolonization of isolated populations. Variation in abundance and migratory status scores were unweighted to indicate their relatively lesser importance for persistence. Cumulative scores were recalculated according to a scale of 1 to 10 to simplify ranking of risk.

Eighty percent of the species fell into moderately high (score 7.8) and high-risk categories (scores 9, 10) (fig. 1). The 20 high-risk species have low frequency and abundance, and one of three body size-vagility combinations (appendix table 2). Small size and low vagility characterized 12 species of amphibians and small mammals. Their persistence in isolated patches of a highly fragmented landscape is problematic because of low frequency and abundance, and poor probability that subpopulations could be rescued or patches recolonized because of limited vagility. The limitation of poor vagility depends on the varying porosity of adjacent altered habitats to movement of dispersing animals. An additional consideration is the very limited geographic distributions of three amphibians.

These species may persist in relatively smaller patches than large species, however, because of their small size and relatively higher potential density. Amphibians may have an additional advantage relative to small mammals because their lower metabolism and energy requirements presume smaller ranges and higher densities. Small patches of late-successional forest are often regarded as poor habitat because of microclimatic and other edge effects, but the impact of edge effects on amphibians and small mammals remains to be shown. Small patches may **be adequate** to support viable populations of amphibians and perhaps small mammals, and may be important sources for recolonization of adjacent altered stands made suitable with time by succession. The elimination of small old-growth patches as poor habitat, therefore, may be imprudent unless they are imminently threatened by blowdown.

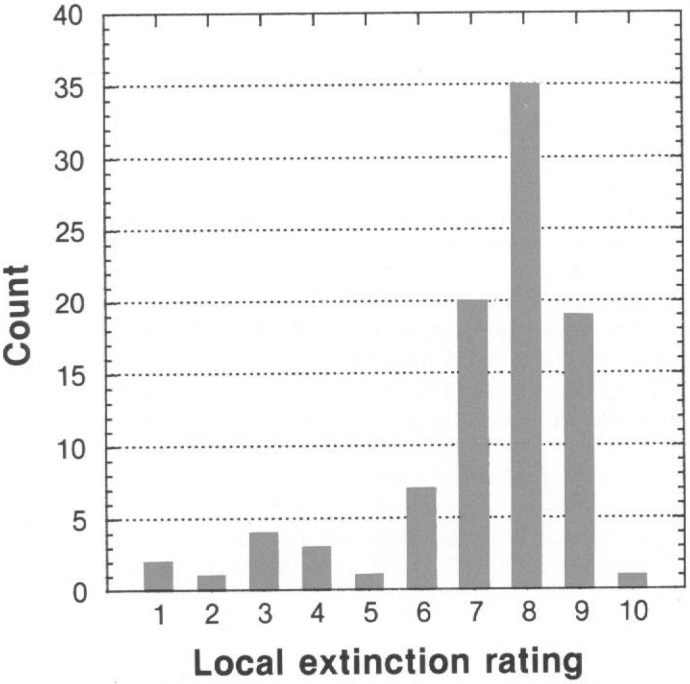

Figure 1—Frequency distribution of weighted risk of local extinction. Scores were calculated as the ranked, weighted sum of population distribution and life-history characteristics as determined by the old-growth community studies (dataset from Lehmkuhl and others, this volume). See appendix table 2 and text for methods.

Another high-risk group includes three squirrel species of small to medium size and moderate vagility. Because of their higher mobility, animals with medium size and moderate vagility are less at risk than smaller species from the isolation of habitat patches and subpopulations. The risk is greater, however, from diminishing patch sizes because of the greater energy demands of larger body size. Persistence for these species is a balance between decreasing patch sizes and increasing isolation.

The third high-risk group is composed of five species of birds and mammals with large size and high vagility. High vagility usually enables these species to overcome patch isolation. Large body size, however, implies greater energy needs and larger home ranges than smaller species have, and consequently, total available habitat and patch size are most important. These species are generalists (elk, mule deer) or tied to special features (for example, bald eagles need tall trees or snags near water), and arguably do not specifically require extensive late-successional forests. Elk and mule deer, however, require some old forest for thermal and hiding cover, and they require winter feeding areas during years of heavy snow. This need is particularly important for deer in areas with snowfall down to sea level, such as southern Alaska and British Columbia (see papers in Meehan and others 1984). Regardless of specific cases, the risk analysis is significant because it indicates the vulnerability of large animals.

Nearly 60 percent of the rated species have moderately high risk scores (7-8) with only slightly less than high risk of local extinction. The large number of species in the group mitigates the lower score, making it perhaps the most important group for management. In common with high-risk species, these animals have low frequency and abundance, but with various combinations of body size and vagility. Combinations of body size and vagility range from small size with low vagility for amphibians and small mammals to small- and medium-size birds and mammals with high vagility. An important group is comprised of medium-size birds and mammals, which include the spotted owl, northern goshawk, pileated woodpecker, marten, and fisher. The vulnerability of the birds primarily is a function of habitat loss and the requirements of medium body size, and secondarily of isolation and vagility. The vulnerability of the marten and fisher, by contrast, is a function of both habitat loss and medium body size, and habitat-population isolation with only moderate vagility.

Timber Harvest Alternatives

A foremost consideration in formulating an adequate answer to the question of alternative timber-harvest strategies is the fact that populations of species closely associated with late-successional forest will always experience some detrimental impacts from loss of habitat. Minimum-fragmentation alternatives do not reduce the impact of lost habitat, but primarily attempt to minimize the additional negative impacts that small habitat patch-sizes, edge effects, and isolation of remaining forest patches have on the forest environment and metapopulation structure. The value of a given timber-management alternative therefore depends on how species respond to changes in patch size and isolation. Animals respond to increasing patch size as a function of their body size: large species with large ranges and low density benefit from larger patches that allow for larger, more persistent populations. Response to declining isolation is a function of vagility: animals with low vagility have greater access to other habitat patches as isolation decreases. We cross-tabulated vagility and body size for the species in our data set to examine how the impact of timber harvest may be reduced by a minimum fragmentation scheme (table 1).

Increasing the patch size and decreasing the isolation of habitat patches reduces impacts on at least 27 species (score 4), probably helps another 20 species (score 3), and likely has little impact on 46 species (table 1). This analysis does not consider qualitative habitat loss through edge effects. Those species that can be identified as interior species may benefit from the reduction of edge through minimum fragmentation practices. Some preliminary evidence from ongoing research indicates that the abundance of a few birds (winter wren, Swainson's thrush, and varied thrush) is higher in patch interiors (A. Hansen and J. Peterson, pers. comm.).

Table 1—Species groups and number of species associated with late-successional forest that are likely to sustain fewer impacts from a minimum-fragmentation clearcutting alternative relative to current maximum-fragmentation practices

Vagility scores	Body-size scores[a]		
	Large - 3	Medium - 2	Small - 1
Low - 3	6 (0)[b]	5 (0)	4 (21)
Moderate - 2	5 (0)	4 (2)	3 (5)
High - 1	4 (4)	3 (15)	2 (46)

[a] Column scores are the sums of vagility and body-size scores (see text) and indicate the relative impact of the alternative, with higher numbers indicating more favorable response of the species group.

[b] The number in parentheses indicates the number of species (from appendix table 2) in that category.

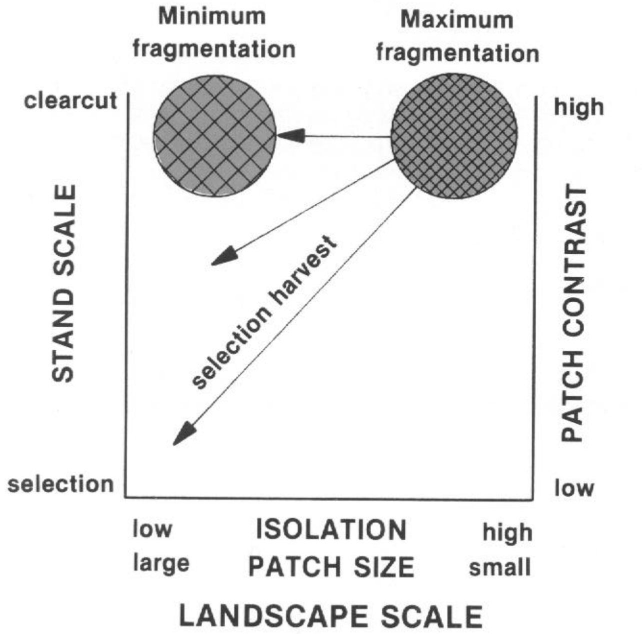

Figure 2—Hypothetical "management space" for appraising the impacts of alternative timber-harvest methods on landscape pattern. The horizontal axis represents a landscape scale of management, where timber harvest determines the size and isolation of remaining forest patches. The vertical axis represents the contrast between forest and harvested areas, which is at a stand scale of management. Current staggered-set clearcutting and minimum fragmentation alternatives act along the horizontal axis (top of figure), whereas selection harvest tends to act at both landscape and stand scales by minimizing the contrast between forest patches and the altered matrix, and thus minimizes the isolation and increases the functional size of patches (diagonal arrows).

Other management options may reduce the impacts of timber harvest. Alternatives such as minimum fragmentation alter the juxtaposition of clearcut units at a landscape scale to alter the size and isolation of remaining forest patches (fig. 2). Management, however, can also act at a stand scale along which selection harvest and clearcutting lie at the extremes. Current staggered-set clearcutting is in the area of greatest impact at the extremes of both stand- and landscape-scale modification (top right of fig. 2). Minimum fragmentation alternatives move management to the left along the landscape axis, and stand-scale impacts and patch contrast remain constant. As harvest changes from clearcut to selection methods, or as other means of maintaining the structural and functional characteristics of harvested stands are used (Harris and others 1982, Nyberg and others 1987), the contrast and edge effects between altered and remnant patches and landscape fragmentation decrease concurrently as shown by the arrows in figure 2.

Conclusions

Reducing timber harvest will always increase the probabilities of persistence for vulnerable wildlife species. Viable populations may exist with some timber harvest, however, especially if harvest practices are modified to minimize the effects of logging at landscape and stand scales. Alternative plans for arranging clearcut units to minimize landscape-scale impacts have been suggested by Franklin and Forman (1987) and are being planned for some National Forests in the Pacific Northwest. Alternative stand-scale practices, such as retaining green trees and coarse woody debris, are only recently being explored. Other beneficial practices include the use of corridors that maintain habitat connectivity across the landscape and facilitate wildlife movement from wilderness or between forest patches across managed landscapes (Harris 1984, Noss 1987, Noss and Harris 1986, Simberloff and Cox 1987). Population viability will also be enhanced if the location of cutting units does not remove habitat refugia or decrease the habitat heterogeneity across the landscape that animal populations depend on during periods of environmental stress. Planning for the replacement over time of late-successional forest patches or structural attributes like snags will ensure the viability of species requiring these key habitats.

We need more research to give managers better information and tools. Verner (1986) gave a good prescription for research into fragmentation effects: emphasis has been on birds for several reasons, but we need more research on mammals, reptiles, and amphibians; more research is needed on the processes affecting wildlife persistence in fragmented landscapes, rather than patterns related to area alone; we need to determine population parameters and model population responses to examine the consequences of fragmentation over space and time, which is not feasible without long-term research; and more emphasis should be placed on the spatial dynamics of fragmentation from a landscape perspective.

We suggest several additional research issues: more emphasis is needed on habitat relationships in managed forests, and the interaction of remnant forest patches and the managed habitat matrix; continued research is needed into the value of late-successional forests for wildlife to assess long-term trends; examination of habitat relationships from a landscape-scale perspective is needed to account for processes working above the stand or patch scale: and study is needed of the ecology of species and species groups that current research has shown to be clearly associated with late-successional forests.

We have used facts and speculation to assess the impacts of timber harvest on the vertebrate community. We can say definitely that the old axiom good timber management is good wildlife management does not apply to species associated with late-successional forest. These species will always sustain some negative impact from logging. Given that logging will continue and wildlife populations will continue to be affected, a larger question is “At what point will forest fragmentation from logging endanger the viability of wildlife populations on public lands?” Models (Franklin and Forman 1987; McLellan and others 1986; B. Noon, pers. comm.) and some field data (Lehmkuhl and others, this volume; Rosenberg and Raphael 1986) suggest that, for most species, we have not yet reached a threshold of fragmentation on most public lands beyond which local population viability is doubtful and management options are few. This is very good news. Nevertheless, some species, such as the spotted owl, will always be exceptionally vulnerable no matter how viable the majority of species remain. The viability of populations of those vulnerable species will be the touchstone of our commitment to maintaining biotic diversity on public forest lands.

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Appendix

Table 2—Risk of local extinction for species associated with late-successional temperate coniferous forest [the species list was modified from Ruggiero and others (this volume) and Brown (1985)]

	Variables[a]										
	Management score										
Species	DE	ST	SP	FR	AB	BO	VA	MI	VR	RISK[b]	RANK
Clouded salamander	2	1	0	3	3	1	3	1	3	30	10
Oregon slender salamander	1	1	0	3	3	1	3	1	1	28	9
Pacific giant salamander	1	1	0	3	3	1	3	1	2	29	9
Larch Mountain salamander	1	1	2	3	3	1	3	1	1	28	9
Siskiyou Mountains salamander	1	1	2	3	3	1	3	1	1	28	9
Van Dyke's salamander	1	1	2	3	3	1	3	1	1	28	9
Olympic salamander	1	1	0	3	3	1	3	1	2	28	9
Bald eagle	1	2	1	3	3	3	1	2	1	29	9
Band-tailed pigeon	2	2	0	3	3	2	1	2	2	28	9
Common raven	1	2	0	3	3	3	1	1	1	28	9
Red tree vole	1	2	0	3	3	1	3	1	1	28	9
White-footed vole	1	1	0	3	3	1	3	1	1	28	9
Elk	2	3	0	3	3	3	1	1	1	28	9
Northern flying squirrel	1	3	1	3	3	1	2	1	3	28	9
Mule deer	2	3	0	3	3	3	1	1	1	28	9
Coast mole	2	1	0	3	3	1	3	1	2	29	9
Western gray squirrel	2	2	0	3	3	2	2	1	1	28	9
Marsh shrew	2	1	0	3	3	1	3	1	1	28	9
Pacific shrew	2	1	0	3	3	1	3	1	1	28	9
Douglas' squirrel	2	2	0	3	3	2	2	1	1	28	9
Western redback salamander	1	1	0	3	2	1	3	1	2	26	8
Cascades frog	1	1	0	3	3	1	2	2	1	27	8
Red-legged frog	1	1	0	2	3	1	2	2	3	26	8
American robin	2	3	0	3	3	1	1	2	2	26	8
Bufflehead	1	2	1	3	3	2	1	2	1	27	8
Blue grouse	2	2	0	3	3	2	1	1	1	26	8
Barrow's goldeneye	2	2	1	3	3	2	1	2	1	27	8
Black-throated gray warbler	2	2	0	3	3	1	1	3	2	27	8
Black-headed grosbeak	2	2	0	3	3	1	1	3	2	27	8
Common merganser	1	2	1	3	3	2	1	2	1	27	8
Cooper's hawk	1	2	0	3	3	2	1	2	1	27	8
Evening grosbeak	1	2	0	3	3	1	1	2	2	26	8
Hutton's vireo	2	2	0	3	3	1	1	2	2	26	8
Hooded merganser	2	2	1	3	3	2	1	2	1	27	8
Northern goshawk	1	2	0	3	3	2	1	1	1	26	8
Nashville warbler	2	2	0	3	3	1	1	3	1	26	8
Olive-sided flycatcher	1	2	0	3	3	1	1	3	1	26	8
Pine siskin	1	2	0	3	3	1	1	2	2	26	8
Pileated woodpecker	1	3	1	3	3	2	1	1	2	27	8
Red-breasted sapsucker	2	2	1	3	3	1	1	2	2	26	8
Swainson's thrush	1	3	0	3	3	1	1	3	2	27	8
Sharp-shinned hawk	1	2	0	3	3	2	1	2	1	27	8
Northern spotted owl	1	3	0	3	3	2	1	1	1	26	8
Townsend's warbler	2	2	0	3	3	1	1	3	2	27	8
Vaux's swift	1	2	1	3	3	1	1	3	2	27	8
Western tanager	1	2	0	3	3	1	1	3	2	27	8
Western screech-owl	2	2	1	3	3	2	1	1	1	26	8
Wood duck	2	2	1	3	3	2	1	2	1	27	8
White-winged crossbill	2	2	0	3	3	1	1	2	3	27	8
Yellow-rumped warbler	1	2	0	3	3	1	1	2	2	26	8
Fisher	1	3	0	3	3	2	1	1	1	26	8

See footnotes on next page.

Table 2—continued

	Variables[a]										
	Management score										
Species	DE	ST	SP	FR	AB	BO	VA	MI	VR	RISK[b]	RANK
Marten	1	3	0	3	3	2	1	1	1	26	8
Shrew-mole	1	1	0	2	3	1	3	1	2	26	8
Forest deer mouse	1	1	0	2	3	1	3	1	3	27	8
Water shrew	2	1	0	2	3	1	3	1	3	27	8
Tailed frog	1	1	0	2	2	1	3	1	3	24	7
Dunn's salamander	1	1	0	2	2	1	3	1	3	24	7
Hammond's flycatcher	1	2	0	2	3	1	1	3	3	25	7
Marbled murrelet	1	2	0	3	3	1	1	1	1	24	7
Northern pygmy-owl	1	2	1	3	3	1	1	1	1	24	7
Northern flicker	1	3	1	3	3	1	1	1	1	24	7
Northern saw-whet owl	1	2	1	3	3	1	1	1	1	24	7
Purple finch	1	2	0	3	3	1	1	1	1	24	7
Rufous hummingbird	1	2	0	2	3	1	1	3	2	24	7
Townsend's solitaire	1	2	0	3	3	1	1	2	1	25	7
Wilson's warbler	2	2	0	2	3	1	1	3	2	24	7
Big brown bat	1	2	1	3	3	1	1	1	2	25	7
Silver-haired bat	1	2	1	3	3	1	1	1	2	25	7
Keen's myotis	1	2	1	3	3	1	1	1	2	25	7
Yuma myotis	1	2	1	3	3	1	1	1	2	25	7
California myotis	1	2	1	3	3	1	1	1	2	25	7
Long-eared myotis	1	2	1	3	3	1	1	1	2	25	7
Long-legged myotis	1	2	1	3	3	1	1	1	2	25	7
Little brown myotis	1	2	1	3	3	1	1	1	2	25	7
Fringed myotis	1	2	1	3	3	1	1	1	2	25	7
Northwestern salamander	1	1	0	2	2	1	2	2	3	23	6
Roughskin newt	1	1	0	2	2	1	2	2	3	23	6
Gray jay	1	2	0	2	3	1	1	1	2	22	6
Hairy woodpecker	1	2	1	2	3	1	1	1	2	22	6
Hermit thrush	1	2	0	2	3	1	1	2	2	23	6
Red crossbill	1	2	0	3	2	1	1	2	2	23	6
Steller's jay	2	3	0	2	3	1	1	1	3	23	6
Western red-backed vole	1	1	0	1	2	1	3	1	3	21	5
Brown creeper	1	2	1	1	3	1	1	1	2	19	4
Red-breasted nuthatch	1	2	1	1	3	1	1	1	2	19	4
Varied thrush	1	3	0	1	3	1	1	2	2	20	4
Ensatina	2	1	0	1	1	1	3	1	2	17	3
Southern red-backed vole	1	1	0	1	1	1	3	1	3	18	3
Hermit & Townsend's warblers	1	2	0	1	2	1	1	3	2	18	3
Western flycatcher	1	2	0	1	2	1	1	3	2	18	3
Golden-crowned kinglet	1	2	0	1	2	1	1	1	2	16	2
Chestnut-backed chickadee	1	2	1	1	1	1	1	1	2	13	1
Winter wren	1	3	0	1	1	1	1	2	2	14	1

[a] DEpendency on late-successional forest: 1 = primary; 2 = secondary. STructural layer used: 1 = horizontal; 2 = vertical (foliage); 3 = both. SPecial management: 0 = none; 1 = snags; 3 = limited distribution. MIgratory status scored as 1 = resident; 2 = short-distance migrant; 3 = long-distance migrant. Other life history variables were scored as 1 = low, 2 = moderate, 3 = high risk.

[b] Risk = 3* (FRequency + ABundance) + 2* (BOdy size + VAgility) + MIgratory status + VaRiance in abundance. Scores for frequency, abundance, and variation were assessed from data presented by Lehmkuhl and others (this volume). Total risk was calculated as the weighted sum.

Old-Growth Inventories: Status, Definitions, and Visions for the Future

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Abstract

Inventories of old-growth forests require a classification system for identifying and arraying forest conditions for a variety of interests. Old growth has value as fish and wildlife habitat, as a timber stratum, as an economic resource, and as a component of biological diversity. It is needed for scientific study, for long-term forest productivity, for recreation, for aesthetics, for spiritual interests, and for watershed protection. Several authors have defined old growth. Their definitions have similar but not identical components, and none suffices for all forest types, nor do they meet the intent of all interests. Recent estimates of known and candidate old growth in Washington, Oregon, and California total to 3.6 million ha. This sum, however, is based on a variety of definitions, forest types, and recency of data. Estimates based on consistent definitions and data sources are not available. Differences between estimates made by the Forest Service and The Wilderness Society of the amount of old growth on National Forests in Washington and Oregon can be partially explained by the stringency of their definitions of old growth and the methods they used to identify old-growth stands. The amount and distribution of old growth on National Forests in the Pacific Northwest in the future will depend on management allocations in reserved (for example, wilderness) and non-reserved (for example, timber production) status.

Current information needs relative to inventories of old-growth forest include descriptions of successional and developmental stages of old-growth forests and criteria for defining old growth for each forest type in the Pacific Northwest. At present, the Forest Service is conducting a regional inventory in the Pacific Northwest, using an attribute-driven approach. This work will provide the most complete inventory to date on National Forest lands. Other recommendations for old-growth inventories include: taking an attribute-based rather than a definition-based approach; developing a map-based rather than just numerical-based product to address the scale, context, and size of old-growth stands; and integrating any adopted definition of old-growth as part of a system for describing the amounts and distributional patterns of older forest.

Introduction-What Constitutes an Old-Growth Inventory?

Without adequate inventories and without a clear understanding of the amount and distribution of old growth it is difficult for the decision maker to determine what is practical or feasible (Ham 1984:69).

Conducting inventories of a natural system across a broad geographic area is a difficult task. Attempting to inventory old-growth forests throughout the Western United States and beyond is challenging because of the large size and great diversity of the area. An old-growth inventory requires an explicit and quantitative classification system to identify and array candidate areas. Potential old-growth stands are first identified by a set of general criteria, and finally classified according to a precise set of stand structural attributes.

This paper was prompted by the need to review existing definitions and inventory estimates of old-growth forests in the Western United States, and to help resolve controversies over old-growth inventories on National Forests by describing the bases of the estimates. Specifically, the objectives of this paper are to describe the proposed definitions that have guided estimates of the amount and distribution of old-growth forests, to review estimates of the amount and distribution of old-growth forests in the Pacific Northwest, to describe the bases for estimates of the amount of old-growth forests on selected National Forests in Washington and Oregon, and to propose methods for improving the reliability of those inventories. This paper is not intended to represent official Forest Service policy on old growth, nor to present a new inventory of old growth. The geographic scope of this paper includes Washington, Oregon, and California for tallying existing inventories; and Washington and Oregon only (the Pacific Northwest Region of USDA Forest Service) for describing definitions of old growth on National Forest land.

Important Considerations for Old-Growth Definitions and Inventories

In current planning and management activities on National Forests, old growth has several values (Sirmon 1985). and one of them is its importance as wildlife habitat (Meehan and others 1984, Meslow and others 1981, Raphael and Barrett 1984, Thomas and others 1988). Old growth provides optimal habitat for some management indicator species, including spotted owl, pileated woodpecker, and marten, and for many other species of plants, fish, amphibians, reptiles, birds, and small mammals (Harris and others 1982, Meslow and others 1981, Raphael 1988c, Raphael and Barrett 1984). It also provides thermal and hiding cover for ungulates, especially in winter (Schoen and others 1984, Wallmo and Schoen 1980). Old growth, therefore, plays an important role in providing for productive populations of some species of special ecological and administrative interest. For some of these species, old growth may be a key factor in providing for continued population viability.

Old growth also has value as a source of timber. It has been defined as forested areas that are past mean annual increment of wood-volume production (DeBell and Franklin 1987). Silviculturally, the structure and age-classes of old-growth forests, with large diameter boles, presence of snags, and less than ideal stocking, represent less than optimal use of growing space for trees. Economically, old-growth stands are valuable as timber because of the large volume and high quality of wood they contain (Society of American Foresters 1984).

Additional values of old growth are as natural research areas for scientific study (Greene 1988, Sheppard and Cook 1988) and its ecological role in providing long-term forest productivity (Franklin and others 1981, Perry and others 1988). Other interests in old growth include its recreational, aesthetic, and spiritual significance (Anderson 1988), its contribution to watershed protection (Sedell and Swanson 1984), and its importance as a contributor to biological diversity (Harris 1984, Luman and Neitro 1980, Norse and others 1986).

Addressing each of these values requires different concepts and definitions of old growth. The wide variety of interests in old growth also requires consideration of several spatial scales for inventories: stand, watershed, province, and State or regional scales. Inventories are the basis for describing the present and future distribution and amount of old growth, and for evaluating management alternatives and options available over time.

Review of Old-Growth Definitions

Several definitions of old growth have been proposed or used for Pacific Northwest forests. Few definitions have been developed independently. In particular, definitions by the Old-Growth Definition Task Group (1986) refined earlier definitions by Franklin and Spies (1984) and Society of American Foresters (1984), which in turn were based on Franklin and others (1981). Most of the Forest Service definitions and those of The Wilderness Society were based on these definitions in detail or in concept. Definitions are of two kinds: those based on timber production criteria, and "ecological definitions" (those based on field observations of vegetational structure and composition rather than on economic value, timber age, or stocking-classes).

Existing Definitions of Old-Growth Forests in the Pacific Northwest

Society of American Foresters-The Society of American Foresters (1984) defined old-growth Douglas-fir forests of western Oregon and Washington as stands that have two or (commonly) more tree species with a range in tree sizes and ages and often including a long-lived dominant (such as Douglas-fir) and a shade-tolerant associate (such as western hemlock); a deep, multilayered canopy; some individual live trees (greater than 25 per ha) either more than 200 years old or greater than about 100 cm in d.b.h.; significant coarse woody debris, including more than 25 snags per ha greater than 6 m tall and more than about 45 metric tons/ha of down wood, and at least 10 snags and logs per ha over 64 cm in diameter and 15 m long. SAP did not provide a definition for other forest types.

Old-Growth Definition Task Group-This task group provided interim, working definitions of old growth in four Douglas-fir and mixed-conifer forest types in the Cascade Range of Washington and Oregon, in northwestern California, and in the Sierra Nevada of California (Old-Growth Definition Task Group 1986). Their definitions (table 1) included criteria for live-tree size, age, density, and associates; canopy structure; snag size and density; and log size and density. Different criteria were developed for the four forest types to reflect differences in moisture regimes and expected site potential Collectively, these definitions are commonly referred to as ecological definitions.

USDA Forest Service-The Forest Service has published old-growth definitions for Washington, Oregon, and California in two regional guides to support the planning process for the management of forest land (table 2). For Washington and Oregon, the Pacific Northwest Regional Guide defined old growth with qualitative criteria (table 2) as well as with quantitative, Forest-specific criteria (as in table 3). In addition to the regional definitions, the draft Forest plans for most National Forests quantified structural parameters for stands of specific forest types. Many of these definitions varied by National Forest.

In the Pacific Northwest Region, a minimum tract size of 4 ha was established as a regional standard, and qualitative guidelines were presented for optimal tract size to support functional patches of old growth:

> Optimum tract size will be related to the needs of dependent wildlife species, such as northern spotted owls or pileated woodpeckers, and the ability to insulate part of the stand from the edge effects in created openings.

In California, the Pacific Southwest Forest Service Regional Guide used qualitative criteria to define old growth (table 2).

The Wilderness Society-The inventory assessment conducted by Morrison (1988) for The Wilderness Society used the ecological old-growth definition of the Old-Growth Definition Task Group (1986). Where inventory data were unavailable, log and snag criteria were not used. Morrison also defined several additional classes and subclasses of old growth (Morrison 1988:10). "Classic" old-growth stands meet all minimum criteria of the Old-Growth Definition Task Group (1986) and contain at least 20 trees per ha that exceed 300 years in age or 100 cm in d.b.h. A subclass of classic old growth is "super" old growth, with trees exceeding 700 years old or 180 cm in d.b.h. Stands meeting the definition of the Old-Growth Definition Task Group (1986), including where inventory data on logs and snags were not available, were termed "early" old growth, and contain at least 20 trees per ha over 200 years old or 80 cm in d.b.h. Such stands may include some older trees but they are in low numbers. "Mature" stands contain more than 50 trees per ha exceeding 80 years old or 53 cm in d.b.h. Such stands fail to meet one or more of the minimum old-growth criteria. Morrison also summarized old-growth tracts more than 122 m from roads or clearcuts.

Old-Growth Research Studies-Stands classified as mature and old growth in the studies by the Old-Growth Forest Wildlife Habitat Program were selected to represent the full range of conditions in Douglas-fir forests more than 200 years old (T. Spies, pers. comm.). They were selected before the criteria used by the Old-Growth Definition Task Group were developed. As a result, not all old-growth stands studied in this research fully meet the criteria established by the Task Group.

Comparison of Four Existing Definitions-The three key definitions outlined above (Old-Growth Definition Task Group, Pacific Northwest Regional Guide, and Society of American Foresters (1984)) describe old growth in Douglas-fir/western hemlock forests in Washington and Oregon (table 4). Only the Pacific Northwest Regional Guide describes old growth for true fir/mountain hemlock forests. In the Douglas-fir/western hemlock type, all three definitions call for live trees of two or more species with a variety of sizes and ages. The Society of American Foresters' (1984) definition is most stringent on tree density and size. The Pacific Northwest Regional Guide does not specify age. All other definitions allow >200 years old as an alternative to tree diameter. Criteria for shade-tolerant associates also vary among definitions. All three definitions agree on qualitative canopy characteristics. Quantitative criteria for snags and logs vary widely, however, with the Society of American Foresters' definition calling for the greatest densities and largest diameters.

Table l-Interim minimum standards for old-growth Douglas-fir and mixed-conifer forests in western Washington and Oregon and in California (from Old-Growth Definition Task Group 1986:4)

Stand characteristic	**Douglas-fir** on western hemlock sites (western hemlock, Pacific silver fii)	Douglas-fir on mixed conifer sites (**white fir,** Douglas-fir)	Douglas-fir on mixed **evergreen** sites (**tanoak,** Douglas-fir)	Sierra mixed-conifer forests (white fir)
Live trees	Two or more species with wide range of ages and tree sizes	Two or more species with wide age range and full range of tree sizes	Douglas-fir and evergreen hardwood species (**tanoak,** Pacific **madrone,** and canyon live oak) associates (40 to 60% of canopy)	Two or more with wide age range **and** full range of **tree** sizes
	Douglas-fir ≥20 per ha of trees >81 cm in diameter or > 200 years old	Douglas-fir, ponderosa **pine,** or sugar pine ≥20 per ha of trees >76 cm in diameter or >200 years old	Douglas-fir or sugar pine **≥15 per ha of trees** **78** 1 cm in diameter or >200 years old	Douglas-fir, sugar pine, or ponderosa pine ≥20 per ha of trees **781** cm in diameter or 7200 years old
	Tolerant associates (western hemlock. western **redcedar,** Pacific silver fir, grand fii, or **bigleaf** maple) 130 per ha or trees >41 cm in diameter	Intermediate and small size-classes are typically white **fir,** Douglas-fir, **and incense-cedar. singly or in mixture**	Intermediate and small size-classes may be evergreen hardwoods or include a component of conifers (e.g., Douglas-fir or white fir)	Intermediate and small size-classes are typically white fir with **incense-**cedar or both in some stands
Canopy	Deep, multilayered **canopy**	Multilayered canopy	Douglas-fii emergent above evergreen hardwood canopy	Multilayered canopy
Snags	Conifer snags 110 per ha that are >51 cm in diameter and **>4.6 m** tall	**Conifer snags 23.7** per ha that are >51 cm in diameter and >4.6 m tall	Conifer snags ≥3.7 per ha that are >51 cm in diameter and >4.6 m tall	Conifer snags ≥7.4 per ha that are >51 cm in diameter and 74.6 m **tall**
Logs	Logs ≥34 metric tons per ha including 10 pieces per ha ≥61 cm in diameter and >15 m long	Logs ≥22 metric tons per bit including 5 pieces per ha >61 cm in diameter and 715 m long	Logs ≥22 metric tons per ha including 5 pieces per ha >61 cm in diameter and >15 m long	Logs ≥22 tons per ha including 5 pieces per ha ≥61 cm in diameter and >15 m long

Table 2-Old-growth definitions from USDA Forest Service Pacific Northwest and Pacific Southwest Regional Guides (units converted to metric)

Pacific Northwest Region (Region 6)-Washington and Oregon
For all National Forests in the Pacific Northwest Region, an old-growth stand is defined as any stand of trees 4 ha or greater generally with the following characteristics:

(a) Stands contain **mature and overmature trees in** the overstory and are well into the mature growth stage
(b) Stands usually contain a **multilayered canopy** and trees of several age-classes
(c) Standing **dead trees and down material** are present; and,
(d) Evidence of **human activities** may be present but may not significantly alter the other characteristics and would be a subordinate factor in a description of such a stand

Pacific Southwest Region (Region 5) -California
Old growth is a stand that is past full maturity and showing signs of decadence, the last stage in forest succession. The definition of old growth by tree age, size, height or density varies by timber type. Among the components of old growth that may be of importance to wildlife species and that may be affected by land-management practices are large trees, old trees, decadence of standing vegetation, much dead and down woody material, uneven-aged vegetation, multi-layered vegetation, moderate foliar-height diversity, and mesic micro-habitats afforded by high canopy closure. High canopy closure does not always correspond to decadence.

Efficacy of Existing Definitions

Society of American Foresters (1984), the Old-Growth Definition Task Group (1986)) Morrison (1988), and Forest Service definitions all describe old-forest conditions as an “old-growth ecological type” with varying degrees of stringency. Thomas and others (1988:253) recommended that old growth be ecologically defined on the basis of the composition of plant and animal species, and the vegetative structure (including sizes and densities of live trees, snags, and down wood, and the number and nature of canopy layers) of stands. Minimum stand size and its effect on specific ecological functions is another critical characteristic, especially as related to providing fish and wildlife habitat. The Forest Service, Pacific Northwest Region, established 4 ha as a criterion for minimum stand size, and alluded to optimal sizes for conserving wildlife species and habitats. Morrison (1988) summarized inventories by two stand size-classes and by degree of isolation from other old-growth stands. The Old-Growth Definition Task Group (1986) cautioned that stands of less than about 32 ha are fully influenced by edge conditions, and should not be expected to provide interior forest conditions.

As Should be expected, none of the definitions suffices for defining, locating, and analyzing old-growth forests for the full variety of resource interests. Nor do any of the definitions cover all forest types in the Pacific Northwest. None of the definitions is part of a classification scheme for describing the full sere of development of old-forest conditions. Information based on successional development and structural changes will be most useful in developing an understanding of the status of old forests and in making future projections of old forests. Any single definition should only be part of a whole system for classifying old forests in a scheme that recognizes the range of young through old-growth and climax forest conditions.

Table 3-SpecifIc definitions of old growth as used in the USDA Forest Service Pacific Northwest Regional Guide for Cedar-Hemlock-Douglas-fir Forest Type (units converted to metric)

- At least **60 percent of the overstory canopy is dominated by large individual trees** in some combination of shade-tolerant and shade-intolerant species.
- The stand contains some **trees** with **stem diameters 81 cm or greater,** an average of **five snags per ha,** and **67 metric tons of logs per ha.**
- Trees have **mature bark characteristics;** for example, Douglas-fir has to have deeply furrowed bark.
- **Crown-height growth has slowed,** giving the tops a more rounded shape; tops may be broken.
- **Limbs are usually heavy and gnarled,** often with **mosses and lichens** present.
- Stands in these forest types will be considered old growth until fewer **than 12 overmature trees remain per ha.**

A Review of Old-Growth Inventories in the Western United States

Amounts of Old Growth

The following discussion reviews old-growth and old-forest inventories in Washington, Oregon, and California. Substantial amounts also occur in Alaska and British Columbia throughout coastal and interior environments, including stands dominated by Douglas-fir, western hemlock, and western redcedar. Much of this additional old-forest area, however, occurs in Sitka spruce and high boreal forest types, including black spruce and white spruce. These forests are ecologically much different than the lower elevation and more coastal forest types dominated by Douglas-fir, Sitka spruce, and western hemlock in Washington, Oregon, and California. Inventory amounts from Alaska and British Columbia are therefore excluded from the summary that follows.

Washington and Oregon-Franklin and Spies (1984) and the Society of American Foresters (1984) estimated nearly 6 million ha of old growth on commercial forest land in the

Table 4-Three old-growth definitions[a]

Stand characteristic	Old-Growth Definition Task Group	Pacific Northwest Regional Guide	Society of American Foresters
Douglas-fir on Western Hemlock Sites			
Live trees	Two or more species; wide range of age & size	Two or more species of several age-classes	Two or more species; wide range of age & size
	Douglas-fir ≥20 per ha of trees d.b.h. >81 cm or >200 yrs	Overmature trees 212 per ha with at least some Douglas-fir with d.b.h. ≥81 cm	≥ 25 trees Per ha with d.b.h. >102 cm or or >200 yrs old
	Tolerant associates ≥30 Per ha	No specific standard	No specific standard
Canopy	Deep, multilayered	Multilayered	Multilayered
Snags	Conifer snags ≥10/ha >51 cm in diameter and >4.6-m tall	≥5/ha	>25/ha >6 m tall and some >64 cm in diameter
Logs	Logs 234 metric tons/ha including 10 pieces/ha ≥6 1 cm in diameter and >15 m long	Logs ≥67 metric tons per ha	>45 metric tons/ha and some >64 cm in diameter and >15 m long '
Fir-Mountain Hemlock			
Live trees	Not addressed	Two or more species of several age-classes	Not addressed
		Dominant trees >12/ha	
		No specific standard	
Canopy		Multilayered	
snags		≥12/ha	
Logs		≥45 metric tons/ha	

[a] To develop their estimates, The Wilderness Society (Morrison 1988) defined "early old growth" with the old-growth criteria of the Old-Growth Definition Task Group (1986). One deviation was that age data in timber-inventory plots were not quantified precisely enough to use stand age (>200 years) as a criterion, as with the Old-Growth Definition Task Group (1986) definition. The Society also established definitions for "classic old growth" and "super old growth."

Douglas-fir region in the mid-1800s, and at present nearly 4 million ha have been harvested. More recently, Spies and Franklin (1988) estimated that about 17 percent of old growth existing in the early 1800s remains in the Douglas-fir region of the Pacific Northwest. In an independent estimate, Norse (1990) suggested that as much as 7.7 million ha of old growth may have been present in western Washington and Oregon before Euro-American settlement, although he acknowledged that this estimate may be high. Because of the absence of historic field inventories, these figures are approximate, and definitions applied to forest conditions are imprecise.

According to draft Forest plans, some 2.5 million ha of forests classified as old growth remain on National Forests in Washington and Oregon both east and west of the Cascade Crest. This estimate was based on the definition of old growth from the Pacific Northwest Regional Guide (table 2), and interpreted in the draft Forest plan by each National Forest. The draft plans were published between 1986 and 1988. The old-growth figures were generally updated to 1985, but some were based on earlier inventories that had not been updated. No information is available on historic amounts of old growth on these National Forests.

The reported 2.5 million ha represent about 25 percent of the total area of National Forest land in these two States. An estimated 1.2 million ha of that area occurs on the 10 National Forests that are located either wholly or predominantly east of the Cascade Crest, and 1.3 million ha occur on the 9 National Forests' located either wholly or predominantly west of the Cascade Crest.

About 0.30 million ha of the 2.5million ha total occur in areas reserved from timber harvest by decrees of Congress, such as in wilderness, Research Natural Areas, and other special reserves, and of that 0.30 million ha, about 0.11 million ha occur in the 10 National Forests east of the crest and 0.19 million ha occur in the 9 forests west of the crest. This leaves a reported 2.2 million ha of old growth on National Forests throughout Washington and Oregon that are not in such reserved lands.

The Wilderness Society (Morrison 1988) also estimated old growth in Oregon and Washington. This estimate, however, covered only six of the nine west-side National Forests in Oregon and Washington, and it used the definition produced by the Old-Growth Definition Task Group (1986). According to Morrison (1988), only 45 percent of the area inventoried as old growth by the Forest Service actually met all criteria set forth by the Old-Growth Definition Task Group.

Haynes (1986) estimated, based on data from the 1970s, that about 1.3 million ha of forest stands more than 250 years old remained on all land (regardless of ownership) in the Douglas-fir region of western Washington and western Oregon. Of this remaining old growth, about 0.4 million ha are protected, mostly in National Parks in Washington. Haynes' estimates were substantially lower than Forest Service estimates. Haynes' definition of old growth included forests older, and thus more scarce, than did the Forest Service definition, and he estimated old growth from stand-age data (Morrison 1988). The precision of estimates made by Haynes and by the Forest Service was not reported.

More recently, Greene (1988) reported that 0.3 1 million ha of old-growth forest stands more than 200 years old occur in North Cascades, Mount Rainier, Olympic, and Crater Lake National Parks. Franklin and others (1988) estimated that 60 percent of the 97 000 ha within Mount Rainier National Park in the central Washington Cascades are forested, and most forests are at least 200 years old.

The Bureau of Land Management (BLM) has defined old growth as stands 4 ha or larger with trees more than 200 years old (R. Metzgar, pers. comm.;[2] 1987 BLM Spotted Owl Environmental Assessment, cited in Greene 1988). In April 1987, the BLM in western Oregon had 0.19 million ha of unsold old growth remaining, with a projected 0.17 million ha remaining by 1990 (Greene 1988). In April 1988, they had 0.19 million ha of old growth on commercial forest land, 0.06 million ha protected by current plans, and 0.13 million ha subject to harvest (R. Metzgar, pers. comm.[2]). The 0.13 million ha were estimated by expanding permanent plot information, not by mapping stands in place, although BLM plans to incorporate all old-growth stands in their geographic information systems during their 1990s inventory. Based on BLM Timber Management Plans implemented from 1980 through 1984, Ohmann and others (1988) reported 0.17 million ha of old growth 200 years old on BLM land in western Oregon. BLM land in western Washington adds a negligible amount, if any, to these old-growth amounts,

Ohmann and others (1988) also reported 2800 ha of old growth on other public lands and 17 000 ha of old growth on forest-industry lands in western Oregon. In these estimates, old growth was defined according to the Old-Growth Definition Task Group (1986).

California--Currently, California has 8.0 million ha of forest land (U.S. Department of Agriculture, Forest Service 1986); 39 percent is in National Forests, 53 percent in private ownership, and 8 percent in other ownerships. In the mid-1800s, 5.1 million ha of the 8.0 million ha were thought to be old growth. About half of these occurred in the Sierra Nevada, a fourth in the North Coast, and the remainder in northeastern California with less than 3 percent in the mountains of southem California (Laudenslayer 1985).

Based on inventories from an earlier date (dates vary, depending on National Forest), Laudenslayer (1985) estimated that about 0.9 million ha of forest stands qualified as candidate old growth on National Forests in California around 1980. This amount was about 17 percent of estimated historic old growth. Candidate old growth was defined as all stands that might meet or do meet structural criteria for old growth as presented in the Pacific Southwest Regional Guide (table 2). On National Forests in California, old growth had not been defined for most forest types and the only data available were by timber-type strata. Even if old growth was defined by forest type, existing inventories would not likely be able

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[1] The nine west-side National Forests are the Olympic, Mount Baker-Snoqualmie, Gifford Pinchot, Mount Hood, Willamette, Deschutes, Umpqua, Siskiyou, and Siuslaw.

[2] On file with Bruce Marcot

and overmature timber-type-strata and stocking-classes. Laudenslayer also estimated that, in the future under Forest Service plans, the 0.9 million ha will decrease to about 0.7 million ha, or about 14 percent of historic amounts. Virtually all old growth on private lands in California may be harvested in the next 30 to 50 years (F. Samson and others, unpubl. manuscript).

In California, Resources Planning Act (RPA) Timber and Wildlife Narratives provide a more recent estimate of candidate old growth. In the Timber Narratives, old growth was defined under the general regional definition (table 2), and in the Wildlife Narratives, overmature forest was based on the definition of old-growth habitat for management indicator species. In 1987, 0.6 million ha of candidate stands qualified as old growth on National Forests in California, with 0.4 million ha on land suitable for timber production (RPA Timber Narrative, Pacific Southwest Region). These candidate stands included forests typed by the Forest Service as containing overstory trees with crown diameters of >7 m and with canopy closure >40 percent (Forest Service stand classes 4N and 4G). Another Forest Service summary reported about 0.8 million ha of overmature forest on National Forests in California in 1985, 0.2 million ha of which occur in wilderness (RPA Wildlife Narrative, Pacific Southwest Region).

Summary-The most extensive estimates of old growth suggest that amounts of old growth and other old forests on National Forests in Pacific States total about 3.6 million ha (table 5). This tally uses the Forest Service's estimate of old-growth amounts in Washington and Oregon. If the more stringent definition and estimate by Morrison (1988) is used, total amounts would be lower.

This tally of current inventories is very approximate. It combines many forest types, including upper elevation, true fii forests in the Washington and Oregon Cascade Range; namely, Pacific silver fir, grand fir, and ponderosa pine forests in eastern Washington and Oregon; mixed-conifer and Jeffrey pine forests in northern California and the Sierra Nevada, and other forest types. The estimate combines data from different years and is based on a variety of definitions of old growth. It includes candidate old-growth forests, an unknown but significant proportion of which would not qualify as ecological old growth (Old-Growth Definition Task Group 1986). The estimate, however, does not include amounts of old growth that may exist on lands of other Federal, Provincial, State, local, commercial, and private administration and ownership throughout the geographic area considered.

Size of Old-Growth Stands

Past clearcutting of old growth has fragmented remaining stands into smaller patches with greater interpatch distance. Fragmentation also alters stand shapes. An unknown proportion of existing old-growth forests occur in relatively inaccessible or unproductive areas, such as in canyon bottoms or along ridges. Such old-growth stands are often linear and narrow. Most or all of such stands may be influenced by edge conditions. Effects of small patch-size, increasing isolation, and edge conditions may adversely affect the persistence of some wildlife populations in old-growth areas.

Harris (1984) summarized the sizes of 319 old-growth stands from 1981 Total Resource Inventory System (TRI) data from the Siuslaw National Forest in the Oregon Coast Range. He noted that 61 percent of the stands were less than 16 ha, the average stand was 28 ha, and the median was 13 ha.

Laudenslayer (1985) noted that on National Forests in California, candidate old-growth stands of all forest types averaged about 16 ha, ranging from an average of 7 ha in the red fir forest type in the north coast to an average of 235 ha in the Jeffrey pine forest type in the Sierra Nevada. Few data are available on the distances between old-growth patches, but old-growth patches are probably becoming increasingly smaller and isolated over time (Harris 1984).

Old-Growth Inventory and Management Direction on National Forest Land in Western Washington and Oregon

Forest Service and The Wilderness Society Estimates

The Wilderness Society estimates of the amount of old growth remaining in Washington and Oregon (tables 6,7; Morrison 1988) and estimates by the Forest Service (table 7; draft Forest plans) differed substantially. Both estimates were derived from Forest Service timber inventories, but these inventories were not designed to measure all characteristics of importance in distinguishing old-growth stands. Both estimates, therefore, required extrapolation from the inventory values.

The two estimates were produced for different purposes with different techniques. The Forest Service estimate was derived from a mapped inventory of old growth for Forest planning, and therefore relied heavily on photo-interpretation, The Wilderness Society estimate was intended to be only a numerical estimate. Although Morrison (1988) did use photo-interpretation, he depended more heavily on plot data from the Forest Service timber-inventory process.

Table S-Estimated current amounts (in millions of hectares) of old growth and candidate old growth on selected lands in the Pacific States of the United States

Area	Estimate	Definition	Reference
Washington and Oregon:			
Forest Service	2.5 (1.3 west-side only)	Old growth variously defined in plans and Regional Guide	Draft National Forest Plans
National Park Service	0.31	Forests >200 yrs old	Green 1988
Bureau of Land Management-Oregon	0.19	Stands of 4+ ha, trees >200 yrs old	R. Metxgar, pers. comm.
Other public lands and forest industry, western Oregon only	0.019	Old-Growth Definition Task Group	Ohmann and others 1988
California:			
Forest Service	0.60	Stands with trees >7.3 m crown diam. and canopy closure >40 Percent	RPA Timber Narrative, Pacific Southwest Region
Total	3.6	Includes all candidate old-growth and excludes old growth on some lands other than National Forests)	

The two estimates were based on different years and on different definitions of old growth. The Forest Service estimates were generally current for 1985, although several estimates were based on older data. Morrison's estimate was based on data updated to 1988. Morrison adhered to the definition proposed by the Old-Growth Definition Task Group (1986), except for down wood and snag density criteria. Morrison also applied the Task Group definition to forest types for which it was not developed. The National Forests used the less restrictive definition published in the Regional Guide, which was modified to reflect conditions specific to each forest type and each National Forest.

The draft Environmental Impact Statements for the Forest Plans show that the operational definitions used by National Forests actually varied from the definition presented in the Regional Guide. These operational definitions generally focused on characteristics for which data were more readily available. Definitions used by the nine west-side National Forests in Washington and Oregon require fewer large trees, large snags, or trees of shade-tolerant species than do either the Old-Growth Task Group or the Regional Guide definitions (see table 4; The Wilderness Society 1988).

Data published by Morrison (1988) allowed us to estimate inventory results by using the less restrictive definitions that the Forest Service used on six National Forests in western Oregon and Washington (table 6). In addition to areas that met all the old-growth criteria of the Old-Growth Definition Task Group (1986), Morrison listed areas that had some old-growth characteristics but failed to meet individual criteria (table 6) Most of these areas would likely meet the less restrictive definition generally used by the Forest Service. All of these areas have developed beyond a mature stage marked only by the presence of trees >53 cm d.b.h., and all contain at least some trees >80 cm d.b.h. These areas were summed and compared to Forest Service old-growth estimates in table 7. This table also shows the sampling error calculated by Morrison for his old-growth estimates. Sampling error (table 7) for the sum of these four, less restrictive old-growth classes would actually be greater than the sampling error calculated only for the old-growth class.

Predictably, these adjustments bring the two estimates closer together. Figures taken from The Wilderness Society report total to 0.8 million ha or 80 percent of the Forest Service estimate of 1.0 million ha (table 7). This compares to The Wilderness Society estimate of 0.4 million ha of old growth on the six National Forests, which represented 45 percent of the Forest Service estimate. When sampling error is taken into account, estimates overlap on two of the six forests. If the 3 years of harvest between 1985 and 1988 were taken into account, the two estimates on the Willamette National Forest would probably also overlap.

Table 6—The Wilderness Society area-estimates in thousands of hectares of old-growth forest and forest conditions that fail to meet one or more old-growth criteria (*sensu* Old-Growth Definition Task Group 1986) as listed in table 4, on 6 National Forests in western Washington and Oregon

National Forest	(1) Old growth[a]	(2) Fails late-seral tree-criterion	(3) Fails snag criterion	(4) Fails large-tree criterion	(1-4) Total[b]	(5) Fails multilayer-canopy criterion	(6) Meets mature-forest criterion	(1-6) Total with mature
Mount Baker-Snoqualmie	120	3	40	29	192	3	41	236
Olympic	43	1	0	21	64	1	8	74
Gifford Pinchot	48	1	23	31	104	0	80	183
Mount Hood	72	0	27	39	138	0	35	173
Willamette	121	29	36	35	221	0	93	314
Siskiyou	57	0	18	34	109	0	7	117
Total	461				829			1097

Source: Morrison (1988).

[a] Includes old growth on all land allocations, including wilderness. Other columns do not include wilderness lands established before the date of the inventory data available from the National Forests.

[b] Columns 1 to 5 all contain stands with at least some trees >80-cm in d.b.h. Column 6 does not.

Table 7-Estimates of old growth in thousands of hectares by the Forest Service and The Wilderness Society (Morrison 1988) including areas that fail to meet one or more old-growth criteria

National Forest	The Wilderness Society old-growth plus other old-forest stands (from table 6)	Forest Service[a] old-growth estimate	Difference	Sampling error (Morrison 1988)
Mount Baker-Snoqualmie	192	270	76	8
Olympic	64	88	23	2
Gifford Pinchot	104	93	10	17
Mount Hood	138	140	2	13
Willamette	221	259	37	25
Siskiyou	109	179	70	19
Total	829	1029		

[a] Derived from draft Forest Plans.

This comparison is not intended to show that both inventories are really the same. Significant differences clearly exist. The comparison indicates that old-growth estimates are sensitive to the definitions on which they are based. This emphasizes the need for a commonly accepted definition of old growth, a better understanding of important old-growth characteristics, and better inventories intended to quantify those characteristics. Inventories must be designed to provide information on individual characteristics rather than to accommodate one fixed definition of old growth. The importance of such an inventory design is highlighted by the fact that the stands classified as "old growth" in the Old-Growth Program research studies (this volume) did not actually meet, nor were they designed to meet, all criteria from the Old-Growth Definition Task Group. An inventory designed around this single definition would fail to inform us about a large amount of forest land that is important wildlife habitat. Improved inventories must be completed soon if we are to make use of information from research (this volume).

Current Management of Old Growth and Old-Growth Allocations in National Forest Plans

What will be the fate of the 1.3 million ha of old growth on the nine National Forests in western Washington and Oregon? Forest-planning alternatives propose the retention of about 0.6 to 1.2 million ha over time. Preferred alternatives of the nine draft Forest plans called for a total of 0.8 million ha of reported old growth to be retained over time, which is about 57 percent of currently inventoried amounts. The proportion of total historic old growth represented by this amount is substantially less and is not quantified.

In current planning and management activities on National Forests, old growth appears as an issue derived from various interests, including recreation, fish and wildlife habitat, timber supply, long-term forest productivity, scientific research areas, and aesthetics. Management-area direction established in Forest plans will determine the future amount and distribution of forest habitat, including some old growth, for wildlife species, and particularly management indicator species on National Forests. In addition, management requirements for standing and fallen dead trees in all areas address a vital component of old-growth forests that also may be found in younger stands. Those snags will probably be smaller, however, and may not persist as long as in old-growth stands.

Actual amounts and distributions of old growth for wildlife species is currently decided by each National Forest through Forest plans. Amounts and distributions result from applying regional standards ("minimum requirements") for maintaining old-forest habitats for spotted owls, marten, pileated woodpeckers, a variety of other primary excavators, and some additional key vulnerable species identified in each of several provinces in the Pacific Northwest Region. Forest plans establish final allocations, but they must meet or exceed the regional standards.

Habitat-management areas for old-growth management indicator species provide one type of allocation where old growth may occur. Other allocations will also contain old growth. As an example, the draft Forest plan on the Willamette National Forest lists the following land allocation-classes that may contain old-growth forest (other National Forests will retain old growth under similar allocations):

Congressionally withdrawn-no harvest
  Wilderness
  National Recreation Areas
  Experimental Forests
  Research Natural Areas

Administratively withdrawn-no harvest
  Proposed Research Natural Areas
  Old-Growth Groves
  Threatened or Endangered Species Habitats (such as for bald eagle)
  Other Special Wildlife Habitats and Habitat Protection areas
    Spotted Owl Habitat Areas
    Pileated Woodpecker Habitat Areas
    Marten Habitat Areas
    Deer and Elk Thermal Cover
    Other Special Habitat (Protection and Enhancement)
  Semiprimitive (Roadless) Areas
  Recreation Sites (Existing and Proposed)
  Mining Claims
  Lands Technically Unsuited for Timber Production

Partial Harvest Categories
  Visual Retention Areas
  Semiprimitive (Roadless) Areas
  Riparian

Full Harvest Categories
  General Forest

Old growth occurring in the full harvest allocation and several other allocations (such as mining claims) would be retained only until the time of harvest or management activity.

Under the Preferred Alternative in the Willamette National Forest draft plan, 52 percent of old growth will be retained through time. This totals about 0.18 million ha (table 8). The remaining 48 percent or 0.17 million ha is planned to be harvested over the next five decades. According to the draft Forest plan, old growth on the Willamette National Forest was defined according to the Old-Growth Definition Task Group (1986; see table 1) with specifications that vary by forest type. Like most of the other draft Forest plans in the region, the Willamette National Forest draft plan quantified and analyzed the effects of land-allocation decisions on the distribution of old-growth forest-stands for specific management indicator species (spotted owls, marten, pileated woodpeckers, and primary cavity excavators). Outside of such management requirements, however, the effects of land-allocation decisions on the size and context of old-growth stands were not analyzed.

Old-Growth Habitat Characteristics of Importance to Wildlife: A Key to Future Inventories

Some wildlife species may have co-evolved with, and depend on, specific amounts and conditions of old-growth forests. Specific kinds, sizes, and patterns of old-growth environments are, therefore, keys to the long-term survival of these species. Land allocations affect the distribution of old growth across

Table 8—Allocation of mature and old-growth forest under the preferred alternative in the draft Forest plan, Willamette National Forest

Category	Area	Percentage
	Hectares	
Withdrawn		
Wilderness	93 600	—
Unsuited for timber production	45 000	—
Minimum management requirement wildlife habitats	27 700	—
No harvest	18 000	—
Subtotal	184 200	52
Harvestable		
Timber harvest areas	167 200	48
Total	351 400	100

Note: On a forest-wide average, about 75 percent of all mature and old-growth areas actually meet the old-growth criteria of the Old-Growth Definition Task Group (1986). This error rate varies slightly by forest type. For example, in the Douglas-fir/western hemlock forest type, 50 percent of the mature ("large sawtimber") stage is old growth and 87 percent of the old-growth stage is actually old growth (J. Mayo, pers. comm., on file with B. Marcot).

the landscape over time and the effectiveness of old growth as habitat for wildlife. Resulting spatial patterns of old growth influence the viability of many wildlife species that depend on the ecological conditions of old forests. Old growth may provide population "reservoirs" for species that find early successional stages of second-growth conifer stands marginal habitat.

What attributes of old growth affect the perpetuation of these old-growth wildlife species? Attributes may be characterized at stand and landscape scales. Attributes at each scale may be useful for guiding future inventories of old growth as wildlife habitat.

At the stand scale, important vegetational structures include the presence of key substrates, food, and resources, especially epiphytic mosses and lichens, which are important as winter food for ungulates and rodents; and the presence of specific thermal and moisture conditions. Other stand characteristics important to old-growth-dependent wildlife are related to long-term productivity of the forest environment. These characteristics include the presence of dead and decaying, standing and down wood as habitat for breeding, feeding, hiding, and other needs; and the presence and density of hypogeous fungi, which are important as food sources for the co-evolved mycophagous small mammals that disperse the mychorrizal fungi needed for conifer growth.

Landscape attributes affecting the perpetuation of old-growth dependent and associated wildlife include the spatial distribution of old growth; the size of stands; the presence of habitat corridors between old-growth or old-forest stands; proximity to other stands of various successional stages and especially for well-developed mature-forest stages and species with different seasonal uses of habitats; and the susceptibility of the old-growth habitat to catastrophic loss (such as wildfire, insects, disease, wind and ice storms, and volcanic eruptions).

Stand size, in combination with its landscape context (the condition, activities, or both on the adjacent landscape that affect the stand), is of major significance in perpetuating old-growth resources and can have a major effect on their use by wildlife. Wide-ranging species may be able to use stands of various structural- , size- , and age-classes. If such stands are separated by unsuitable habitat or disruptive activities, however, the remaining old-growth stands become smaller in effective (interior) size, more fragmented, and possibly not suitable for occupancy or for successful reproduction. An old-growth inventory that quantifies such stand and landscape attributes is a prerequisite for evaluating possible context and landscape effects on species' presence.

The Mature and Overmature (MOM) Forest Inventory on National Forest Land

Rationale for an Old-Forest Inventory

An old-growth inventory must respond to a set of clearly stated goals and objectives (Thomas and others 1988). These goals directly determine the classification schemes, parameters to be gauged, spatial scale of resolution for the inventory, and acceptable scales for the reliability of the information. They also help guide how the inventory process and its results are integrated into other resource information needs (see Davis and Henderson 1977). At present, goals and objectives for conducting an inventory of old-growth forests in the Pacific Northwest vary among groups with different interests in how the old-growth resource is managed.

An old-growth inventory can be category driven or attribute driven. With a category-driven inventory, old-forest stands are tallied into one or more classes, which are defined *a priori*. By contrast, in an attribute-driven approach, the classifier describes forest stands by a set of structural characteristics deemed pertinent to old-forest conditions. These stands are then classified *a posteriori* based on a specified set of stand attributes. The utility of both approaches depends on the purpose of the inventory. For old-growth inventories, the attribute-driven approach—when used with a classification of seral stages of old forests—is more flexible than a category-driven approach. As Smith (1982a:1) observed, It is better to invent additional patterns than to warp those observed to fit preconceived ones.

With either approach, we must specify what is being inventoried. Inventories of old-growth forests include the presence or amount of various stand characteristics, and distributions of old growth at different scales of resolution and geographic areas. Amounts should be displayed as totals by State, by Federal and State agency jurisdiction, by administrative unit within agencies, by individual and corporate ownership, by ecophysiographic province, or by other geographic divisions. Size and context should include contiguous sizes and the shapes of old-growth stands and their relation to adjacent landscape conditions and activities, including the proximity of other old-growth stands. Distribution includes defining the spatial scale at which an old-growth inventory should be conducted. This scale greatly affects the kinds of stand attributes that can be used as inventory criteria and the resolution at which such attributes should be known.

For example, a stand-by-stand inventory could include a complete census of appropriate characteristics for each vegetative unit. By contrast, a forest-wide inventory may use a stratified sampling approach to provide reliable information at the scale of vegetation types. Then, some of the characteristics of any given stand are known only as a probability-that is, an estimate of the proportion of all stands in a stratum that have particular structural characteristics.

An old-growth inventory must be designed with a specified degree of reliability. The degree of error and confidence in the statements of amount and distribution should be known, at least qualitatively. The reliability of an inventory is a function of many factors. These include the correctness and usefulness of the classification scheme used; the quality of the sampling design by which remote-sensing images are interpreted and vegetation surveys in the field are conducted; the consistency with which inventory criteria are applied across various land units, taking into account the need to vary criteria by forest type and land form; the availability and quality of remotely sensed images: the expense and training involved in having people interpret the remotely sensed images; the experience and training of field crews; and the sample sizes used in field verification testing and from which subsequent classification strata are derived.

Inventory of Mature and Overmature Forest

A large-scale, attribute-driven inventory of mature and overmature forests has been instituted on National Forests in Washington and Oregon as part of an inventory of all vegetation stands. The main objective of the inventory of mature and overmature forest is to provide a set of data to which a solid, basic set of definitions of the developmental stages of old forests can be applied. This inventory will provide an accurate inventory of old-growth stands; allow for the use of multiple definitions of old-growth forest conditions; and be accessible on a geographic information system (GE) for analysis of distributional conditions. Plans also call for a periodic update of the inventory with remote imagery, although this technology needs further testing.

The inventory of mature and overmature forest was designed to enhance the existing Vegetative Resource Survey, which is the standard inventory of all vegetation stands on National Forests in the Pacific Northwest Region. This enhancement resulted in a redefinition of mapping criteria and a greater emphasis on sampling stand attributes that are considered to be of importance in old forests. These attributes include the size, shape, and location of stands; the multicanopy structure of the stands: mixes of tree, shrub, and herbaceous species; the diameters and heights of live trees; canopy closure within each canopy layer and for the stand as a whole; the size, distribution, and decay states of standing and down dead trees; and heterogeneous characteristics of stands with small canopy openings.

Information about these attributes will allow interpretations about the values of stands from several different viewpoints. One interpretation that could be made would be whether stands meet a specific definition of old growth. This interpretation, however, would be an outcome of the basic information that was collected, rather than being the driving force for the design of the inventory.

The Mature and Overmature (MOM) Inventory follows the two-stage design of the existing Vegetative Resource Survey. The first stage is done by photo-interpretation. In this step, each forest stand is delineated on photos and maps. For each delineated stand, information is recorded on the number of canopy layers (up to three); canopy closure of the entire stand; the presence of snags; clumpiness of the canopy; the presence of large, remnant trees from stands that previously occupied the site; and volume. In addition, for each of the canopy layers, information is recorded on tree species, canopy closure, crown diameter of dominant trees, clumpiness, and visible snags. All of this information is derived from photo-interpretation and is ground verified on about 10 percent of all stands.

After the photo-interpretation is completed, stands are arrayed according to their attributes to determine an appropriate distribution for additional, detailed ground plots. The ground plots are the second stage of the inventory. In other inventories, the standard design calls for lumping the stands into defined strata to develop a sampling strategy. With the MOM Inventory, strata are avoided so that plot data can later be combined in several different ways to address various concerns. Instead of developing strata, the sample plots are distributed so that the full array of stand conditions are sampled. This process involves arraying the stands according to species composition, number of canopy layers, tree density or stocking, canopy closure, and crown diameters. The ground plots follow a IO-point design and include detailed information on live-tree species including height, density, diameter, and form by canopy layer; snag density, diameter, height, and decay state; diameter, length, and decay state of logs; and the presence of indicator plant species in the understory. This last category is used to classify the stand by plant association.

Because this plot information can be collected only for a sample of stands, it will not be available for all the stands that are photo-interpreted. Data from the MOM Inventory can be analyzed in two different ways to draw inferences about stands that were not sampled. First, a collection of stands can be defined based on any combination of the photo-interpreted characteristics. Plot data can then be summarized for all stands in this collection that were ground sampled. Because these collections of stands are not being defined as a priori strata, the values of attributes for such a summary could vary widely.

The second analysis opportunity is to develop correlations between characteristics that were photo-interpreted and characteristics that were measured in plots. For each stand, this comparison would allow us to identify photo-interpreted characteristics with some degree of certainty, and to identify ground-sampled characteristics with some known degree of reliability. Currently, the ability to correlate ground-sampled characteristics with photo-interpreted characteristics is the largest unknown in the inventory design, and the reliability of inferences about these ground-sampled characteristics is also unknown.

The combined MOM and Vegetative Resource Inventories will result in five products:

- A stand map for each forest stored on a GIS.
- A data card for each stand containing the photo-interpreted data for that stand. This information will be stored in the attribute file of the GIS.
- A database containing all plot data.
- Summarized plot data for collections of stands defined according to any combination of the photo-interpreted characteristics.
- Statistical correlations between photo-interpreted characteristics and plot-sampled characteristics.

The MOM-Inventory process is currently being implemented on the Siuslaw and Willamette National Forests as part of the Vegetative Resource Inventory. It is expected to be completed on all nine of the west-side forests in Oregon and Washington by 1994.

Recommendations for Old-Growth Inventories

We offer the following recommendations for developing a multipurpose, old-growth inventory. First, an old-growth inventory should be attribute-based rather than definition-based. An example is the inventory of mature and overmature forests currently being conducted by the Pacific Northwest Region of the Forest Service.

Second, an old-growth inventory should be map-based to address landscape issues, including that of scale. Map-unit sizes should be small enough to identify old growth where edge effects eliminate interior habitat. A map-based approach would also benefit from further exploring the use of Landsat as a tool for updating inventories over time. In addition, a map-based inventory would benefit from the application of a geographic information system for evaluating the data, especially the landscape and spatial conditions of stand size, shape, and context. The MOM Inventory is currently being installed on GIS to facilitate the evaluation of spatial components.

Third, any adopted definition of old growth should be part of a system of describing the amount and distribution of various stages of forests, especially older ones. The full classification system would include descriptions of the total vegetation inventory from seedling to old-growth successional stages, including noncommercial forest lands and nonforest vegetation. Specifically, the Old-Growth Task Group definitions should be the basis for ecological definitions used in a broader framework. In this manner, a consistent definition can be applied to the attribute-based data and also allow analyses of stand conditions that meet various other definitions.

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Ecological Definitions of Old-Growth Douglas-Fir Forests

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Abstract

We examined the potential for definitional and indexing approaches to identifying old-growth Douglas-fir stands. An interim definition created by the Old-Growth Definition Task Group uses multiple structural characteristics of forest stands-specific levels of large or old live trees, snags, logs, and foliage canopy layers. This definition and numerous variants with different parameters and parameter values were tested for their ability to discriminate old growth from young and mature natural forests with an independently collected data set. The criteria used in the definitions appear appropriate but variants of the definition differ significantly in their ability to distinguish old-growth in particular geographic areas. Definitions that used density of all large (>lOO cm in diameter at breast height) trees, rather than just Douglas-fir, performed best. Further refinement of definitions should probably be site specific. Developing approaches that recognize the continuous variability in old-growth stands are recommended for the whole region. These approaches could be simple indices based on multiple structural characteristics or using discriminant analysis; examples are provided to demonstrate the merits of both concepts. Maintaining a holistic perspective on old-growth forest ecosystems is critical in these and other current efforts to characterize old growth by individual attributes.

Introduction

Old-growth forest is a biological or ecological concept that presumes ecosystems systematically change as they persist over long periods. An ecosystem has, in effect, a series of linked life stages, progressing from origin (birth) to old age (senescence), which vary in composition, function, and structure. Such progressions can take a very long time in forests because the dominant organisms, trees, typically live very long.

Characterizing old-growth forests is possible based on these concepts. Obviously, a series of ecological attributes must be considered because of the many relevant compositional, functional, and structural features. For practical reasons, however, a working definition-one for everyday use in gathering stand data-emphasizes structural and compositional rather than the conceptually important functional features that are difficult to measure.

A generic definition of old-growth forests, applicable to most temperate and subalpine forests, is possible. Old-growth forests are later stages in forest development that are often compositionally and always structurally distinct from earlier successional stages. For example, forests at low to moderate elevations in western Washington and Oregon often shift from strong dominance by Douglas-fir in early stages of succession to mixed stands with large amounts of western hemlock and other tolerant species at mid to late stages in succession (Franklin and Hemstrom 1981). Even where both early- and late-successional forests are composed of the same species, such as many sites with ponderosa or lodgepole pine, the old stands differ from young stands in structure; for example, old stands have a much larger range in tree sixes. The age at which forests become old growth varies widely with forest type or species, site conditions, and stand history.

Structurally, old-growth stands are characterized by a wide within-stand range of tree sizes and spacing and include trees that are large for the particular species and site combination. Decadence is often evident in larger and older trees. Multiple canopy layers are generally present. Total organic matter accumulations are high relative to other developmental stages. Functionally, old-growth forests are characterized by slow growth of the dominant trees and stable biomass accumulations that are constant over long periods. Respiration reduces net annual additions of living organic matter to low amounts relative to earlier successional stages, despite high gross primary productivity in old-growth stands. All climax forests” forests that appear to have stable composition and structure in the absence of a major disturbance”qualify as old growth, although most old-growth forests are not climax; that is, they still contain seral species and are undergoing slow directional changes in composition and structure. Not all virgin or primeval forests are old growth and not all old-growth stands are totally free of human disturbance. Old-growth forests could theoretically originate after either human or natural disturbance because they are defined by composition, structure, and function and not by origin or naturalness.

General characterizations of old-growth forest are conceptually important, but specific definitions are essential to forest-land management. Inventories to identify the quantity and location of old-growth forests require such specificity. Forest policy, including the allocation of forest lands to various uses, are partially based on these inventories. Old-growth forests need to be characterized so that important attributes can be retained and attempts made to create similar forests. Characterizations are also needed by scientific researchers.

In this paper, we will consider the state and future of old growth in the Pacific Northwest. Our primary focus is on the mesic temperate forests dominated by Douglas-fir and located west of the crest of the Cascade Range in Washington, Oregon, and northern California. We review the history and adequacy of the existing old-growth definition and explore directions for future development of such characterizations including local refinement and extension to other forest types, developing indices with continuous scales of variation, and using statistical methods, such as discriminant analysis.

Old-growth forests in our study area vary widely in their age and ecological state (for example, in composition and structure), which reflects a similar wide variability in their history and physical environments. Old-growth Douglas-fir forests are from about 200 to over 1000 years old, they undergo gradual but significant autogenic change during those centuries of existence and may also be subjected to varying numbers and intensities of disturbance events, such as windstorms. As a consequence, old-growth Douglas-fir forests can differ substantially in their degree of “oldgrowthness”-that is, in the degree to which they express the various structural and functional features associated with these forests; this variability must be considered in efforts to define and manage old growth.

Current Definition of Old-Growth Douglas-Fir Forests

Historical Development of the Interim Definition

The history of the interim definition of old-growth Douglas fir forests (Old-Growth Definition Task Group 1986) is discussed in detail by Marcot and others (this volume). It began with National Science Foundation funding of the Coniferous Forest Biome in 1969, as part of the International Biological Program (Edmonds 1982), and of subsequent ecosystem studies, particularly at the H. J. Andrews Experimental Forest. The USDA Forest Service also contributed to this research. These studies provided a wealth of data and concepts on the nature of old-growth forests and associated streams (see Blinn and others 1988, McKee and others 1987).

In 1976 the research group associated with this work received a request from a National Forest planner for assistance in characterizing old-growth forests; as he put it, “We know that old-growth forests are more than just some big old trees, but we don’t know how else to describe them. Could your group provide us with a more complete characterization?” A workshop, convened at Wind River, Washington, in 1977, produced the synthesis entitled, “Ecological Characteristics of Old-Growth Douglas-Fir Forests” (Franklin and others 1981).

All current attempts at ecological definitions of old-growth Douglas-fir are based on the 1977 synthesis and subsequent research, much of it under the auspices of the Forest Service’s Old-Growth Forest Wildlife Habitat Program. These studies clarify the distinctiveness of old-growth forests in composition, structure, and function and, perhaps even more important, the complexity of most naturally regenerated forests developing after wildfire, windstorm, or other catastrophic events in the Pacific Northwest, regardless of successional stage. For example, the structural complexity of young natural forests is high because of the carryover of large snags,, logs, and even large live trees from the predisturbance stand; conditions in these natural stands obviously contrast with the simplified structure of most young forests managed for timber production. Past old-growth studies also illustrate the need to use multiple attributes to characterize old-growth forests and the value and validity of emphasizing structure in working definitions. Among the first iterations of old-growth definitions based on these ecosystem concepts are those by the Society of American Foresters (1984) and Franklin and Spies (1984).

In 1985, an interagency group-the Old-Growth Wildlife Habitat Research and Development Program Steering Committee-created the Old-Growth Definition Task Group to develop an interim definition of old-growth Douglas-fir forests. The group was composed of technical experts from the USDI Bureau of Land Management, Oregon State University, and National Forest and Research branches of the Forest Service. The draft reports they wrote were extensively reviewed by management groups and scientists and revised before the interim definitions were published (Old-Growth Definition Task Group 1986).

The Interim Definition and Its Adequacy

The interim definition consist of separate definitions for old-growth Douglas-fir forests under three broad environmental conditions indexed by plant series (table 1). The three definitions are based on multiple structural criteria: density of live trees of large or old Douglas-firs and of associated medium- to large shade-tolerant tree species; multiple canopy layers; standing dead tree (snag) densities, including larger sizes; and logs, including total weight and a minimum number of large pieces. The rationale for selection of specific characteristics is discussed in the original publication (Old-Growth Definition Task Group 1986).

Although the definitions have been cussed and discussed since their publication, no data have been available to test their adequacy in discriminating old-growth from young and mature forests. Forest-inventory procedures usually do not collect data on all of the characteristics used in the definitions; however, Morrison (1989) was able to effectively use USDA Forest Service inventory plot data by adapting the definitions to the more limited set of parameters that were included in the inventories.

Spies and his associates have provided the first complete and independent data set (Spies and others 1988; Spies and others, in press; Spies and Franklin, this volume) appropriate for testing the performance of one of the interim definitions-the definition developed for stands on western hemlock and mid-elevation Pacific silver fir sites (table 1). This interim definition is the only one subsequently addressed in this paper. The data are from 196 young, mature, and old-growth stands in the Oregon and southern Washington Cascade Range and Oregon Coast Ranges (Spies and others 1988; Spies and others, in press; Spies and Franklin, this volume). Stands were selected that contained Douglas-fir and appeared to have originated after a high-intensity or stand-regenerating wildfire. None of the stands were selected according to any preconceived set of old-growth criteria. Five systematically spaced plots were used to characterize each of the selected stands. Stands were classified as young (<80 years old), mature (80-199 years old), and old (>200 years old), according to the ages of the dominant Douglas-fir trees. The 85 age-defined old-growth stands from this data set are the standard against which the performance of the various definitions and other discriminating procedures are tested.

Table l-Interim minimum standards for old-growth Douglas-fir forests in western Washington and Oregon[a]

Stand characteristic	Douglas-fin on western hemlock sites (western hemlock, Pacific silver fir)	Douglas-fir on mixed-conifer sites (white fir, Douglas-fir	Douglas-fir on mixed-evergreen sites (tanoak, Douglas-fir)
Live trees	Two or more species with wide range of ages and tree sizes	Two or more species with wide age range and full range of tree sizes	Douglas-fir and evergreen hardwood (tanoak, Pacific madrone, and canyon live oak associates (40 to 60 percent of canopy)
	Douglas-fir ≥ 20 per ha of trees > 81 cm diameter or > 200 years old	Douglas-fir, ponderosa pine, or sugar pine ≥ 20 per ha of trees >76 cm diameter or >200 years old	Douglas-fir or sugar pine ≥ 15 per ha of trees > 81 cm diameter or > 200 years old
	Tolerant associates (western hemlock, western redcedar, Pacific silver fir, grand fii, or bigleaf maple) ≥ 30 per ha of trees >41 cm diameter	Intermediate and small size-classes are typically white fir, Douglas-fir, and incense-cedar, singly or in mixture	Intermediate and small size-classes may be evergreen hardwoods or include a component of conifers (e.g., Douglas-fii or white fir)

See footnote on next page.

Table l-continued"

Stand characteristic	Douglas-fir on western hemlock sites (western hemlock, Pacific silver fii)	Douglas-fir on mixed-conifer sites (white fir, Douglas-fir	Douglas-fir on mixed-evergreen sites (tanoak, Douglas-fir)
Canopy	Deep, multilayered Canopy	Multilayered Canopy	Douglas-fir emergent above evergreen hardwood Canopy
Snags	Conifer snags ≥ 10 per ha which are >51 cm diameter and >4.6 m tall	Conifer snags ≥ 3.7 Per ha that are >51 cm diameter and >4.6 m tall	Conifer snags ≥ 3.7 per acre that are>51 cm diameter and >4.6 m tall
Logs	Logs ≥34 metric tons Per acre including 10 pieces Per ha >61 cm diameter and >15 m long	Logs 222 metric tons per acre including 5 pieces per acre ≥61 cm diameter and >15 m long	Logs ≥ 22 metric tons per acre including 5 pieces per acre ≥ 61 cm diameter and >15 m long

[a] From Old-Growth Definition Task Group (1986). Plant series are shown in parentheses.

The selection of attributes used in the interim definition generally appear appropriate; that is, they are important features of old-growth forest (Spies and others 1986, Spies and others 1989) and several discriminate old-growth from younger forest stages (Spies and Franklin, this volume). Analyses (Spies, this volume; Spies and Franklin, this volume) have identified other features that distinguish old-growth forests, such as coverage of western yew, coverage of herb and deciduous shrub species, and measures of crown decadence in overstory trees.

The parameter values chosen in the interim definition were intended as "minimum standards," and they do fall well below average or characteristic values for measured stands. The values were, in fact, selected as a "lowest common denominator," with the intent that most old-growth stands would meet the criteria and most young or mature forests would not. As an example, the 85 old-growth stands sampled by Spies and his associates average 66 tons per ha of logs (Spies and others 1988), and the minimum standards call for only 35 tons per ha on western hemlock sites (Old-Growth Definition Task Group 1986). Similarly, large snags averaged about 12 per ha in the old-growth samples versus the task group requirement for 10 per ha.

Table 2-Performance of the interim definition for Western Hemloc kSeries

Parameter and minimum standard	Province			
	Oregon coast Ranges	Oregon Cascade Range	Southern Washington Cascade Range	All
Douglas-fir > 80 cm in d.b.h. (> 20 Per ha)	96	94	77	89
Shade associates > 40 cm in d.b.h. (2 30 Per ha)	72	76	97	83
Snags > 50 cm in d.b.h. >5 m tall(>10 per ha)	68	74	92	79
Log biomass (34 tons per ha)	92	88	97	92
All criteria	52	56	70	60

[a] Performance is the percentage of old-growth stands fulfilling individual and collective minimal standards based on stand means ± standard deviation. 15 percent of mature stands also fulfilled all criteria.

[b] From Old-Growth Definition Task Group (1986).

The interim definition does **not perform as well as expected** in distinguishing this set of old-growth stands, however, even though parameter values are well below mean measured values for old-growth stands (table 2). For example, only 70 percent of the 24 old-growth (>200-year-old) stands sampled by Spies and his associates in the Washington Cascade Range met all minimum criteria, even when 1 standard deviation around the mean stand value is allowed. Percentages were even lower for the Oregon Coast (52 percent) and Cascade (56 percent) Ranges (table 2). Furthermore, the interim definition did not completely exclude mature and young stands; discrimination was poorest in the Coast Range, where 30 percent of the mature (80- to 199-year-old) stands also met the minimum standards for old growth.

The mediocre performance of the interim definition results from at least two factors. First, the statistical distribution of measured stand attributes, such as number of large snags, are skewed so that the median values lie well below the means. Hence, many stands fail to fulfill minimum values even though average values for old-growth stands indicate that a higher percentage should meet them. Second, a higher percentage of stands fulfill individual criteria than can fulfill all of the criteria (table 2). For example, old-growth stands measured in the southern Washington Cascade Range meet the four criteria 77, 92, 97, and 97 percent of the time, but only 70 percent of the stands meet all four criteria simultaneously.

Revising the Interim Definition

Several approaches are possible for modifying the interim definition: adjust the values in the interim definition so that it does a better job of either characterizing or distinguishing old-growth Douglas-fir stands, developing more site-specific versions of the definition, such as for individual habitat types or restricted geographic regions; or a combination of the two approaches.

Fifteen iterations of a revised interim definition for old-growth Douglas-fir forests on western hemlock sites were developed by using different variables and parameter values as minimum standards. The selection of variables and range of values were based on conditions encountered in the old (>200-year-old) stands sampled by Spies and his associates. Four different large-tree variables were tried: Douglas-firs >80 cm in d.b.h. and >100 cm in d.b.h. and density of all trees >80 cm in d.b.h. and >100 cm in d.b.h. The range of values used in the 15 definitions are

Douglas-fir >80 cm in d.b.h.	10-20 per ha
Douglas-fir >100 cm in d.b.h.	l10-20 per ha
All trees >80 cm in d.b.h.	20 per ha
All trees >100 cm in d.b.h.	10-15 per ha
Shade-tolerant trees >40 cm in d.b.h.	10-30 per ha
Snags >50 cm in d.b.h. and >5 m tall	4-10 per ha
Log biomass	30-34 tons per ha

The definitions were tested by determining the proportion of stands in the old-growth data set that they correctly identified based on having values within 1 standard deviation of the mean stand value. Generally, definitions were judged by their ability to identify old-growth stands (minimize Type I error), although their ability to exclude mature and young stands (minimize Type II error) were also considered.

The best revised definition correctly identifies 82 percent of the old-growth (>200-year-old) stands sampled by Spies and his associates (table 3). This definition uses density of large trees of all species rather than just Douglas-fir. It also uses much lower parameter values than those used in the original definition: all trees >100 cm in d.b.h. 10 per ha; shade-tolerant trees >40 cm in d.b.h., 10 per ha; large snags, 4 per ha; and log biomass, 30 tons per ha. These substantially lower values relax the criteria to the point where 24 percent of the mature stands also meet the old-growth criteria. A definition that uses a value of 15 per ha for all trees >100 cm in d.b.h. performs almost as well in identifying old growth but does much better at discriminating against mature stands. Old-growth stands in the Oregon Coast Ranges were the most difficult to distinguish correctly under any of the definitions, including the original.

Among individual attributes, density of large trees best differentiates old growth from young and mature stands of natural origin; coarse woody debris (snags and logs) does poorest. This is true of all versions of the definition and reflects the substantial similarities between natural stands of all age-classes. It is also consistent with the finding of Spies and Franklin (this volume) that the best classification success in discriminant analyses is achieved using an equation based on overstory attributes.

Table 3-Performance[a] of the "best-performing" revision of the interim definition of old growth for the Western Hemlock Series

	Province			
Parameter and minimum standard	Oregon Coast Ranges	Oregon Cascade Range	Southern Washington Cascade Range	All
All species > 100 cm in d.b.h. (≥ 10 per ha)	96	96	92	95
Shade associates > 40 cm in d.b.h. (≥ 10 per ha)	88	88	100	92
Snags > 50 cm in d.b.h. >5 m tall (≥4 per ha)	84	94	100	94’
Log biomass (30 tons per ha)	92	92	100	95
All criteria	76	80	92	82’

[a] Performance is the percentage of old-growth stands fulfilling individual and collective minimal standards based on stand means ±1 standard deviation. 24 percent of mature stands also fulfilled all criteria.
[b] From Old-Growth Definition Task Group (1986).

The revised definition continues to focus on minimum standards, with the objective of improving its ability to distinguish old from young and mature stands. An alternative approach would be to use mean values and associated variances for characterizing old-growth stands. By replacing the minimum standards or values with mean or median values, the definition would provide a much better perspective on what an average old-growth stand is like. Obviously, such a definition would do much more poorly than one based on minimum standards at distinguishing old-growth stands from other stages in forest succession. It would decrease the probability of "poor quality" stands-stands with few old-growth structural features-being included in an old-growth pool.

Substantial efforts to further refine one general definition of old-growth forests for the Western Hemlock Series is probably not warranted at this time. First, appropriate data sets are not available for old-growth stands over large geographic areas-for example, old-growth Douglas-fir forests on Western Hemlock Series sites in the central and northern Washington Cascade Range, Olympic Mountains, British Columbia, and the northern Oregon Coast Ranges. Data sets are very limited for old-growth Douglas-fir on other series or habitat types in southwestern Oregon or in eastern Washington and Oregon. Even within geographic areas that have been sampled, sampling has avoided old-growth stands of species other than Douglas-fir, such as western redcedar or western hemlock. Further development of general definitions seem pointless until such data are available.

A second and perhaps more important reason for suspending efforts at further refinement of a general definition is the large variability in old-growth stands apparent from the existing data sets. We infer from this high variability that regional variations in environment and disturbances (stand ages and disturbance histories) are very important (Spies and Franklin, this volume). As data are added from additional geographic areas, the range of variability known for old-growth forests can only be expected to increase. A definition that attempts to encompass these increasing amounts of variability becomes less and less valuable as a tool for identifying and characterizing old-growth stands in specific locales.

Further development of old-growth definitions should probably be directed toward developing more site-specific definitions, such as for specific habitat types, geographic locales, or both.

We believe that all classificatory work, whether as discrete types or along gradients, should be locally fine-tuned for maximum value. An example might be to define old-growth on the Western Hemlock/Swordfern and closely related habitat types in the northern Oregon Cascade Range. The Area Ecology program of the Forest Service's Pacific Northwest Region (6) provides an excellent opportunity to carry out locale-specific efforts of this type-that is, quantifying more specifically the characteristics of old growth with much more intensive sampling.

The interim Douglas-fir definition can be effectively extended to other forest types. Because the definition was. by direction, for old-growth Douglas-fir and not for old-growth conifer forests in general, Douglas-fir had to be a component of all of the stands, but most other temperate and subalpine old-growth stands in the Douglas-fir region follow a similar pattern in stand structural attributes. As suggested in the interim definition, The Douglas-fir old-growth criteria in table 1 can be modified for use with other species or types. The major change is replacement of Douglas-fir as the dominant species...Sitka spruce or western redcedar can be substituted... [and] In old-growth western hemlock or Pacific silver fir forests, these species would dominate all size classes including the [larger trees]. (Old-Growth Definition Task Group 1986). The revised definition, which uses density of large trees of all species rather than just Douglas-fir, is already better adapted for use in these other forest types than was the original interim definition. Obviously, data would have to be gathered to provide parameter values for these forest types because very little currently exists; such stands were excluded from the Old-Growth Forest Wildlife Habitat Program.

Characterizations by Using Continuous Scales

The problem with these categorical approaches to old-growth characterization is that they attempt to pigeon-hole old-growth forests, which exhibit continuous temporal and spatial variability. Systems of characterization based on continuous scales of variability avoid this problem and allow us to recognize varying degrees of old-growthness. They also mesh well with the approach to old-growth inventory recently suggested by a multi-interest consensus group facilitated by the Pacific Northwest Region of the Forest Service; this group agreed that stands should be characterized in terms of structural attributes rather than simply identified as falling in or out of a specific old-growth definition (Marcot and others, this volume). Alternative approaches to old-growth identification include developing indices based on multiple characteristics and discriminant analysis. Our explorations of indices follow; results of discriminant analysis are mainly reported elsewhere (Spies and Franklin, this volume).

Indices to successional stage are probably best comprised of characteristics that are ecologically important, such as providing wildlife habitat, and functional features of the ecosystem as well as those strongly related to forest age. Many stand-structure attributes exhibit one of two typical patterns of change (table 4, fig. 1): a U-shaped curve, such as is typical of the amount of coarse woody debris with highest amounts early and late in succession; and an S-shaped curve rising to an asymptote from low values early in succession, which is typical of average tree size. As discussed by Spies and Franklin (1988), these two general patterns of development are useful in constructing an old-growth index by simply summing absolute or transformed values of characteristics, so that the highest index numbers occur in the later stages of stand development (fig. 2). We illustrated this scheme with three stands (Spies and Franklin 1988): a stand with high densities of large trees and large amounts of coarse woody debris has an index value of more than 0.75; a young stand with high amounts of woody debris inherited from the previous old stand is indexed at 0.5; and a young stand lacking both woody debris and large trees has an index value below 0.25.

We constructed and tested four versions of a more complex structural index by using both pooled and province-specific data sets. Attributes used in this index are amount of crown decadence of Douglas-fir (broken tops, dead tops, broken tops with upturned leaders, and multiple tops); density of large trees defined in the four versions as Douglas-firs >80 cm in d.b.h., Douglas-firs >100 cm in d.b.h., all trees >80 cm in d.b.h., and all trees > 100 cm in d.b.h. density of shade-tolerant associates either >25 cm or >40 cm in d.b.h.; density of large snags; and log biomass, using 60 tons per ha as the base value. Two versions of each index were constructed and tested for each province: one based on mean values for that province and another using means for the pooled (multiple province) data set.

Table 4—Classification[a] of ecosystem characteristics according to their expected pattern of change during succession in Douglas-fir forests

Characteristics following a U-shaped curve (curve 1)	Characteristics following an S-shaped curve (curve 2)
Amount of coarse woody debris	Average tree size
Number of large snags	Diversity of tree sizes
Coarse woody debris as percentage of total ecosystem biomass	Incidence of broken tops
Heterogeneity of understory	Forest floor depth
Plant species diversity	Surface area of boles and branches
Mammal diversity	Wood biomass

[a] From Spies and Franklin 1988

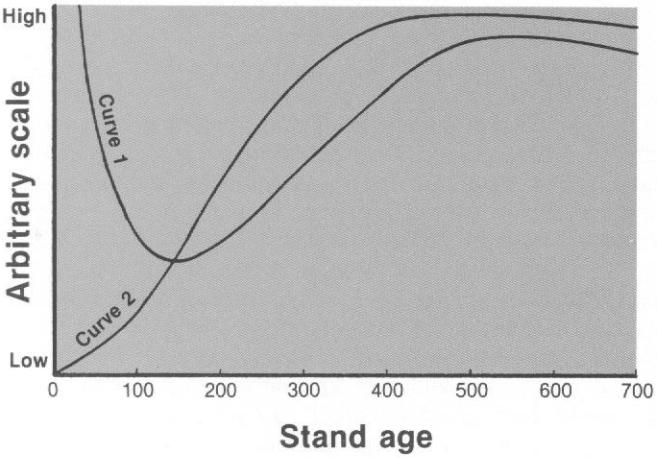

Figure 1—Generalized curves of change in ecosystem attributes with long developmental periods in a Douglas-fir forest sere (from Spies and Franklin 1988).

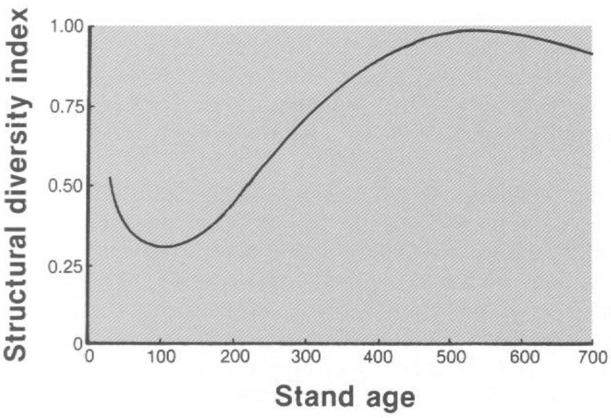

Figure 2—Hypothetical index of structural diversity in relation to stand age in a Douglas-fir forest sere (from Spies and Franklin 1988).

This set of five structural attributes works well at indexing forest stands along an age gradient in most of its forms (see, for example, figs. 3, 4). One version performs particularly well with the complete set of stands, as well as the stands in both the Oregon and southern Washington Cascade Range (figs. 3, 4). This version uses density of all trees >80 cm in d.b.h. and of shade-tolerant trees >40 cm in d.b.h., along with the measures of Douglas-fir crown decadence, large-snag density, and log biomass. Other versions also work well, however—particularly in specific provinces. We infer from the variability in performance among versions that fine-tuning indices for more limited geographic areas is needed, just as with the definition. The high degree of overlap between natural young, mature, and old stands using these indices (fig. 3, 4), is important to note, however.

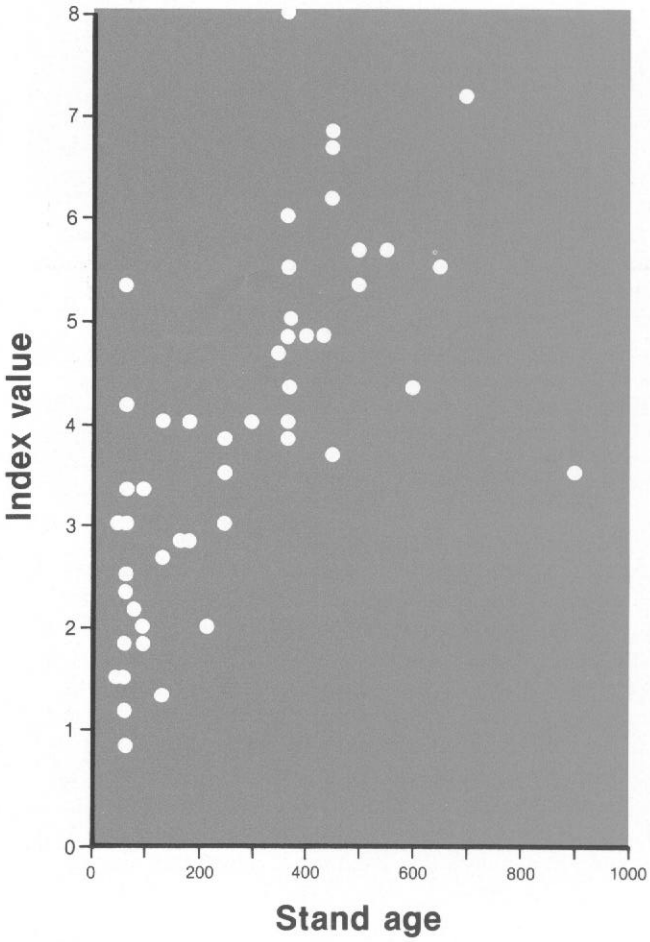

Figure 3—Test of a forest structure index to degree of old-growth development by using data from a set of natural forest stands in the southern Washington Cascade Range. This index uses Douglas-fir crown decadence, density of all trees > 80 cm d.b.h., density of shade-tolerant trees > 40 cm d.b.h., density of large snags, and log biomass (tons/ha); it was constructed with data only from the southern Washington Cascade Range.

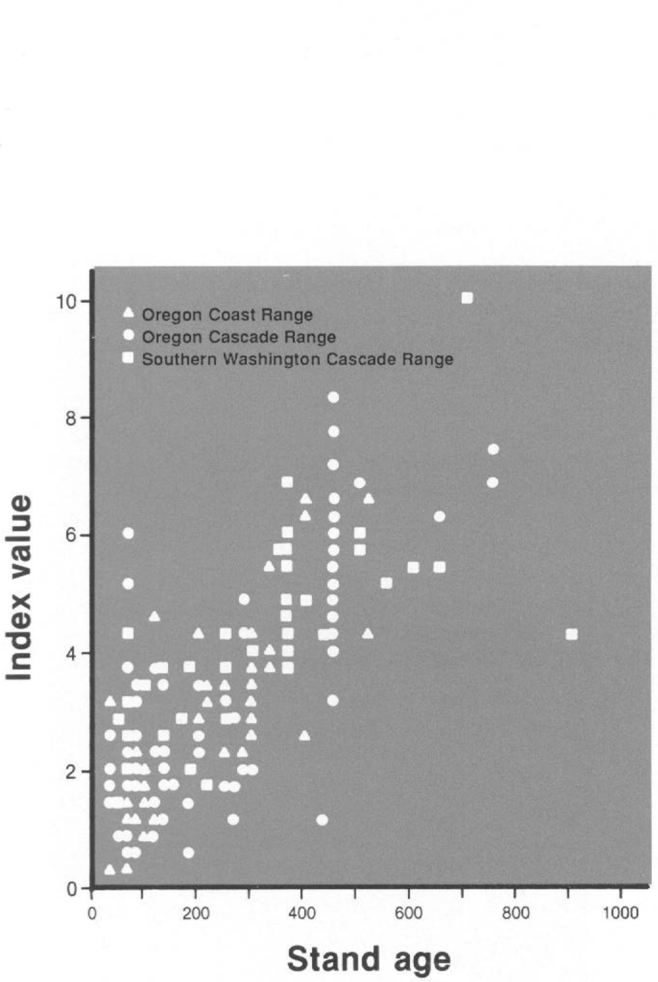

Figure 4—Test of a forest structure index to degree of old-growth development with data from natural forest stands in the Oregon and Washington Cascade Range and the Oregon Coast Range. The index uses Douglas-fir crown decadence, density of Douglas-fir >100 cm d.b.h., density of shade-tolerant trees >25 cm d.b.h., density of large snags, and log biomass (tons/ha); it was constructed with data from all provinces.

The best approach to accurately identifying old-growth stands and assigning them to a successional stage appears to be discriminant analysis (Spies and Franklin, this volume). Although this procedure is not actually indexing, it is based on multiple structural attributes (as we have applied it) and deals statistically with the wide variability in old-growth forests. Numerous equations have been developed and tested by using various combinations of attributes as reported elsewhere (Spies and Franklin, this volume). The equation that has the best classification success (94 percent of the old-growth stands accurately identified) uses an overstory attribute set: standard deviation d.b.h., mean tree diameter, density of Douglas-firs >100 cm in d.b.h., and total tree density.

Conclusions

The interim definition has worked well in identifying the essential characteristics of old-growth Douglas-fir forests. It has provided a basis for considering issues of inventory and allocation. Perhaps our current understanding of old-growth forests is now sufficient to allow interested parties to discuss the nature of this highly variable phenomenon objectively.

The merit and utility of using multiple ecological attributes and of the specific variables selected in the interim definition has been demonstrated. A version with different parameters of the definition is proposed based on existing data sets, but generic definitions will always be less useful than those developed for a more limited geographic area. Hence, further improvements in the definition should be its refinement for specific habitat types and geographic locales and extension to other forest types.

Indices and discriminant analyses are superior to general definitions in distinguishing old-growth Douglas-fir forests where that is the objective. Such approaches more easily incorporate the wide variability in old-growth forests in time and space and fit well with current concepts of forest inventory based on ecological attributes. Indexing allows recognition of various degrees of "old-growthness," as well as consideration of variability in individual attributes, such as snags or large trees, that may be important in management.

All three approaches—definition, indexing, and discriminant analysis—have merit and specific applications in considering policy, management, and research issues associated with old-growth Douglas-fir forests.

We hypothesize, based on the high structural variability in old-growth Douglas-fir forests, multiple developmental or successional routes to old-growth-like forests. If this hypothesis proves correct, it could have important management implications. Specifically, stands appear to differ widely in density and other structural features as a consequence of varied histories. Hence, developing multi-aged and multi-sized stands through partial cutting may be one alternative to long rotations in re-creating stands that resemble existing old-growth forests functionally and structurally. These stands could be created by retaining selected green trees, as well as large snags and logs, at the end of each harvest cycle.

Much additional research on old-growth forests is urgently needed. Although millions of research dollars have been directed to northern spotted owls and other vertebrates (as demonstrated by this volume), almost no funds are being expended on studies of old-growth forests as ecosystems. This lack is true for Douglas-fir forests and even more so for other coniferous forests on both sides and at the summit of the Cascade Range.

Our failure to study old-growth forests as ecosystems is increasingly serious in considerations of old-growth issues. Without adequate basic knowledge of the ecosystem, we risk losing track of its totality in our preoccupation with individual attributes or species. Definitional approaches to old growth based on attributes, including those that we have presented here, predispose us to such myopia. The values and services represented by old-growth ecosystems will he placed at ever greater risk if we perpetuate our current ignorance about these ecosystems. It will also increase doubts about our ability to manage for either old-growth ecosystems or individual attributes (for example, species and structures) associated with old growth. We must increase ecosystem understanding and management emphasis on holistic perspectives as we plan for replacement of old-growth forests. How can we presume to maintain or re-create what we do not understand? Some may presume that ignorance (on ecological values of old growth) is bliss, but this attitude creates high risk that we will continue to be blindsided by subsequent discoveries.

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Part 3

Douglas-Fir Forests of Oregon and Washington

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Composition, Function, and Structure of Old-Growth Douglas-Fir Forests

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Abstract

Ecological characteristics of old-growth Douglas-fir forests are examined in terms of compositional, functional, and structural features. Old-growth forests typically include distinctive animal and plant species-that is, organisms that are most abundant in such forests. Functional behavior of old-growth forests differs from functional behavior under other forest conditions. Productivity is typically high, but most energy is used to maintain the large mass of living material; growth and mortality are in approximate balance over long periods. Nutrient and sediment yields from old-growth forests are typically very low. Old-growth forests also differ from younger forests in their effects on hydrologic cycles in areas where cloud or fog precipitation, rain-on-snow events, or both are important. The structural characteristics of old-growth forests are the basis for most of their unique compositional and functional attributes. Specifically, important structural components are large individual old trees-whether live, dead and standing (snags), or dead and fallen (logs)-in both terrestrial and associated aquatic environments. Old-growth forests also have stand attributes that are very different from younger and, especially, from managed forests. The distinctive communities of microbes, invertebrates, higher plants, and animals that occur in old-growth forests are integrally related to the collective structural attributes.

Introduction

In the Pacific Northwest, the term "old-growth forests" typically connotes stands 200 to over 1000 years of age that contain large, coniferous trees, especially Douglas-fir. Such forests once covered millions of acres, but have been drastically reduced by logging and other forest clearing (Marcott and others, this volume; Morrison 1988). The remaining acreage is in high demand for a variety of conflicting uses, such as a source of merchantable logs and as habitat for animals and plants. As a result, the disposition of unreserved old-growth Douglas-fir has recently become very controversial.

A clearer understanding of the major ecological characteristics of old-growth Douglas-fir forests is relevent to the ultimate resolution of this controversy. Until about 20 years ago, little was known about the ecological nature of these forests. For example, foresters and wildlife managers have sometimes referred to old-growth stands as "cellulose cemeteries” and ‘biological deserts.” Research over the last two decades has dispelled such notions, however, and provided insights into the distinctive ecological qualities of old-growth forests. Scientific studies, sponsored largely by the National Science Foundation (for example, Edmonds 1982, Franklin and others 1981) and, more recently, the USDA Forest Service’s Old-Growth Forest Wildlife Habitat Program (this volume), have documented many important differences between younger and older forests and, especially, between managed and unmanaged forest ecosystems.

In this paper, we provide an overview of the key ecological features of old-growth Douglas-fir forests. Our paper is divided into three sections: composition, function, and structure. Composition receives relatively little attention here, however, because it is the primary focus of many of the papers in this volume. We emphasize the structural characteristics of old-growth Douglas-fir forests because they determine many of the distinctive compositional and functional features of these forests. Structure is also the element that foresters manipulate to achieve specific functional or compositional goals.

Composition

Old-growth Douglas-fir forests are now known to have high biological diversity in groups as varied as plants (see Franklin and others 1981; Spies, this volume), vertebrates (see this volume), invertebrates (see Moldenke and Lattin, this volume; Schowalter 1989), and aquatic organisms (see Gregory and others, in press).

Alpha (species) diversity of both plants and animals is often highest early in succession before tree-canopy closure occurs, lowest in the heavily shaded young forest, and recovers to intermediate as the forest matures and evolves into old growth (fig. 1). High diversity of plant species early in succession is a combined result of the survival of forest species and the addition of weedy generalist species (Halpern 1988, Schoonmaker and McKee 1988); this combination may also occur with other classes of organisms. Habitats and environmental resources appear to be relatively limited in a fully stocked young forest (Spies and Franklin, this volume). As a result, species diversity, as well as structural and functional diversity, is probably lowest in this stage of forest development. Old-growth forests contain many highly specialized species, and several of these organisms appear to have clear preferences for old-growth habitats, based on their patterns of abundance. Ruggiero and others (1988) have argued that such preference should be interpreted to reflect a dependence on that habitat for survival over the long term.

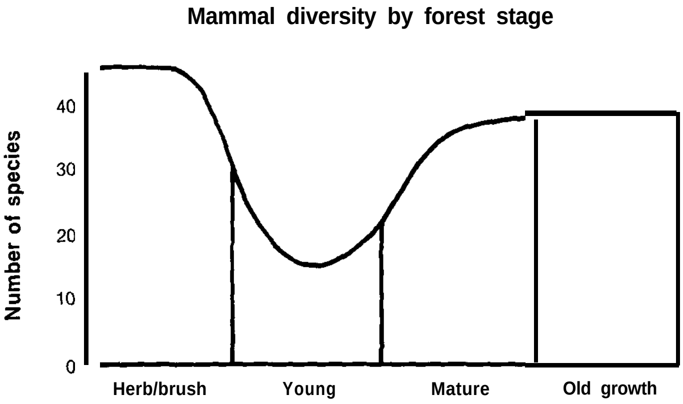

Figure I-Generalized relationship of mammal species diversity to successional stage in Douglas-fir forests.

The major point here is that old-growth forests are biologically diverse ecosystems with several constituent species that appear to be closely associated with these forests. From a biological standpoint, such a conclusion is not surprising. Many species would be expected to become adapted to a habitat (old-growth forest) that has occupied large areas for long periods. That some of these species would become sufficiently specialized to require old-growth conditions for their survival also seems reasonable.

Function

Function refers to the work that an ecosystem does and the rate at which it is carried out. Examples of forest ecosystem functions are production, the capture of the sun’s energy through photosynthesis and its conversion to organic substances; regulation of nutrient cycling, including accumulation and conservation of nutrients: regulation of hydrologic cycles; and provision of habitat for organisms. We will briefly consider production and nutrient and water cycling; the habitat function of old-growth forests is covered in the section on old-growth structure.

Production

Old-growth forests are productive ecosystems, fixing and processing large amounts of solar energy. The huge foliar surfaces-the greenness-of typical old-growth Douglas-fir stands makes this evident; trees do not retain leaves that are respiring more energy than they are fixing through photosynthesis. Stand leaf areas are often very high in old-growth stands, commonly with 9 to 15 m^2 of leaf surface per square meter of ground surface. Young stands are typically in the range of 6 to 8 m^2 (Franklin and Waring 1980). Individual old-growth trees may have 60 to 70 million needles with 4000 m^2 of leaf surface (Pike and others 1977). Obviously, such large photosynthetic factories could not be maintained if they were failing to support themselves.

Distinguishing between productivity as measured by biologists and that measured by foresters is important. Gross production in ecological terms is equivalent to the amount of energy fixed photosynthetically per unit area per unit time. Ecologists define net primary production as the biomass increment plus mortality, including litterfall and materials removed by grazing. Foresters define productivity as wood biomass increment, which describes only a portion of the ecosystem's total net productivity. Comments on the low productivity of old-growth forests therefore refer only to the relatively low rates of new wood production. Available data indicate that productivity of old and young forests is typically comparable but that the vast majority of production in old-growth forests is used in respiration and maintenance (Grier and Logan 1977).

Despite high respiration rates, most old-growth forests appear to maintain or increase their amounts of wood. Only one long-term study of timber growth and yield in an old-growth Douglas-fir forest is available (DeBell and Franklin 1987). Over 36 years, wood volumes remained constant even though the stand was subjected to serious attacks by several pests. Live-tree volume losses were high because of mortality, but this loss was offset by substantial stand growth. A high annual wood increment [15.8 m /ha (1582 bd ft/acre)] was measured in a IO-year study of growth and mortality in a 250-year-old Douglas-fir stand on the Mount Hood National Forest (Bemtsen 1960). Even an extraordinarily high annual mortality of 14.1 m^3/ha (1156 bd ft/acre) resulting from a major windstorm and bark beetle outbreak that occurred during this period failed to completely offset growth.

The conclusion that old-growth forests are generally stable in biomass or board foot accumulations is logical. That foresters have long recognized the basic stability of wood accumulations in old-growth forests is evident in their expression of "storing wood on the stump." We have also begun to realize that significant tree and forest growth occurs well beyond culmination of mean annual increment (for example, Williamson and Price 1971). Indeed, by cutting forests before or at culmination, we are cutting them at the transition from ecologically young to mature forests; growth and biomass accumulation are very far from complete at this stage.

Nutrient and Water Cycling

More data are available on the protective functions of old-growth forests-their effects on nutrient and water cycling and on soil erosion-than on any other functional aspect. Old-growth forest systems are highly retentive of nutrients. Large amounts are tied up in both living and dead organic material. Although the release of energy and nutrients from dead organic materials is often slow, it makes old-growth forests extremely conservative-nutrients are tightly retained within the ecosystem. Typically, only small amounts of nutrients leach into the ground water and subsequently appear in streams (for example, Fredriksen 1972, Sollins and others 1980). Soil erosion is also low in old-growth forests relative to rates typical of early stages in forest succession (Swanson and others 1982). The combination of low losses of dissolved nutrients and of particulate matter results in the high water quality of old-growth watersheds.

We are learning that old-growth forests have distinctive and often unexpected effects on hydrologic cycles. At the time of an earlier synthesis of old-growth characteristics (Franklin and others 1981), old and young forests were assumed to have similar net effects on water cycles, but this assumption has not proved true. One example is in effects on condensation of cloud or fog moisture, In a study at mid-elevations in the northern Oregon Cascade Range, fog drip from old-growth foliage was found to contribute up to 30 percent (89 cm or 35 in) of measurable precipitation per year (Harr 1982). This discovery came after clearcutting of some experimental watersheds reduced, rather than increased, water yields. Because old-growth forests typically have deep, multilayered canopies and comparatively high leaf areas, we can expect them to be more effective than young forests at condensing and precipitating moisture and atmospheric particulates The differences between age-classes will probably be most profound where low clouds or fog are an important part of the microclimatic environment.

The snow hydrology of old-growth forests is also distinct from that of younger stands and, especially, clearcits. Differences result mainly from a reduction in the potential for rain-on-snow flood events (Harr 1986). Several factors are responsible, including reduced snow accumulation in old-growth stands because of canopy interception, and protection of accumulated snow from the direct impacts of warm air masses and rain.

Structure

Structural characteristics of old-growth forests are extremely important whether the concern is with the ecology of these forests or their management. Many, and probably most, of the distinctive compositional and functional characteristics of old-growth forests are a direct consequence of their structural features (fig. 2). Hence, structure is the key to understanding the ecosystem dynamics of old-growth forests. Also, structure is what the forest manager can manipulate to achieve various objectives; this structural manipulation is what silviculture is about.

Old-growth forests, and unmanaged forests in general, tend to exhibit high structural diversity. In fact, structural diversity offers some of the strongest contrasts between unmanaged forests and intensively managed, commercial timber stands. Some key structural elements of old-growth forests are obvious: wide ranges in tree sizes, including trees of large diameter and height; deep, dense tree canopies; and abundant dead wood (Franklin and others 1981, Spies and others 1988) (fig. 3). Some of these attributes consist of individual structures (for example, large live trees, large snags, and large logs) and others are stand attributes (for example, multiple canopy layers and understory heterogeneity).

Individual Structural Features

Large live trees, large snags, and large logs are individual structural features that have been identified as key elements of old-growth Douglas-fir forests (for example, Franklin and Spies, this volume; Franklin and others 1981; Maser and others 1988; Old-Growth Definition Task Group 1986; Spies and others 1988). We will consider each briefly.

Large old-growth trees-The most conspicuous of the individual structural components of old growth are the large, and very old, live trees. These old trees are typically Douglas-fir, although many other species-such as western redcedar, Sitka spruce, and noble fir-may play similar roles depending on site conditions and stand history. Although size varies with site conditions and age, old-growth Douglas-fir trees are very large, with diameters of 1 to 2 meters and heights of 50 to 90 meters. Because individual trees are often 350 to 750 years old, their long and unique histories give them highly individual forms, in contrast to the uniformity of trees in young (40-80 yr) or mature (80-250 yr) stands.

The large, deep, irregular crown, that is characteristic of many old-growth Douglas-fir trees, is as ecologically important as the massive trunk. Branches are typically irregularly distributed and include large, multiple, fan-shaped arrays. Surfaces of these large branches or branch arrays are covered by thick organic accumulations, which play important roles as habitat for both plants and animals.

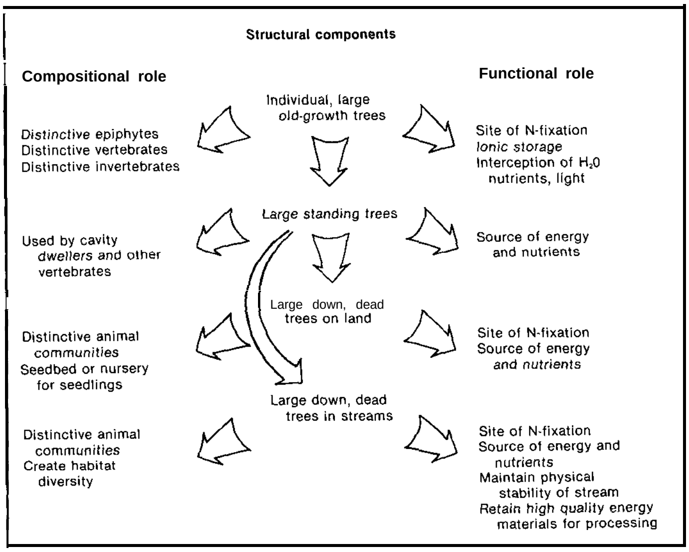

Figure 2-Relationship of some structural components of old-growth forest to distinctive habitat and ecosystem functions (from Franklin and others 1981).

The large, old, live trees are important contributors to the distinctive functions of old-growth forests. Canopies are sites for nitrogen-fixing foliose lichens, such as Lobaria oregana (Franklin and others 1981). They are also locales for condensation of moisture, precipitation of other atmospheric materials, and interception of snow. Large trees provide diverse habitats for a myriad of organisms, including epiphytic plants, birds, and mammals. Invertebrate communities are especially rich-an old-growth stand may contain more than 1500 species. A comparative study of canopy arthropods in an old-growth forest and in an adjacent plantation illustrates this richness (Schowalter 1989). Sixty-one species occurred in the old-growth canopy and one arthropod in four (individuals, not species) was a predator or parasite on another arthropod. In contrast, the plantation canopy supported only 16 species and only one in a thousand individuals was a predator or parasite; most individuals were herbivores, mainly aphids. Large trees also serve the important function of providing a source for the large snags and logs that are two other important forest structures.

Large snags-Most old-growth forests contain significant numbers of tall, large-diameter snags >50 cm d.b.h. and >20 m tall) (Franklin and Spies, this volume; Franklin and others 1981; Spies and others 1988). Snags have a variety of functional roles in forests but are probably best known as essential habitat for many species of vertebrate and invertebrate animals (this volume, Brown 1985, Maser and others 1988, Thomas 1979). Large snags are particularly important for primary cavity excavators, such as the pileated woodpecker (see Part IV, this volume).

Figure 3—Structural features of old-growth Douglas-fir forests include a range in tree sizes (including large, old trees), large snags, and abundant logs.

Large logs-Logs are nearly as conspicuous in old-growth forest stands as are large live trees. In numbers, as well as in volume and weight of organic matter, they are an important structural component of natural stands (Spies and others 1988). Large logs typically persist for very long periods-up to several centuries for some species, such as Douglas-fir and western redcedar. Logs gradually decompose, undergoing a variety of physical and chemical changes. For these reasons, logs are present in a variety of decay states in most natural stands (Harmon and others 1986).

Large logs are important contributors to the distinctive compositional and functional features of old-growth stands (Harmon and others 1986). Logs represent major long-term sources of energy and nutrients as well as sites for nitrogen fixation. Logs may also provide physical stability by protecting sites from erosion and other geomorphic processes. Large woody debris is a dominant element in aquatic ecosystems associated with unmanaged Douglas-fir forests, controlling the distribution of habitats, providing substrate, and helping to retain materials within stream reaches.

Large logs provide essential habitat for many plant and animal species (see Parts V and VI, this volume). In addition to microbial and fungal species, many vascular plants use logs as habitat. A classic example is the reproduction of tree species on rotting logs ("nurse logs"), which is particularly well represented in the coastal rainforests (Harmon and Franklin 1988). Invertebrate communities are currently not well known but certainly include hundreds of species in a typical old-growth stand. And, as this volume documents, many vertebrate species use logs as habitat to a considerable extent.

Stand Structural Features

Old-growth forests also have important stand-scale structural features. Unfortunately, our emphasis on individual structures has tended to obscure the existence and importance of such stand features. We emphasize, however, that the character of old-growth forests is not reducible to a few individual structures or characteristics.

Tree size-class distributions provide a simple example of stand-scale structure. Because of the large number of small trees found in old-growth forests, average diameters and heights in old-growth stands may be similar to those in young stands. The range of values, however, is much greater in old growth, and size-class distributions tend strongly towards much larger numbers of the smaller trees.

Multiple canopy layers or, more specifically, the continuous distribution of foliar surfaces from the top of the crown to the ground, is another stand-scale structural feature. Such canopy distributions are significant in creating greater quantities and greater diversity of animal habitat.

Understory heterogeneity is another stand-scale characteristic that is highly variable in old-growth stands. Understories in old-growth stands tend to be much patchier than in younger forest stands. This variability is partially a response to varied overstory conditions. Gaps are important structural features of old-growth stands and typically persist for long periods (Spies and others 1990). Well-developed understories of herbs, shrubs, and small trees characterize such open habitats, Heavily shaded sites ("antigaps"), also characteristic of old-growth forests, produce areas of bare litter from which green plants may be almost totally absent. Interestingly, except on dry sites, the distribution of gaps and antigaps in old-growth stands appears to be controlled primarily by the canopy density of western hemlock and other shade-tolerant codominants and not by the canopy distribution of dominant Douglas-firs.

Any consideration of old-growth forest structure must include both individual and stand structural features. Better understanding and quantification of the roles of known structural elements are needed along with basic research designed to identify additional stand-scale attributes.

Conclusions and Management Implications

Old-growth forests in the Douglas-fir region appear to provide specialized habitat for a unique array of species. These forests are also very productive in an ecological sense. Major contrasts in compositional, functional, and structural features exist between old-growth and managed young-growth stands. Differences between old-growth and unmanaged young-growth stands are less pronounced, however, because many structural features-such as large snags and logs-are carried over from the old stand to the new under natural disturbance regimes (Spies and others 1988).

Several management strategies can be used to accommodate plant and animal species associated with old-growth forests and to sustain old-growth forests as ecosystems. Retaining existing old-growth forests is, in many respects, the safest strategy. Much is still unknown about the composition, structure, and function of these ecosystems. How can we propose to recreate replicas of existing old-growth forests if we are still ignorant of many of the parts and how they are related? Furthermore, the existing old-growth forests are, at least to some degree, unique products of historical events; they are thus not completely reproducible. Any approach that emphasizes preservation of existing old growth must also include some strategy for replacing the stands that will inevitably be lost to natural catastrophes, such as fire, windstorm, and volcanic eruption.

Managing forest stands on long rotations is a second strategy for maintaining old-growth-like habitats. Natural developmental sequences (Franklin and Spies, this volume) show that old-growth conditions typically begin to emerge at 175 to 225 years (fig. 4). Silvicultural treatments could accelerate the development of old-growth structural and compositional features, such as the presence of large trees and intermediate canopy layers.

Partial cutting (sometimes referred to as partial or green-tree retention) is another approach to recreating old-growth-like forest structures in managed stands (fig. 4c). Cuttings of this type typically retain 10 to 40 percent of the living trees (fig. 5), as well as snags and logs. Proposals for this type of cutting practice have been reinforced by observations of mixed-age-structure stands (see sere illustrated in fig. 4b), such as Douglas-fir forests originating after the 1902 wildfires in southwestern Washington and a 1921 blowdown on the Olympic Peninsula. These naturally developed forests show that many of the structural elements of old growth can develop in less than 100 years if large structural “legacies” remain from the previous stand. Partial cutting can be used as either a substitute for or supplement to long rotations; that is, the strategies are not mutually exclusive.

Providing a low density of individual structures, such as large live trees, large snags, and large logs on clearcut areas is another strategy. This approach can be used to provide habitat for animal species that depend on specific types of structures, such as snags, but are otherwise tolerant of cutover habitats. Such approaches, which are designed to provide for a continuing supply of large snags and logs, are currently being widely applied on State and Federal forest lands (fig. 6).

Developing sound management strategies obviously requires dramatically expanded knowledge of natural forest ecosystems and how they work, including but not confined to old growth. The relationships of forest structure and function to various plant and animal species are critical and must include considerations of “lesser” organisms, such as invertebrates and fungi, as well as the vertebrates.

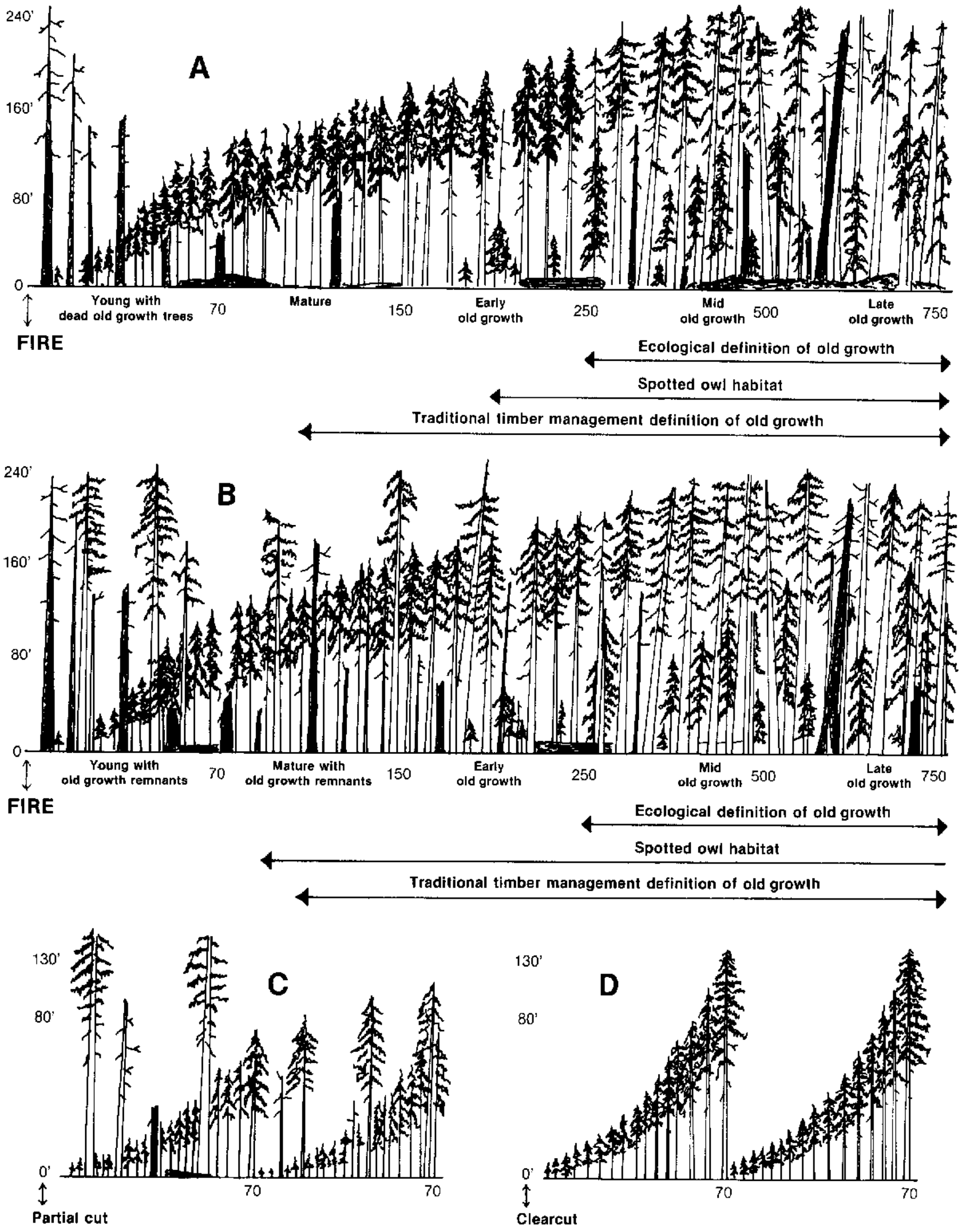

Figure 4—Structural diagrams for successional seres associated with: (A) natural succession after total destruction of an old-growth forest stand; (B) natural succession after partial destruction of an old-growth forest stand; (C) succession under a partial cutting regime to maintain two tree size- and age-classes; and (D) succession under a clearcutting regime with a single age-class. Note the similarity in structures between (B) and (C).

Figure 5—Partial cutting is one strategy for recreating old growth-like forest structures in shorter periods (such as 80-120 years) than would be required after clearcutting; 8 to 12 dominant mature (about 120 years) Douglas-fir trees were retained for the next rotation on this cutover (H. J. Andrews Experimental Forest, Blue River Ranger District, Willamette National Forest).

Figure 6—Retention of individual structural features—such as a few large green trees, snags, and logs—on clearcut areas, provide suitable habitat for some wildlife species; such practices are becoming common on commodity lands on northwestern National Forests (Innis Block, Blue River Ranger District, Willamette National Forest).

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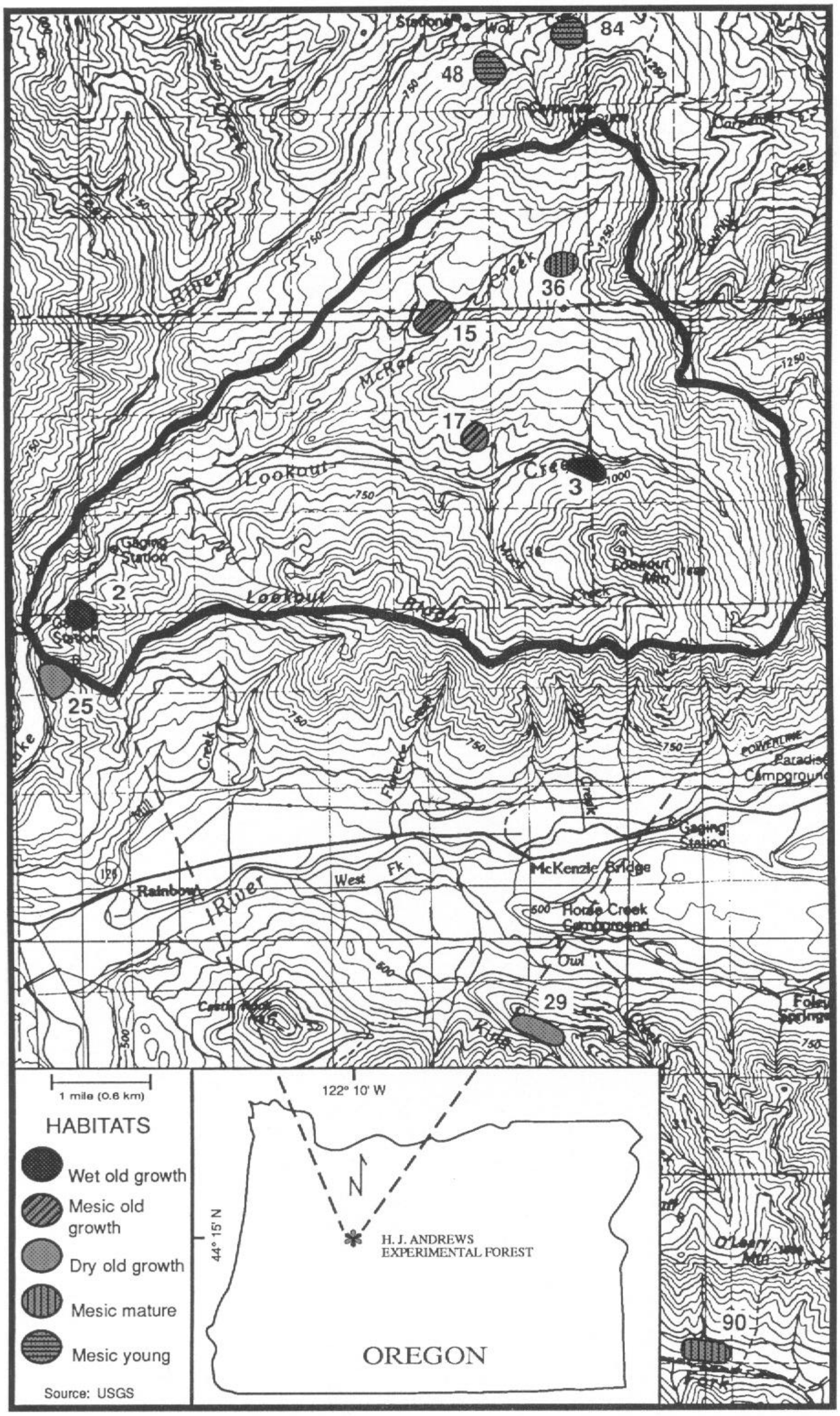

Location of sample stands (numbered and coded by habitat) and of the H. J. Andrews Experimental Forest, Oregon.

Annual Changes in Seasonal Production of Hypogeous Sporocarps in Oregon Douglas-Fir Forests

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Abstract

Sporocarps of hypogeous ectomycorrhizal fungi were harvested from 10 Douglas-fir stands representing a variety of natural habitats. Results are presented in a landscape context by assuming that the reported sporocarp production is representative of Western Hemlock Zone forests in the central western Cascade Range of Oregon. Over all stands, sporocarps were harvested from 5400 m^2 and yielded a total dry standing biomass equivalent to 1.3 kg per ha. The maximum single-stand sample biomass equaled 9.9 kg per ha. Forty-seven species of hypogeous fungi were recorded. Elaphomyces granulatus, Gautieria monticola, Hysterangium coriaceum, Leucogaster rubescens, and Rhizopogon parksii accounted for 73 percent of the biomass.

In contrast to epigeous species in the study area, hypogeous sporocarp production was higher in spring than in fall, Individual fungal species showed strong seasonal trends; most had spring production peaks. Year-to-year variation in relative biomass for individual species was greater in spring than in fall. The major species in this study were also major species in studies from young Douglasfir stands in the Oregon Coast Range. Gautieria monticola, in particular, seems to be a widespread dominant species in Western Hemlock Zone forests of western Oregon.

Introduction

Cooke (1972) defines mycocoenologists as “mycologists with ecological orientation, [or] ecologists with mycological interests.” Arnolds (1981) considers a mycocoenological approach to ecological research as one that usually uses sample plots (quadrats) to inventory macrofungi in stands of well-defined plant communities or selected habitats. The goals of such research are to describe the fungal composition of a particular plant community and to draw conclusions about relationships between fungi and vegetation on a quantitative and qualitative basis.

Vegetation has long been used to assess site quality and to help identify the importance of various environmental factors (Cajander 1949). In the Pacific Northwest, quantification and classification of vegetation in combination with autecological observations has furthered development of the plant association and habitat type concepts (Daubenmire 1968, Hemstrom and others 1987, Zobel and others 1976). The prevailing regional system of plant community classification in the

Pacific Northwest greatly facilitated the execution of mycocoenological research by freeing the investigator of the need to conduct elaborate vegetation studies to classify sample stands. This study was part of a regional characterization of Douglas-fir forests from which Spies and others (1988) provided the habitat classification.

Studies of the community ecology of macrofungi have lagged far behind those of vascular plants. Several daunting challenges face the would-be mycocoenologist. Arnolds (198 1) provides a summary of some of these difficulties: fungal species concepts are often poorly understood and defined; collections are difficult to identify morphologically and often require considerable research to reach independent taxonomic decisions; research is limited to the study of sporocarps (fruiting bodies), which are strongly seasonal (Hueck1953), are subject to yearly variation caused by variable weather patterns, and exhibit varying, largely unknown, rates of decay and predation; sporocarp production is not necessarily related to the abundance or activity of the mycelial colony; and, autecological research is lacking both in the field, where it is hampered by the concealed nature of the fungal colonies and in the laboratory where it is constrained by the investigators' inability to relate the conclusions to field situations with confidence.

Fungi that produce hypogeous (belowground) sporocarps (broadly referred to as truffles) pose additional challenges. The sporocarps are not only hidden from view, but are also often preferentially sought and consumed by small animals (Ure and Maser 1982). Although quantitative community studies of epigeous (fruiting above the ground) fungi have been reported since at least 1933 (Haas), Fogel (1976) was the first to provide a quantitative assessment of hypogeous sporocarp production. Most of the fungal species producing hypogeous sporocarps are thought to be ectomycorrhizal (fungi which develop mutually beneficial associations in the exterior layers of the roots of certain plants) (Castellano and others 1989; Trappe 1962, 1971). Mycorrhizal fungi act as extensions of the root system in forest trees and are thus important to their nutrition (Tmppe and Fogel1978).

Currently, the only practical way to compare the relative functional importance of species of ectomycorrhizal fungi in an ecosystem is by estimating sporocarp production. Potential functional roles of hypogeous species range from essential symbiosis with the roots of over-story trees (Harley and Smith 1983) to provision of sporocarps as food for animals (Vogel and Trappe 1978).

Several recent studies focused on sporocarp production by hypogeous fungal species in the Coast Range of western Oregon. Fogel (1976) was the first to quantitatively analyze the seasonal distribution of hypogeous sporocarps; he used sporocarp dry weight and number to calculate mid-dates of fruiting for individual species and populations.

In a 13-month study including the end of a severe winter drought, Fogel and Hunt (1979) observed a strong fall peak in total sporocarp dry weight. Fogel (1981) reviews techniques for quantifying hypogeous sporocarps and correlates sporocarp production with temperature and moisture. Hunt and Trappe (1987) point out that documenting all species of hypogeous fungi in a forest stand requires longterm collecting over several years. Underestimation of species richness due to small stand samples and infrequent fruiting of some species was noted by Hunt and Trappe (1987). After 32 months of collection with a total sample area of 1536 m^2, their species-area curve still had not stabilized.

The cited studies were confined to single, similar, second-growth Douglas-fir stands on Marys Peak in the Oregon Coast Range, which had all developed over 35 to 65 years after clearcut logging and burning. An obvious need existed to characterize the occurrence of hypogeous sporocarps in a landscape context from a variety of natural habitats over a wider forest area.

This research aims at broadening the data on year-to-year changes in the seasonal distribution of sporocarp production and reports the sporocarp abundance of major species (Hering 1966) of hypogeous fungi found in 10 forest stands in the H. J. Andrews Experimental Forest (Oregon Cascade Range physiographic province). Standing crop sporocarp biomass was measured within five Douglas-fir forest habitats covering a range of moisture- and age-classes. To obtain a representative sample of the major species and to document the differences in sporocarp production that are largely induced by yeartoyear changes in weather patterns, the study spanned a 4-year period. Seasonal variation in fruiting pattern was anticipated through intensive spring and fall sampling. The following specific objectives were addressed: identification of the major fungal species that produce hypogeous sporocarps in Douglas-fir stands typical of the central Oregon Cascades; characterization of the seasonal fruiting aspect as determined by the major species; and determination of yeartoyear changes in the seasonal distribution of each major species as measured by sporocarp biomass.

Materials and Methods

Study Area

The H. J. Andrews Experimental Forest occupies the 6400-ha drainage of Lookout Creek, a tributary of the McKenzie River (see frontispiece). Elevations range from 420 to 1630 m. The area is typical of the western slopes of the central Cascade Range in Oregon. The experimental forest has been administered by the USDA Forest Service as part of the Willamette National Forest for scientific, educational, and management purposes since its establishment in 1948.

A cool-summer Mediterranean climate prevails in the study area. Average annual precipitation ranges from about 2300 to 2800 mm, depending on topography. About 90 percent of the precipitation occurs from October through April; summers are dry. Above 900-m elevation, winter snowpacks accumulate to a depth of 1 m or more. Temperatures are moderate and range from -2 (mean January minima) to 28 °C (mean July maxima). Potential evapotranspiration exceeds precipitation from mid-May to September (Bierlmaier and McKee 1989, Franklin and Dyrness 1971).

Inceptosols dominate the three general soil types that are characteristic of the experimental forest (Bemtsen and Rothacher 1959, Brown and Parsons 1973, Dymess and others 1974, Franklin and Dymess 1973). Steeper slopes and ridgetops often support a residual Brown Podzolic gravelly clay loam formed from andesite or basalt. Residual Reddish Brown and Yellowish Brown Lateritic silty clay loams associated with breccia and tuff parent material are commonly found on midslopes. Gentle slopes and benches are often occupied by a colluvial clay loam.

The study area lies generally within the Western Hemlock Zone of Franklin and Dymess (1973). Studies of forest communities within the Western Hemlock Zone reveal a generalized pattern of occurrence along a moisture stress gradient (Zobel and others 1976). Characteristic understory vascular plant species are used to describe the community types. For example, abundant sword fern and Oregon oxalis typify moist sites. Mesic sites may be occupied by Oregongrape and Pacific rhododendron. Towards the dry end of the scale, salal increases in dominance. The driest sites capable of supporting forest vegetation are occupied by plant communities of the Douglas-fir series. In these communities, Douglas-fir is often considered climax and oceanspray is an important shrub (Hemstrom and others 1987). A temperature gradient reflecting elevation is also noted (Zobel and others 1976). The coolest extreme is represented by the Western Hemlock-Pacific Silver Fir/Twinflower association, transitional to associations in the Pacific Silver Fir Zone.

Sampling

Ten Douglas-fir forest stands were selected for sampling by age and moisture status. Age-classes were <80,80 to 199, and 2200 years of age and are referred to in this paper, respectively, as young, mature, and old-growth. Relative moisture-classes prevailing at these sites were identified by generalized vascular plant habitat or community types by Spies and others (1988).

Five habitat combinations were selected (wet old-growth, mesic old-growth, dry old-growth, mesic mature, and mesic young); two stands of each were sampled. Each stand, occupying about 5 ha of relatively homogeneous forest, represented a subset of typical stands originally located by other researchers as part of a regional forest characterization (Spies and others 1988). Stand locations (see frontispiece) and selected descriptive characteristics of each stand (table 1) are presented.

Stands were sampled in each season over 6 to 7 weeks. In spring, stands on lower elevation south slopes were sampled first, those on higher elevation north slopes last. We thereby condensed the sample period relative to temperature and moisture conditions that strongly influence fruiting. The fall sampling strategy was reversed with stands on higher, northerly slopes sampled first. Field work was initiated in the spring of 1983 and continued through spring of 1986.

Hunt and Trappe (1987) note the difficulty in determining adequate sampling size and sampling procedures for hypogeous sporocarps because fruiting differs so much by species and abundance in time and space. Additionally, Fogel(1976, 1981) and States (1985) report the clustered distribution of fruit bodies. Accordingly, welldistributed small plots were used in the conduct of this study.

For each stand sample, sporocarps were harvested from 25 circular 4-m^2 plots for a total sample area of 100 m^2. Plots were placed systematically about every 25 m along three transects running parallel to the slope contour and spaced about 75 m apart. New transects were established for each stand sample; no plots were resampled. In western Oregon conifer forests, most hypogeous sporocarps are produced at or above the mineralorganic soil interface (M. Castellano, G. Hunt, D. Luoma, J. Trappe, pers. obs.). In each plot, the forest floor was raked back to a 5- to IO-cm depth, thereby exposing sporocarps in the upper soil layers. The number of sporocarps from each collection in a plot was recorded. In the laboratory, sporocarps were identified to species, dried in a dehumidifier cabinet set to maintain <l5 percent relative humidity, and weighed to the nearest 0.01 g to determine biomass. Major species are those with 25 percent of the total biomass in the study (Hering 1966).

The terms “dominant” and “subdominant” within categories refers to sporocarp biomass as an indicator of a species’ importance relative to other species. Cooke (1955) measured the dominance of epigeous sporocarp by estimating fruiting body volume, and concluded his measure had “physiognomic rather than competitive significance.” Cain and Castro (1959) note that the term “dominance” is applied to different phenomena but argue against restrictive meanings because the

Table 1—Selected characteristics by habitat of 10 Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon

Habitat[a]	Stand (#)	Age[b] (yr)	Basal area[b] (m^2/ha)	Stem density[b] (#/ha)	Coarse soil[b, c] (% vol.)	Median elevation (m)	Aspect	Slope[d] (deg.)
WOG	2	450	81	280	47	550	NNE	30-35
	3	450	101	526	19	800	N	0-35
MOG	15	450	146	392	8	800	SW	0-15
	17	450	108	670	13	770	SSE	10-30
DOG	25	200	49	443	55	550	W	30-35
	29	200	47	463	52	700	SW	30-40
MM	36	130	71	408	33	1160	W	15-30
	90	84	38	433	25	930	SSW	10-30
MY	48	69	58	1410	48	1050	NW	20-30
	86	79	52	1535	59	930	NW	20-30

[a] WOG = wet old-growth, MOG = mesic old-growth, DOG = dry old-growth, MM = mesic mature, MY = mesic young.

[b] Unpublished data from T. Spies (see Spies and others 1988).

[c] Fragments >2 mm.

[d] Wet old-growth stand 3 occupied a series of slumps causing high slope variability.

differences are clear enough in context. Dominance (also co- and subdominance) of a species indicates predominance as expressed by some measure that may or may not reflect ecological influence in the dynamics of the community.

The term "stand sample" refers to the total 100-m^2 collection area (from 25 plots) for a given stand at a given seasonal harvest in a given year. This report uses data collected from 54 stand samples over 4 years, 28 stand samples in spring and 26 in fall. Seasons were defined by equinox and solstice calendar dates. Twelve stand samples were taken in wet old growth, 10 in mesic old growth, 12 in dry old growth, 8 in mesic mature, and 12 in mesic young habitats.

Analysis

Because of the unequal number of stand samples in the various seasonal categories, sporocarp biomass values were standardized to equivalent biomass, expressed in grams per hectare, and used to report seasonal results and relative values. The total biomass for a species in a category was divided by the appropriate fraction of a hectare sampled in that category to obtain equivalent biomass. Relative annual biomass of each species by season was calculated as a percentage of a species' total seasonal biomass (equivalent g/ha within each year).

Results

Total sporocarp production

Sporocarps were harvested from 5400 m^2 and yielded a dry weight biomass of 697 g, equivalent to a standing biomass of 1.3 kg per ha. The maximum single-stand-sample total biomass was 99 g dry weight or 9.9 kg per ha. Forty-seven species of hypogeous fungi were recorded during the study. Fourteen species accounted for 94 percent of the total biomass. Five major species—*Elaphomyces granulatus* Fr., *Gautieria monticola* Harkn., *Hysterangium coriaceum* Hesse, *Leucogaster rubescens* Zeller & Dodge, and *Rhizopogon parksii* Smith—accounted for 73 percent of the biomass.

Year-to-year variation

Spring fruiting was dominated by a different fungus each year: *Hysterangium coriaceum* in year one, *Gautieria monticola* in year two, and *Elaphomyces granulatus* in year three (table 2). Eighty percent of the spring biomass of *Elaphomyces granulatus* in year three was attributable to one extreme stand sample of 99 g. This value represents a particularly interesting outlier because it was obtained from a single 4-m^2 plot containing 54 sporocarps. If a more "reasonable" (for this sample size, 1000 m^2) stand-sample value of 35 g for *E. granulatus* were assumed, then *Gautieria* would have been the spring biomass dominant in year three also. *Elaphomyces granulatus* was a subdominant in year two. *Rhizopogon parksii* was not found in spring.

Fall sporocarp production was dominated by *Rhizopogon parksii* with >50 percent of the total biomass (table 2) in all years. In each year, one stand sample contributed a large proportion of *R. parksii's* fall biomass (29, 36, and 70 percent in years 1, 2, and 3, respectively). *Elaphomyces granulatus* was a fall subdominant in years one and two. *Leucogaster rubescens* was a fall subdominant in year three. *Hysterangium coriaceum* was not found in fall. Year one, with the least biomass, had relatively equal distribution of fall and spring biomass (table 2).

Table 2—Annual sporocarp biomass (equivalent g per ha) of major species by season in a 5400-m^2 total sample from 10 Douglas-fir stands, H.J. Andrews Experimental Forest, Oregon

	YEAR 1		YEAR 2		YEAR 3	
Species	Spring (n = 8)	Fall (n = 8)	Spring (n = 10)[a]	Fall (n = 9)	Spring (n = 10)	Fall (n = 9)
Elaphomyces granulatus	65	109	231	82	1234	87
Gautieria monticola	4	30	790	19	525	19
Hysterangium coriaceum	293	—	142	—	80	—
Leucogaster rubescens	10	21	84	43	13	131
Rhizopogon parksii	—	170	—	672	—	491
Seasonal g per ha	372	330	1247	917	1852	728
Yearly g per ha	351		1091		1319	

[a] 3 spring stand samples from a 4th year were included.

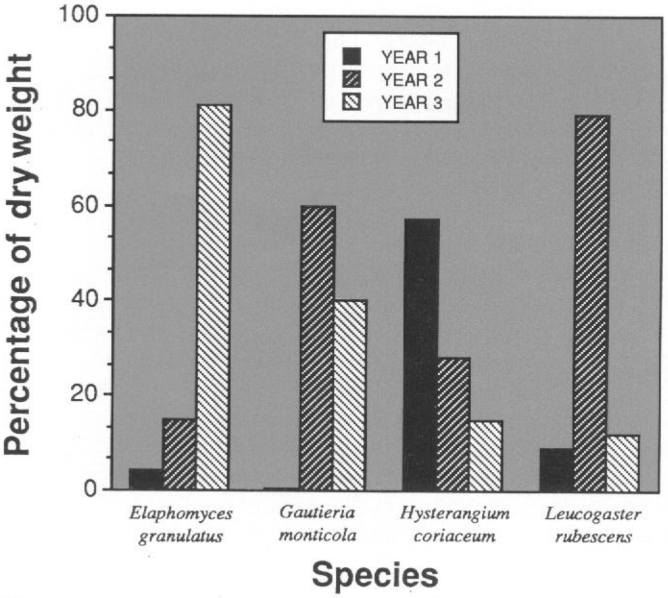

Figure 1—Major species year-to-year variation in spring relative sporocarp biomass in a 2800 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

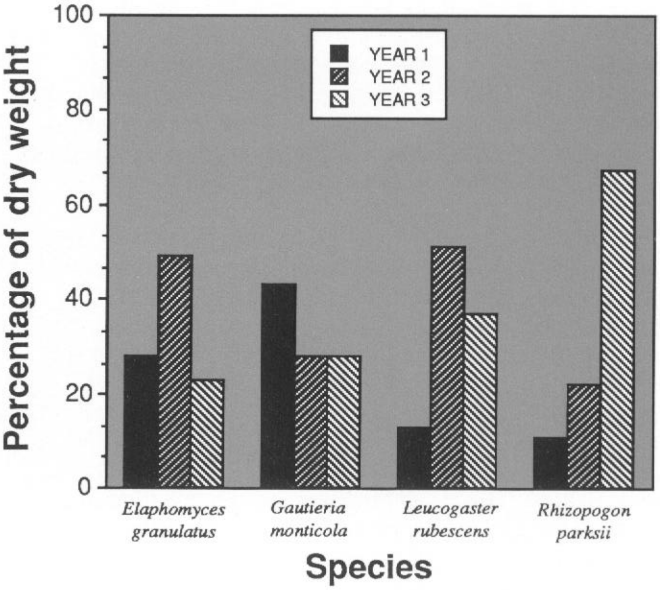

Figure 2—Major species year-to-year variation in fall relative sporocarp biomass in a 2600 m^2 total sample from ten Douglas-fir stands, H. J. Andrews Experimental Forest, Oregon.

The yearly proportion of each species seasonal sporocarp biomass is shown (figs. 1, 2). Variation in relative biomass from yeartoyear for individual species was greater in spring than in fall. Three spring species had one year with >60 percent of their total seasonal biomass. In fall, only *Rhizopogon parksii* had such a strong single-year dominance.

Discussion

This paper seeks to put the results in a landscape perspective by generalizing seasonal sporocarp production as being representative of Western Hemlock Zone forests in the central Cascade Range of Oregon. The most extensive previous studies of hypogeous sporocarp production were confined to single stands (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987). Their major goals were to quantitatively estimate sporocarp production, to determine phenology of production, and to characterize the hypogeous fungal-species community composition.

Fogel (1976) and Hunt and Trappe (1987) show that sporocarp biomass production of single species differs from year to year. In a 3-year study with small (50-m^2) monthly samples, Fogel (1976) had four major species in common with this study. The species and biomass ranges of the annual standing crop were as follows: *Elaphomyces granulatus,* *0* to 90 *g* per ha; *Gautieria monticola,* 13 to 432 g per ha; *Hysterangium coriaceum* (as *H. separabile* Zeller), 294 to *572 g* per ha; and *Rhizopogon parksii, 89* to 252 g per ha. Other major species of Fogel's (1976) study include: *ffymenogasterparksii* Zeller *&* Dodge, 76 to 435 g per ha; *Hysterangium setchellii* Fischer (as *H. crassum* [Tul. *&* Tul.] Fischer), 517 to 1206 *g* per ha; *Truncocolumella citrina* Zeller, *30* to *2336 g* per ha; and *Tuber* spp., 0 to 380 g per ha. *Hysterangium setchellii* and *Truncocolumella citrina* were moderately important, while *Hymenogaster parksii* and *Tuber* spp. were minor species in Luoma (1988).

Fogel (1976) provides seasonal information on *Hysterangium coriaceum* by reporting fruiting period (monthly range) and mean calender day of fruiting with number of days standard deviation. *Hysterangium* taxonomy was not well known at the time of his study so that *H. separabile* is the species reported and may not entirely equate with what is now accepted as *H. coriaceum*. Fogel(1976) made collections of *H. separabile* throughout the year and lists it as an "opportunistic" species. The mean fruiting date, however, in each of 3 years was in April with a standard deviation of 11 **days**—the smallest of the eight species reported. Fogel(1976) lists *Rhizopogon parksii as* a characteristic fall species.

Data from Dinner Creek, Oregon (Fogel and Hunt 1979, Hunt and Trappe 1987), gathered over 2 years, revealed five major species. *Three-Gautieria monticola, 8* to 85 g per ha; *Leucogaster rubescens,* 316 to *338 g* per *ha:* and *Rhizopogon parksii,* 116 to 463 g per ha-were also major species in the current study. *Two-Leucophleps magnata Harkn.,* 21 to *189 g* per ha; and *Truncocolumella citrina, 0 to 749 g* per ha-had moderate importance in Luoma (1988).

Hunt and Trappe (1987) sampled sporocarp production in a 1.5-ha stand for 21 months. Monthly production was estimated from twelve **4-m^2** plots. Major species in common with the present study were *Gautieria monticola, 769* to 1527 g per ha and *Hysterangium coriaceum, 106* to 204 g per ha. Other major species were *Hysterangium setchellii, 746 to 842 g* per ha and *Melanogaster* sp. nov., 108 to 225 g per ha.

Hunt and Trappe (1987) also report fruiting middate mean, and standard deviation for selected species. Over 2 years, *Hysterangium coriaceum* was collected from February to December but its middate was in April with a standard deviation of *8* days. *Rhizopogon parksii* was found only from September to December.

In this study, total spring equivalent biomass ranged from 0.4 to 1.8 kg per ha. These values were consistently greater than or equal to the fall range of 0.3 to 0.9 kg per ha (table 2) and contrast with Fogel and Hunt's (1979) marked fall biomass peak in the 1st year of sampling at Dinner Creek. Hunt and Trappe (1987) found comparable biomass between spring and fall during the 2d year of sampling at Dinner Creek. Fogel(1976) reports that spring and fall biomass were comparable but data in Hunt and Trappe (1987) show that Fogel had a marked spring biomass peak in each of 3 years. The single-sample maximum biomass of 9.9 kg per ha reported here supplants the unpublished values (1.4, 1.7 kg per ha) of Luoma and Hunt cited in table 6 of Hunt and Trappe (1987).

Total sporocarp biomass was substantially less in both spring and fall of year one compared to the other years. The low spring values may have been influenced by record high temperatures in May 1983. A 14-day period with only a trace of rain encompassed 12 days in which high temperatures reached more than 25 °C (mean monthly high = 18.7 °C) and included the highest May temperature (40°C) recorded at the H. J. Andrews station. Low sporocarp production in fall was coincidental with well below average September and October precipitation in 1983 (Bierlmaier and McKee 1989; F. Bierlmaier, unpubl. data).

Year one had the maximum production for one species in spring and another species in fall (figs. 1.2). Year two showed highest relative sporocarp biomass for two species in spring and two species in fall. One species had maximum spring biomass and one species had maximum fall biomass in *year three. Hysterangium coriaceum* was not found in the fall and *Rhizopogonparksii* was not found in spring; otherwise, no strong trends were in these data. In this data set, a single year with maximum relative biomass of two species occurring in the same season is the nominal distribution. Year two had both such species maximums for spring and fall.

Weather patterns (particularly the timing and duration of drought periods) likely account for much of the yeartoyear seasonal variation observed in this and other studies (Fogel 1981). Although it is ecologically meaningful for a given year, such variation detracts from attempts to characterize general trends in importance or dominance (as measured by sporocarp biomass) by season and habitat. Such a characterization will be presented elsewhere in the scientific literature (Luoma and others, in press).

Conclusions

Relatively few species (five) of hypogeous fungi accounted for most of the total biomass (73 percent). Many species showed strong seasonal variation in relative biomass production. For the major species, spring had greater year-to-year variation in sporocarp production and higher total biomass production than did fall. The range of standing biomass values for the species reported in this study is similar to the values reported for hypogeous sporocarps by other researchers. All of the major species in this study were also major species in one or more of the studies from young Douglas-fir stands in the Oregon Coast Range (Fogel 1976, Fogel and Hunt 1979, Hunt and Trappe 1987). In Western Hemlock Zone forests of western Oregon, *Gautieria monticola* seems to be a widespread sporocarp dominant, *Hysterangium coriaceum* a predominantly spring species, and *Rhizopogon parksii* characterizes the fall fruiting aspect. In contrast to epigeous mycorrhizal fungi, hypogeous sporocarp production is generally higher in spring than in fall (Fogel 1976; Hunt, unpubl. data).

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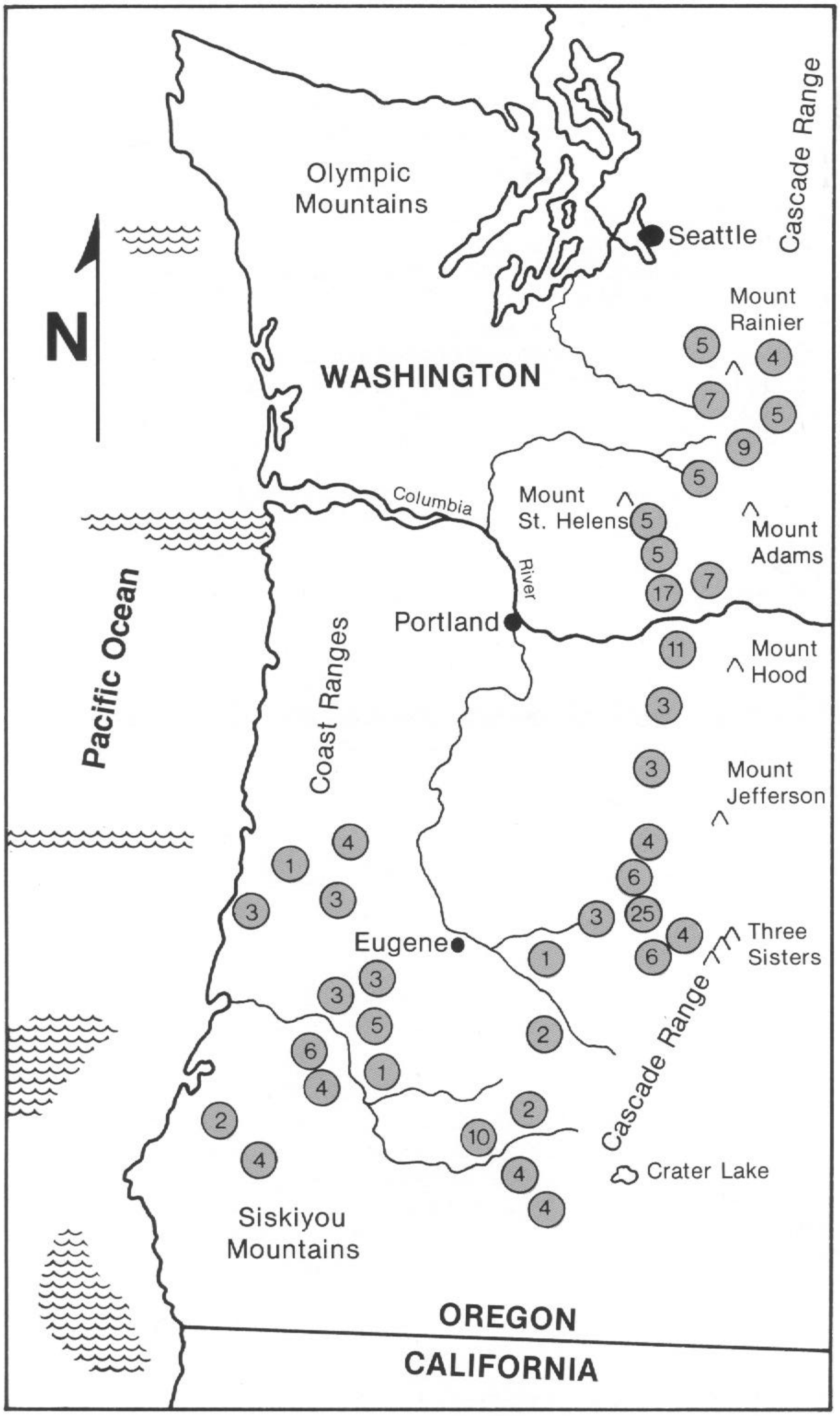

Location of stands in western Oregon and Washington. Numbers indicate total number of stands in an area.

The Structure of Natural Young, Mature, and Old-Growth Douglas-Fir Forests in Oregon and Washington

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Abstract

Structural characteristics of forest overstories, understories, and forest floor and coarse woody litter accumulations were related to stand age, geography, and relative site moisture in 196 Douglas-fir stands in western Oregon and Washington. Stands ranged in age from 40 to 900 years and typically originated after wildfire. A series of multivariate analyses was used to identify structural attributes that distinguished old-growth (>195 years old) from mature (80-195 years old) and young (40-80 years old) age-classes. Separate analyses of four attribute sets-overstory, stand condition (degree of damage and disease), understory vegetation, and forest floor and coarse woody litter indicated that the age-classes differed in numerous attributes. Discriminant models that used overstory characteristics, such as tree density, density of large Douglas-firs, and variation in tree diameter, and models combining variables from the four different attribute sets were most successful in distinguishing the age-classes. Age-classes represent portions of a continuous gradient of structural variation associated with age, based on ordinations with canonical discriminant analysis. Old-growth stands from different geographic provinces and relative site moisture-classes differ considerably in structure. Much of this variation in old-growth structure was associated with variation in densities of shade-tolerant trees and characteristics of the understory vegetation. Variation in old-growth-forest structure strongly suggests that low to moderate disturbance during the life of the stands has had an important influence on stand structure. The study provides a basis for defining and taking inventory of old-growth conditions as well as for managing the natural diversity of old-growth and earlier successional Douglas-fir forests in western Oregon and Washington.

Introduction

Douglas-fir forms dense, long-lived coniferous forests that dominate the mountainous landscapes of western Oregon and Washington. The structure and habitat quality of these forests varies greatly as a consequence of forest succession, disturbance, and plant community and environmental factors. The loss of the habitat structure associated with natural and old-growth Douglas-fir forests is a matter of intense public debate. The range of variability in the ecological structure of these forests is becoming more and more limited as the majority of forest lands are committed to short rotations for wood products. Information about natural Douglas-fir forest structure, its variability, and the processes that determine it are needed to identify wildlife habitat relationships, to inventory critical habitat conditions, and to provide management targets for silvicultural manipulations, habitat reserve areas, and the maintenance of biological diversity.

Little quantitative information has been available on variation in natural Douglas-fir forests over a wide range of ages. Franklin and others (198 1) describe the general ecological characteristics of old-growth Douglas-fir forests. They identify large live trees, large snags, and large logs as major distinctive features of these old ecosystems. Juday (1976) examines the species composition and some structural attributes in old-growth forests in the Oregon Coast Range. Alaback (1984) compares the structure of old-growth and second-growth western hemlock-Sitka spruce forests in southeastern Alaska. Most quantitative studies in Douglas-fir forests have focused on woody-debris components (Agee and Huff 1987, Graham and Cromack 1982, Sollins 1982, Spies and others 1988) or live tree components (Grier and Logan 1977; Franklin and DeBell 1988; Spies and others, unpubl. manuscript) in detailed studies of relatively few stands.

The major objectives of this study were to identify distinctive attributes and contrast the ecological structures of old-growth, mature, and young Douglas-fir forests; and to contrast the old-growth forest structure of different physiographic provinces and relative site moisture-classes in western Oregon and Washington. Several general questions were addressed: Are overstory, understory, and debris components equally distinctive among age-classes? Do different structural components change at the same rate and in the same manner with stand development and succession? How similar is old-growth forest structure among site moisture-classes from different physiographic provinces?

Study Area

Douglas-fir-dominated forests were studied in Washington and Oregon in three physiographic provinces: the southern Washington Cascade Range, the Oregon Cascade Range, and the southern half of the Coast Ranges of Oregon (Franklin and Dymess 1973). These provinces are characterized by steep, deeply dissected terrain with well-developed soil. Parent materials are Tertiary basalts and andesites in the Cascade Range, and early Tertiary sedimentary rocks in the Coast Range. The climate is wet in winter and dry in summer. Annual precipitation is heavy, ranging from 800 to over 3000 mm. Highest amounts of precipitation occur near the upper western slopes of the Coast Range and in the Cascade Range in Washington and northern Oregon (Franklin and Dymess 1973). Lowest precipitation occurs on the eastern slopes of the Coast Range and in the southern Oregon Cascades.

The study area encompasses two major vegetation zones: the Western Hemlock Zone and the lower elevational portion of the Pacific Silver Fir Zone (Franklin and Dyrness 1973). Western hemlock and Pacific silver fir are the climax species on most sites in these zones; on dry sites, Douglas-fir may be climax. In southern Oregon, the northern margin of the Mixed Conifer Zone was sampled. In the Coast Range, the eastern margin of the Sitka Spruce Zone was sampled.

Most Douglas-fir stands in the region originated after catastrophic wildfire (Franklin and Hemstrom 1981); see Franklin and Dymess (1973) for a generalized, natural successional sequence. Young stands originating from wildfires are typically dominated by Douglas-fir, although western hemlock or red alder may dominate in some areas. By 200 years, many stands exhibit old-growth characteristics (Franklin and others 1981, Spies and Franklin 1988), such as codominance of western hemlock in the overstory, diverse vertical distribution of foliage, and large accumulations of woody debris (Spies and others 1988). True climax forests are rare because pioneer Douglas-fir can persist in stands for over 1000 years (Franklin and DeBell 1988; Franklin and others 1988; Spies and others, unpubl. manuscript), and wildfires occur more frequently than 1000 years on most sites.

Methods

General Design

A total of 196 Douglas-fir stands in Washington and Oregon representing different ages (40 to 900 years) and site conditions were sampled during 1983 and 1984 (see frontispiece). All stands originated after wildfires, which killed all or nearly all the overstory trees. We sampled along two gradients: a chronosequence of Douglas-fir stands on sites with moderate moisture, and a full range of site-moisture conditions for old-growth Douglas-fir stands (≥200 years old). Resources were not available to sample extremes of site moisture for stands <200 years old. Consequently, the results of the Chronosequence analyses are based only on moderate or mesic sites (from young through old growth), and site-moisture analyses are based only on old-growth stands. To maintain a similar geographic distribution among ages of sampled stands, sampling was concentrated in areas in each province that contained all three of the following broad age-classes: young (<80 years), mature (80-195 years), and old growth (2195 years).

Site Moisture Classification

Stands >200 years were tentatively assigned during field reconnaissance into three broad moisture-classes-dry, moderate, and moist-based on observations of vegetation composition (Franklin 1979, Zobel and others 1976), physiography, and soils. Dry sites occur on steep upper slopes of southerly aspects, commonly with skeletal soils. Plant communities of

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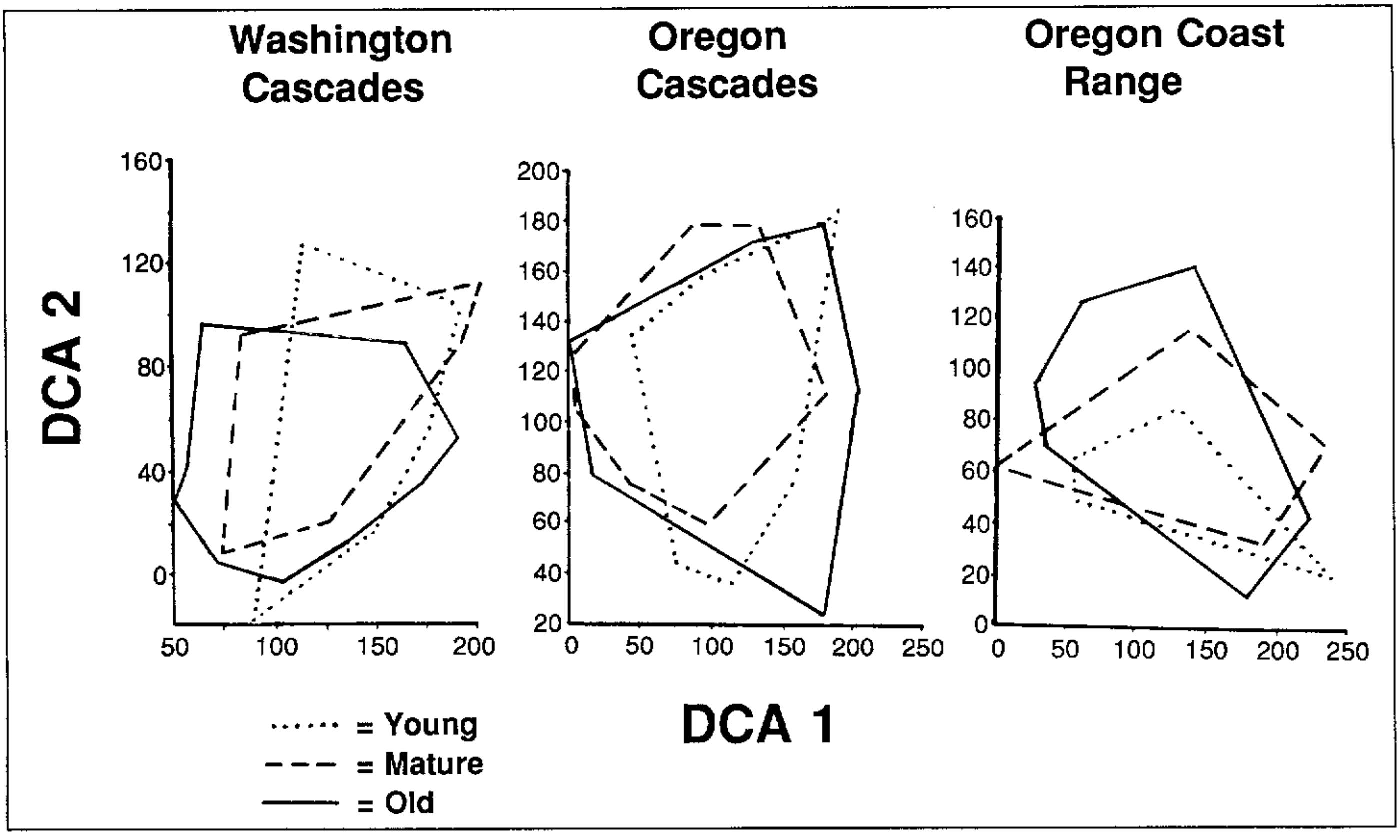

Figure 1—Ordination of old-growth, mature, and young stands along first two axes from a detrended correspondence analysis (DCA) of understory vegetation.

this moisture-class are characterized by Douglas-fir/*Holodiscus discolor*[1] and western hemlock/*Gaultheria shallon* plant associations (Franklin 1979). Moderate sites are on deeper soils of mid to low topographic position. Plant communities of this moisture-class were characterized by western hemlock/*Berberis nervosa*, western hemlock/*Berberis nervosa*/*Polystichum munitum* and related associations. Moist sites occur on lower northerly slopes, wet benches, and river terraces where plant communities include western hemlock/*Polystichum munitum*, western hemlock/*Oxalis oregana*, and western hemlock/*Oplopanax horridum* and other related types.

After field sampling was completed, the site-moisture classifications were refined for each province using detrended correspondence analysis (DECORANA) (Gauch 1982), a multivariate data-reduction and ordination program for ecological data. Moisture classifications also were done separately for each of three subprovinces (north, central, and south) in the Oregon Cascade province, because it spanned a very large and diverse area. The moisture classifications consequently relate to specific provinces or subprovinces. Refinements to the classification were made subjectively, based on the environmental interpretation of the ordination axes.

DECORANA was also used to help reduce differences in environment among the age-classes. Analysis of understory vegetation data from all stands indicated that young and mature stands sampled a broader range of environment than originally intended. Scatter plots of the DECORANA stand scores were used as a guide for deleting stands within an age-class that were outliers from the general range of stands of the other age-classes. This editing procedure, which was done subjectively, based on both the DECORANA analyses and knowledge of the site conditions, resulted in selection of 177 stands from the 196 for comparing age-classes. Although the distributions of the stands differed somewhat with respect to the ordination scores, the stand scores of the age-classes still overlapped considerably (fig. 1).

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[1] In this botanical chapter herbaceous plants and lichens are referred to by their scientific names for accuracy and the convenience of the reader.

Stand Selection and Plot Measurements

Stand size ranged from about 4 to 20 ha. Within each stand, five circular plots were systematically located. In some of the very small stands, only three or four plots were established. Plots were spaced either 100 or 150 m apart, depending on stand size, with wider spacing in large stands. The locations of the plots were determined before the field sampling by the size and shape of the stand as seen on aerial photographs.

Each plot was a nested set of circular plots of six sizes: 0.002 ha, 0.02 ha, 0.05 ha, 0.1 ha, and 0.2 ha. In the 0.1 -ha plot, trees over 50 cm in d.b.h. and snags over 0.1 m tall with upper diameters >l0 cm were measured (10 cm in d.b.h. for snags>1.4 m tall) and recorded by species, diameter, height-class, and decay-class using the five-class system of Cline and others (1980). Trees were classified into one of the following height-classes: 1 to 2 m; 2 to 4 m; 4 to 8 m; 8 to 16 m; 16 to 32 m; 32 to 48 m; 48 to 64 m; >64 m. Additional measurements on trees included coding of condition of crowns and boles, presence of disease and disturbance indicators, and presence of natural and excavated cavities on the readily visible lower third of the bole. Additional measurements on snags included the presence of natural cavities and excavations, and heights that were estimated visually after heights of a few snags or trees on each plot were measured with a clinometer and tape. The 0.2-ha plot was used during the second field season to record information on snags >50 cm in d.b.h. and >15 m tall, which occurred with low densities in most forests. The 0.05-ha plot **was used to record the information described above for trees** 50 cm in d.b.h. All logs >10 cm in diameter (large end) that projected into the 0.05-ha plot were measured. Log measurements included length (within plot), horizontal diameter at both ends, species and decay-class using a five-class scheme developed for Douglas-fir logs (Fogel and others 1973, modified by Sollins 1982). The decay-classes were used for all species because no classification was available for the other species.

Understory vegetation information was recorded by species in the three smallest plots. The number, species, and height by class of all tree seedlings and saplings 1 m tall to 5 cm in d.b.h. was recorded in the 0.05-ha plot. The percentage cover of tall shrubs was estimated by species over the 0.05-ha plot. The percentage cover of all vascular plants, mosses, and lichens (including foliose lichens from the canopy that had fallen to the forest floor) was estimated by species in the 0.02-ha plot. All vascular plants were identified to species or genus, but only selected mosses and lichens were identified to species. The number, species, and height-class of all tree seedlings <1 m tall were recorded in four 0.002-ha plots systematically located in the 0.05-ha plot. The depth of the L, F, and H litter layers was recorded to the nearest millimeter at three points in each 0.002-ha plot (12 points in each 0.05-ha plot) by use of a trowel and ruler.

Data on slope, aspect, topographic position, and shape of topographic cross section were collected from the 0.l-ha plot. The heights of two to four trees on each plot were measured with a clinometer and tape. Tree ages were determined for young and mature stands by increment coring at breast height of at least one dominant Douglas-fir per plot, adding 5 to 7 years for growth to breast height (depending on site), and averaging the plot estimates to obtain an age estimate for the stand. For old-growth stands, age estimates were made from stumps in nearby clearcuts, along trails or roads, or, sometimes, from increment cores on dominant trees. Data collected by Hemstrom (1979) were used to estimate ages of the stands in Mount Rainier National Park.

Calculations and Analyses

The density of trees, and volume and number of logs and snags, were computed by species, decay-class, and various size-classes for each plot in a stand. Diversity of tree heights (H') (Pielou 1977) was calculated for the height-classes, based on either density of trees or basal area of trees in each class. Volume was computed by using the formula for a cone. Stand values were then calculated as the means and variances of the plot values. Logs in decay-classes 1 to 4 were considered round in cross section. For decay-class 5 logs, which are flattened in cross section, vertical diameters were estimated by multiplying the horizontal diameter by 0.439, a ratio determined from a sample of 20 logs (J. Means, unpubl. data). We estimated the upper diameters of snags by using a taper value of 0.12 cm/dm determined from diameters and lengths of class 1 to 3 logs. Plot areas were not area-corrected for slope because such corrections result in an overestimate of stand characteristics as compared with level ground (Mueller-Dombois and Ellenberg 1974).

The potential number of variables available to characterize the forest stands is extremely large-perhaps over 2000 if characteristics of species are included. Therefore, the analysis began with a multi-step process of variable selection and data reduction, with aggregation of species information into life-form-group variables (appendix table 10) to reduce the number of variables. The only exception was Douglas-fir, which retained its species identity for several tree characteristics. Variables were *then* divided subjectively into four attribute-sets: overstory, stand condition (tree and snag characteristics related to vigor, damage, disease, or animal use), understory, and debris. In each of these sets, 15 to 30 variables were subjectively chosen, based on documented or hypothesized importance to wildlife habitat, ecosystem function, and successional development (appendix table 11).

Four separate but related analyses were used for each attribute-set and the combination of all attributes. First, a stepwise discriminant analysis (SAS 1987) was conducted on each set with either the three age-classes for the entire study area, or nine province/site moisture-classes. A significance level of $P < 0.15$ was used to include or exclude a variable from the model. The distributions of all variables were examined before analyses, and square-root or logarithmic transformations were used where appropriate to produce normal or close-to-normal distributions. The stepwise analyses typically selected 8 to 12 variables for each attribute-set with significant discriminatory power for the particular class models. These new smaller attribute-sets were then used in the next three analytic steps.

Canonical discriminant analysis (SAS 1987), a data-reduction technique, was the next step, which extracted a small set of new variates that maximized differences between the classes. The correlations of the original variables with the new variates was used to evaluate the dependence structure of the variables associated with differences in the classes. The stand scores of the variates were plotted to evaluate the relative distinctness or degree of overlap among the age- or old-growth province/moisture-classes.

Discriminant analysis was then used to determine the classification error rate by a jackknife procedure based on the variables selected in the stepwise analysis (Lachenbruch and Mickey 1968). This procedure generates a relatively unbiased estimate of the error or success rate of the discriminant models. Within-class covariate matrices were used in the discriminant analysis of the age-classes, and pooled covariate matrices were used in the analysis of the Province/moisture-classes.

The fourth and last analysis on the variables from the stepwise analysis consisted of combining the best variables from each of the four attribute-sets and conducting another series of stepwise discriminant analyses, canonical discriminant analyses, and error-rate analyses.

Results

How Do Old-Growth Forests Differ From Younger Forests?

Overstory (trees >5 cm in d.b.h..)-Tree density, mean stand diameter, and basal area were most important in discriminating among age-classes (table 1). Tree density was about twice as high in young stands as it was in mature and old-growth stands (table 2). Basal area increased with age-class, and mean tree diameter was highest in mature stands, which lacked the smaller diameter, shade-tolerant trees common in the old growth (table 2). The high variability in old-growth stand structure was evidenced by old growth's having the highest standard deviation of tree diameter at breast height (table 2). Diversity of tree heights (H'), which had weak discriminating power, was actually highest in mature stands, probably because tree densities were more evenly distributed across the height-classes in mature stands than in young or old-growth stands, where tree densities are concentrated in the shortest height-classes.

Most of the variance between age-classes could be reduced to a single canonical variate related to the standard deviation of tree diameter and the density of large trees (>100 cm in d.b.h.) (table 3). A second minor variate was related to mean tree diameter and tree density. Ordination of the stands, based on their canonical variate scores, revealed relatively distinct age-class means but considerable within-age-class variation and moderate overlap between the mature stands and the old-growth and young stands (fig. 2a).

Stand condition-Percentage of snags with natural cavities, percentage of Douglas-fir boles with resinosis, and percentage of tree crowns with broken tops were important in the discriminant model (table 1). Nearly all measures of tree decadence were much higher in old growth than in the younger age-classes (table 2). The percentage of Douglas-firs with broken-topped crowns was nearly 10, and it was nearly 3 times higher in old growth than in young and mature stands. The percentage of broken tops in old growth is probably much higher than we measured because many smaller breaks or older, obscured breaks were not counted. The percentage of trees with excavated cavities was <1 in all age-classes, although the percentage in old growth was several times that of the other age-classes. Both old-growth and young stands had similar percentages of fall scars. The bark of small, shade-intolerant trees in young stands is easily scarred; in old-growth, thin-barked, shade-tolerant species also scar relatively easily, and falling trees and large limbs can cause scarring even on thick-barked shade-intolerant trees.

Most of the between-class variation could be accounted for by the first canonical variate, which is related to tree crowns with broken and dead tops (table 3). The second, minor variate was related to fall scars and dead tops. Age-class means were not well separated, and considerable overlap occurred between the mature stands and the old and young stands, although the distributions of the old and young age-classes overlapped only slightly (fig. 2b).

Understory vegetation-Cover of herbs, density of shade-tolerant saplings, and cover of deciduous shrubs were important in the discriminant model (table 1). Herb and deciduous-shrub cover increased with stand age-class. As expected, the density of shade-tolerant saplings was highest in old growth, but, unexpectedly, shade-tolerant saplings were lowest in mature stands and intermediate in young ones (table 2).

Table l-Variables and their *F* values in final models selected by stepwise discriminant analyses of forest age-classes based on different subsets of variables (all variables significant at $P \leq 0.05$)

		Variable set							
Overstory	*F*	Stand condition[a]	*F*	Understory	*F*	Debris	*F*	Combined set	*F*
Tree density	22.1	Snags with natural cavities	7.6	Percentage herb cover	8.6	5-to 15-m-tall snag density	22.2	Shade-intolerant tree species density	14.8
Tree d.b.h. mean	20.3	Resinosis Douglas-fir	6.4	Density shade-tolerant saplings	7.7	Decay class 2 log volume	14.3	100~cm-d.b.h. Douglas-fii density	7.4
Total basal area	18.4	Broken-topped croyts	6.4	Percentage cover deciduous shrubs	6.1	>5-m-tall and >50-cm-d.b.h. snag density	9.8	>5-m-tall and >50-cm-d.b.h. snag density	7.1
>lOO-cm-d.b.h. Douglas-fii density	10.3	Sweeping boles, all spp.	4.6	Density of sub-canopy saplings	4.7	50-cm-d.b.h. snag density	6.7	1.5- to 5-m-tall snag density	5.7
Tree spp. richness in stand	1.5	Trees with excavated cavities	4.1	Percentage total vegetation cover	4.0	Snag volume	6.3	Decay-class 2 log volume	5.5
Shade-tolerant species density	5.2	Snags >50-cm-d.b.h. with natural cavities	3.9	Coefficient of variation of herb cover	3.4	Decay class 4 snag volume	5.9	Tree d.b.h. standard deviation	5.1
Tree d.b.h. standard deviation	5.0	Broken-topped crowns, Douglas-fir	3.6			1.5- to S-m-tall snag density	5.1	Snag volume	5.0
Broad-leaved species basal area	4.8	Trees with root-collar cavities	3.4			Decay class 5 snag volume	4.5	Decay class 5 snag volume	4.9
Shade-intolerant species density	4.0	Douglas-firs with fall scars	3.4			Log volume	3.7	Percentage herb cover	4.3
Diversity of tree heights (H') based on density	3.6	Trees with leaning boles	3.2					Broken-topped tree crowns	4.2
	3.6	Snags >50-cm-d.b.h. with excavated cavities	3.2					Decay class 4 snag volume	4.0
								Broad-leaved tree species basal area	3.6
								>50-cm-d.b.h. snag density	3.6

[a] All variables are percentages.

The first canonical variate, which explained most of the variation, was related to the density of shade-tolerant saplings, density of subcanopy saplings, and density of herb cover (table 3). The second, minor variate was related to graminoid cover and herb cover. All of the age-class distributions overlapped in the ordination (fig. 2c). Only a portion of the old-growth distribution was distinct from the young and mature stands; these old-growth stands had high densities of shade-tolerant saplings and high cover of herbs.

Debris-Density of snags 5 **to 15 m tall, decay-class 2 log-**volume, and density of large snags were important variables in the discriminant model (table 1). The density of snags 5 to 15 tall decreased with age-class (table 2), but decay-class 2 log-volume and density of large snags increased with age-class. In general, small snags and logs were more numerous in young stands and large ones were most numerous in old growth. Although not selected by the stepwise discriminant analysis, the combined-depth of the F and H litter layers was deeper in old growth (x = 21 mm) than in young (x = 15 mm) or mature stands (x = 14 mm).

The density of snags less than 15 m tall was related to the first canonical variate, which explained most of the between group variation (table 3). The ordination along this variate separated the old-growth from young and mature forest, which overlapped almost entirely (fig. 26). The second, minor variate, which was related to log volume and the coefficient of variation of numbers of large logs per ha (table 3), distinguished mature stands from both old-growth and young stands, although the overlap among classes was high (fig. 2d). The high coefficient of variation for large logs in mature stands may result from the scarcity amounts of logs of this size and the patchy mortality in these stands from root pathogens and bark beetles, or from an occasional remnant old-growth tree or a large snag that falls to the forest floor.

Table 2--Means’ and confidence limits[b] of characteristics selected in stepwise discriminant analyses of young, mature, and old-growth forests

	Age-class		
Characteristic’	Young	Mature	Old-growth
Overstory:			
Tree density	935 (758-l 154)	452 (373-548)	448 (394-5 11)
Tree d.b.h. mean	21 (19-25)	34 (30-39)	31 (28-34)
Total basal area	44 (39-50)	59 (53-65)	69 (64-74)
>lOO-cm-d.b.h. Douglas-fir density	0.5 (0.2-0.73)	2.5 (0.99-4.73)	19 (16-23)
Tree spp. richness (no./stand)	5.6 (4.7-6.6)	5.1 (4.3-5.9)	5.5 (4.9-6.0)
Shade-intolerant spp. density	490 (333-719)	243 (171-346)	63 (49-79)
Shade-tolerant spp. density	277 (165-416)	132 (64-223)	270 (199-353)
Tree d.b.h. standard deviation	12 (10-14)	22 (20-24)	32 (30-34)
Broad-leaved spp. basal area	0.01 (0.0-0.08)	0.01 (0.0-0.08)	0.001 (0.0-0.004)
Diversity (H′) of tree heights based on density	2.6 (2.4-2.9)	2.8 (2.5-3.0)	2.6 (2.5-2.8)
Stand condition:			
Boles with fall scars (%)	5.5 (3.5-7.9)	4.3 (2.7-6.3)	6.6 (5.3-8.3)
Resinosis, Douglas-fir (%)	0.3 (O-1.2)	1.0 (0.2-2.3)	2.2 (1.2-3.4)
Broken-topped crowns, all spp. (%)	1.7 (0.8-2.9)	4.6 (3.2-6.4)	6.3 (5.2-7.7)
Sweeping boles, all spp. (%)	.12 (9-16)	15 (12-20)	(11-16)
Trees with excavated cavities (%)	co.001 (0-0)	0.06 (O-0.2)	0.1 (0.06-0.3)
Snags >50-cm-d.b.h. with natural cavities (%)	21 (9-36)	7.8 (2.0-17.4)	7.0 (3.0-12.8)
Broken-topped crowns, Douglas-fir (%)	1.3 (0.1-3.8)	4.2 (1.6-7.9)	11 (8-15)
Root-collar cavities (%)	3.4 (1 .0-7.3)	(3.3Y1.3)	12 (9-17)
Boles with fall scars, Douglas-fir (%)	3.7 (1.6-6.5)	2.4 (0.9-4.6)	3.0 (1.8-4.5)

	Age-class		
Characteristic[c]	Young	Mature	Old-growth
Boles with lean (%)	11 (8-14)	12 (9-15)	15 (13-17)
Snags >50-cm-d.b.h. with excavated cavities (%)	19 (8-35)	24 (12-40)	8.9 (4.1-15.7)
Understory:			
Herb cover (%)	(1.5-4.1)	5.1 (3.3-8.1)	6.4 (4.7-8.7)
Shade-tolerant saplings density	228 (104-400)	84 (22-186)	335 (233-456)
Deciduous shrub cover (%)	6.8 (4.1-11.2)	(5.6Y4.1)	12 (9-16)
Subcanopy tree saplings density	14 (1-46)	11 (0-37)	53 (29-84)
Total understory cover (%)	46 (33-62)	57 (44-72)	52 (43-62)
C.V. herb cover	81 (66-97)	80 (66-94)	75 (66-84)
Debris:			
5- to 15-m-tall snag density	(59-1O3)	60 (44-79)	(8-18)
Decay-class 2 log volume	2.0 (0.9-4.5)	8.3 (3.9-17.8)	16 (9.6-26.9)
>50-cm-d.b.h. and >5-m-tall snag density	5.6 (3.1-8.9)	6.1 (3.6-9.3)	12 (10-15)
>50-cm-d.b.h. snag density	25 (18-32)	14 (10-20)	24 (20-28)
Snag volume	132 (92-189)	85 (62-119)	159 (128-199)
Decay-class 4 snag volume	(36-83)	(13-42)	(23-45)
1.5- to 5-m-tall snag density	(41-72)	(31-5s2)	24 (20-28)
Decay-class 5 snag volume	(14-41)	(6-23)	(9-22)
Log volume	223 (163-305)	124 (93-165)	266 (219-324)

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[a] Means are back-transformed to linear values from either a logarithmic or square root transformation.

[b] 95% confidence limits of the mean; Scheffe’s procedure. Limits are asymmetrical about the mean because of transformations.

[c] Units: basal area in square meters per hectare density in number/per hectare; volume in cubic meters per hectare and diameter in centimeters.

Table 3-Percentage explained variance and correlation coefficients of the first two canonical variates of analyses of age-classes based on different sets of characteristics (only the 2 highest correlations are shown for each canonical variate, except for the combined analysis where the variables with the 4 highest correlations are shown)

Characteristic	Variate 1	Variate 2
Overstory:		
Percentage of variance explained	91	9
Correlation coefficients		
Tree d.b.h. standard deviation	0.89	0.20
>100-cm-d.b.h. Douglas-fir density	0.85	-0.12
Tree diameter mean	0.33	0.63
Tree density	-0.50	0.63
Stand condition:		
Percentage of variance explained	85	15
Correlation coefficients		
Broken-topped crowns, all spp. (%)	0.56	0.40
Broken-topped crowns, Douglas-fir (%)	0.56	0.04
Trees with conks on lower bole (%)	0.19	0.37
Dead-topped crowns, all spp. (%)	0.54	-0.34
Understory:		
Percentage of variance explained	74	26
Correlation coefficients		
Shade-tolerant tree sapling density	0.54	-0.56
Subcanopy tree sapling density	0.53	-0.09
Graminoid cover (%)	-0.11	0.70
Herb cover (%)	0.50	0.60
Debris:		
Percentage of variance explained	82	18
Correlation coefficients		
5- to 15-m-tall snag density	0.83	-0.10
d-m-tall snag density	0.61	0.04
Log volume	-0.32	0.63
>60-cm-diameter log C.V. density	0.09	-0.60
Combined:		
Percentage of variance explained	89	11
Correlation coefficients		
Tree d.b.h. standard deviation	0.88	0.18
>100-cm-d.b.h. Douglas-fir density	0.85	-0.10
Shade-intolerant tree spp. density	-0.79	0.08
>5-m-tall snag density	-0.54	0.04
Tree d.b.h. mean	0.33	0.55
>60-cm-diameter log density	0.04	0.50
>50-cm-d.b.h. snag density	0.08	-0.43
Snag volume	0.20	-0.39

Combined variable set-When all classes of variables are considered together, overstory and debris variables are the most important in the discriminant model (table 1). Density of shade-intolerant overstory trees appeared to separate the age-classes (table 2). The density of large-diameter Douglas firs increased dramatically with age-class; snag volume distinguished mature stands, which had the lowest volume, from *young* and old-growth stands, which had relatively high snag volumes (table 2).

A high percentage of between-class variation was accounted for by the first canonical variate, which was positively correlated with the standard deviation of tree diameter and density of large Douglas-firs and negatively correlated with density of shade-intolerant trees (table 3). The second variate was related to log and snag volume. The age-classes were relatively distinct when the stands were ordinated along the two variates, although overlap still occurred (fig. 2e).

The scores of the first canonical variate were closely related to stand age in an approximately logistic relation (fig. 3a) illustrating the continuous nature of habitat variation. The changes with stand age begin to level-off by 400 to 500 years, reflecting changes in variation in tree diameter and density of large Douglas-fir. The scores of the second canonical variate followed a different pattern with stand age, rising to a peak between 100 and 200 years, and then declining (fig. 3b). This pattern reflects changes in both average tree diameter, which is high between 100 and 200 years, and amounts of coarse woody debris which are high both early and late in succession.

Classification error among attribute types-The variable sets differed in their capacity to distinguish among the age-classes (table 4). The highest classification success was achieved by overstory- and combined-attribute sets. Tree condition- and understory-attribute sets had the lowest success percentages. The overstory discriminant model achieved a slightly higher classification success for old-growth stands than did the combined-attribute model. In the combined-attribute model, however, no young stands were classified as old-growth; in the overstory model, 5 percent of the young stands were classified as old growth. In all but the understory- and debris-attribute models, mature stands were the least successfully classified age-class, which is not surprising because mature stands are intermediate in the more or less continuous process of stand development and succession.

How Does Old-Growth Structure Differ Among Geographic Provinces and Site Moisture-Classes?

Overstory-Basal area of shade-tolerant tree species and basal area of broad-leaved tree species were most important in the discriminant model (table 5). Old-growth stands in the Washington Cascades generally had the highest basal areas of shade-tolerant trees of all provinces, although old growth on moderate sites in the Oregon Cascades had the highest total basal area of any single province moisture-class (table 6). In general, moist sites had higher basal areas of shade-tolerant tree species than did moderate or dry sites. The basal area of broad-leaved tree species, although typically less than 0.1 m^2 per ha, was highest in the Coast Range. The broad-leaved trees in old growth in the Coast Range primarily are bigleaf maple, which is most common on the east side of the mountain range. The density of large-diameter Douglas-firs

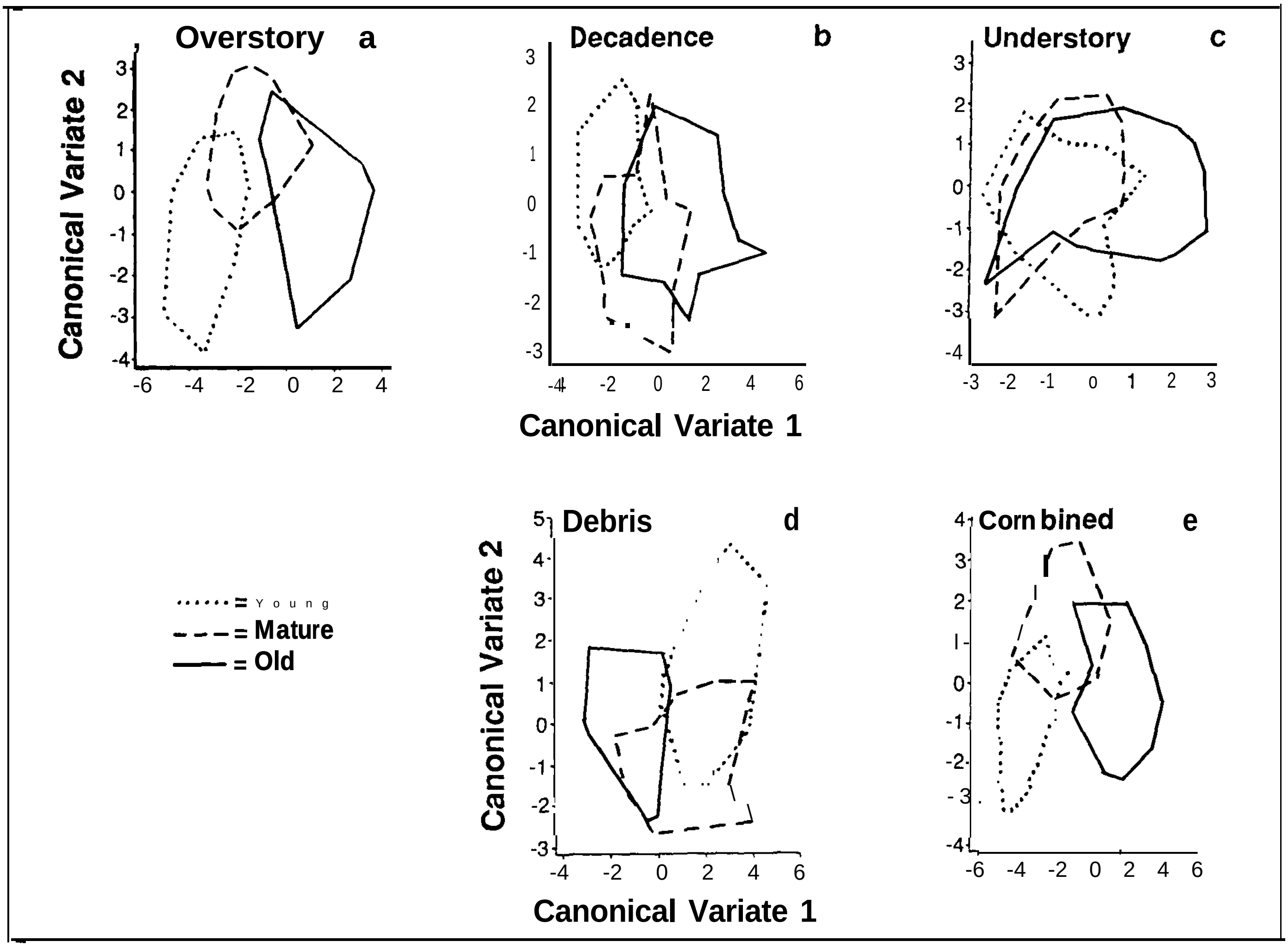

Figure 2—Ordinations of old-growth, mature, and young stands along first two canonical variates from analyses of overstory attributes (a), stand condition attributes (b), understory attributes (c), debris attributes (d), and a combination of all attribute sets (e).

was typically lowest in the Washington Cascades and did not exhibit a strong pattern related to moisture-class, except for a decrease in density with increasing moisture in the Coast Range. The density of subcanopy trees generally decreased with increasing site moisture, probably as a result of increasing basal area of shade-tolerant trees in the upper canopy that creates low-light conditions unfavorable to understory trees.

Basal area of shade-tolerant species and density of shade-intolerant species were related to the first canonical variate, which accounted for 49 percent of the variation (table 7). This variate essentially distinguished dry sites of the Oregon Cascades and Coast Range from all other old-growth sites (fig. 4a). The second variate was related to variation in tree diameter, density of subcanopy trees, and basal area of broad-leaved trees (table 7). Stands positioned along this variate ranged from moist Washington and Oregon stands with high standard deviations of tree diameter to dry Washington stands with lower variation in tree diameter and high densities of subcanopy trees (table 7).

Stand condition-Percentages of natural root-collar cavities, of trees with arching boles, and of trees with fungal conks on the lower bole were important in the discriminant model (table 5). Natural root-collar cavities were most abundant in stands in the Washington Cascades, where western hemlock-which often roots on rotten wood and forms stilted roots-was very common; root-collar cavities were least common in the Coast Range stands (table 7). The percentage of arching boles, perhaps an indicator of steep slopes and soil creep or disease-weakened stems, was highest in the Coast Range. The percentage of trees with fungal conks in

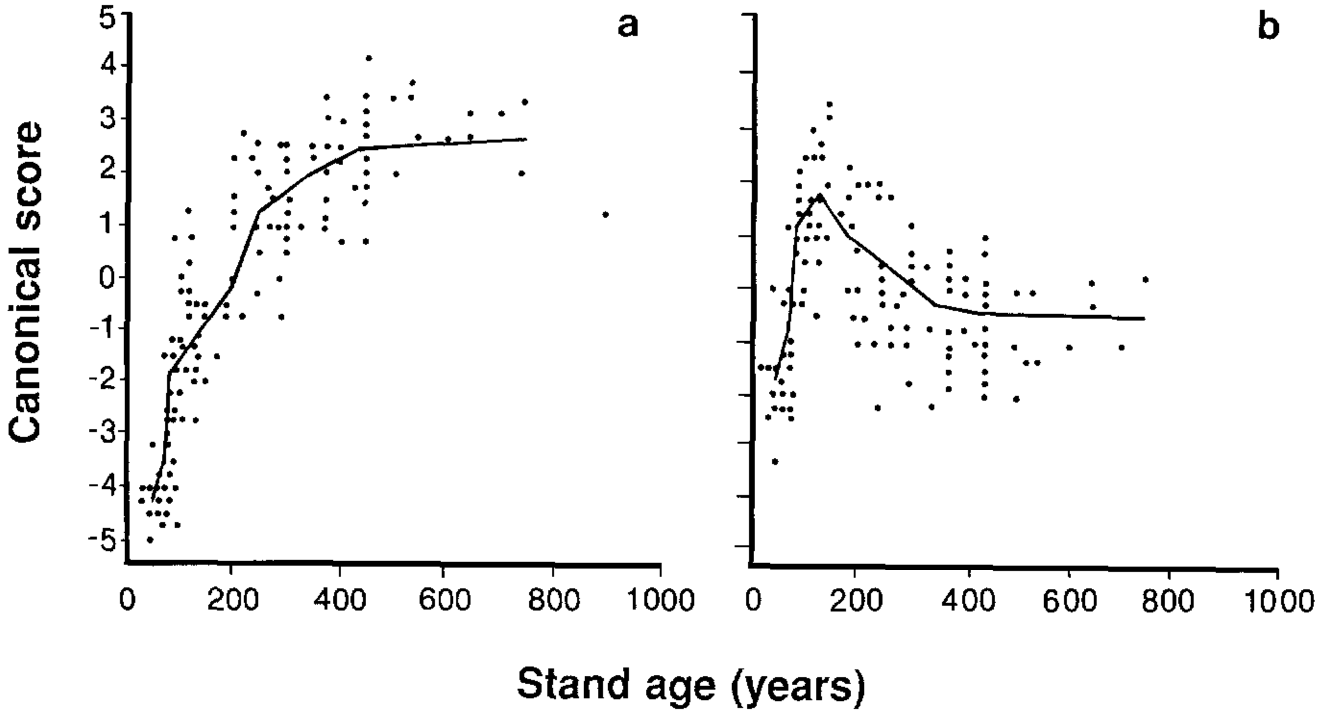

Figure 3—Relation of canonical variates 1 (a) and 2 (b) from combined-attribute set to stand age. Curves are fit to variate means from age-classes (years): <60; 60-80; 80-120; 120-160; 160-200; 200-300; 300-400; 400-600; >600.

Table 4—Summary of discriminant classifications of age-classes based on different sets of characteristics[a]

	Percentage classified into age-class by discriminant function														
	Variable set														
	Overstory			Tree condition			Understory			Debris			Combined		
From age-class	Y	M	O	Y	M	O	Y	M	O	Y	M	O	Y	M	O
Young (n = 37)	**81**	14	5	**68**	27	5	**54**	32	5	**65**	30	5	**84**	16	0
Mature (n = 44)	16	**73**	11	32	**43**	25	23	**64**	14	18	**68**	14	11	**73**	16
Old-growth (n = 96)	0	6	**94**	6	17	**77**	18	27	**55**	5	13	**82**	0	10	**90**

[a] Values in bold indicate correctly classified percentages.

the stands, an indicator of disease incidence, was highest in the Coast Range on all sites, and generally highest on dry sites in all provinces.

The percentages of trees with arching boles and fungal conks were related to the first canonical variate, which explained 51 percent of the variance (table 7). The second variate was related to the percentage of large snags with excavated cavities and Douglas-fir boles with sweep. Coast Range stands and the dry Oregon stands were separate from all other classes when plotted against the two variates (fig. 4b), although considerable variation was found within groups and overlap among groups.

Understory vegetation—Important variables in the discriminant model included percentage cover of graminoids, total vegetation, evergreen shrubs, and deciduous shrubs (table 5). Coast Range stands had the highest cover of graminoids on all sites (table 6). Total cover by understory vegetation also tended to be higher in the Coast Range and did not exhibit a strong relation to site moisture, except perhaps in the Oregon

Table S-Variables and their *F* values in final models selected by stepwise discriminant analyses of province-moisture classes based on different subsets of variables (all variables significant at $P \leq 0.05$)

				Variable set					
Overstory	*F*	Stand condition[a]	*F*	Understory	*F*	Debris	*F*	Combined set	*F*
Shade-tolerant tree spp. basal area	7.6	Trees with root-collar cavities	6.0	Graminoid cover (%)	11.0	F and H litter layer depth	8.7	Shade-tolerant tree spp. basal area	7.5
Broad-leaved tree spp. basal area	4.3	Arching boles	4.8	Total vegetation cover(%)	9.8	30- to 60-cm-diameter log density	4.9	Deciduous shrub cover (%)	6.1
>100-cm-d.b.h. Douglas-fir density	3.1	Conks on lower bole	3.8	Evergreen shrub cover (%)	8.3	Snag volume	3.9	100-cm-d.b.h. tree density (%)	5.3
subcanopy tree spp. density	3.1	Dead-topped crowns	3.8	Decidous shrub cover(%)	7.6	Decay class 5 snag volume	2.7	Total vegetation cover (%)	4.9
Total basal area	2.9	Snags with natural cavities	3.3	Herb cover (%)	5.8			Subcanopy tree spp. density	4.5
>100-cm-d.b.h. tree		Broken-topped crowns	2.9	Subcanopy tree spp. sapling density	3.1			>100-cm-d.b.h. Douglas-fir density	4.3
Shade-intolerant tree spp. basal area	2.1	Resinosis, Douglas-fir	2.6	Evergreen shrub cover C.V.	2.8			F and H litter layer depth	3.8
		Multiple-stem crowns	2.6					Sweeping boles, Douglas-fir (%)	3.7
		Snags with excavated cavities	2.4					Evergreen shrub cover (%)	3.6
		>50-cm-d.b.h. snags with excavated cavities	2.8					Herb cover (%)	3.2
		Sweeping boles, Douglas-fir	2.1					Broken-topped crowns (%)	3.2
								Conks on lower bole (%)	3.0
								Dead-topped crowns(%)	2.9
								Broad-leaved tree spp. basal area (%)	2.5
								&Q-cm-diameter logs C.V. density	2.4
								Snag volume	2.1

[a] All variables are percentages.

Cascades, where it increased with site moisture. Evergreen shrub cover tended to be higher on dry sites in all provinces. Canonical variates analysis indicated that two variates were required to account for most of the variation between the classes (table 7). Cover of graminoids was most closely related to the first canonical variate, and cover of evergreen shrubs was related to the second variate. Ordination of the stands along the first two variates separated the Coast Range stands from the Cascade stands and suggested a gradient of increasing moisture from top to bottom (fig. 4c).

Debris-The combined depth of the F and H litter layers and the density of medium-diameter logs were important in the discriminant model (table 5). The litter layers were generally thinnest in the Coast Range and thickest in the Washington Cascades, except on moist sites, where the litter layers of the Oregon Cascades were thickest (table 6). The forest floor depth was typically highest on moist sites and lowest on dry sites, except in the Coast Range. Snag volumes were highest in the Washington Cascades on all sites and highest on moist sites in all provinces.

Depth of the F and H litter layers and the density of medium-diameter logs were related to the first and second canonical variate (table 7). Ordinations of stands along the first canonical variate (fig. 4d) separated Coast Range stands and dry Oregon stands, which had relatively thin litter layers and low amounts of coarse woody debris, from all other classes. As with the other discriminant models, dry old growth in the Washington Cascades was more similar to moderate sites in Washington and Oregon than to dry sites in the other provinces.

Table 6—Means[a] and confidence limits[b] for characteristics selected in stepwise discriminant analyses of province-moisture-classes of old-growth forests

	Moisture-class								
	Dry			Moderate			Moist		
Characteristic[c]	Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
Overstory:									
Shade-tolerant tree spp. basal area	29 (13-51)	2.3 (0-11.0)	2.2 (0-10.9)	36 (23-53)	20 (11-33)	16 (6-32)	60 (38-86)	39 (26-55)	31 (10-63)
Broad-leaved tree spp. basal area	<0.1 (0-0.1)	<0.1 (0-0.1)	0.3 (0-36.1)	<0.1 (0-0)	<0.1 (0-0)	0.1 (0-8.0)	<0.1 (0-0.1)	<0.1 (0-0.1)	0.1 (0-30.1)
>100-cm-d.b.h. Douglas-fir density	5.6 (0.05-20.4)	18 (5-41)	29 (11-57)	15 (6-29)	21 (10-36)	24 (9-46)	15 (1.6-24.9)	20 (10-34)	18 (2-25)
Density subcanopy trees	86 (14-218)	67 (6.9-187)	43 (1-145)	36 (5-94)	29 (3-83)	53 (5-151)	0.6 (0-31)	23 (2-70)	0
Total basal area	56 (39-79)	61 (43-87)	65 (46-93)	70 (56-89)	73 (58-93)	70 (51-96)	90 (66-124)	81 (65-101)	72 (45-115)
>100-cm-d.b.h. tree density	7.6 (0.4-23.7)	22 (7-46)	30 (11-58)	22 (11-37)	25 (13-41)	27 (11-51)	32 (15-56)	32 (19-49)	25 (5-62)
Shade-intolerant tree spp. basal area	26 (0-52)	58 (32-84)	60 (34-85)	33 (15-50)	53 (36-70)	51 (27-74)	30 (8-52)	43 (26-59)	39 (4-73)
Stand condition:									
Root-collar cavities (%)	24 (7-52)	3.6 (0-17.9)	2.9 (0-16.2)	22 (10-39)	13 (4-26)	8.6 (0.7-25.5)	27 (10-52)	14 (5-28)	19 (2-57)
Arching boles (%)	2.4 (0-9.4)	1.5 (0-7.7)	11 (3-24)	1.8 (0.1-5.6)	2.3 (0.2-6.4)	9.4 (2.8-19.9)	2.3 (0-8.2)	1.8 (0.1-5.4)	4.8 (0-18)
Conks on lower bole (%)	0.5 (0-2.9)	2.4 (0.3-6.5)	5.9 (2.0-11.8)	0.4 (0-1.6)	0.6 (0-2.1)	1.0 (0-3.8)	0.2 (0-1.8)	1.0 (0.1-2.7)	0.8 (0-5.0)
Dead-topped crowns (%)	4.0 (0.9-9.4)	2.0 (0.1-6.2)	1.9 (0.1-6.1)	3.4 (1.3-6.6)	2.6 (0.8-5.4)	1.0 (0-3.8)	2.5 (0.5-6.3)	3.9 (1.7-7.0)	0.3 (0-3.7)
Snags with natural cavities (%)	11 (0-37)	13 (1-40)	22 (4-54)	18 (6-36)	2.8 (0-12.1)	14 (2-39)	20 (5-50)	13 (3-28)	20 (1-66)
Broken-topped crowns (%)	4.2 (0.8-10.4)	4.8 (1.0-11.3)	6.1 (1.7-13.3)	5.5 (2.4-10.0)	8.3 (4.4-13.4)	4.4 (1.1-10.0)	5.9 (2.0-11.8)	9.7 (5.6-14.9)	8.4 (1.8-20.0)
Resinosis, Douglas-fir (%)	0.3 (0-6.8)	2.2 (0-12.1)	5.7 (0.1-19.5)	0.9 (0-5.2)	1.0 (0-5.5)	6.3 (0.5-18.9)	0.1 (0-4.4)	3.6 (0.4-10.1)	0.7 (0-12.5)
Multiple-stemmed crowns (%)	5.3 (0.6-14.8)	1.4 (0-7.4)	10 (3-23)	3.6 (0.8-8.6)	4.3 (1.1-9.6)	8.4 (2.3-18.4)	4.2 (0.5-11.4)	2.7 (1.8-10.8)	5.8 (0.1-20.0)
Snags with excavated cavities (%)	10 (0-33)	13 (1-38)	19 (3-48)	5.9 (0.5-17.3)	3.6 (0-13.2)	10 (1-30)	5.5 (0-21.0)	3.0 (0-11.5)	16 (0-57)
Snags >50-cm-d.b.h. with excavated cavities (%)	16 (0-69)	15 (0-64.5)	11 (0-57)	3.9 (0-22.9)	2.7 (0-20.1)	35 (4-94)	8.9 (0-43.9)	2.6 (0-18.6)	28 (0-120)
Sweeping boles, Douglas-fir (%)	24 (3-62)	16 (1-50)	20 (2-57)	21 (6-44)	11 (2-29)	23 (4-57)	12 (1-37)	5.0 (0.2-18)	23 (1-78)

See footnotes on next page.

Table 6—continued

	Moisture-class								
	Dry			Moderate			Moist		
Characteristic[c]	Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
Understory:									
Graminoid cover (%)	<0.01 (0-0.01)	0.3 (0-16.8)	0.7 (0-36.6)	<0.01 (0-0.01)	<0.01 (0-0.01)	0.1 (0-26.2)	0.04 (0-1.3)	<0.01T0.1 (0-0.01)	(0-26.2)
Total vegetation cover (%)	49 (20-91)	43 (16-83)	72 (36-122)	42 (23-67)	54 (32-82)	51 (24-90)	44 (20-78)	64 (41-93)	66 (22-134)
Evergreen shrubs cover (%)	21 (5-49)	17 (3-43)	34 (12-68)	12 (3-25)	18 (7-34)	21 (6-45)	2.3 (0-12.8)	16 (7-31)	1.2 (0-18.3)
Deciduous shrub cover (%)	14 (4-50)	11 (3-38)	21 (6-73)	16 (7-37)	9.5 (4-22)	6.7 (2.0-21.0)	13 (4-37)	15 (7-33)	9.0 (2.0-49.0)
Herb cover (%)	6.3 (1.9-21.1)	4.9 (1.5-16.4)	3.5 (1.1-11.7)	6.8 (3.0-15.2)	7.3 (3.3-16.5)	3.9 (1.3-11.5)	11 (3.9-31.3)	17 (7.8-36.6)	5.0 (0-25.1)
Subcanopy tree sapling density	169 (14-498)	194 (21-540)	13 (0-169)	25 (0-127)	30 (0-138)	7.1 (0-123.1)	4.4 (0-103.3)	61 (3-190)	0.8 (0-168.6)
C.V. evergreen shrub cover (%)	78 (36-136)	72 (32-129)	62 (25-115)	97 (63-139)	65 (38-99)	102 (56-161)	148 (94-215)	79 (50-115)	133 (59-236)
Debris:									
F and H litter layer depth	28 (11-52)	14 (4-33)	7.7 (0.7-22.0)	29 (17-45)	22 (12-36)	5.2 (0.3-16.2)	35 (18-58)	39 (25-55)	7.0 (0-27.0)
30- to 60-cm-diameter log density	163 (80-335)	70 (34-144)	61 (30-125)	225 (139-365)	152 (94-247)	124 (65-238)	226 (122-422)	162 (102-257)	138 (53-362)
Snag volume	170 (64-447)	64 (25-170)	71 (27-188)	232 (121-145)	202 (105-387)	166 (69-393)	290 (125-670)	207 (112-385)	208 (56-764)
Decay-class 5 snag volume	5.9 (0-34.5)	5.2 (0-32.6)	1.7 (0-22.5)	24 (7-52)	23 (6-61)	10 (0-39)	8.1 (0-33.9)	24 (8-51)	12 (1-66)

[a] Means are back-transformed to linear values from either a logarithmic or square root transformation.
[b] 95% confidence limits of the mean, Scheffe's procedure. Limits are asymmetrical about the mean because of transformations.
[c] Units: basal area in square meters per hectare; density in number per hectare; volume in cubic meters per hectare; litter depth in millimeters.

Combined variable set—Basal area of shade-tolerant trees, cover of deciduous shrubs, and density of large-diameter trees were important in the discriminant model (table 5). The first canonical variate, which explained only 37 percent of the variance between classes, was related to basal area of shade-tolerant trees, depth of the F and H litter layer, and basal area of broad-leaved trees (table 7). The second canonical variate was related to basal area of shade-tolerant trees, density of subcanopy trees, and cover of evergreen shrubs. Ordinations of stands along the two variates again resulted in relatively good separation of Coast Range stands and dry Oregon stands from the other classes, as well as better separation of the other classes, than had been achieved by the models that used individual variable sets (fig. 4e). Site moisture appears to increase from upper left to lower right.

Classification error among attribute sets—Analysis of total error rates of classification indicated that the province-site moisture types were not easily distinguishable (table 8). The combined-attribute set and the overstory set provide the best discriminant models, although the successful percentages were relatively low. When just the three province-classes were considered, the success of the discriminant models was considerably better, especially for the combined-attribute and stand-condition models (table 8). When the three site moisture-classes were considered alone the models were not very successful in discriminating these classes, even for the combined-attribute model. These results suggest that differences in old-growth habitat structure are driven more by geographic variation than by variation associated with local-site moisture and that combinations of several different attribute types are needed to resolve the differences. The

Table 'I-Percentage of explained variance and correlation coefficients *(r)of* the first 3 canonical variates of analyses of province-moisture-classes based on different sets of characteristics (only the 2 highest correlations are shown for each canonical variate except for the combined analysis sets where variables with the 4 highest correlations are shown)

Characteristic	Variate 1	Variate 2	Variate 3
Overstory:			
Percentage of variance explained	49	2s	11
Correlation coefficients			
Shade-tolerant tree spp. basal area	0.97	0.09	-0.06
Shade-intolerant tree spp. density	0.50	0.16	0.14
Tree d.b.h. standard deviation	0.16	0.53	0.29
Subcanopy tree spp. density	-0.34	-0.53	0.07
Broad-leaved tree spp. basal area	-0.44	0.48	0.45
>100-cm-d.b.h. Douglas-fir density	-0.31	0.20	0.29
Stand condition:			
Percentage of variance explained	51	18	11
Correlation coefficients			
Conks on lower boles (%)	0.63	-0.26	0.23
Arching boles (%)	0.56	0.33	0.003
Snags SO-cmd.b.h. with excavated cavities (%)	0.27	0.47	0.02
Sweeping boles, Douglas-fir (%)	0.11	0.45	0.15
Snags with natural cavities (%)	0.11	0.23	0.52
Trees with swollen knots (%)	0.27	-0.10	-0.46
Understory:			
Percentage of variance explained	44	30	13
Correlation coefficients			
Graminoid cover (%)	0.82	0.08	-0.30
Herb cover (%)	-0.46	-0.24	0.21
Evergreen shrub cover (%)	0.11	0.69	0.47
Total vegetation cover (%)	0.15	-0.02	0.44
Evergreen shrub cover C.V. (%)	0.02	-0.55	-0.61
Debris:			
Percentage of variance explained	48	30	12
Correlation coefficients			
F and H litter layer depth	0.83	-0.54	-0.03
30- to 60-cm-d.b.h. log density	0.80	0.25	0.14
Snag volume	0.68	0.32	0.07
Decay class 5 snag volume	0.44	0.10	-0.64
>6O-cm-diameter log density C.V.	-0.55	-0.03	0.46
Combined set:			
Percentage of variance explained	37	22	16
Correlation coefficients			
Shade tolerant spp. basal area	0.72	-0.58	0.14
F and H litter layer depth	0.70	0.04	0.42
Broad-leaved tree spp. basal area	-0.63	-0.14	-0.13
Conks on lower bole (%)	-0.53	0.34	0.13
Subcanopy tree density	0.06	0.50	-0.24
Evergreen shrub cover (%)	-0.25	0.47	0.03
Snag volume	0.43	-0.44	0.03
Sweeping boles (%)	0.10	0.53	-0.48
Herb cover (%)	0.36	-0.13	0.47
Broken-topped crowns (%)	0.02	-0.16	0.42
>100-cm-d.b.h. tree density	-0.17	-0.22	0.41

results also suggest that the broad moisture-classes developed in each province are not comparable across provinces or even within large provinces, such as the Oregon Cascades.

Of the three provinces, the Coast Range old-growth types were most successfully identified in the discriminant model based on combined attributes (table 9). The Washington Cascade old-growth types were the next most-successfully classified types-except for Washington dry old-growth types, which were often classified as dry or moderate Oregon Cascade types. The moderate and moist Oregon Cascade types were not distinctive in the models; the moderate types often were classified as other Cascade moisture types or Coast Range types, and the moist types often were classified as other Oregon Cascade types or Washington Cascade types. These results suggest that the Oregon old-growth types are somewhat intermediate in habitat structure between the Washington types to the north and the Coast Range types to the south and west.

Discussion

Limitations of the Chronosequence

In characterizing habitat structure in relation to stand age, the assumption has been that space can be substituted for time-an assumption that is violated to different degrees in most chronosequence studies because of differences in site and stand history. In this study, the effects of site differences were controlled somewhat by maintaining similar levels and ranges of site characteristics across the age-classes. Stand history could not be controlled except by restricting the stands primarily to those that regenerated naturally after stand-replacing wildfire. Differences in climate, establishment, and subsequent minor and moderate rates of disturbance also could not be controlled and can leave a strong imprint on stand structure (Spies and others, unpubl. manuscript). Given these caveats, successional interpretation of differences in age-classes must be made with caution..

Differences Amcmg Age-classes

Multivariate analyses indicated that forest habitat structure differs among age-&asses in numerous ways. The variables selected by stepwise discriminant analyses were not the only variables that exhibited significant differences among age-classes. They have high discriminating power, but are not necessarily the most discriminating set (Legendre and Legendre 1983). Other variable sets that were not selected may have equal or possibly somewhat greater discriminating power, and the subset of variables selected by the stepwise process is not stable against small changes in the, data set (SAS 1987). Variables with the highest F values, however, typically stable against small changes in the sample set, and the general kind of variables selected were very stable against changes in sample sets. Several different stepwise analyses run on different subsets of the data, for example,

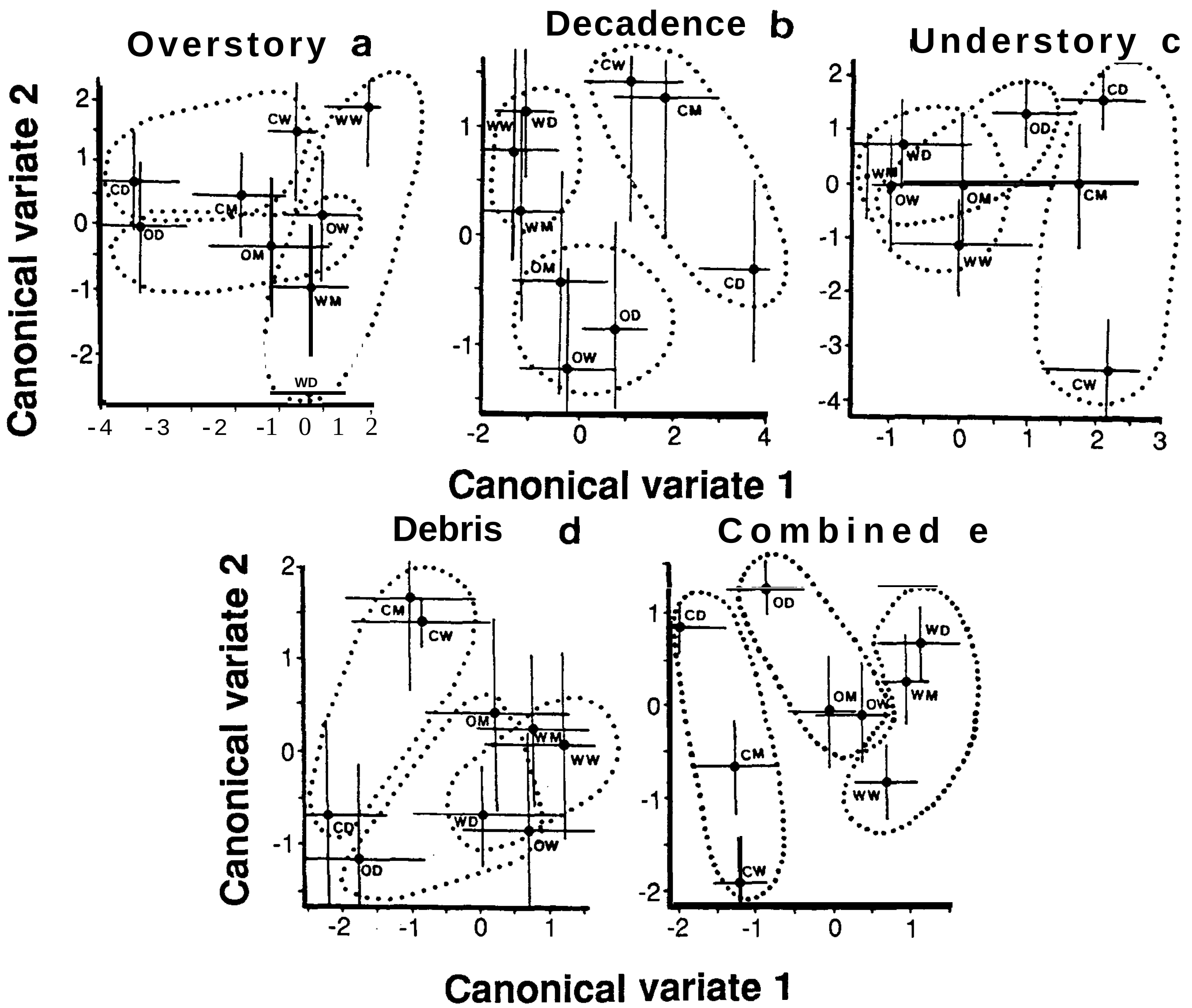

Figure 4-Ordinations of province-moisture class means (with standard deviations) of old-growth stands along first two canonical variates from analyses of overstory attributes (a), stand-condition attributes (b), understory attributes (c), debris attributes (d), and a combination of all attribute-sets (e). First letter indicates province: Oregon Cascades (0); Washington Cascades (W); Coast Range (C). Second letter indicates moisture class: Dry (D), Moderate (M), Moist (W). Dotted lines encompass province distributions.

still indicated that overstory attributes had the highest discriminating power. These characteristics of the analyses suggest generalizing the results not on the basis of the discriminating power of a single specific structural attribute or exact size-class of attributes, but rather on the general type or gross features of the attributes.

The high discriminating power of overstory attributes for age-classes is not surprising because the age-classes were based on the age of overstory trees. Within the overstory set, two general processes contribute to the structural changes. The first is associated with stand development: the decline in stand density and the increase in tree size. The second is more related to successional changes: the increase in variation in tree diameter as the density of large-diameter Douglas-firs increases and the density of smaller-diameter, Shade-tolerant trees increases. Variation in tree diameter increased strongly with succession, but diversity of tree heights (H') did not, which probably reflects the fact that the Height-classes were too broad to be sensitive to height diversity.

Table S-Summary of discriminant classifications of province-moisture-classes based on different sets of attributes

From classes	Percentage classified into class by discriminant function Variable set Overstory	Stand condition	Understory	Debris	Combined
Nine province- and moisture-classes	44	33	42	30	56
Three province-classes alone	66	71	61	56	81
Three moisture-classes alone	57	43	58	55	65

Table 9-Summary of discriminant classifications of province- and moisture-classes based on combined sets of attributes[a]

From class		Percentage classified into class by discriminant function								
		Dry			Moderate			Moist		
Moist	Province	Washington	Oregon	Coast	Washington	Oregon	Coast	Washington	Oregon	Coast
DRY	Washington	44	44	0	0	11	0	0	0	0
DRY	Oregon	0	**67**	33	0	0	0	0	0	0
DRY	Coast	0	11	67	0	0	22	0	0	0
Moderate	Washington	20	**5**	0	50	10	0	**10**	5	0
Moderate	Oregon	0	15	0	0	35	10	0	30	10
Moderate	Coast	0	0	0	0	0	91	0	0	9
Moist	Washington	0	0	0	17	8	8	58	8	0
Moist	Oregon	5	**5**	0	5	14	5	14	55	0
Moist	Coast	0	0	0	0	20	0	0	0	**80**

[a] Values in bold type indicate correctly classified percentages.

The developmental and successional changes of stands, which are described above, account for most of the variation in overstory structure associated with stand age.

Debris attributes were not as powerful in discriminating the age-classes. This difference is probably because the time since disturbance provides a better measure of debris amounts than does stand age (Spies and others 1988). Woody debris attributes operate with a different cycle than overstory attributes. Woody debris amounts actually are highest early in succession and lowest in mid-succession for many Douglas-fir ecosystems. This difference produces a more U-shaped pattern of development with stand age, which tends to reduce the discriminating power of these characteristics for natural forest age-classes. Because natural disturbances typically do not destroy much of the debris biomass in large pieces of wood, these features are present in natural stands of all ages to some degree (Spies and others 1988).

Stand-condition attributes alone did not exhibit good discriminatory power, probably because of high variability associated with non-age-related factors. Characteristics such as percentage of broken-topped crowns increased with stand age; however, topography and the history of windstorms at a site are likely to play an equally important role. The difficulty of observing tall canopies from the ground may also have contributed to the poor discrimination.

Understory characteristics exhibited the lowest discriminatory power for age-classes. Although forest understories are likely to be strongly controlled by the overstory, the important overstory characteristics are not necessarily closely linked to stand age. Overstories casting dense shade, for example, may occur in dense, young Douglas-fir stands and in old-growth stands with dense hemlock canopies. Despite their low discriminatory power, many of the understory characteristics exhibited trends associated with the age-classes.

Among the strongest trends in understory characteristics was the increase in percentage of herb cover with stand age-class. An increase in herb cover in late-successional forests has been observed in Sitka spruce-western hemlock forest in southeastern Alaska (Alaback 1982). Higher herbaceous cover in old growth might be explained by changes in understory light intensity and microclimate. Light intensity under old-growth forest canopies dominated by western hemlock is lower than under mature or young forest canopies dominated by Douglas-fir (Spies and others 1990). Low light might favor more shade-tolerant herbs over evergreen shrubs such as salal that often form dense clonal patches in mature- and young-forest understories. The more competitive, light-demanding shrubs such as salal could limit the development of herbaceous plants in the understories of younger forests (Long and Turner 1974). In addition, a more moderated microclimate in old-growth understories might favor more mesic understory species.

The high discriminatory power of overstory attributes does not mean that other attributes are unimportant in characterizing the habitat structure of natural young, mature, and old-growth forests. Other attributes with more subtle changes or greater variability can play important roles in the habitat and ecosystem function of these forests. These characteristics must be considered along with the characteristics of the overstory when habitat relations and land-management objectives are identified. The discriminatory power of the overstory attributes, however, can be used advantageously when simple indicators of forest habitat condition are sought, such as when aerial-photo inventories of habitat conditions over large areas are needed. We can infer that overstory characteristics such as densities and sizes of trees might be reasonably successful in identifying old-growth habitat from aerial photographs.

Regional and Site Differences in Old-Growth Forests

The study indicates that regional gradients exist in the structure of old-growth forest habitat, and to a lesser degree, gradients in structure occur within provinces in relation to site moisture. Given the large geographic area covered in the study, finding regional patterns stronger than within-region site differences is not surprising.

One of the prime drivers of habitat differences among the provinces was the basal area of shade-tolerant trees, primarily western hemlock. The study area ranged from near the southem limit of the species toward the middle part of its range (Harlow and Harrar 1969). This area encompasses relatively steep gradients in species composition and stand structure (Franklin and Dymess 1973).

Disturbance history also plays a role in the regional differences. The southern and eastern Coast Range, where most of the Coast Range stands were located, probably has experienced more fires in the last several hundred years than the two Cascade provinces (Juday 1976). Fire disturbance is evidenced by the fact that fire-sensitive subcanopy trees and shade-tolerant trees such as western hemlock are less common in the Coast Range than in the Cascades; forest floor layers are much thinner there, and the percentage of Douglas-firs with fire scars on moderate sites in the Coast Range was 1.6 but only 0.4.and 0 on similar sites in the Oregon and Washington Cascades. Stand ages of old growth in the Coast Range are younger, averaging 330 years compared with over 420 years for the Cascade Range stands (Spies and others 1988).

Differences in climate and site productivity also played a role in the regional patterns that were observed. Coast Range stands averaged almost 400 meters lower in elevation than Cascade stands, and winter minimum temperatures are 2 to **5** °C higher than in the Cascades (Franklin and Dymess 1973). Trees can grow faster in the Coast Range than in the Cascades, which is evidenced by the relatively high densities of large-diameter (>100 cm in d.b.h.) trees in the Coast Range, despite the younger average stand age.

Differences in the moisture-related habitat structure of sites were not as great as regional patterns, but several general trends were apparent. The overstories on dry sites generally have a low abundance of shade-tolerant species, which probably reflects drier conditions, greater fire frequencies, and younger stand ages. The low density of shade-tolerant species on these sites suggests that canopies are more open, which allows greater understory development. The greater density of subcanopy trees such as chinkapin or possibly Pacific dogwood on these sites, and the relatively high cover of total understory vegetation and graminoids supports this conclusion. Moist old-growth sites, by contrast, have relatively high cover of herbaceous species. The relatively high cover of evergreen shrubs on drier sites follows a similar finding by Zobel and others (1976) for the central Oregon Cascades, although they primarily associated the higher evergreen understory cover with low nitrogen availability.

Differences in debris characteristics associated with moisture conditions of sites have been identified by Spies and others (1988). Amounts of debris and numbers and sixes of debris pieces generally increase with site moisture, probably as a result of higher site productivity, lower fire frequencies (which can consume some of the wood), and possibly because of lower rates of decay resulting from excessively high moisture in the wood (Harmon and others 1986). Thicker litter layers on moist sites probably reflect the infrequency of fire and higher litter-fall rates associated with dense canopies of western hemlock and other shade-tolerant species.

Differences in stand condition across moisture-classes were associated with either species-composition differences, age/disturbance factors, disease, or tree vigor. The higher percentage of root-collar cavities on moderate and moist sites is related to the higher abundance of western hemlock on these sites. The higher incidence of broken tops on moderate and moist sites, which contain the oldest trees, may be related to the fact that with increasing age, trees are more likely to experience wind storms that cause crown damage. The higher incidence of fungal conks on dry sites, which are characterized by steep south and west-facing slopes, is similar to the findings of Boyce and Wagg (1953) who observed a higher incidence of conk rot in old-growth Douglas-fir on steep slopes and southerly aspects. Our percentages of fungal conk incidence (1 to 6 percent) are much lower than the percentage incidence of conk rot (Boyce and Wagg 1953), but we surveyed only the lower one-third of the tree boles for fungal conks, which are only one indicator of the disease.

Conclusions and Management Implications

The structure of natural Douglas-fir forests in western Oregon and Washington is extremely diverse because of numerous processes operating at different spatial and temporal scales. Stand development and succession are important processes that determine forest habitat; however, regional flora, disturbance, local site potential, and climatic patterns are also important. We should not assume that the old-growth forest structure will be the same at one location or area as at another until we have a better understanding of how these processes interact and affect structure. Nor should we assume that the young and mature forests of today will produce the same old-growth forest structure in the future as the one that we see today. Management of old growth in western Oregon and Washington should be sensitive to the regional diversity of old-growth conditions. It should recognize the fact that natural young and mature forests have also provided important habitat and ecosystem functions that may be lost if only old-growth forest areas are used to provide habitat diversity for an entire landscape.

These results indicate that differences in forest structure associated with stand age and regional and local geography are numerous; they are characterized by multiple continua in forest structure rather than discrete classes. Changes in forest habitat structure do not stop when stands become 200 years old, the age often used for the onset of old-growth conditions. The results of this study suggest that structural changes continue until stands are at least 400 to 500 years. Additional changes likely happen after this time, but they may be more gradual and may move toward less structural diversity as stands become dominated by western hemlock and other shade-tolerant species.

The variability in old-growth forest structure strongly suggests varied developmental histories. Many, if not most, old-growth stands have been affected by low to moderate amounts of disturbance during their histories. Such disturbances have contributed to the development of multiple size- and age-classes. Structurally distinguishing old-growth stands with continuous age-class distributions from those composed primarily of a few (3 to 5) tree cohorts may be difficult, but this difficulty suggests that one method for creating stands that resemble old growth is to leave an overstory of dominant green trees at the time of final cutting.

The young and mature stands examined in this study are not the equivalent of intensively managed, even-aged plantations. Many natural young and mature stands have some of the attributes of old-growth stands that may not be present in young, managed stands. Perhaps the greatest difference between natural and managed stands is the lower number and volume of large snags and logs in managed plantations (Spies and Cline 1988). Many young natural forests less than 80 years old have high amounts of carry-over of woody debris, although some young natural stands have little carry-over (Spies and others 1988). Other structural differences between young and mature natural forests and their managed equivalents are less well known. Managed plantations, however, generally will have fewer tree species, more uniform tree sizes and spacing, and no large remnant overstory trees. Understories of young natural and managed stands may be less spatially heterogeneous if overstory density is controlled. Over several rotations, a decline in the population of some understory species may occur if those species are sensitive to the short interval between major canopy and forest-floor disturbances in short-rotation plantations.

The concept of the "intensively managed stand" is, however, an ideal that has not yet been realized in many forests. It is also subject to change if management objectives are broadened to include a greater array of ecological values. Lessons from the natural forests in this study will be useful as our concept of forest management evolves with society's needs.

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Appendix

Table 10-Tree life form groups used in analysis

Shade-intolerant dominant trees:
- Subalpine fir
- California red fir
- Noble fir
- Incense-cedar
- Engelmann spruce
- Sitka spruce
- Sugar pine
- Western white pine
- Douglas-fir

Shade-tolerant dominant trees:
- Pacific silver fir
- White fir
- Grand fii
- Port-Orford-cedar
- Alaska-cedar
- Western redcedar
- Western hemlock
- Mountain hemlock

Table 10-continued

Subcanopy trees:
- Pacific madrone
- Golden chinkapin
- Pacific dogwood
- Western hemlock

Broad-leaved dominant trees:
- Bigleaf maple
- Red alder
- Oregon ash
- Tanoak
- Bitter cherry
- Oregon white oak
- Willow
- California-laurel

Table ll-Variables used in stepwse discriminant analyses

Overstory (>5-cm-d.b.h.)	Stand condition*	Understory	Debris
Total basal area	Broken-topped crowns, Douglas-fir	Shade-tolerant sapling density	F and H litter layer depth
Tree density	Broken-topped crowns, all spp.	Subcanopy sapling density	Snags SO-m-tall density
Basal area, standard deviation	Sweeping boles, Douglas-fir	Cover vegetation c2 m tall (%)	10- to 30-cm-diameter log C.V. density
Tree density, standard deviation	Sweeping boles, all spp.	C.V. herb cover	30- to 60-cm-diameter log C.V. density
Tree d.b.h. mean	Multiple-stemmed crowns, all spp.	Lichen cover (%)	Snag >5-m-tall and 50-cm-d.b.h. density
Tree d.b.h. standard deviation	Multiple-stemmed crowns, Douglas-fir	Moss cover (%)	5-to 15-m-tall snag density
Number of overstory trees	Dead-topped crowns, Douglas-fir	Fern cover (%)	SO-cm-d.b.h. snag density
Trees >100-cm-d.b.h. density	Dead-topped crowns, all spp.	Herb cover (%)	Snags >50-cm-d.b.h. density
Tree height diversity (H') based on basal area	Broken-topped crowns with upturned leaders, Douglas-fir	Evergreen shrub cover (%)	10- to 30-cm-diameter logs density
Tree height diversity (H') based on stem density	Broken-topped crowns with upturneds leaders, all spp.	Deciduous shrub cover (%)	30- to 60-cm-diameter log density
Douglas-fir basal area	Forked bole	Total understory cover (%)	60-cm-diameter log density
Douglas-fir >100-cm-d.b.h. density	Arching boles.	C.V. evergreen shrub cover	Decay-class 1 log volume
Shade-tolerant tree spp. basal area	Boles with fall scars, Douglas-fir	C.V. deciduous shrub cover	Decay-class 2 log volume
Shade-intolerant tree spp. basal area	Boles with fall scars, all spp.	C.V. >2-m-tall vegetation cover	Decay-class 3 log volume
Subcanopy tree spp. basal area	Trees with swollen knots, Douglas-fir		Decay-class 4 log volume
Broad-leaved tree spp. basal area	Conks on lower boles, Douglas-fir		Decay-class 5 log volume
Shade-intolerant tree spp. density	Conks on lower bole, all spp.		Decay-class 1 snag volume
Shade-tolerant tree spp. density	Resinosis, Douglas-fir		Decay-class 2 snag volume
Subcanopy tree spp. density	Resinosis, all spp.		Decay-class 3 snag volume
Trees with root-collar cavities	Trees with excavated cavities		Decay-class 4 snag volume
Trees with natural cavities	Snags with natural cavities		Decay-class 5 snag volume
Snags with excavated cavities	Snags >50-cm-d.b.h. with excavated cavities		Ratio log-volume decay-class 4 + 5 to total log volume
	Snags >50-cm-d.b.h. with natural cavities		Log volume
			Snag volume
			Snag volume (C.V.)

[a] All variables are percentages.

Plant Species Diversity and Occurrence in Young, Mature, and Old-Growth Douglas-Fir Stands in Western Oregon and Washington

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Abstract

The objective of the study was to characterize differences in vascular plant diversity and species abundance among young (30-80 years old), mature (80-195 years old), and old-growth (195-900 years old) Douglas-fir forests. A chronosequence of Douglas-fir stands was sampled in each of three physiographic provinces: southern Washington Cascade Range; Oregon Cascade Range; and southern Oregon Coast Range. The cover of all vascular plants was recorded in 177 stands, each consisting of 4 to 5200 m^2 plots. Measures of species diversity were calculated for the overstory and understory strata of each stand. Species diversity in the three provinces showed an age-class effect ($P < 0.1$) in 6 of the 12 tests performed. Diversity tended to remain constant or increase slowly with age-class. The frequency of occurrence of species showed an age-class effect ($P < 0.1$) in 15 to 20 percent of understory species tested in the three provinces. Similar results were obtained in analyses based on species cover, although relative differences between old growth and the other age-classes were greater. Species occurring with greatest frequency and abundance in old growth included Pacific yew, an understory *tree;* Cornus *canadensis*[1] and *Tiarella trifoliata var unifoliata,* understory herbs; and *Lobaria* spp., foliose canopy lichens. Four factors contributing to late-successional change in these communities are hypothesized: changes in resources, changes in horizontal heterogeneity, changes in vertical heterogeneity, and long periods without intense fire.

Introduction

The plant compositional changes during the middle to late stages of succession in Douglas-fir forests are poorly known. Most research has concentrated on early successional changes after catastrophic disturbances (Dyrness 1973, Halpern 1987, Isaac 1940, Long 1977). These studies have focused on the first 50 years of a potentially 1000-year-long ecological process-less than a twentieth of the sere!

Plant species diversity within stands appears to be highest in the early stages of succession in western coniferous forests (Habeck 1968, Schoonmaker and McKee 1988), and plant community changes are rapid during the early stages of succession (Long 1977). After canopy closure, less dramatic

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[1] In this botanical chapter, herbaceous plants and lichens are referred to by their scientific names for accuracy and the convenience of readers.

but distinct changes may continue for many centuries. For example, in Sitka spruce-hemlock forests, where stand development requires hundreds of years, understory communities continue to change for at least 300 years (Alaback 1982). Stewart (1986a, in press) reported that canopy structure and composition influenced understory development in several mature and old-growth Douglas-fir stands in the Oregon Cascades.

Few examples of plants that are restricted to old-growth Douglas-fir forests or find optimal habitat in old growth have been reported. Franklin and others (1981) suggest that some mycotrophic plants, such as pinesap, and lichens, such as *Lobaria oregana* find optimal habitat in old growth, but they do not present any data. Moir and others (1979) reported that *Tiarella unifoliata* had higher cover in old than in young growth in a chronosequence of stands on similar sites from Mount Rainier National Park. No plant community studies have reported how diversity measures change with time in the later stages of Douglas-fir forest succession.

The objective of this study was to contrast the composition of natural young, mature, and old-growth Douglas-fir stands in western Oregon and Washington, emphasizing distinctive features of old growth. The specific objectives were to characterize the species diversity in overstories (tree stratum) and understories (herb, shrub, and seedling stratum) of the three forest age-classes, and to identify plant species that differ in frequency of occurrence and abundance among the forest age-classes.

Study Area

The study was conducted in Douglas-fir-dominated stands in Washington and Oregon in three physiogmphic provinces: the southern Washington Cascade Range, the Oregon Cascade Range, and the southern half of the Oregon Coast Ranges (Franklin and Dymess 1973). These provinces are all characterized by steep, deeply dissected terrain with well-developed soil. Parent materials are Tertiary basalts and andesites in the Cascade Range and early Tertiary sedimentary rocks in the Coast Range. The climate is mild and wet in winter and cool and dry in summer. Annual precipitation is heavy, ranging from 800 to over 3000 mm. Highest amounts of precipitation occur near the upper western slopes of the Coast Range and in the Cascade Range in Washington and northern Oregon (Franklin and Dymess 1973). Lowest precipitation occurs on the eastern slopes of the Coast Range and in the southern Oregon Cascades.

The study area primarily encompasses the Western Hemlock Zone and the lower elevational portion of the Pacific Silver Fir Zone (Franklin and Dymess 1973). Western hemlock and Pacific silver fir are the climax species on most sites in these zones; on dry sites, Douglas-fir may be climax. In southern Oregon, the northern fringes of the Mixed Conifer Zone (Franklin and Dymess 1973) were sampled. In the Coast Range, the eastern margin of the Sitka Spruce Zone was sampled.

Most Douglas-fir stands in the region originated after catastrophic wildfire (Franklin and Hemstrom 1981); see Franklin and Dymess (1973) for a generalized, natural successional sequence. Young stands originating from wildfires are typically dominated by Douglas-fir, although western hemlock or red alder may dominate in some areas. By 200 years, many stands exhibit old-growth characteristics (Franklin and others 1981; Spies and Franklin, this volume), such as codominance of western hemlock in the overstory, diverse vertical foliage distribution, and large accumulations of woody debris (Spies and others 1988). True “climax” forests composed entirely of shade-tolerant species are rare because pioneer Douglas-fir can persist in stands for over 1000 years (Franklin and DeBell 1988), and wildfires have occurred more frequently than this on most sites.

Methods

General Design

A total of 196 Douglas-fii stands in Washington and Oregon representing different ages (40 to 900 years) and site conditions were sampled during 1983 and 1984 (for a map of the stand locations, see Spies and Franklin, this volume). All stands originated after wildfires, which killed most or all of the overstory trees. Where remnant old-growth trees occurred in young and mature stands, their densities were typically less than 1 per 10 ha. Similar geographic distribution among ages of sampled stands was maintained by sampling in areas in each province that contained all three of the following broad age-classes: young (<80 years), mature (80-195 years), and old-growth (>195 years). These age-classes were then used in the analyses.

To control site variation across the age-classes, a subset of 177 stands were selected based on field observations, site data, and DECORANA ordinations (Spies and Franklin, this volume). In general, the age-classes in a province had similar means and ranges of site conditions (table 1). Drier and wetter plant associations were sampled in old-growth stands (Spies and Franklin, this volume) but were not included in the chronosequence analysis. Old-growth stands occurred on slightly drier aspects than mature or young stands in the Washington Cascades and were intermediate to young and mature stands in the other provinces. Old growth did tend to occur at slightly lower topographic positions, but elevations and slope percentages were intermediate to young and mature stands. Plots from DECORANA ordinations (fig. 2, in Spies and Franklin, this volume) indicated that the overall vegetation composition was similar among the age-classes.

Table 1—Means and ranges of age and site characteristics for young (Y), mature (M), and old-growth (O) stands in 3 physiographic provinces

	Washington			Oregon			Coast		
Characteristic	Y	M	O	Y	M	O	Y	M	O
Stand age (yr)									
mean	65	130	425	60	115	395	55	100	315
range	42-75	80-190	210-900	30-79	84-180	195-750	40-70	80-120	130-525
Aspect[a]									
mean	1.2	1.1	0.9	1.1	0.7	0.9	0.9	1.0	0.9
range	0.3-2.0	0.1-2.0	0.0-2.0	0.1-1.9	0.0-1.8	0.0-2.0	0.1-1.4	0.4-1.7	0.1-1.9
Slope %									
mean	40	45	35	37	44	40	40	53	50
range	13-66	19-73	9-80	8-71	3-90	2-92	16-70	26-75	19-85
Elevation (m)									
mean	709	747	730	844	808	808	302	487	403
range	472-1167	483-1124	378-1049	474-1428	326-1478	437-1284	86-473	260-1022	153-909
Latitude (deg)									
mean	46.3	46.2	46.2	44.2	43.9	44.1	43.6	43.9	43.8
range	45.8-46.9	45.1-46.8	45.8-46.9	42.8-45.5	42.9-45.4	42.8-45.6	43.2-44.3	43.0-44.5	43.1-44.5
Topographic[b] position									
mean	2.9	2.8	2.2	2.5	2.7	2.6	3.3	3.3	2.8
range	2-4	2-4	1-4	2-4	1-4	1-4	2-4	2-4	2-4

[a] Cosine transformation: northeast = 2.0, southwest = 0.

[b] 1 = valley bottom; 2 = lower 1/3 slope; 3 = middle 1/3 of slope; and 4 = upper 1/3 of slope.

Given the large geographic area of the study and the large size of sample stands (see below), the analysis could not be stratified by individual plant associations (Hall 1988). Each age-class in the chronosequence, however, encompassed a similar range of mesic to dry-mesic plant-association groups of the Western Hemlock Series (Hall 1988). The major association groups were: Western Hemlock/Rhododendron-Salal (CHS3); Western Hemlock/Salal-Oregongrape (CHS1); Western Hemlock/Rhododendron, Cool (CHSC); Western Hemlock/Forb, Dry (CHF2); Western Hemlock/Rhododendron, Mesic (CHSM); Western Hemlock/Salal-Oregongrape, Dry (CHSD); and Western Hemlock/Shrub, Dry (CHC2). In addition, no significant difference among age-classes was found in the percentage cover ($P < 0.05$) of the following key plant association indicator species: *Gaultheria shallon*; *Xerophyllum tenax*; *Rhododendron macrophyllum*; *Holodiscus discolor*; *Berberis nervosa*; *Athyrium felix-femina*; *Rubus spectabilis*; *Oplopanax horridum*; *Oxalis oreganum*; and *Polystichum munitum*.

Every effort was made to control site variation. True chronosequences should have similar soils, sites, climates, climate histories, and disturbance and establishment histories (Oliver 1982), but these assumptions are violated to various degrees in most chronosequence studies. Given the wide geographic range of this study, the inferences about successional change should be viewed with caution, and more as working hypotheses than as established facts.

Stand selection and plot measurements

Stand size ranged from about 4 to 20 ha. Within each stand, five circular plots were established systematically. In a some very small stands, only three or four plots were established. Plots were spaced either 100 or 150 m apart, depending on stand size, with the wider spacing used in large stands. The locations of the plots were determined before the field sampling by the size and shape of the stand as seen on aerial photographs.

Each plot consisted of a set of nested circular plots of four sizes: 0.002 ha, 0.02 ha, 0.05 ha, and 0.1 ha. Each plot size sampled different aspects of forest structure (see Spies and Franklin, this volume). Within the 0.1-ha plot, trees over 50 cm in diameter at breast height (d.b.h.) were measured and recorded by species, d.b.h., and height. The 0.05-ha plot was used to record the information described above for trees 5 to 50 cm d.b.h.

Information on understory vegetation was recorded by species in the three smallest plots. The percentage cover of tall shrub species and trees less than 8 m tall was estimated by species over the 0.05ha plot. The percentage cover of all vascular plants, mosses, and lichens (including canopy foliose lichens, Lobaria *oregana* and *L. pulmonaria,* that had fallen to the forest floor) was estimated by species in the 0.02-ha plot. Species occurring in the 0.05-ha plot were also recorded and used in presence/absence analyses. All vascular plants were keyed to species or genus. For mosses and lichens, only a selected subset were identified to species or genus.

Data on slope, aspect, topographic position, and shape of topographic cross section were collected from the 0.1-ha plot. Tree ages were determined for young and mature stands by increment coring of 1 to 4 dominant Douglas-fir per plot (5 20 per stand) at breast height, adding 5-7 years for growth to that height (depending on site), and averaging the plot estimates to obtain an age estimate for the stand. For old-growth stands, age estimates were made from stumps in nearby clearcuts, along trails or roads, or sometimes from increment cores on dominant trees. Data collected by Hemstrom (1979) were used to estimate ages of the stands in Mount Rainier National Park.

Calculations and Analyses

Species richness and diversity were calculated separately for the overstory (trees >5 cm d.b.h.) based on basal area, and for the understory vascular plants based on percentage cover. Because about 25 percent of the stands were sampled with fewer than 5 plots, a smaller subset, 144 stands, was used to calculate mean species richness and diversity for each age-class. Stands were selected for each age-class so that the mean number of plots per stand or area was the same for each age-class in a province. Species diversity was calculated as No and N_2 (Hill **1973),** the reciprocal of Simpson's index. No is simply the total number of species in a stand. N2 is calculated as:

$$1/p_i2$$

where p_i is the proportional abundance of the *ith* species.

Analyses of species frequency and abundance in the age-classes were conducted for overstory and understory species occurring at least five times within a province. Preliminary analyses of species distributions by latitude and elevation were conducted in each province. Many species were elevationally and latitudinally restricted in the provinces. Consequently, each province was divided into ecological zones (table 2), based on inspections of sample and species distributions. The zones were typically large enough to include several stands of different age-classes. If a species did not occur in any stands within a zone, then none of the sample stands from that zone were used in the age-class analyses for that species. Consequently, sample sizes differ among species. The objective of the stratification was to restrict the analysis of species to age-class relationships within zones where the species could occur, based on their ranges and environmental conditions. It had the effect of reducing the number of zero values for some species and increasing the power of the statistical analyses. Chi-square analyses were used to test for an age-class effect in the frequency of occurrence of each species. Kruskal-Wallis nonparametric analyses were used to test for differences in species abundance (either percentage cover or basal area) among the age-classes. All analyses were conducted using SAS (SAS Institute Inc. 1987).

Table 2-Latitudinal-elevation zones used in determining species distributions for age-class analyses

Province	Zone	Elevational range (meters)	Latitudinal range (degrees)
Oregon Cascades	1	1000-1500	42.5-43.5
	2	400-1000	42.5-43.5
	3	950-1200	43.6-44.8
	4	400-950	43.6-44.8
	5	300-950	44.9-45.6
Oregon Coast Range	1	50-800	43.0-44.0
	2	100-800	44.1-44.5
	3	800-100	44.1-44.5
Washington Cascades	1	350-1100	45.8-46.6
	2	600-1200	46.6-47.0

Results

Species Diversity

Overstory-Species richness (No) was significantly different (*P* < 0.05) among the age-classes only in the Coast Range, where old-growth stands had the highest numbers of overstory species, and mature stands the lowest numbers (fig. 1). Overstory species diversity (N_2), on the other hand, showed an age-class effect only in the Cascade provinces, where old growth had the highest diversity.

Understory-Species richness was marginally significant ($P < 0.09$) among age-classes in the Coast Range (fig. 2); old growth had the highest number of species and young stands had the lowest. Understory species diversity (N_2) showed a significant age-class effect in the Washington Cascades and the Coast Range. Old growth had the highest values in both provinces; young stands had the lowest values in the Washington Cascades, and mature stands had the lowest values in the Coast Range.

Species Occurrence

Overstory-Species differing significantly (*P* < 0.1) in basal area among the age-classes were either shade-tolerant species that had highest basal areas in old-growth stands or shade-intolerant species with highest basal area in young stands (table 3). Western hemlock, Pacific yew, and bigleaf maple

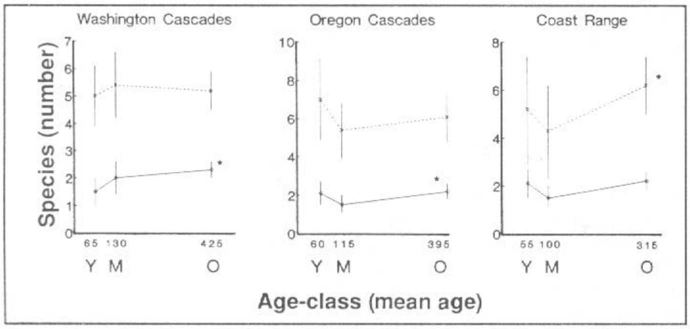

Figure 1—Species diversity of the overstory stratum in relation to age-class in Douglas-fir stands from three physiographic provinces. Dotted line is N_o and solid line is N_2. Vertical bars are Scheffe's 95 percent confidence intervals. Significant age-class effect of ANOVA is indicated by '*' ($P < 0.05$).

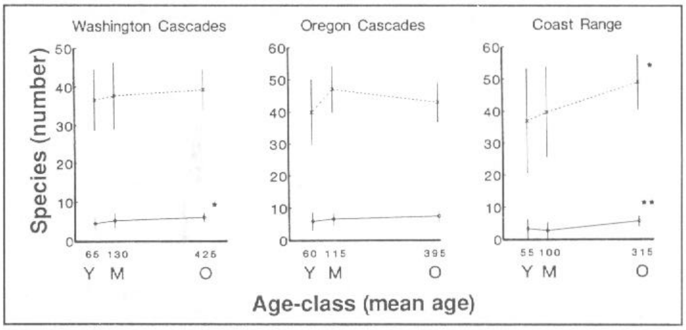

Figure 2—Species diversity of the understory stratum in relation to age-class in Douglas-fir stands from three physiographic provinces. Dotted line is N_o and solid line is N_2. Vertical bars are Scheffe's 95 percent confidence intervals. Significant age-class effect in ANOVA is indicated by '*' ($P < 0.1$) or '**' ($P < 0.05$).

Table 3—Basal area (m^2/ha) of trees species (>5 cm d.b.h.) in young (Y), mature (M), and old-growth (O) Douglas-fir stands in 3 physiographic provinces

Species	Washington			Age-class[a] effect	Oregon			Age-class[a] effect	Coast			Age-class[a] effect
	Y	M	O		Y	M	O		Y	M	O	
Pacific silver fir	0.4	0.2	5.4	***	<0.1	0.1	0.9		0	0	0	
White fir	0	0	0		9.8	11.8	3.3		0	0	0	
Grand fir	<0.1	<0.1	<0.1		0.4	1.2	0.5		<0.1	0	1.6	
Noble fir	<0. 1	0.3	0.4		0	0	0		0	0	0	
Bigleaf maple	0.1	0.2	<0.1	**	0.7	0.5	<0.1	*	0.5	0.4	1.6	+
Red alder	<0.1	0.3	0		0.6	0.3	0.0	*	1.6	2.1	0.1	*
Pacific madrone	0	0	0		<0.1	0.2	0.1		2.2	0.1	0.4	+
Incense-cedar	0	0	0		0.5	3.2	2.0		0	0.1	1.7	
Golden chinkapin	0	0	0		1.0	0.3	0.3		0.4	0.2	0.2	
Pacific dogwood	<0.1	0.2	<0.1		0.3	0.1	0.1		0.2	0.1	0.4	
Sugar pine	0	0	0		0.4	1.4	2.0		0	0	0	
Western white pine	0	<0.1	0.1		0.1	<0.1	<0.1		0	0	0	
Douglas-fir	38.5	36.0	31.3		28.6	48.8	47.8	***	36.4	47.1	49.8	
Pacific yew	<0.1	<0.1	0.7	***	0.2	0.1	0.67	**	0	0	0.4	*
Western redcedar	1.0	4.4	6.3		2.1	1.3	7.4		<0.1	2.8	2.9	+
Western hemlock	7.4	15.0	24.0	***	7.9	1.5	14.0	***	4.2	6.1	9.9	+

[a] P values in Kruskal-Wallis test: + = <0.10; * = <0.05; ** = <0.01; *** = <0.001.

were the only species with significant differences among age-classes in all three provinces. The basal area of Pacific yew, an understory tree, typically was 5 to 74 times higher in old growth than in the younger age-classes in the two Cascade provinces. In the Coast Range, no overstory-size stems (that is 5 cm d.b.h.) of yew were encountered in any stands younger than 200 years. The basal area of Douglas-fir was significantly different among age-classes only in the Oregon Cascades. Bigleaf maple, an early to mid-successional species in the Cascade provinces, had highest basal area in old growth in the Coast Range.

Understory—A total of 26 of 129, 35 of 171, and 13 of 98 species were found to differ in percentage frequency among the age-classes ($P < 0.1$) in the Washington, Oregon, and Coast provinces, respectively (table 4). Most species attained their maximal age-class frequency in old-growth or mature stands. Only two plants, Pacific yew and *Lobaria* spp., were significant in all provinces; they both reached their highest frequency of occurrence in old growth. Other species with maximal frequency of occurrence in old growth included: *Cornus canadensis*, *Linnaea borealis* var *longiflora*, and *Tiarella trifoliata* var *unifoliata* in the Cascade provinces, and *Synthyris reniformis* in the Coast Range province. Species occurring more frequently in mature and young stands than in old-growth stands included: *Holodiscus discolor*, *Anemone lyallii*, and *Pteridium aquilinum*. Although differences were significant for many species, most species were relatively common, occurring 25 percent or more of the time in at least two of the age-classes. This overlap includes the old-growth-associated species mentioned above, except for Pacific yew and *S. reniformis* in the Coast Range province, where these species either did not occur or occurred infrequently in mature and young stands.

Table 4—Percent frequency of occurrence of species showing an age-class effect ($P < 0.1$) in old-growth, mature, and young stands in 3 physiographic provinces (species are listed from top to bottom in order of decreasing frequency in old growth)

Species	O	M	Y	Sig.[a]
		Washington		
Trees				
Pacific yew	90	70	46	**
Pacific silver fir	90	60	62	*
Douglas-fir	27	30	69	*
Bigleaf maple	9	67	40	+
Grand fir	0	30	0	***
Shrubs				
Vaccinium membranaceum	80	50	15	***
Rubus lasiococcus	60	40	23	+
Gaultheria ovatifolia	43	20	8	*
Holodiscus discolor	10	50	39	*
Rubus parviflorus	3	30	39	**
Lonicera spp.	0	10	23	*
Herbs				
Achlys triphylla	100	100	77	**
Clintonia uniflora	87	70	54	+
Cornus canadensis	87	60	54	*
Tiarella trifoliata unifoliata	80	70	39	*
Trientalis latifolia	40	70	77	*
Campanula scouleri	33	40	69	+
Pyrola picta	20	80	62	***
Galium triflorum	16	60	61	**
Osmorhiza chilensis	7	50	31	**
Anemone lyallii	3	20	0	+
Grass				
Melica harfordii	0	20	0	**
Ferns and club mosses				
Polystichum munitum	73	100	100	*
Pteridium aquilinum	57	80	100	**
Lycopodium clavatum	30	10	0	*
Lichen				
Lobaria spp.	80	30	23	***
		Oregon		
Trees				
Pacific yew	79	44	61	**
Douglas-fir	49	68	78	+
Bigleaf maple	29	59	54	*
Noble fir	0	17	20	*
Shrubs				
Chimaphila umbellata	84	64	50	*
Chimaphila menziesii	74	80	100	+
Holodiscus discolor	26	52	33	+
Amelanchier alnifolia	21	44	17	+
Gaultheria ovatifolia	5	5	24	+
Oemleria cerasiformis	3	23	27	*
Salix spp.	0	0	17	*
Herbs				
Linnaea borealis longiflora	98	80	89	*
Goodyera oblongifolia	98	80	89	+
Coptis laciniata	62	46	20	*
Tiarella trifoliata unifoliata	58	36	33	+
Cornus canadensis	58	28	56	*
Monotropa uniflora	30	23	0	+
Vancouveria hexandra	81	100	56	***
Galium triflorum	63	92	56	**
Fragaria vesca	24	55	53	*
Disporum hookeri	58	72	39	+
Galium oreganum	18	29	0	+
Collomia heterophylla	11	32	7	+
Montia sibirica	9	36	22	*
Arenaria macrophylla	6	36	0	***
Anemone lyallii	7	33	25	+
Pyrola aphylla	5	23	40	**
Galium aparine	4	27	8	+
Plagiobothrys figuratus	4	27	17	+
Senecio bolanderi	2	20	6	*
Hypericum perforatum	0	0	17	*
Ferns				
Blechnum spicant	49	22	20	+
Pteridium aquilinum	43	88	100	***
Polypodium glycyrrhiza	17	38	0	+
Lichen				
Lobaria spp.	91	64	39	***
		Coast		
Trees				
Western hemlock	91	78	33	**
Pacific yew	55	0	0	**
Shrubs				
Berberis nervosa	100	78	67	*
Acer circinatum	91	56	50	*
Herbs				
Disporum hookeri	91	67	50	*
Anemone deltoidea	87	56	50	+
Adenocaulon bicolor	86	57	33	*
Linnaea borealis longiflora	74	56	17	*
Achlys triphylla	78	67	17	**
Synthyris reniformis	64	14	0	**
Smilacina racemosa	64	29	17	+
Goodyera oblongifolia	68	14	83	**
Lichen				
Lobaria spp.	87	33	17	***

[a] Significance level (P) in chi-square test for age-class effect: + = <0.1, * = <0.05, ** = <0.01, *** = <0.001.

The cover of many understory species also differed among the age-classes, with at least marginal significance ($P < 0.1$) (table 5). Thirty species, 45 species, and 14 species differed among the age-classes ($P < 0.1$) in the Washington, Oregon, and Coast provinces (table 5). Mean species cover was highest in old-growth 37 times, highest in mature 30 times, and highest in young stands 22 times in the three provinces. Eight species differed significantly in all three provinces. Five of these, Pacific yew, *Goodyera oblongifolia*, *Linnaea borealis* var *longiflora*, *Achlys triphylla*, and *Lobaria* spp. had highest cover in old growth; the remaining three, *Adenocaulon bicolor*, *Anemone lyallii*, and *Pteridium aquilinum* had higher cover primarily in mature stands. The cover by Pacific yew and *Lobaria* spp. in young and mature stands was typically less than one-tenth of the cover in old-growth stands (table 4). Other species with highest cover in old growth included: *Chimaphilla umbellata*, *Berberis nervosa*, *Cornus canadensis*, and *Tiarella trifoliata* var *unifoliata*.

Table 5—Ratios of mean species cover in mature (M) and young (Y) stands to mean species cover in old growth for species showing an age-class effect ($P < 0.1$) (species are listed from top to bottom in order of decreasing mean cover in old growth)

Species	M	Y	Sig.[a]
	Washington		
Trees			
Silver fir	0.05	0.03	***
Pacific yew	0.06	0.04	***
Cascara	>100	8	*
Douglas-fir	7.9	13	*
Bigleaf maple	86	15	**
Grand fir	>100	0	***
Shrubs			
Vaccinium membranaceum	0.09	0.03	***
Vaccinium alaskaense	0.10	0.05	**
Vaccinium parvifolium	0.24	0.37	**
Chimaphila umbellata	0.48	0.11	***
Holodiscus discolor	3.8	1.3	+
Rubus parviflorus	>100	>100	**
Herbs			
Tiarella trifoliata unifoliata	0.09	1.00	+
Corallorhiza mertensiana	0.13	<0.01	*
Clintonia uniflora	0.13	0.14	*
Cornus canadensis	0.36	0.24	***
Linnaea borealis longiflora	0.50	0.30	***
Goodyera oblongifolia	0.85	0.11	*
Trientalis latifolia	1.6	1.7	*
Achlys triphylla	1.7	0.63	+
Anemone deltoidea	3.5	2.5	*
Pyrola picta	4.9	2.8	*
Adenocaulon bicolor	6	7	*
Galium triflorum	12	16	**
Anemone lyallii	19	<0.01	+
Aster canescens	0.03	63	*
Osmorhiza chilensis	>100	>100	**
Ferns			
Pteridium aquilinum	3.0	17	***
Grass			
Melica harfordii	>100	0	
Lichen			
Lobaria spp.	0.01	0.02	***
	Oregon		
Trees			
Pacific yew	0.02	0.10	***
Western hemlock	0.33	0.54	**
Western redcedar	0.63	2.3	*
Cascara	7	9.8	*
Bigleaf maple	12	22	*
Noble fir	>100	>100	*
Shrubs			
Rubus nivalis	0.22	0.27	+
Chimaphila umbellata	0.95	0.24	*
Berberis nervosa	1.7	0.95	*
Chimaphila menziesii	1.7	4	**
Rosa gymnocarpa	2.7	0.85	*
Gaultheria ovatifolia	<0.01	18	*
Amelanchier alnifolia	44	44	+
Oemleria cerasiformis	66	16	+
Salix spp.	0	>100	*
Herbs			
Tiarella trifoliata trifoliata	<0.01	<0.01	*
Tiarella trifoliata unifoliata	0.10	0.01	**
Pyrola asarifolia	0.11	0.31	*
Coptis laciniata	0.28	0.03	**
Cornus canadensis	0.33	0.27	+
Linnaea borealis longiflora	0.34	0.41	***
Vancouveria hexandra	0.61	0.09	**
Goodyera oblongifolia	0.79	0.14	**
Achlys triphylla	0.8	0.04	***
Pyrola aphylla	0.72	2.47	**
Pyrola picta	1.3	4.2	**
Anemone deltoidea	2.1	0.59	*
Hieracium albiflorum	3.0	0.24	+
Galium oreganum	3.2	<0.01	*
Adenocaulon bicolor	3.3	0.99	**
Campanula scouleri	4.6	0.37	*
Galium triflorum	5.2	0.95	***
Montia sibirica	5.0	14	*
Collomia heterophylla	6.9	<0.01	*
Fragaria vesca	6.7	0.93	*
Arenaria macrophylla	24	<0.01	***
Senecio bolanderi	27	2.4	+
Anemone lyallii	32	2.3	*
Stachys rigida	>100	0	+
Plagiobothrys figuratus	0	>100	*
Ferns			
Pteridium aquilinum	9.1	18	***

See footnote on next page.

Table 5—continued

Species	M	Y	Sig.[a]
Grasses and rushes			
Festuca occidentalis	3.0	0.11	*
Bromus vulgaris	5.7	0.28	+
Luzula parviflora	>100	>100	+
Lichen			
Lobaria spp.	0.39	0.02	***
		Coast	
Trees			
Pacific yew	<0.01	<0.01	**
Western hemlock	0.25	0.02	**
Golden chinkapin	0.57	0.08	+
Shrubs			
Acer circinatum	0.02	1.08	**
Berberis nervosa	0.18	0.18	**
Herbs			
Synthyris reniformis	<0.01	0.01	*
Goodyera oblongifolia	<0.01	0.35	*
Linnaea borealis longiflora	0.06	0.07	**
Achlys triphylla	0.40	0.08	*
Anemone deltoidea	1.6	0.13	*
Adenocaulon bicolor	1.25	0.1	+
Corallorhiza maculata	4.4	1.4	+
Ferns			
Pteridium aquilinum	1.3	1.4	*
Lichen			
Lobaria spp.	0.03	0.009	***

[a] Significance level (P) in chi-square test for age-class effect: + = <0.1, * = <0.05, ** = <0.01, *** = <0.001.

Several species differed in cover among age-classes ($P < 0.1$) only in one province (table 5). For example, in the Washington Cascades, *Vaccinium* spp. and *Clintonia uniflora* had many times more cover in old growth than in mature or young stands. In the Oregon Cascades, *Coptis laciniata* and *Pyrola asarifolia* had much higher cover in old growth relative to the younger age-classes. In the Coast Range, *Acer circinatum* and *Synthyris reniformis* had highest cover in old growth.

The analyses based on percentage cover differed in two ways from the analyses based on percentage occurrence. First, more species showed significant differences among the age-classes in tests based on cover (90 species) than in tests based on occurrence (76 species). Second, for many species, such as Pacific yew and *Tiarella trifoliata* var *unifoliata*, relative differences among age-classes were greater for percentage cover than for percentage occurrence. The results indicate that the significant species are not strongly restricted to one age-class but differ in their development in the age-classes.

Discussion

Species Diversity

Various patterns of plant species diversity during succession have been hypothesized (Odum 1969, Pielou 1966, Whittaker 1965) including increases and decreases, and multiple peaks in diversity. Because this study did not examine the earliest stages of forest succession, the entire pattern of changes in diversity in Douglas-fir forests cannot be examined with these data. Other studies (Halpern 1987, 1989; Schoonmaker and McKee 1988), however, show that after stand-replacing disturbance in old-growth Douglas-fir stands, plant species diversity (both N_0 and N_2) increases to a peak early in succession as shade-intolerant herbs and shrubs invade the surviving community of shade-tolerant forest species. These studies indicate that as a forest canopy develops and closes, between 20 and 40 years, diversity declines to a low point when the dense tree canopy shades-out all but the most shade tolerant of the understory species.

The results of this study indicate that after canopy closure, the trend in understory diversity was to increase slightly from young to old growth. The increase may, in fact, be stronger than indicated by this study. The wide age range of the old-growth age-class may mask a steeper increase, followed by a decline in diversity as the stand becomes entirely composed of shade-tolerant tree species such as western hemlock. In the Coast Range, where old growth was almost 100 years younger than the Cascade old growth and had a lower basal area of hemlock, understory richness and diversity showed the strongest increase with age-class. Habeck (1968) found that forests dominated by western hemlock in Montana had lower species richness than earlier stages containing a mix of early- and late-successional species. This finding suggests that within the old-growth age-class, diversity may be high in the early stages of old growth (from 200 to 400 years) and low in the later stages (after 400 years), when western hemlock reaches dominance in the stand (Spies and others, unpubl. manuscript).

The overstory component of diversity appears to follow the general pattern described above, with peaks early and late in succession. The tendency for overstory diversity to be higher in young stands than in mature stands in the Oregon Cascades and Coast Range suggests that early successional species, such as red alder, bitter cherry, and madrone persist in young stands and drop out during the mature stage. During the old-growth stage, shade-tolerant species reach the canopy, contributing to an increase in canopy tree diversity during this period. A decline in overstory diversity probably occurs as Douglas-fir drops out of the stands.

Species Occurrence

The list of species associated with succession should be viewed as a first approximation, requiring further verification and more controlled study. Given that 398 individual nonparametrical statistical tests were conducted, about 40, or 10 percent of the tests, might be expected to yield significant results at $P < 0.1$ by chance. Consequently, the statistical tests should be viewed with caution. The results do suggest, however, that many species were different among the age-classes because about 20 percent of the tests in both analyses were significant"and many of those were significant at $P < 0.01$. The results should also be viewed with caution because some species that increase or decrease in abundance with stand age may have occurred too infrequently to show statistical significance. The influence of site and historical factors in this geographically broad chronosequence study can never be fully evaluated; however, the similarities in average site and vegetation characteristics (see Methods) do not indicate that these factors played a strong role in the community and species patterns among the age-classes.

Several of the species most common in old growth have been associated with late-successional coniferous forests in other studies. *Tiarella unifoliata* was most common in late-successional forests in Montana (Habeck 1968) and Washington (Moir and others 1979). Pacific yew reached highest abundance in late-successional cedar forests in Montana (Habeck 1968, McCune and Allen 1985). Alaback (1982) found that C. *canadensis* and *Vaccinium alaskaense* had highest biomass in old growth in a chronosequence of Sitka spruce/western hemlock stands in southeastern Alaska.

Some species had different successional relationships than were reported in other studies. Habeck (1968) found that *Vaccinium membranaceum,* a species associated with old growth in this study, was most frequent in early-successional stands in Montana, and *Adenocaulon bicolor,* which was most abundant in mature stands in this study, was most frequent in late-successional stands in Montana (Habeck 1968). Alaback (1982) found that V. parvifolium, which had highest percentage cover in old growth in the Washington Cascades, had high biomass in mature stands and low biomass in old growth in southeastern Alaska. Many factors, such as climate, genetics, competition, and disturbance regime, could lead to geographically different successional distributions for a single species.

Even within this study, some species did not show consistent successional patterns. For example, bigleaf maple had lowest basal area in old growth in the Cascade provinces but highest basal area in old growth in the Coast Range. This pattern may be because bigleaf maple has not yet dropped out of Coast Range old-growth stands, which are younger than the stands in the Cascade provinces. In addition, the lower basal area of western hemlock, a competitor for light, in old growth in the Coast Range may allow bigleaf maple to persist longer than it does in the Cascade stands.

Factors Contributing to Successional Change

Assuming that many of the patterns of vegetation and stand age are a consequence of forest succession, four related mechanisms of change in understory communities and plant species abundance are hypothesized.

The first mechanism is change in resources, particularly light, and competitive abilities to capture those resources. Old-growth forests develop many areas of dense hemlock canopies in addition to the relatively open Douglas-fir canopies and canopy gaps. Small, very shade-tolerant herbs and shrubs such as *Clintonia, Syntheris, Tiarella,* and *Cornus* are favored in the deep-shade areas. In mature and young forests"with more uniform, open canopies"aggressive, less shade-tolerant shrubs such as Gautheriu shallon often form large, dense patches that may exclude smaller, less-competitive herb and shrub species (Long and Turner 1974). The increase of shade-tolerant herbs and shrubs in coniferous forest development has been observed by Alaback (1982) and Stewart (1988). Some shade-tolerant understory herbaceous plants and tree species such as Pacific yew and westem hemlock may also be favored in old growth by cool, moist microclimates during the dry, warm season. Although the relative microclimates of the age-classes have not been quantified, old-growth understories are likely to be relatively cool and humid during the dry season because they are protected from radiation and drying winds by deep, multiple canopy layers. In addition, soil moisture may be higher as a consequence of the large accumulations of litter on the forest floor (Spies and Franklin, this volume) and pieces of decomposed wood that store moisture in the soil.

A second mechanism of understory change may be an increase in the horizontal spatial heterogeneity of resources and environments. As Douglas-fir stands develop, they become a mosaic of canopy gaps, and dense hemlock canopies overlying a forest floor with accumulations of woody debris, tip-up mounds, and shrub patches. This structural heterogeneity may create a shifting mosaic of resources and environments that favors species that can both tolerate low light and spread laterally to take advantage of increased light. In addition, if canopy gaps also represent areas of low root occupancy, then soil moisture and nutrients may be relatively more available. Species that can take advantage of resource heterogeneity include *Linnaea* borealis, *Rubus lasiococcus* and Clintonia unifrora, which spread rapidly by stolons or rhizomes (Antos and Zobel 1984) to occupy gaps that form above or near the plant. These species can apparently persist with low abundance in shaded areas but may require canopy gaps to survive for long periods in some stands.

A third mechanism in plant community change is the increase in vertical environmental diversity, specifically the increase in the height and number of canopy layers. The canopies of old-growth trees provide moist, cool environments that favor the growth of foliose lichens such as *Lobaria oregana* (Pike and others 1975). Because the canopy flora was not sampled directly, other epiphytic plant species may also be associated with tall, structurally and environmentally diverse canopies.

A fourth mechanism may be sensitivity to fire and slow rates of reestablishment and growth after fire. Fire-sensitive species such as western hemlock and Pacific yew are typically killed by moderate to high-severity fires and can take relatively long periods to reach maturity, growing slowly in the understory for many years. They are often present as scattered seedlings and saplings in young and mature stands but do not reach maximum size and density until the old-growth stage, one hundred to several hundred years later. This distribution does not mean that old-growth stands where these species occur have been free of fire during their entire development. Many old-growth stands have had a history of patchy low-intensity fires (Morrison and Swanson 1990), which miss individuals of these species or only injure them. Best development of these species appears where a stand has not been subjected to low-intensity fire for several centuries, however.

Conclusions and Management Implications

The majority of species did not show any differences in their frequency or abundance within the age-classes. At least 20 percent of the species did differ among the age-classes, and many of those were more frequent and abundant in old growth. Most species associated with old growth, however, were not restricted to old-growth forests and could be found with moderate frequencies and abundances in at least one younger age-class. Of all the species showing an age-class effect, only Pacific yew and *Lobaria* spp. showed strong preference for old-growth in all three provinces, suggesting that these species would suffer the greatest decline in regional populations if most of the current old growth is clearcut and converted to short-rotation plantations. Many of the ecological conditions that favor old-growth-associated plant species can be found in lesser amounts in younger unmanaged forests. Gaps, deeply shaded and cool understories, and accumulations of woody debris on the forest floor can be found in at least small areas in many unmanaged young and mature stands. Conditions such as long periods since catastrophic disturbance, development of massive tree crowns, and buffered canopy microclimates, which favor Pacific yew and *Lobaria* are not typically found in unmanaged young or mature stands that regenerated after stand-replacing fire, however.

The suggestion that the composition of the forest understory community changes with overstory succession has important implications for using vegetation to assess site conditions and for maintaining biological diversity in managed landscapes. The abundance (cover) of many understory species is used to classify forests into plant associations used for management. If the influence of succession on understory plant communities is not taken into account, then understory plant communities may incorrectly estimate site conditions and potential (Spies and Barnes 1985). Stewart (1988) has found that many understory species in Douglas-fir forests are influenced by tree canopies and warns that understory communities may reflect canopy-disturbance history more than site quality. Species such as *Tiarella*, which may be affected by changes in light intensity and understory microclimate, will have limited value in identifying plant associations and indicating physical site conditions. A better understanding of the autecologies of many understory shrubs and herbs, will help resolve uncertainty of the indicator value of some understory species.

The effect of forest management on understory and overstory species composition is not well known. This lack is partly a consequence of the limited research studies but is also a result of the varied nature of “managed” stands. Managed forests range from young stands that originated from railroad logging in the early 1900’s to second- and third-rotation stands on non-Federal lands that have been burned, sprayed with herbicides, planted, fertilized, or thinned. Speculating on how old-growth-associated plant species might be affected by some specific management practices may be useful, however. Management effects can be divided into effects on the initial plant population in an old-growth stand from activities such as clearcutting and site preparation, and effects on recovering plant populations from activities such as stand-density control and short rotations. Initial old-growth populations of many species will suffer at least temporary declines as a consequence of clearcutting and site preparation, especially broadcast burning. The current practice of clearcutting removes all the overstory trees, leaving no habitat for canopy epiphytes such as Lobaria. In landscapes where no large canopy trees occur and no plans are made to grow them, Lobaria and other canopy plant species will probably decline to very low populations. Where site preparation includes broadcast burning, fire-sensitive species such as Pacific yew, Chimaphila, and Linnaea will show strong declines (Halpern 1987) without return to old-growth populations for at least 20 years. If stands are planted to high densities and not thinned, then recovery of understories may be delayed if very dense canopies develop and shade-out the understory. On the other hand, if canopy density is controlled by planting density, precommercial thinning, or both, then forest understories may recover more quickly. If species composition is strongly controlled during this process to favor one species such as Douglas-fir, however, then both canopy and understory diversity will be reduced. The practice of short rotations may reduce populations of understory and overstory species associated with old growth before their populations can recover from the effects of clearcutting and burning. In the long term, the combination of clearcutting, site preparation, and short rotations could greatly reduce populations of some old-growth-associated plant species.

By creating and managing microsites, however, managers have many opportunities to maintain populations of plant species associated with old growth in managed stands and landscapes. Leaving some live canopy trees in cutting units can maintain canopy species that might recolonize the young forest canopy more rapidly than if no refuge trees were present. Leaving large Pacific yew trees in cutting units may provide for this species, but no studies have evaluated how well such trees survive broadcast burning, hotter drier microclimate, and increased herbivory from ungulates. Using cooler, more patchy site-preparation fires, or not using fire on some sites, could help maintain fire-sensitive species. Creating more diverse canopies by planting a mix of conifers, allowing hardwoods to regenerate, thinning dense stands, and cutting canopy openings could help create a more heterogenous understory environment and allow plant species populations to recover more rapidly. Finally, growing some stands on long rotations would help maintain species such as Pacific yew that require long recovery after catastrophic disturbance. Possibilities for maintaining populations of old-growth-associated species in managed stands and landscapes appear to be good, but additional information is needed about the autecologies of many understory species and the effects of management practices on those species to develop more specific management recommendations.

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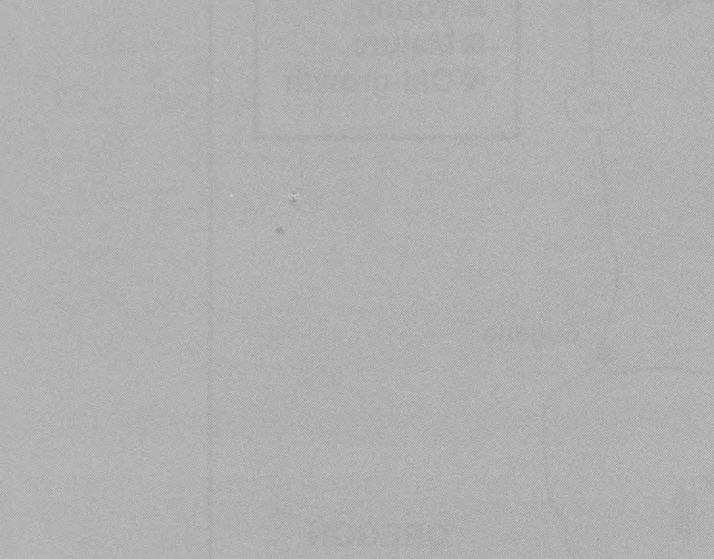
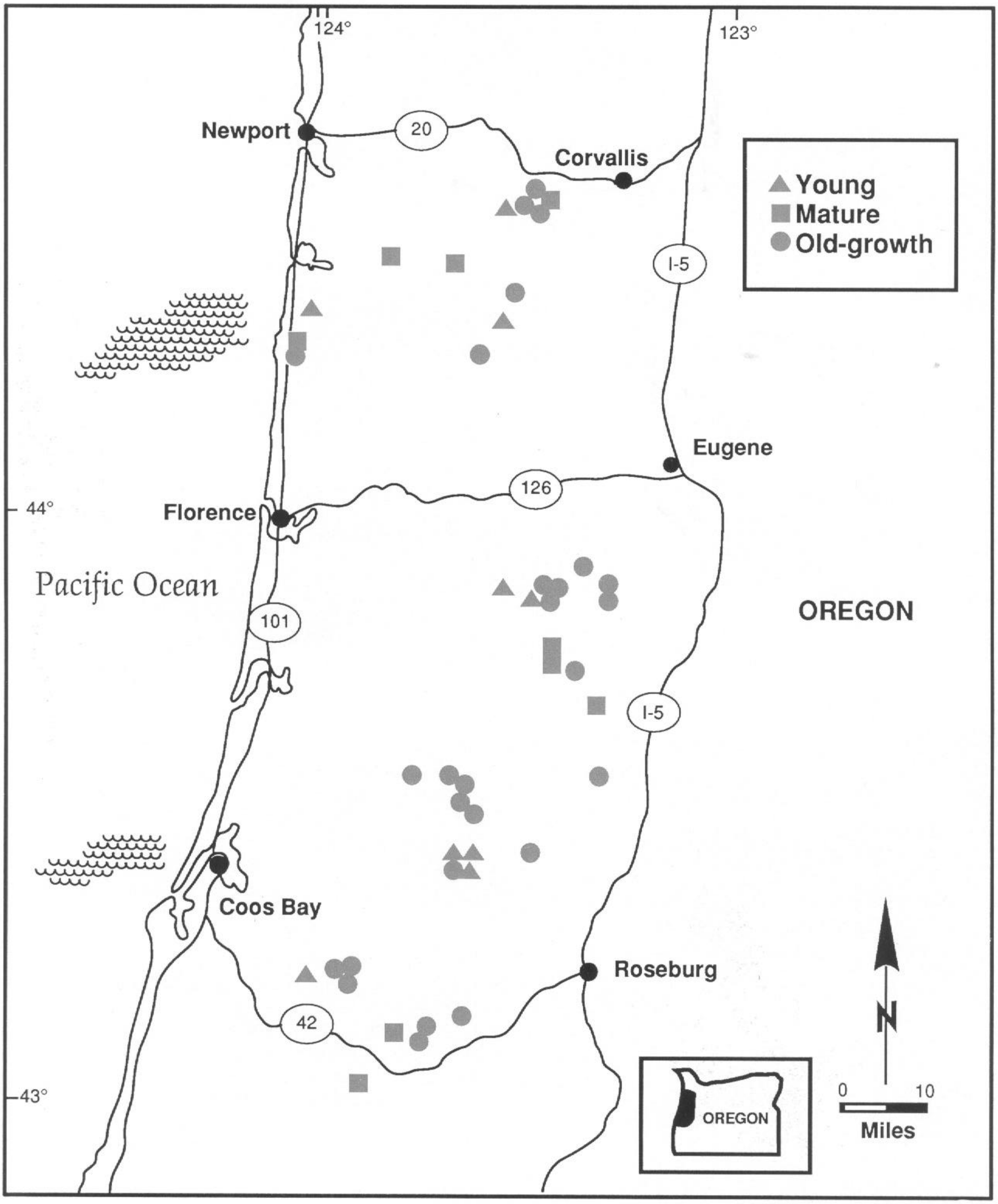


Part 4

Diurnal Forest Birds of Oregon and Washington



Location of study sites.

Spring Bird Communities in the Oregon Coast Range

Andrew B. Carey, Mary Mae Hardt, Scott P. Horton, and Brian L. Biswell

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Abstract

Our objectives were to determine the value to birds of old-growth forests relative to mature and young forests in the southern Oregon Coast Range. Special emphasis was placed on cavity-using birds. We studied birds in 45 stands in 1985 and 33 stands in 1986. Over 60,000 individuals of 91 species were counted; 989 observations on the foraging activities of cavity-using birds were recorded; 277 nests of cavity users were found and described; snag densities were estimated by four size-classes and three decay-classes. We calculated a birds-per-area index (BAI) from the counts and diversity indices from the BAI. Bird species diversity and total bird abundance did not differ significantly among the young, mature, and old-growth stands. Fourteen species were most abundant in old growth; 10 were cavity users (including the crevice-nesting brown creeper and the spotted owl). Two species that do not nest in cavities, the western flycatcher and the varied thrush were also abundant in young and mature stands. Two, the marbled murrelet and the olive-sided flycatcher, were rare in young and mature stands. All the cavity users (including the brown creeper) selected very large snags for nesting; snags of the average sizes used by these birds were larger than those normally produced in young stands. Under current conditions, the cavity-using birds depend on old growth.

Introduction

"Are there unique features, species, or important values associated with old-growth forests?" ask Franklin and others (1981). They review the literature and ongoing research and conclude that old-growth forests provide specialized habitats and differ from both natural and managed younger forests. Research shows some differences between managed forests and old-growth forests in avian community composition (Hagar 1960) and total bird abundance and constancy of abundance (Bowles 1963). And although 18 or more species of vertebrates appear to find optimal conditions in old growth, quantitative avifaunal studies across stages of forest development are lacking in the Douglas-fir forests of western Oregon and Washington (Meslow and Wight 1975, Meslow and others 1981). The Old-Growth Forest Wildlife Habitat Program was chartered to quantify the value of old growth to wildlife (Carey and Spies, this volume; Ruggiero and Carey 1984). We began our research in the Oregon Coast Range in 1985 under the aegis of the Old-Growth Program.

Our objectives were to determine the value to birds of old growth relative to young and mature Douglas-fir forests in the Oregon Coast Range. In particular, we wanted to determine if the bird communities in old growth differed from the bird communities in mature and young forest in total abundance, diversity (numbers of species and the degree to which the communities were dominated by a few species), composition of species, and structure (ranked abundance of the species) because these are all components of biodiversity; simple presence or absence of species does not reflect all the important aspects of biodiversity, and few species in the Pacific Northwest are so specialized that they would be expected to be confined to old growth (Meslow and others 1981). We also wanted to determine which species reached maximum abundance in old growth and which, if any; were found exclusively in old growth. We placed special emphasis on cavity-using birds because Mannan and others (1980), in an unreplicated study, report cavity-using birds to be strikingly more abundant in old growth than in younger stands. And Cline and others (1980), Mannan and others (1980). and Meslow and others (1981) express concern over the loss to timber management of large, Douglas-fir snags that are important to cavity-using birds.

Franklin and others (1981) list some structural features unique to old-growth (as compared to young and mature) forests that could be important to birds; we wished to determine whether these features were important. These features and their putative value to birds (and the tests we made) include:

- Large, old Douglas-fir trees have deeply furrowed bark that provides a unique environment for bark arthropods and may be important foraging substrates for bark-foraging birds, especially the brown creeper. We test the hypotheses: (a) young, mature, and old-growth stands do not differ in the density of large (>lOO cm in diameter-at-breast height, d.b.h.) Douglas-fir; (b) abundance of bark-foraging birds is not positively correlated with the densities of large Douglas-fir trees; (c) bark-foraging birds do not differ in abundance among young, mature, and old-growth stands; (d) brown creeper abundance is not correlated with the density of large Douglas-fir trees; (e) brown creeper abundance does not differ among young, mature, and old-growth stands. Rejection of the last two hypotheses would imply that brown creepers forage in large trees out of proportion to their availability relative to small trees. We examined the foraging behavior of brown creepers to test this implicit hypothesis.

- Two or more age-classes of conifers that form an overstory, midstory, and sometimes an understory result in a vertical diversity of coniferous foliage that may support a diversity and abundance of birds that forage among the foliage of trees (foliage foragers) that exceeds that in young or mature forests. We test the hypotheses: (a) foliage-height diversity does not differ among young, mature, and old-growth stands; (b) the abundance of foliage foragers does not differ among young, mature, and old-growth stands; (c) the diversity of foliage foragers does not differ among young, mature, and old-growth stands; (d) the diversity of foliage foragers is not correlated with foliage-height diversity; (e) the abundance of foliage foragers is not correlated with foliage-height diversity.

- Large, standing, dead trees may provide important nesting substrate for cavity-using birds. We test the hypotheses: (a) the density of large snags does not differ among young, mature, and old-growth stands; (b) the abundance of cavity-using birds does not differ among young, mature, and old-growth stands; (c) cavity-using birds do not use large snags for nesting out of proportion to their availability relative to small snags.

- Spatial diversity of vegetation brought about by gaps in the canopy caused by the death of large trees may provide for a greater diversity and abundance of birds in the understory and on the ground. We test the hypotheses: (a) spatial diversity of vegetation does not differ among young, mature, and old-growth stands; (b) the diversity and abundance of birds associated with the forest floor do not differ among young, mature, and old-growth stands.

Our final objective was to determine if the complex moisture-temperature gradient governing plant community composition in the Pacific Northwest (Franklin and Dymess 1973) resulted in differences in bird species diversity or species abundances among old-growth stands on different parts of the gradient (wet, mesic, and dry sites). Franklin and others (1981) discuss the value of streams in old growth. We do not address streams here because the influence of small streams and seeps on upland, spring bird communities in the Oregon Coast Range was reported by Carey (1988).

Methods

Experimental Design

Study stands were selected under the vegetation community ecology portion of the Old-Growth Program (Carey and Spies, this volume), but we were unable to find enough stands for three complete replicates of the Program’s design: three young, three mature, three wet old-growth, three dry old-growth, and three mesic old-growth stands. Forty-five stands were studied in 1985: 8 young, 10 mature, 14 mesic old-growth, 8 dry old-growth, and 5 wet old-growth stands (see frontispiece). In 1986, because of cuts in funding, only 33 stands were studied: 6 young, 8 mature, and 10 mesic old-growth, 5 dry old-growth, and 4 wet old-growth stands. Young and mature stands were not classified into moisture-classes, but spanned the same moisture gradient that the old-growth stands spanned. We could not find stands of 100 ha or more as called for in the research plan. Stand size averaged 29 ha, ranging from 14 to 62 ha. Two small old-growth stands studied in 1985 were replaced with larger stands in 1986. Study stands were in four large clusters: between Corvallis and Yachats, west of Drain, northwest of Roseburg, and between Roseburg and Coos Bay, Oregon. The clusters covered the southern Coast Range western hemlock forest type but also included the coastal Sitka spruce forest type near Yachats, the Umpqua Valley margin mixed-conifer forest type northwest of Roseburg, and the southwest Oregon mixed-evergreen forest type near Remote. Each cluster contained young, mature, and old-growth stands, but not enough stands of each type to be treated separately.

Douglas-fir was a dominant species in each stand. Young stands were 40 to 72 years old; mature stands were 80 to 120 years old, old-growth stands were 200 to 525 years old. One old-growth stand had a mixed-aged canopy of trees 130 years old and old-growth trees of unknown age, d.b.h. of 100 cm or more, and density of 17.4 per hectare. The old-growth and mature stands and three of the young stands originated after catastrophic wildfire. Five of the eight young stands originated after human disturbance (logging or clearing) as evidenced by stumps, old roads, or railroad grades.

Sampling Plan

We located 12 points 100 m apart along a transect through each stand; our stands were not large enough to use the Program's recommended 150 m between points. Because stands were small and we maintained a 75-m buffer along stand edges, the points systematically covered the interior of each stand. The smallest stands were too small for 12 points. One stand had only 7 points (dropped in 1986), one had 10 points (dropped in 1986). and three had 11 points (two dropped in 1986). These points served as centers for nested circular plots for describing vegetation and for bird counts; they also delineated segments of 30-m-wide strip transects used to sample snags.

Sampling Techniques

Birds-Pilot studies (Manuwal and Carey, in press) compared line transects, variable-circular plots, and territory mapping as methods for estimating bird abundance and describing bird communities for contrasting young, mature, and old-growth forests. Variable-radius circular plots (Reynolds and others 1980) with 12 sampling points and six visits gave the best return per unit effort in determining species presence and abundance, but densities differed from territory mapping by 13 to 41 percent. Major differences were overestimates from counting birds more than once, particularly birds of species whose home ranges were large relative to spacing between the plots or that could be detected at long distances (for example, more than 75 m).

With the pilot study as the basis for our sampling, we recorded all birds seen or heard during 6 to 11, early morning, 8-minute visits during late April, May, and June at each of the sampling points in the stands. Species not commonly recorded at sampling points were recorded if seen while the observer walked between points and during searches for nests and observations of foraging behavior that immediately followed the count surveys; 4 to 5 hours were spent in each stand on a sampling day. Sampling was not done on windy or rainy days. The minimum number of visits to a stand was six in a year. We tried to visit stands with less than 12 points more often than the stands with 12 points (appendix tables 14, 15). For example, the maximum was 11 visits to the stand with 7 points. In 1985, all but three stands had six to eight visits, with the range caused by rainy days, observer illness, and other random events. In 1986, all but two stands were visited seven times (the two had six visits). As predicted by the pilot study, species richness reached an asymptote before 72 8-minute counts (six visits to a stand with 12 points) had been done.

We estimated the distance to each bird detected that was not flying through or over the stand during the 8-minute counts. Distance estimation was aided by two flags 25 m from each point, flags midway between points, and by rangefinders. Distances more than 100 m were not recorded because we and our field biologists concluded that estimating distances beyond 100 m with a 20-percent precision was impossible.

We made a strong effort to avoid counting the same bird more than once from the same point. We and our field biologists believe that we were successful in minimizing double counting. If a bird could be heard from more than one point, it was recorded only at the point closest to it. The average (among species) third quartile of detection distances was 51 ± 0.4 (SE) m and did not differ among young, mature, and old-growth stands. Because we used only detections within the third quartile for calculating abundance indices (see section on data analysis), any bias (dependence) from assigning a bird to only one point should have been minimized.

Controlling for differences among observers-Eleven biologists counted birds in 1985 and eight counted in 1986. Five counted birds in both years. **All** had experience in bird identification before employment, and all were trained for 2 to 3 weeks before sampling each year they participated in sampling.

Training consisted of instruction and practice in the field and written protocols that documented objectives, methods, assumptions of techniques, and consequences of violating assumptions. Protocols were reviewed in group discussions and implemented in the field both by groups and by pairs of biologists. All were provided with binoculars, field guides to bird identification, recordings of bird calls and songs in northern California and southern Oregon, as well as opportunities to review recordings based on national and regional bird calls and songs. **A** written, phonetic guide to bird calls and songs (Carey and others 1990) was developed by the group, based on their experiences in the southern Coast Range, and all observers were provided with a copy. Training in bird identification, identification of calls and songs, and aural distance estimation in the field was provided to the group before sampling began; individuals had opportunities to practice alone. The biologists were trained in the use of rangefinders and ocular estimation of distance on courses with targets at various, measured distances. Targets were placed at measured distances near offices so rangefinders could be calibrated daily (flags 25 m from each station allowed checking of rangefinders during actual surveys).

During surveys, rangefinders were used to check ocular and aural estimates of distances to birds. Flags at 25-m intervals along the transect allowed observers to continually check their distance estimates for birds that were too far away to be visually or aurally located in a specific tree. We and our field biologists believed that we maintained a high degree of accuracy in bird identification and distance estimation throughout the sampling.

Observers were in three Oregon locations in 1985, with four in Corvallis, two in Lorane, and five in Winchester: In 1986, three biologists were in Corvallis and five were in Sutherlin. Within each geographic area, observers were systematically rotated among the stands being sampled; young, mature, and old-growth stands were sampled in each area. Biologists in each geographic area (three areas in 1985, two areas in 1986) regularly met to discuss the birds seen and heard and to review one another's data sheets. Regular telephone contact was maintained between the geographically separated groups during the sampling season to discuss methodology and the birds being seen and heard.

Nests and foraging behavior-After each morning's bird counts, we searched the stands for nests and recorded foraging behaviors of cavity-using birds. Nests, nest trees, and nest environments were described (Nelson 1989). For foraging behaviors, we recorded the vertical location by foliage strata (upper, middle, or lower canopy; understory; shrub layer; ground), the horizontal location (mainstem; inner, center, or outer branch; log), the species of tree, the substrate (bole; large, medium, or small branch; twig; shrub), the condition of the tree (live good, live poor, snag decay-class), the d.b.h. of the tree (0-9, 10-19, 20-49, 50-99, and ≥ 100 cm), the dominance status of the tree (suppressed, subordinate, dominant/codominant), and the object (foliage, bark, live wood, dead wood, flower, bud, insect, and other) for the first foraging activity observed for each bird seen.

Vegetation-Vegetation was characterized on two scales: 13-m-radius plots for ground cover, shrub, and midstory variables; and 25-m-radius plots for site and overstory variables. Cover variables included fallen trees by three decay-classes (combined from Franklin and others 1981): 1, intact; 2, bark sloughing to absent, sapwood well-decayed; 3, tree completely in contact with the ground, bark absent, and all wood well-decayed). Other cover variables were herbs, ferns (mostly sword fern), berry-producing deciduous shrubs (mostly blueberry and blackberry), other deciduous shrubs (mostly oceanspray, filbert, and maple), evergreen shrubs (mostly salal, Oregongrape, Pacific rhododendron), broad-leaved evergreen midstory trees, deciduous midstory trees, and needle-leaved midstory trees, Overstory variables included canopy cover of three classes of trees (deciduous, broad-leaved evergreen, and needle-leaved evergreen), counts of snags by three decay-classes (combined from Cline and others 1980): 1, bark and branches mostly intact, sapwood firm; 2, limbs stubs to limbs absent, sapwood soft; 3, well-decayed, bark and sapwood sloughed). We also counted trees by diameter-classes (10-49 cm, 50-99 cm, and 1100 cm) for Douglas-fir, western hemlock, cedars-Port-Orford-cedar, incense-cedar, and western redcedar, Pacific madrone, giant chinkapin, bigleaf maple, other conifers (mostly grand fir), and other deciduous trees. Snags sampled along the transects were measured and described in more detail than those in the circular plots, and their use for nesting and roosting by cavity-using birds was compared to that of snags generally available (Nelson 1989).

Data Analysis

Observations of moving birds, birds more than 75 m from a sampling point, or birds recorded only once in a stand were discarded before calculating indices of birds per effort (BEI) and birds per area (BAI). We did this to avoid counting individual birds more than once, eliminate the observations with the most error (the most distant observations), reduce among-observer differences in effective detection distances, eliminate transient species from the counts, and maintain comparability with the results of the bird community studies in the Oregon Cascade Range, the southern Washington Cascade Range, and the regional analysis of the Old-Growth Program data.

The recorded observations for each species were examined to determine if the rate of cue (call, song) emission varied with time. The black-headed grosbeak, Swainson's thrush, and western tanager were not detected during the early counts. We subtracted the sampling done in the first 5 to 18 days (depending on species) from the effort to adjust for the periods when each species was not present (or not singing). From these reduced data, we calculated bird species richness (number of species by stand) and an index to abundance based on effort-mean number per count per species per stand (BEI).

For analyses related to community structure and bird species diversity, we calculated an index to abundance based on area sampled per species (BAI). Placing the birds on an area-sampled scale allowed calculation of diversity indices and examination of community structure (ranked abundance) (Hutto and others 1986). Such analyses cannot be done reliably with simple count data.

First, we eliminated effort and observations of observers who seemed to have especially poor sensitivity to the calls or songs of particular species (these are known as “window species” for that observer, Kepler and Scott 1981). Poor sensitivity was defined as having a mean number per count less than 50 percent of the median (among observers) mean number per count. For the 2 years, 15 of 929 observer-bird species combinations were dropped. Window species did not appear to reflect differences in the hearing, experience, or awareness of the observers. They seemed to be unique interactions between particular species and individual observers.

We then examined the detections-versus-distance curves by stand type to determine if differences existed among young, mature, and old-growth stands (we found none). From the distributions of birds detected over distance, we calculated the third quartile detection distance for each species. We used this distance as an effective radius of detection for that species and calculated the area sampled around each point. The third quartile proved to be a good approximation of the shoulder in the detection curve-the distance at which a marked decline in numbers of birds was detected. The abundance index was calculated as the numbers of cues of individual birds detected within the third quartile divided by the area sampled (number of points times area sampled per point times the number of visits per point). Abundances are reported on a birds-per40-ha scale. We calculated coefficients of variation for the density indices for each stand and stand-class.

For species that were detected mostly (≥ 270 percent) by their songs, we deleted observations of nonsinging birds; later we doubled the BAI of the songs-only species, on the assumptions we were recording only males and that all males were mated (Emlen 1977, Reynolds and others 1980).

Many sources of bias and error are possible in count indices and cue-density indices (Dawson 1981, Emlen 1977, Hutto and others 1986, Verner 1985; see Ralph and Scott 1981 for an extensive treatment). But our BAI require fewer assumptions and incorporation of less error and bias than the abundance index, BEI (Carey 1983, Ramsey and others 1987, Raphael 1987a). Our BAI is a measure of bird density only to the extent that bird call-and-song counts per unit area are a measure of density. Some birds may not be counted, and some may be counted twice. If such a sampling error differs among bird species, among groups of observers, or among stand types, then the BAI (and the BEI) would be biased.

Placing the birds on an area-sampled scale helped to account for differences in detectability among species. Elimination of long-distance detections and window species was designed to reduce among-observer variability. The remaining among-observer variability was evenly apportioned among the stands through our systematic rotation of observers. Calculating species-by-species third quartiles of detection distances was an effort to reduce the errors in identification of species and estimation of distances in the area of marked decline in detectability. We could not use mathematical models of the decline in detectability because the 27 species for which we had numbers of detections sufficient to model detectability differed markedly in the shape of the detectability curves. And we could not relate the shape of the detectability curve to either the cue quality (strength and pitch of calls and songs) or to the vertical position of the species in the canopy. Therefore, we could not choose a model to fit all species, or several models that could be applied to species of like songs and calls or like positions in the canopy.

In both years, five species exhibited “spikes” (high counts in the first few meters followed by a sharp reduction in counts and eventual additional decline in dectectability), six species had “donuts” (low counts in the first few meters, followed by higher counts, then by declining counts), four species had spikes and donuts, and eight species differed in pattern between years. We could not relate patterns to cue quality or usual location of the species in the canopy. Deletion of nonsong cues from songs-only species did reduce the spikes. Using the the third quartile distances typically encompassed the bulk of the donut. Thus, we effectively reduced some of the error from differences among species. Error in the BAI was likely to be greater in the less abundant and less detectable species, simply because of sample sizes. We chose diversity indices (Magurran 1988) and made comparisons of community structure with these errors in mind.

Margalef’s index (MI) accounts for variability in species richness by weighting the number of species by the total number of birds present; thus, MI based on BAI should be a better measure of richness than number of species based on simple counts. The Berger-Parker index (BPI) expresses the degree to which the most abundant species dominates the community and is thus robust to errors in the estimates of species of low abundance. We used Kendall’s coefficient of concordance (Zar 1984) to test differences among age-classes and moisture-classes in the ranked abundance of species, and we used Kendall’s coefficient of rank correlation and its graphical representation (Sokal and Rohlf 1981) to display the results of the analyses of ranked abundance. We applied this analysis only to species that occurred in at least 90 percent of the stands in any one stand type (young, mature, dry old-growth, mesic old-growth, wet old-growth) to eliminate rare species from the data set. In 1985, these tests were based on the 16 most abundant species, and, in 1986, on the 14 most abundant species. All these species were detected 100 times or more during the counts. Error in the estimates of species of low abundance was not important to the analyses of community structure.

We used direct gradient analyses (box-and-whisker plots and scatter plots) to explore our data. We were particularly interested in how much variability was in each variable-where that variability lay in relation to stand-age and environmental gradients, how observations on each variable were distributed in a statistical sense, and how variability changed along the distributions. Correlation coefficients (linear correlations, correlations with log-transformed variables, and rank correlations) were used to identify redundancies among the variables and to quantify bird species' responses to gradients and relations between gradients.

Parametric and nonparametric (Kruskal-Wallis tests) analyses of variance, Mann-Whitney U-tests, and median tests were used to examine the statistical significance of comparisons among categories. Bartholomew's test for gradients in proportions was used to examine patterns of abundance (proportions of stands in which the species was present) of birds of low abundance across age-classes (Fleiss 1973); all recorded observations were used to determine presence and absence. Because our study sites and sampling points were not Selected randomly, levels of significance are biased. But because we intentionally sampled a wide range of variation in stands in the southern Coast Range, we maximized variability and the significance levels should be conservative (Gauch 1982)-our P-values are probably larger than those a random sample would have produced. The generalizability of statistical or mathematical models and predictions derived from the data is unknown, however. As with any study, extrapolation beyond the bounds of the conditions examined would be risky; the degree of risk is unknown. We recognize that the power of statistical tests is low when variability is high and sample sizes are small. We caution the reader that failure to detect differences under these conditions does not necessarily indicate that differences do not exist, only that the data did not support rejection of the null hypothesis.

We examined bird community attributes and species' abundances on two levels of gradients. The first level included stand age (in years, sometimes log-transformed), stage of forest development (young, mature, old-growth), and moisture categories (dry, mesic, wet). These first-level gradients reflect complex interactions of site and the process of forest development. The second level included gradients based on cover-classes and counts made at the sampling points or along transects. These values were averaged for each stand, classes were combined, and the BPI was calculated. The second-level gradients we developed were density of trees 100 cm or more in d.b.h.; diversity of canopy conifer sizes (BPI based on density of trees in the three size-classes); density of broad-leaved evergreens (Pacific madrone and giant chinkapin) in the canopy; density of slightly to moderately decayed snags 50 cm or more in d.b.h.; density of slightly to moderately decayed snags 100 cm or more in d.b.h.; cover of deciduous trees in the midstory and understory; cover of ferns, herbs, and berry-producing shrubs less than 2 m tall; cover of evergreen shrubs less than 2 m tall; and the proportion of cover less than 2 m tall that was ferns, herbs, and berry-producing shrubs.

Results

Characteristics of Old-Growth Stands

Old-growth stands were easily distinguishable from young and mature stands on the basis of density of Douglas-fir trees by diameter-class (table 1). Discriminant analysis using the three density variables correctly classified 93.6 percent of the stands ($P < 0.01$); one mature stand was classified as old growth, one as young; one young stand was classified as mature. The density of coniferous trees 100 cm or more in d.b.h. was positively correlated with stand age (fig. 1, $r = 0.78$, $P < 0.01$).

The vertical diversity of conifers (as measured by the BPI) in the canopy was positively correlated with stand age (fig. 2, $r = 0.51$, $P < 0.01$) and varied almost three-fold among stands. The BPI was significantly different among the young, mature, and old-growth stand types (Kruskal-Wallis test,

Table 1-Density of Douglas-fir by diameter-class and age-class of stands in the southern Oregon Coast Range, 1985-86; 8 young, 10 mature, and 29 old-growth stands were sampled

		Density (stems per hectare)		
Diameter-class	Age-class	Mean	Standard error	Mode
10-49 cm	Young	269.7	29.0	213.4
	Mature	118.8	19.2	74.8
	Old	27.4	6.2	.0
50-99 cm	Young	29.3	6.9	20.4
	Mature	64.4	8.1	54.0
	Old	24.8	2.6	33.6
≥ 100 cm	Young	1.5	.6	.0
	Mature	6.6	2.6	.0
	Old	22.3	1.8	16.6

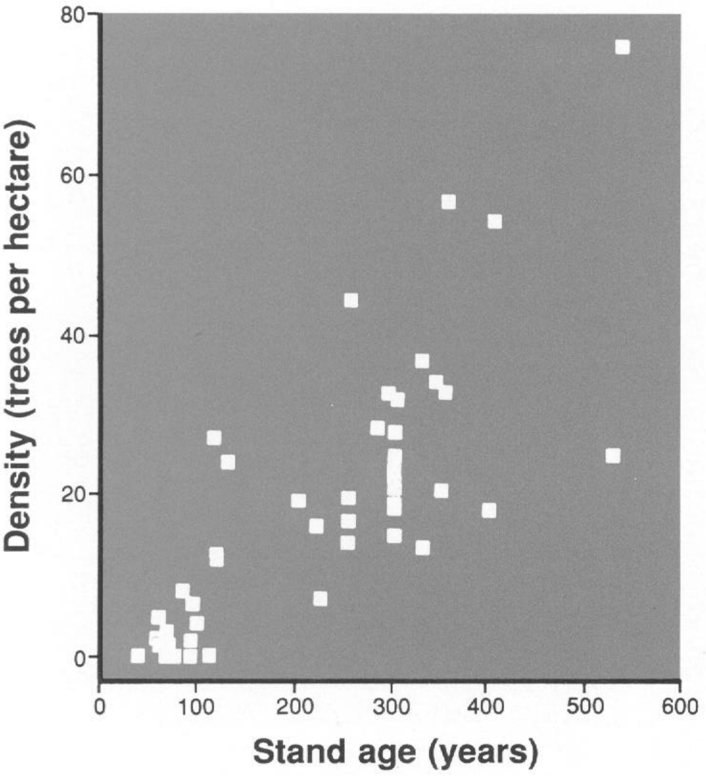

Figure 1—The density of trees 100 cm or larger in d.b.h. versus stand age in the southern Oregon Coast Range, 1985-86.

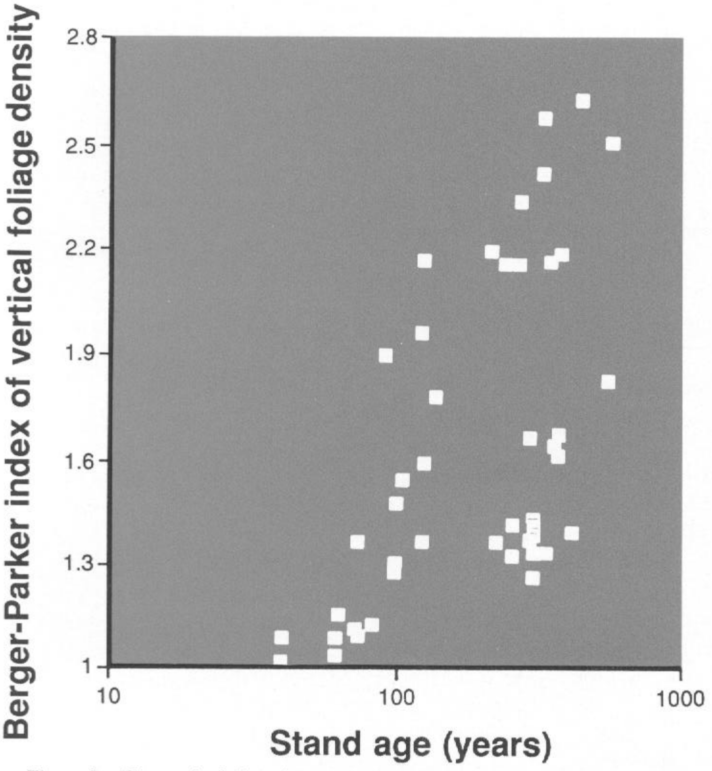

Figure 2—The vertical diversity of conifer foliage in the canopy versus stand age in the southern Oregon Coast Range, 1985-86.

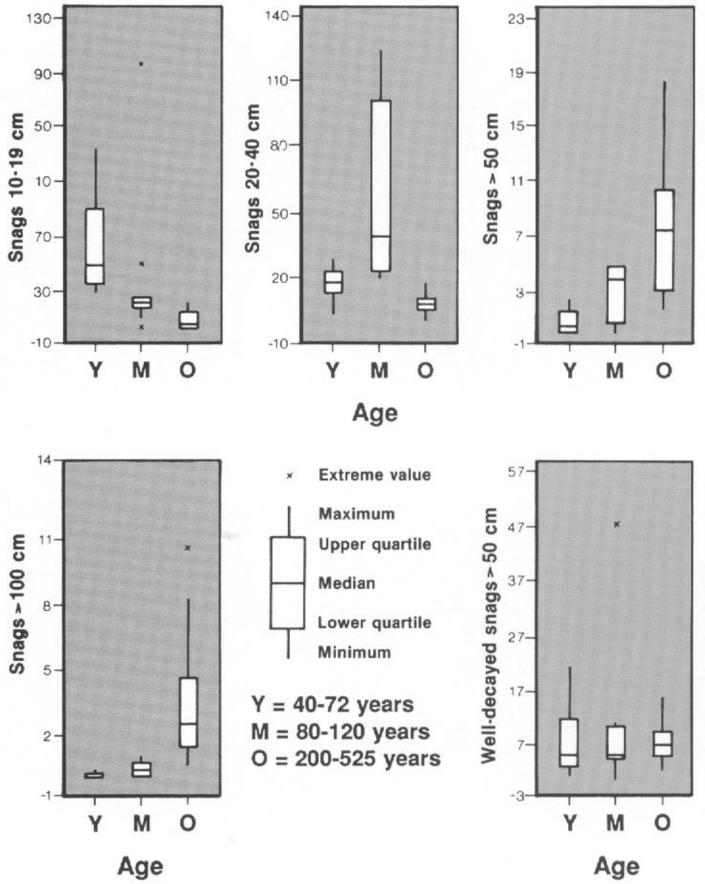

Figure 3—Snag densities by size-class and stand age-class in the southern Oregon Coast Range, 1985-86.

$P < 0.01$), reflecting that the values of BPI were very small in young stands (median = 1.1) and large in mature (median = 1.5) and old-growth (median = 1.7) stands. The variability of the BPI increased with stand age. Canopy height was correlated positively with stand age ($r = 0.59$, $P < 0.01$). Total canopy cover and cover of coniferous trees in the canopy decreased with stand age (Kruskal-Wallis, $P < 0.01$; $r = 0.50$ and 0.49 respectively, $P < 0.01$).

Total midstory cover increased with stand age ($r = 0.436$, $P < 0.01$) and was much greater in old growth than in mature or young stands (Kruskal-Wallis, $P < 0.01$). The number of coniferous trees in the midstory increased with stand age ($r = 0.52$, $P < 0.01$; Kruskal-Wallis $P = 0.01$).

Small-diameter (10-19 cm) snags decreased rapidly with stand age-class (fig. 3; table 8; $r = -0.62$, $P < 0.01$); 20- to 49-cm-d.b.h. snags were most abundant in mature stands; large (>50-cm d.b.h.), moderately decayed (classes 1 and 2) snags increased with stand age ($r = 0.60$, $P < 0.01$). Very large (>100-cm d.b.h.), moderately decayed snags showed marked association with old growth, being 10 times more

Table 2—Density of snags by diameter-class and age-class in 8 young, 10 mature, and 29 old-growth stands in the Oregon Coast Range, 1985-86

		Density (stems per hectare)		
Diameter-class	Age-class	Mean	Standard error	Mode
>100 cm	Young	0.08	0.05	0.0
	Mature	.33	.12	.3
	Old	3.27	.47	1.8
>50 cm	Young	.79	.34	.0
	Mature	4.33	1.52	4.8
	Old	7.32	.84	6.7
20-49 cm	Young	17.63	2.60	13.6
	Mature	55.61	12.62	32.1
	Old	8.35	.84	9.1
10-19 cm	Young	64.90	56.87	36.1
	Mature	39.09	23.17	18.2
	Old	6.95	4.65	6.4

abundant there, on average, than in mature forests (fig. 3, table 2; $r = 0.73$, $P < 0.01$). Very large, moderately decayed snags were not commonly found in young forests (mode = 0.0). Very large, well-decayed (class 3) snags were equally abundant among the age-classes.

No variables measured in the understory were significantly correlated with stand age. The proportion of total vegetative cover that was canopy cover decreased with stand age ($r = -0.50$, $P < 0.01$; Kruskal-Wallis, $P < 0.01$). Significant relations among understory variables and moisture-class were found in old growth. Herbs, ferns, berry-producing shrubs, and total vegetative ground cover increased with moisture (Kruskal-Wallis, $P < 0.10$). Evergreen shrubs, deciduous shrubs, and total shrub cover decreased with moisture (Kruskal-Wallis, $P < 0.10$). The proportion of understory cover that was herbs, ferns, and berry-producing shrubs was highly correlated with moisture (fig. 4; $r = 0.76$, $P < 0.01$; Kruskal-Wallis ranks: 7.5, 15.2, 26.2, $P < 0.01$). The combined cover of evergreen and other deciduous shrubs was negatively correlated with moisture-class (Kruskal-Wallis ranks: 22.2, 13.9, 6.8, $P < 0.01$). The proportion of understory cover that was herbs, ferns, and berry-producing shrubs was negatively correlated with the cover of evergreen and other deciduous shrubs when applied to the old-growth data set ($r = -0.64$, $P < 0.01$) and the total data ($r = -0.66$, $P < 0.01$). Discriminant analysis of preassigned moisture-classes using the understory proportion was significant ($P = 0.0000$) and correctly classified 62 percent of the 29 old-growth stands; 100 percent of the wet stands and 88 percent of the dry stands were correctly classified. Twelve percent of the dry stands were classified as mesic, 38 percent of the mesic stands were classified as dry, and 25 percent of the mesic stands were classified as wet. The proportion of understory cover that was herbs, ferns, and berry-producing shrubs proved to be a good indicator of site moisture and of the gradient in understory cover that ranges from forbs and ferns to heavy cover of salal.

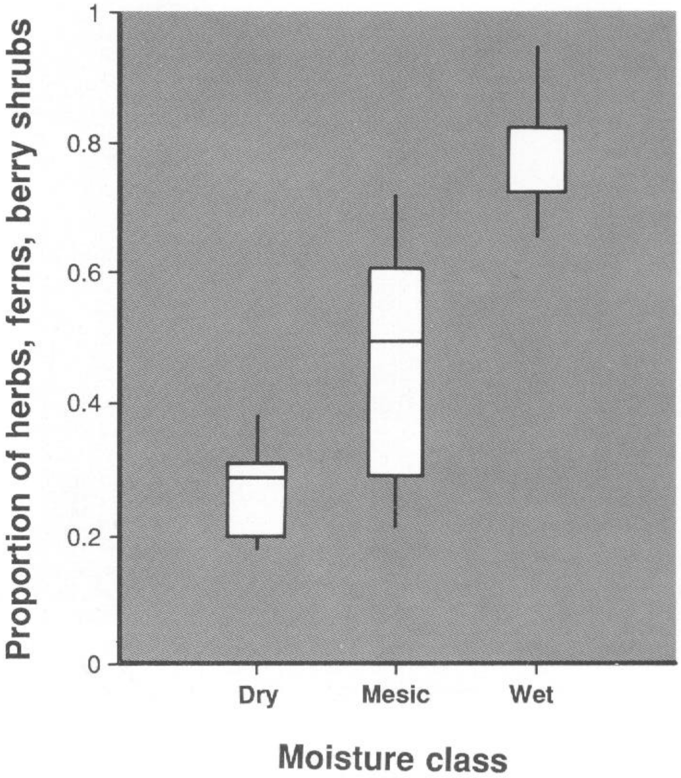

Figure 4—The proportion of cover less than 2 m tall that was composed of herbs, ferns, and berry-producing shrubs by moisture-class of old-growth stands in the southern Oregon Coast Range, 1985-86.

Birds

We recorded 37,402 birds of 84 species in 1985 and 23,089 of 79 species in 1986. A complete list of the 91 species and their numbers was reported by Carey (1988). When we counted only stationary birds within 75 m of the sampling points and deleted observations of birds that occurred less than twice in each of the stands, we obtained 26,811 observations of 51 species in 45 stands in 1985 and 16,741 observations of 46 species in 33 stands in 1986 (appendix tables 10, 11). Eliminating observations of birds more than 75 m from the observer resulted in a 28-percent reduction in number of observations; combined with BAI calculations, almost 40 percent of observations were discarded. The precision of the estimates, however, was not affected. Coefficients of variation averaged 43.6 ± 3.4 percent for BAI, 44.1 ± 6.7 percent for BEI, and 38.6 ± 6.7 percent for total counts for the 15 most abundant species. Total counts were highly correlated with the BEI ($r = 0.99$, $P < 0.01$) and BAI ($r = 0.97$, $P < 0.01$), indicating that no information was lost within species. The

Table 3—Species comprising 75 percent of all observations in 45 stands in 1985 and 33 stands in 1986 in the southern Oregon Coast Range

	1985		1986	
Species	Rank	Number	Rank	Number
Winter wren	1	4589	2	2347
Western flycatcher	2	3725	1	2448
Chestnut-backed chickadee	3	3382	4	1639
Hermit warbler	4	2748	3	1802
Golden-crowned kinglet	5	2225	5	1422
Wilson's warbler	6	1774	6	1075
Brown creeper	7	1365	7	1051
Varied thrush	8	1087	8	875

Table 4—Mean number of species per stand by age-class and moisture-class, based on counts of stationary birds within 75 m of sampling points in the southern Oregon Coast Range, 1985-86 (species must have occurred at least twice in a stand to be counted)

	Age-class				Moisture-class			
Year	Young	Mature	Old	P[a]	Dry	Wet	Mesic	P
1985	20.6	20.6	20.8	0.98	21.8	20.2	21.0	0.51
Samples[b]	8	10	27		8	14	5	
1986	20.7	16.4	19.4	0.01	21.2	19.5	17.0	0.24
Samples[b]	6	8	19		5	10	4	

[a] Kruskal-Wallis test.

[b] Number of stands sampled with around 84 8-minute counts each.

correlation between total counts and BAI was much lower across species ($r = 0.74$, $P < 0.01$), reflecting the information gained by accounting for differences in detectability.

The same eight species accounted for 75 percent of all observations in both years (table 3). Seven species were recorded in 1985 that were not recorded in 1986: black-capped chickadee (39 observations, primary habitat: deciduous and deciduous/conifer forests), mountain quail (three observations, early stages of forest development), ruby-crowned kinglet (two observations, late stages of coniferous forest development), ruffed grouse (two observations, deciduous forests), Townsend's solitaire (seven observations, early and late stages of forest development), white-breasted nuthatch (two observations, late stages of forest development), and western wood-pewee (two observations, late stages of forest development) (habitat associations from Brown 1985). Species recorded only in 1986 were chipping sparrow (four observations, early stages of forest development) and house wren (seven observations, shrub stages of forest development). Lists of species' BAI by age-class are in appendix tables 12, 13. Sampling efforts are in appendix tables 14, 15.

Table 5—Mean values of Margalef's index (MI) of richness and the Berger-Parker index of dominance (BPI) applied to avian species birds-per-area index by age- and moisture-class in the southern Oregon Coast Range, 1985-86

	Age-class				Moisture-class			
Index year	Young	Mature	Old	P[b]	Dry	Mesic	Wet	P
MI, 1985	3.2	3.2	3.1	0.99	3.3	3.0	3.2	0.34
BPI, 1985	4.6	4.0	4.1	.39	3.9	4.2	4.0	.47
Samples[a]	8	10	27		8	14	15	
MI, 1986	3.3	2.6	3.0	0.01	3.3	3.0	2.6	0.14
BPI, 1986	4.5	4.6	4.8	.89	5.6	4.5	4.4	.15
Samples[a]	6	8	19		5	10	4	

[a] Number of stands sampled per class.

[b] Kruskal-Wallis test.

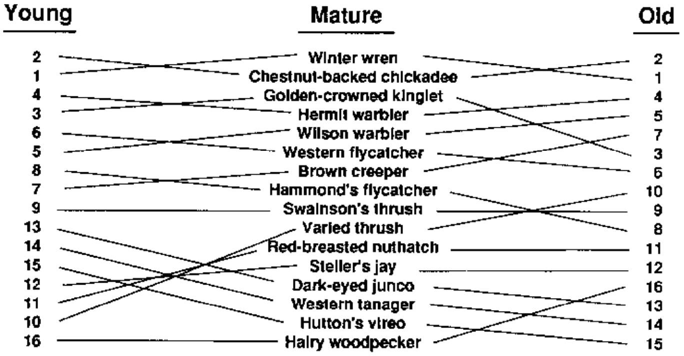

Figure 5—The ranked abundance of bird species in young, mature, and old-growth stands in the southern Oregon Coast Range, 1985.

Species Diversity

The mean number of species per stand (based on counts) did not vary with age-class (Kruskal-Wallis, $P = 0.98$) or moisture-class ($P = 0.51$) in 1985. In 1986, mature stands had fewer species than young or old-growth stands (table 4; Kruskal-Wallis, $P < 0.01$), but no significant difference was found among moisture-classes (Kruskal-Wallis, $P = 0.24$). The difference in richness was due to the absence of some uncommon species in the mature stands. Margalef's index to richness displayed the same pattern as the counts—mature stands had fewer species than young and old-growth stands in 1986 but not in 1985 (table 5). Margalef's index did not differ significantly among moisture-classes. The Berger-Parker index of dominance (and evenness) showed no differences among stand types (table 5).

Patterns of Abundance

The mean number of birds counted per stand in 1985 (570) did not differ significantly ($P = 0.85$) among age-classes; in 1986, fewer birds were counted in mature stands (mean = 471) than in young (mean = 489) and old-growth (mean = 528) stands (analysis of variance, $P < 0.05$). Ranked

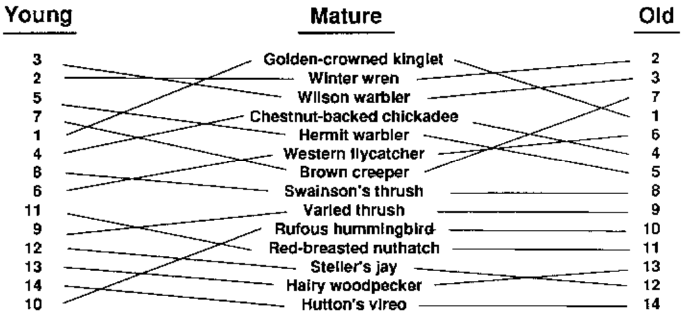

Figure 6—The ranked abundance of bird species in young, mature, and old-growth stands in the southern Oregon Coast Range, 1986.

Table 6—Mean birds-per-area indices (numbers per 40 ha) of birds associated with old-growth forests in the southern Oregon Coast Range, 1985-86

	Age-class			
Species	Young	Mature	Old-growth	P^a
Brown creeper	16.66	28.66	34.24	**
Chestnut-backed chickadee	52.06	61.88	101.62	**
Hairy woodpecker	.74	1.10	1.79	*
Olive-sided flycatcher	.06	.03	.47	*
Pileated woodpecker	.02	.25	.41	**
Red-breasted nuthatch	3.14	6.48	9.30	**
Red-breasted sapsucker	.12	.90	1.02	**
Varied thrush	4.82	15.12	14.75	**
Western flycatcher	49.28	34.57	60.84	**
Woodpeckers[b]	.88	2.25	3.22	**
Other cavity users[c]	71.88	97.08	145.27	**
Bark foragers[d]	20.68	37.39	46.35	**

[a] * $P < 0.10$ in 1 year; ** $P < 0.10$ in 2 years; Kruskal-Wallis test.
[b] Hairy woodpeckers, pileated woodpeckers, and red-breasted sapsuckers.
[c] Red-breasted nuthatch, chestnut-backed chickadee, brown creeper, and northern pygmy-owl.
[d] Hairy woodpecker, pileated woodpecker, red-breasted sapsucker, brown creeper, and red-breasted nuthatch.

abundance did not differ among age-classes in 1985 (for 16 species, fig. 5) or in 1986 (for 14 species, fig. 6) (Kendall's coefficient of concordance, $P < 0.01$, Kendall's coefficient of rank correlation, $P < 0.01$ for all pairwise comparisons). Nine species reached maximum abundance in old growth (table 6), including all the common cavity-using birds. The varied thrush was more abundant in mature and old-growth stands than in young stands. The varied thrush was the only species associated with old forests that also showed a preference for a moisture-class (wet stands in both years, Kruskal-Wallis test, $P < 0.05$). Moisture preferences of other species will be discussed below in relation to the gradient in proportion of understory cover that was herbs, ferns, and berry-producing shrubs. Woodpeckers as a group, other cavity users as a group, and bark gleaners reached maximum abundance in old growth (table 6). Foliage foragers (black-throated gray warbler, chestnut-backed chickadee, golden-crowned kinglet, Hammond's flycatcher, hermit warbler, Hutton's vireo, purple finch, western flycatcher, western tanager, black-headed grosbeak, and yellow-rumped warbler) and forest-floor birds (American robin, blue grouse, dark-eyed junco, hermit thrush, song sparrow, Swainson's thrush, varied thrush, Wilson's warbler, winter wren, and wrentit) as groups did not differ significantly in abundance among age-classes ($P > 0.10$, 1985 and 1986). Eleven species were most abundant in young stands (table 7). One, the purple finch, was listed by Brown (1985) as preferring old growth; our data suggest that it does not.

Table 7—Mean bird-per-area indices of species associated with young forests in the southern Oregon Coast Range, 1985-86

	Age-class			
Species	Young	Mature	Old-growth	P^a
Black-headed grosbeak	3.90	0.79	0.37	*
Dark-eyed junco	7.76	4.39	2.06	*
Evening grosbeak	2.96	5.66	1.63	**
Hammond's flycatcher	27.97	20.26	6.94	*
Hermit warbler	69.59	41.18	48.34	*
Hutton's vireo	6.66	.78	1.62	**
Nashville warbler	1.84	.69	.71	*
Purple finch	4.12	.74	1.70	**
Orange-crowned warbler	3.20	1.18	1.41	*
Warbling vireo	2.41	.12	.26	*
Western tanager	5.12	1.34	1.46	*

[a] * $P < 0.10$ in 1 year; ** $P < 0.10$ in 2 years; Kruskal-Wallis test.

Table 8—Mean proportion of young, mature, and old-growth stands in which selected species of low abundance occurred in the southern Oregon Coast Range, 1985-86; all observations recorded were used

	Age-class			
Species	Young	Mature	Old-growth	P^a
Hairy woodpecker	0.88	1.00	1.00	*
Northern flicker	.56	.88	.93	**
Northern pygmy-owl	.38	.75	.59	*
Olive-sided flycatcher	.31	.38	.78	**
Pileated woodpecker	.69	.94	1.00	**
Red-breasted sapsucker	.31	.44	.87	**
Spotted owl	.00	.00	.24	**
Marbled murrelet[b]	.00	.50	.83	*
Vaux's swift[b]	.00	.29	.39	**

[a] Test of the hypothesis that the species increased in abundance with age-class, using Bartholomew's test for a gradient in proportions; * $P < 0.05$, ** $P < 0.01$.
[b] Data from 1986 only.

Proportional occurrences of species of low abundance reinforced many of the associations with old growth shown by densities in table 6 (table 8). All of these species showed a significant increase in abundance across the three age-classes (Bartholomew's test, $P < 0.05$). In addition, the northern flicker and northern pygmy-owl increased in abundance with stand age. All patterns displayed in tables 4 to 6 were consistent between years, except that evening grosbeaks were less than one-tenth as abundant in old-growth and mature stands and twice as abundant in young stands in 1986 as in 1985. All abundances were of the same magnitude between years except that chestnut-backed chickadees were one-third, orange-crowned warblers one-fourth, and western tanagers one-half as abundant in 1986 as in 1985.

Three species that were not commonly found within 75 m of the sampling points were the marbled murrelet, the spotted owl, and Vaux's swift. They showed a pattern of increasing abundance with age-class (table 8; Bartholomew's test, $P < 0.05$). The marbled murrelet was recorded only in mature and old-growth stands near Corvallis (Carey 1989; Nelson and others, in press).

Responses to Gradients

Bark foragers (hairy woodpeckers, pileated woodpeckers, red-breasted sapsuckers, brown creepers, and red-breasted nuthatches) were not significantly correlated (using Pearson product-moment correlation) with the density of large trees in 1985 and showed only a weak positive Pearson correlation in 1986 ($r = 0.45$, $P < 0.01$) because of a positive response by the red-breasted nuthatch. A simple linear regression of bark-forager abundance on large-tree density had a positive slope significantly different from zero ($P < 0.05$) in both years. When we truncated the gradient at 20 large trees per hectare (about the mean value for trees $\geq$ 100-cm in d.b.h. in old growth) the increase in the slope was marked. When we examined the correlations between large trees and bark-forager abundances for young and mature stands separately from old growth, significant positive Pearson correlations were found in both years (1985, $r = 0.71$; 1986, $r = 0.75$; $P < 0.01$). Brown creeper abundances were positively correlated with the density of large trees in both years ($r = 0.75$ in 1985, $P < 0.01$; $r = 0.62$ in 1986, $P < 0.05$). Positive Pearson correlations were found for pileated woodpeckers in 1985 and red-breasted sapsuckers in 1986. Spearman rank correlations were positive and significant in both years for brown creepers and bark foragers, as a group, across the entire large-tree gradient ($P < 0.10$).

Few positive Pearson correlations were found between cavity-using birds and densities of small, medium, large, and very large snags. When we examined young and mature stands alone, the red-breasted nuthatch, chestnut-backed chickadee, brown creeper, and northern pygmy-owl, as a group, were positively correlated with the density of very large ($\geq$ 100-cm-d.b.h.) snags ($r = 0.71$ in 1985, $P < 0.01$; $r = 0.73$ in 1986, $P < 0.05$). Chestnut-backed chickadees accounted for most of this positive response ($r = 0.62$ in 1985, $P < 0.05$; $r = 0.67$ in 1986, $P < 0.05$). Positive rank correlations ($P < 0.10$) were found between very large snags and all cavity-nesting species, brown creepers, woodpeckers as a group, and other cavity nesters as a group in both years (except hairy woodpeckers in 1985 and northern flickers in 1985 and 1986). Rank correlations with very large snags (0.28-0.55) were higher than rank correlations with large snags (0.17-0.45), indicating that very large snags accounted for a substantial portion of the correlations with large snags.

Only one consistent pattern of positive response was obtained when we examined forest-floor-associated birds relative to the proportion of vegetative cover less than 2 m tall that was herbs, ferns, or berry-producing shrubs, which is also a site-moisture indicator, and the cover of evergreen shrubs. The varied thrush was positively correlated with the proportion of herbs, ferns, and berry-producing shrubs in both years ($P < 0.05$, Pearson's $r = 0$-44-0.54) and negatively correlated with evergreen shrubs in both years ($P < 0.05$, Pearson's $r = -0.43$ in both years), reflecting its preference for wet sites. Rank correlations between ground-associated birds as a group and the proportion of herbs, ferns, and berry-producing shrubs were positive in both years ($r = 0.35, 0.37$, $P < 0.05$).

We found no consistent pattern of positive responses between the abundance and diversity (MI, BPI) of foliage foragers and coniferous foliage-height diversity (BPI). Similarly, we found no consistent pattern of positive responses when we examined the diversity of hardwood-associated species (black-throated gray warbler, black-headed grosbeak, Hutton's vireo, purple finch, Swainson's thrush, warbling vireo, black-capped chickadee, ruffed grouse, and downy woodpecker) in relation to total deciduous hardwood cover (shrub, understory, and midstory). Rank correlations between the abundance of hardwood-associated birds as a group and hardwood cover were significant in both years ($r = 0.33,0.44$, $P < 0.05$).

Nests

We located 277 active nests of nine species of cavity-using birds. All species preferred Douglas-fir snags more than 50 cm in d.b.h. Mean nest-tree d.b.h. ranged from 54 cm for the northern pygmy-owl to 113 cm for the red-breasted sapsucker; the mean was 94 cm (Nelson 1989).

Foraging Behavior

We recorded 989 foraging bouts by six species of cavity-using birds (table 9). Pileated woodpeckers concentrated their activities in the upper and mid-canopy in Douglas-fir, as did red-breasted nuthatches. Pileated woodpeckers concentrated on tree boles, whereas the nuthatches used small, medium, and large branches in addition to the tree bole. Pileated

Table 9-Percentage of common (≥ 14 percent) foraging activities by bird species, location in the forest, tree characteristics, and object for cavity-using birds in the Oregon Coast Range, 1985-86

	Red-breasted sapsucker	Hairy woodpecker	Pileated woodpecker	Chestnut-backed chickadee	Red-breasted nuthatch	Brown creeper
Sample size	99	156	33	323	65	313
Vertical location:						
Upper canopy	19		54	17	38	
Midcanopy	47	35	22	36	49	30
Lower canopy	23	14		22		30
Understory		26		20		32
Horizontal location:						
Mainstem	86	72	83		37	87
Inner branch				16		
Center branch				35	40	
Outer branch				52	16	
Tree species:						
Douglas-fir	44	71	82	43	71	65
Western hemlock	15			21		17
Bigleaf maple	35					
Substrate:						
Tree bole	84	72	75	12	31	89
Large branch				20	22	
Medium branch				48	19	
Small branch					29	
Tree condition:						
Live	85	64	35	92	76	84
Decay-class 1			34			
Decay-class 2		23	24			
Diameter-class:						
0-9 cm				22		
10-19 cm						
20-49 cm	59	38		34	26	41
40-100 cm	28	45	48	43	65	41
>100cm			40			
Tree status:						
Suppressed	18	19		27		
Subordinate	44	22		20		24
Dominant	34	52	80	44	80	62
Object:						
Foliage				54		
Bark	24	48	34		14	79
Dead wood		30	51		31	
Live wood (sap)	60				32	

woodpeckers preferred large trees ranging from live trees in good condition to snags that were slightly to moderately decayed. Nuthatches concentrated on live trees.

Red-breasted sapsuckers and chestnut-backed chickadees also used the upper canopy, but made greatest use of the middle to lower canopy, as did hairy woodpeckers and brown creepers. Sapsuckers, woodpeckers, and creepers concentrated on the boles of trees, whereas chickadees foraged among branches, especially the outer branches. Chickadees foraged mostly on small branches. Douglas-fir was the primary species used, but sapsuckers also used bigleaf maple and western hemlock. All concentrated on live trees in good condition, with hairy woodpeckers making significant use of moderately decayed snags. Chestnut-backed chickadees foraged across diameter-classes, whereas woodpeckers and creepers tended to prefer dominant trees with diameter-classes reflecting stand age; sapsuckers used subordinate trees the most, followed by dominant trees, and thus foraged on smaller trees, on average, than did woodpeckers and creepers. Chickadees concentrated on foliage, sapsuckers on live wood (sap), hairy woodpeckers on dead wood and bark, and creepers on bark.

Foraging behavior mostly was consistent across the stand age-classes. Pileated woodpeckers were seen rarely in young and mature stands (4 of 42 observations). Pileated woodpeckers were observed foraging on fallen trees more (15 percent), a greater variety of trees, more on snags, and mom on trees more than 100 cm in d.b.h. in old growth than in young or mature stands. Hairy woodpeckers used branches on trees more in old growth than in younger stands (42 percent bole use in old growth versus 84 percent and 73 percent in mature and young stands, respectively). Hairy woodpeckers used more live trees in poor condition and slightly decayed trees in mature and old-growth stands than they did in young stands. They also foraged more on large trees in old-growth than in young and mature stands; trees 20 to 49 cm in d.b.h. were used the most in young and mature stands. Only three red-breasted sapsuckers were observed foraging in young stands. Red-breasted nuthatches tended to use the lower canopy more as stand age increased (percentage of use = 0,8, and 12 in young, mature, and old-growth stands) and increased their use of very large trees. In young stands, nuthatches selected trees greater than 50 cm in d.b.h. over trees 20 to 49 cm in d.b.h. But in mature stands, they selected for the 20- to 49-cm diameter-class. Use of diameter-classes by chickadees reflected availability. Nuthatches foraged more on dead wood in young stands (27 percent) than in mature (0 percent) or old-growth stands (6 percent).

Discussion

Forest Development

The Douglas-fir-dominated forests of the southern Oregon Coast Range displayed a clear pattern of development over the range of ages we studied: 40 to 525 years. Both the distribution of diameter at breast height in live trees (table 1) and the patterns of abundance of snags (fig. 3) provide good models of forest development: attainment of dominance by some trees, suppression of subordinate trees, and the opening of the canopy through death of dominant trees. Young stands were characterized by high densities of l0- to 49-cm d.b.h. Douglas-firs (table 1); high stocking rates had resulted in mortality from suppression that produced high densities of small- and medium-diameter snags (table 2, fig. 3). Relatively large numbers of well-decayed large snags from the previous stand were carried over into the young and mature stands. Young stands were even-aged, had low values for coniferous foliage-height diversity (fig. 2), and high values of canopy cover, Midstory and understory layers were undeveloped. Mortality from competition (suppression) continued into the mature age-class, which also tended to be even-aged and to have a low foliage-height diversity. Canopy cover decreased with age, but mortality in the mature stands began to produce snags of the size and condition favored by cavity-nesting birds (moderately decayed snags >50-cm d.b.h.; Cline and others 1980, Nelson 1989). Mature stands were approaching a phase of rapid development, including increases in tree size, abundance of large snags, and vertical stratification of the canopy.

Tree size (fig. 1) and foliage-height diversity (fig. 2) continued to increase with age through the oldest stands studied. Mortality rates of dominant trees slowed; however, the slightly to moderately decayed snags most used by cavity-using birds (mean diameter of snags used for nesting was 94 cm, Nelson 1989) occurred in much lower densities in old growth than the smaller snags did in the younger stands (fig. 3). Tree death in young and mature stands is usually due to suppression, but tree death in old growth is usually due to butt rot, windthrow, or fire (Franklin and others 1987). Canopy cover was at a minimum, and midstory and understory development at a maximum, in old-growth stands. Because of the wildfire history of the Coast Range, 500 years is about the maximum age of old-growth stands there (Juday 1976); 500 years is also the time of peak accumulation of coarse woody debris, including snags (Spies and others 1988). The structure of the old-growth (200-525 years old) forests differs significantly from young and mature forests. Attendant to these structural differences are compositional differences in the makeup of the overstory, the development of a shade-tolerant midstory and understory, and, depending on moisture conditions, a greater development of shrub and forest-floor vegetation.

Bird Communities

Bird communities in the southern Coast Range were dominated by eight common species (table 3); no marked differences were observed in community structure (figs. 5,6) among young, mature, and old-growth forests. Total abundance of birds was about equal among age-classes. Species diversity, as measured by richness, Margalef’s index, and the Berger-Parker index, did not differ in a biologically significant way among age-classes, although mature stands seemed to support a slightly less rich and less abundant bird community. All three age-classes were closed-canopied, maturing coniferous forest; all the study stands were in landscapes dominated by forest communities.

Forty percent of the bird species present in spring communities were migrants and, of these, only the Vaux’s swift (a cavity nester) and the olive-sided flycatcher showed an association with old growth. About one-fourth of the resident birds were cavity users; all showed an association with old growth; and, in addition, the marbled mm-relet and the/winter wren increased in abundance with stand age.

Bird communities in old growth differed from those in young and mature stands, primarily in the abundance and diversity of cavity-using birds (including the crevice-nesting brown creeper and the sometimes cavity-using spotted owl). This compositional change in the bird communities was continuous throughout the age gradient studied, with young forests supporting the fewest cavity users and old-growth forest supporting the most. The cavity users that were abundant in young stands, the brown creeper and the chestnut-backed chickadee, were the only two that made significant use of well-decayed (class 3) snags for nesting (Nelson 1989). As carryovers from the old-growth stands preceding the young and mature stands, these large and very large, well-decayed snags were equally abundant in the three age-classes studied. Our findings suggest that given present conditions, cavity-using birds depend on old growth to support the numbers of birds necessary to ensure viable populations.

Hypotheses Examined

Large trees-Old growth is unique in the number of large, live trees, and bark-foraging birds showed a strong (r = 0.73) numerical response to large-tree density in young and mature stands. Brown creepers, especially, showed a consistent, positive association with large trees throughout the age gradient and increased in abundance with age, being twice as abundant in old-growth as in young stands. Creepers selected the dominant trees in each age-class for foraging and concentrated their foraging on the bark on the tree boles. But brown creepers were abundant birds-even more abundant; in young stands than many of the species associated with young stands (tables 6,7). Large, live trees may not be a necessity for creepers, but they certainly contribute to maintaining large populations. We conclude that live, old-growth trees are an important habitat element for bark-foraging birds, particularly brown creepers.

The other bark foragers were cavity-using birds whose association with large, live trees may reflect, in part, their associations with large, dead trees. They did not concentrate their foraging on the bark on the boles of large, live trees to the extent creepers did. Indeed, the hairy woodpecker used large branches on old, live trees as well as the boles. The red-breasted nuthatch used branches more than boles. The pileated woodpecker used snags as well as live trees. And the red-breasted sapsucker foraged on a greater variety of species than the brown creeper did.

Vertical diversity-Old growth had a much greater vertical diversity of coniferous foliage than young or mature stands did. But the foliage-foraging species did not respond numerically to the gradients in diversity or stand age. The diversity of foliage foragers did not increase with increasing foliage-height diversity. Greater foliage-height diversity (and the attendant diversity of species) of old growth apparently did not strongly influence the bird communities.

Snags-The abundance and diversity of cavity-using birds was positively correlated with large snags. Snags used by cavity-nesting birds began to increase in availability in mature stands but were abundant only in old-growth stands. Ten of the 14 species associated with old growth (tables 6,8) are cavity users. Two, the spotted owl and Vaux's swift, are dependent on old growth (Carey 1989). The only cavity-nesting species that was abundant in young stands was the chestnut-backed chickadee, which used well-decayed, large snags as well as moderately decayed, large snags for nesting. Large, and especially very large, moderately decayed snags are of major importance to cavity-using birds. These kinds of snags may be difficult to maintain in managed stands.

Spatial diversity-We found that canopy cover decreased and midstory development increased with age, but understory vegetation reflected moisture more than canopy cover. Bird species responding to ground cover less than 2 m tall seemed to be responding to the abundance of forbs and berry-producing bushes relative to evergreen shrubs on a wet-to-dry gradient, rather than to stage of forest development, although the varied thrush responded to both. We found no clear pattern of increased ground cover with age. Spatial diversity associated with old growth apparently did not exert a strong influence on bird communities.

The Value of Old Growth to Birds

Old growth seems especially important to cavity-using birds. These birds select large snags out of proportion to their availability even in the midst of abundant, small snags (<50-cm d.b.h.) (Nelson 1989). Mean diameter at breast height of snags used for nesting was 94 cm-an old-growth diameter. The bulk of the snags used were of diameters that do not occur until after at least 80 years of growth.

The pileated woodpecker, hairy woodpecker, and red-breasted sapsucker were rare in young stands and most abundant in old growth, though not as abundant as the secondary cavity users. The home-range size of woodpeckers exceeds our average stand size, however; the average home-range size of the pileated woodpecker in the Oregon Coast Range is 480 ha (Mellen 1987). Thus, the presence of old-growth stands may provide nesting habitat for woodpeckers and allow them to forage in nearby younger forests to a greater degree than would be possible without old growth.

The chestnut-backed chickadee was most abundant in old growth but also abundant in younger stands. The red-breasted nuthatch was three times as abundant in old growth as in young stands but still relatively abundant in young stands.

These small species prefer large, tall snags (Nelson 1989). But unlike most other cavity-using birds (Nelson 1989) chickadees nested in large, well-decayed snags. Young stands developing after harvest of second-growth stands would be devoid of these large, well-decayed snags. Loss of these carryovers from old growth would reduce the quality of young stands as chickadee habitat.

The Vaux's swift uses large, hollow snags for nesting (Gabrielson and Jewett 1940). These swifts will forage over clearcuts, but 56 of the 61 swifts we recorded in the Coast Range were in old growth. The large, hollow trees used for roosting and nesting are not commonly found in young or mature stands (Carey 1989).

The brown creeper, strictly speaking, is not a cavity nester; rather it builds a nest under loose bark (Ehrlich and others 1988). The heavily furrowed bark of old-growth Douglas-firs has been postulated as harboring an abundant arthropod fauna that serves as food for brown creepers (Mariani 1987). Our data show that brown creepers prefer to forage on the largest trees available and that creeper abundance increases with the abundance of large trees. Creepers were abundant in all age-classes. They preferred large snags for nesting (mean d.b.h. was 83 cm) and selected the largest snags available; nest-snag diameter increased with age. Creepers used both moderately and well-decayed snags more frequently than the cavity-using birds did (with the exception of the chestnut-backed chickadee).

The only noncavity nester closely tied to old growth was the olive-sided flycatcher, an aerial insectivore that nests high on the branches of coniferous trees (Ehrlich and others 1988, Gabrielson and Jewett 1940). The tall trees and broken canopy of old growth provides a much better foraging environment than the dense, closed-canopy young and mature forests in the Coast Range.

Western flycatchers, although most abundant in old growth, were abundant in the other age-classes as well. The varied thrush was most abundant in mature and old-growth stands, but relatively abundant in young stands as well. The association with older stands might reflect a subtle influence of canopy openings on ground cover or an influence of tall canopies on ground moisture.

Little information exists on the inland ecology of marbled murrelets; Nelson and others (in press) reviewed what is known about the marbled murrelet in Oregon. Additional information on the ecology of murrelets is needed before the importance of old growth to them can be determined.

We found no evidence that other bird species we studied found old growth to be a more favorable environment than young or mature stands. Many species, however, were not sampled adequately. And we studied the bird communities only during the spring. We believe our data were sufficient to conclude that loss of old growth would negatively affect cavity-using bird populations. We predict that effects would be severe for woodpeckers, the Vaux's swift, and the spotted owl.

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Appendix

Table 10—Mean standardized counts (number per stand visit) of birds within 75 m of sampling points in young, mature, and old-growth forests in the southern Oregon Coast Range, 1985

	Stand age-class		
Species	Young (n = 8)	Mature (n = 10)	Old (n = 27)
American robin	1.00	1.53	0.81
Band-tailed pigeon	.09	.14	.12
Black-capped chickadee	.00	.05	.16
Black-headed grosbeak	.83	.21	.08
Black-throated gray warbler	1.31	.34	.39
Blue grouse	.00	.13	.09
Brown creeper	2.05	4.30	4.86
Chestnut-backed chickadee	7.11	8.76	12.34
Common raven	.00	.00	.05
Dark-eyed junco	2.14	1.06	.68
Downy woodpecker	.00	.04	.00
Evening grosbeak	.89	2.40	.72
Golden-crowned kinglet	6.71	7.63	6.44
Gray jay	.34	.68	.30
Hairy woodpecker	.45	.37	.61
Hammond's flycatcher	3.59	2.99	1.08
Hermit thrush	1.22	.34	.50
Hermit warbler	11.33	7.59	8.81
Hutton's vireo	1.26	.25	.24
MacGillivray's warbler	.00	.00	0.13
Mountain quail	.00	.00	0.02
Nashville warbler	.21	.16	0.04
Northern flicker	.04	.04	0.10
Northern pygmy-owl	.00	.00	0.03
Olive-sided flycatcher	.00	.00	0.15
Orange-crowned warbler	.75	.26	0.31
Pileated woodpecker	.00	.17	0.14
Pine siskin	.09	1.05	0.71
Purple finch	1.25	.18	0.36
Red-breasted nuthatch	1.12	2.98	3.28
Red-breasted sapsucker	.00	.17	0.28
Red crossbill	.00	.08	0.00
Ruby-crowned kinglet	.00	.03	0.00
Ruffed grouse	.00	.00	0.01
Rufous hummingbird	.24	.11	0.41
Rufous-sided towhee	.00	.00	0.09
Song sparrow	.00	.00	0.08
Spotted owl	.00	.00	0.01
Steller's jay	.68	1.47	1.37
Swainson's thrush	3.83	4.91	3.77
Townsend's solitaire	.00	.03	.03
Varied thrush	1.42	3.93	3.61
Warbling vireo	.17	.00	.00
Western flycatcher	10.46	8.98	2.88
Western tanager	1.78	.60	.71
Western wood-pewee	.00	.00	.01
White-breasted nuthatch	.00	.03	.00
Wilson's warbler	6.49	6.40	4.73
Winter wren	11.58	13.97	15.35
Wrentit	.24	.62	.25
Yellow-rumped warbler	.41	.00	.04

Table 11—Mean standardized counts (number per stand visit) of birds within 75 m of sampling points in young, mature, and old-growth forests in the southern Oregon Coast Range, 1986

	Stand age-class		
Species	Young (n = 5)	Mature (n = 8)	Old (n = 19)
American robin	0.76	0.82	0.35
Band-tailed pigeon	.00	.14	.20
Black-headed grosbeak	1.22	.22	.17
Black-throated gray warbler	1.45	.36	.38
Blue grouse	.00	.00	.03
Brown creeper	2.84	4.66	6.08
Chestnut-backed chickadee	3.60	4.89	10.95
Chipping sparrow	.00	.04	.02
Common raven	.00	.00	.10
Dark-eyed junco	2.60	1.48	.65
Downy woodpecker	.00	.00	.02
Evening grosbeak	1.02	.27	.13
Golden-crowned kinglet	4.61	7.50	7.36
Gray jay	.67	.52	.34
Hairy woodpecker	.13	.41	.99
Hammond's flycatcher	6.05	3.32	.96
Hermit thrush	1.63	.25	1.48
Hermit warbler	11.60	6.18	8.79
House wren	.00	.00	.06
Hutton's vireo	1.41	.04	.33
MacGillivray's warbler	.05	.00	.36
Nashville warbler	.07	.00	.00
Northern flicker	.00	.05	.06
Northern pygmy-owl	.00	.04	.02
Olive-sided flycatcher	.00	.00	.07
Orange-crowned warbler	.25	.00	.04
Pileated woodpecker	.00	.00	.23
Pine siskin	.15	.09	.62
Purple finch	.45	.05	.27
Red-breasted nuthatch	1.42	2.91	5.75
Red-breasted sapsucker	.00	.45	.62
Red crossbill	.00	.00	.05
Rufous hummingbird	.33	.13	.46
Rufous-sided towhee	.00	.00	.12
Song sparrow	.20	.00	.08
Spotted owl	.00	.00	.04
Steller's jay	.73	1.04	1.02
Swainson's thrush	5.83	4.83	4.06
Varied thrush	1.27	4.52	5.14
Warbling vireo	.88	.00	.00
Western flycatcher	8.86	7.34	15.17
Western tanager	.98	.15	.48
Wilson's warbler	5.85	5.36	4.85
Winter wren	8.14	11.00	12.69
Wrentit	.17	.16	.24
Yellow-rumped warbler	.07	.00	.07

Table 12—Mean birds-per-area index (numbers per 40 ha) of birds in young, mature, and old-growth forests in the southern Oregon Coast Range, 1985

	Stand age-class					
	Young (n = 8)[a]		Mature (n = 10)		Old (n = 27)	
Species	Mean	N[b]	Mean	N	Mean	N
American robin	2.52	45	4.37	93	2.12	125
Band-tailed pigeon	.13	4	.27	10	.30	28
Black-capped chickadee[c]	.00	0	.00	0	.10	3
Black-headed grosbeak[c]	3.65	29	.75	8	.59	16
Black-throated gray warbler[c]	9.35	54	2.04	15	3.86	69
Blue grouse[c]	.23	2	.41	6	.40	15
Brown creeper	14.22	90	25.85	217	32.74	704
Chestnut-backed chickadee	78.38	325	88.86	492	132.85	1811
Common raven	.84	2	.00	0	.20	16
Dark-eyed junco[c]	5.88	54	3.11	36	1.42	42
Downy woodpecker	.45	1	.11	3	.06	4
Evening grosbeak[d]	2.35	31	9.20	156	2.69	128
Golden-crowned kinglet	54.09	248	73.47	406	62.02	970
Gray jay	1.17	19	1.75	40	1.21	60
Hairy woodpecker	1.05	22	9.92	25	1.42	93
Hammond's flycatcher[c]	23.80	107	20.29	128	8.06	121
Hermit thrush	3.14	37	1.25	20	1.53	58
Hermit warbler[c]	73.62	463	48.23	372	56.58	1170
Hutton's vireo[c]	6.89	41	1.45	12	1.79	37
MacGillivray's warbler[c]	.43	2	.00	0	1.64	22
Mountain quail[c]	.07	1	.18	3	.11	5
Nashville warbler[c]	1.89	11	1.38	11	.86	16
Northern flicker	.23	5	.10	3	.33	25
Northern pygmy-owl	.03	1	.00	0	.12	10
Olive-sided flycatcher	.00	0	.59	1	.65	24
Orange-crowned warbler[c]	5.00	37	2.24	21	1.97	50
Pileated woodpecker	.04	1	.42	14	.38	31
Pine siskin[c]	1.19	15	4.12	70	2.64	122
Purple finch[c]	5.82	49	1.04	12	2.09	57
Red-breasted nuthatch	2.58	52	6.41	169	7.08	465
Red-breasted sapsucker	.62	1	.46	11	.75	48
Red crossbill[d]	.13	3	.19	4	.04	2
Ruby-crowned kinglet	.00	0	.77	1	1.02	3
Ruffed grouse[c]	.00	0	.06	1	.05	2
Rufous hummingbird	6.46	10	5.48	11	13.53	71
Rufous-sided towhee	.19	4	.21	5	.19	12
Song sparrow[c]	.00	0	.15	2	.32	11
Spotted owl	.00	0	.00	0	.07	3
Steller's jay	1.94	36	3.71	82	3.45	212
Swainson's thrush	11.41	103	13.79	148	10.41	286
Townsend's solitaire	.12	2	.09	2	.19	11
Varied thrush[c]	5.59	61	13.59	196	13.85	505
Warbling vireo[c]	1.26	7	.14	1	.06	1
Western flycatcher	48.40	462	36.80	457	62.12	1935
Western tanager[c]	6.50	40	1.92	15	1.89	46
White-breasted nuthatch	.08	1	.07	1	.02	1
Wilson's warbler[c]	42.76	280	39.23	336	30.52	661
Winter wren[c]	76.71	426	89.18	669	107.44	1997
Yellow-rumped warbler[c]	2.96	16	.29	2	1.33	25

[a] Number of stands sampled.

[b] Number of birds counted.

[c] More than 70 percent of the detections of these species were of singing males. Mean densities reported are twice the densities of singing males.

[d] More than 50 percent of all detections of these species were of flying birds not included in the estimates.

Table 13—Mean birds-per-area indexes (numbers per 40 ha) of birds in young, mature, and old-growth stands in the southern Oregon Coast Range, 1986

	Stand age-class					
	Young (n = 6)[a]		Mature (n = 8)		Old (n = 16)	
Species	Mean	N[b]	Mean	N	Mean	N
American robin	1.84	23	2.10	36	0.91	37
Band-tailed pigeon	.07	1	.53	11	.36	18
Black-headed grosbeak[c]	4.15	26	.83	7	.74	14
Black-throated gray warbler[c]	8.78	48	2.70	20	2.21	39
Blue grouse[c]	.00	0	.00	0	.21	5
Brown creeper	19.09	83	31.47	192	35.75	515
Chestnut-backed chickadee	25.73	105	34.79	200	70.39	957
Chipping sparrow[c]	.10	1	.08	1	.09	3
Common raven	.00	0	.08	1	.37	11
Dark-eyed junco[c]	9.64	52	5.67	42	2.67	47
Downy woodpecker	.00	0	.00	0	.06	3
Evening grosbeak[d]	3.58	40	2.01	31	.57	21
Golden-crowned kinglet	45.75	139	80.95	335	64.12	623
Gray jay	2.28	26	1.50	24	.82	30
Hairy woodpecker	.43	5	1.27	21	2.16	84
Hammond's flycatcher[c]	32.14	130	20.23	113	5.81	77
Hermit thrush[c]	4.60	34	.99	10	3.15	76
Hermit warbler[c]	65.56	369	34.04	262	40.11	733
House wren[c]	.00	0	.00	0	.23	6
Hutton's vireo[c]	6.44	40	.10	1	1.46	28
MacGillivray's warbler[c]	1.06	6	.00	0	1.74	33
Nashville warbler[c]	1.80	5	.00	0	.55	5
Northern flicker	.00	0	.22	5	.15	8
Northern pygmy-owl	.00	0	.12	2	.10	4
Olive-sided flycatcher[c]	.11	1	.00	0	.29	8
Orange-crowned warbler[c]	1.40	9	.11	1	.85	18
Pileated woodpecker	.00	0	.08	2	.43	24
Pine siskin[d]	1.00	11	.13	2	1.56	57
Purple finch[c]	2.41	16	.44	4	1.31	28
Red-breasted nuthatch	3.69	43	6.54	118	11.52	446
Red-breasted sapsucker	.18	2	1.34	23	1.30	53
Red crossbill[c]	.07	1	.30	6	.52	25
Rufous hummingbird	11.08	12	7.42	12	11.76	45
Rufous-sided towhee	.14	1	.21	2	.56	13
Song sparrow[c]	1.13	5	.00	0	.57	8
Spotted owl	.00	0	.00	0	.44	6
Steller's jay	2.08	27	2.65	47	2.14	89
Swainson's thrush	29.96	110	19.22	123	16.35	213
Varied thrush[c]	4.15	31	17.64	179	15.60	371
Warbling vireo[c]	3.55	27	.10	1	.46	11
Western flycatcher	40.15	267	32.33	301	59.55	1305
Western tanager[c]	3.74	22	.76	6	1.02	19
Wilson's warbler[c]	39.12	162	38.25	223	25.88	358
Winter wren[c]	46.59	209	69.91	443	63.51	946
Wrentit	.42	6	.46	9	.45	21
Yellow-rumped warbler[c]	.46	2	.00	0	.51	7

[a] Number of stands sampled.

[b] Number of birds counted.

[c] More than 70 percent of the detections of these species were of singing males. Mean densities reported are twice the densities of singing males.

[d] More than 50 percent of all detections of these species were of flying birds not included in the estimates.

Continue

Table 14—Total bird-observation effort (number of stations times number of visits) in the southern Oregon Coast Range, 1985

Stand number	Number of of stations	Number of visits	Total effort
701	7	11	77
702	12	7	84
703	11	6	66
704	12	7	84
705	12	7	84
706	12	7	84
717	12	7	84
718	12	7	84
719	12	7	84
721	12	7	84
726	12	7	84
728	12	6	72
732	10	8	80
733	12	7	84
737	12	8	96
740	12	6	72
741	12	7	84
742	12	7	84
750	12	7	84
755	12	7	84
760	12	7	84
761	12	7	84
764	12	7	84
765	12	7	84
806	12	8	96
810	12	8	96
812	12	8	96
815	12	8	96
817	12	6	72
818	12	9	108
819	12	6	72
821	11	6	66
835	12	6	72
837	12	6	72
838	12	8	96
839	12	6	72
840	12	8	96
845	12	8	96
847	12	8	96
848	12	8	96
860	11	9	99
861	12	6	72
862	12	8	96
865	12	6	72
870	12	8	96

Table 15—Total bird-observation effort (number of stations times number of visits) in the southern Oregon Coast Range, 1986

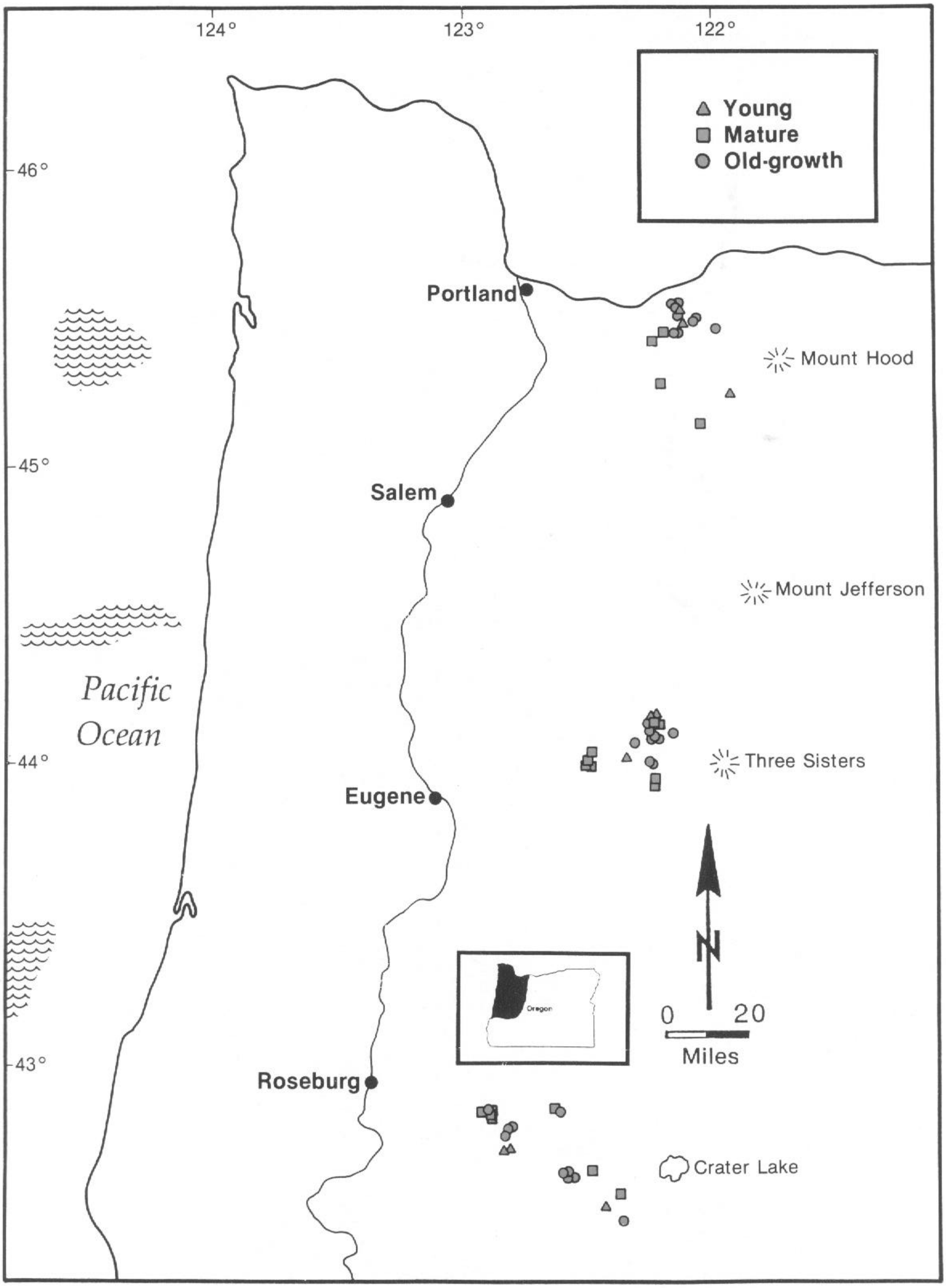
Stand number	Number of of stations	Number of visits	Total effort
702	12	7	84
704	12	7	84
705	12	7	84
718	12	6	72
719	12	7	84
720	12	7	84
722	12	7	84
726	12	7	84
733	12	7	84
737	12	7	84
742	12	7	84
750	12	7	84
755	12	7	84
761	12	7	84
764	12	7	84
765	12	6	72
806	12	7	84
810	12	7	84
812	12	7	84
815	12	7	84
818	12	7	84
819	12	7	84
835	12	7	84
838	12	7	84
839	12	7	84
840	12	7	84
845	12	7	84
847	12	7	84
848	12	7	84
860	11	7	77
861	12	7	84
862	12	7	84
870	12	7	84

Table 16—Standard deviations (and percent coefficients of variation) for age-class means of densities of birds associated with old-growth forests in the southern Oregon Coast Range, 1985

	Age-class					
Species	Young		Mature		Old-growth	
Brown creeper	7.2	(51)	12.4	(48)	18.2	(56)
Chestnut-backed chickadee	22.7	(29)	36.1	(41)	54.5	(41)
Hairy woodpecker	1.3	(118)	1.0	(111)	1.1	(79)
Olive-sided flycatcher	.0	—	.2	(317)	1.2	(200)
Pileated woodpecker	.1	(300)	.5	(121)	.5	(134)
Red-breasted nuthatch	1.5	(58)	6.0	(93)	3.5	(49)
Red-breasted sapsucker	.2	(283)	1.1	(233)	1.0	(137)
Varied thrush	7.2	(129)	10.5	(77)	10.3	(75)
Western flycatcher	10.9	(23)	16.6	(45)	16.3	(26)

Table 17—Standard deviations (and percent coefficients of variation) for age-class means of densities of birds associated with old-growth forests in the southern Oregon Coast Range, 1986

	Age-class					
Species	Young		Mature		Old-growth	
Brown creeper	6.3	(39)	14.4	(45)	10.8	(30)
Chestnut-backed chickadee	9.3	(36)	18.6	(53)	22.8	(32)
Hairy woodpecker	.5	(125)	1.0	(81)	1.6	(72)
Olive-sided flycatcher	.3	(254)	.0	—	.4	(145)
Pileated woodpecker	.0	—	.2	(200)	.5	(107)
Red-breasted nuthatch	2.7	(75)	6.3	(97)	7.0	(60)
Red-breasted sapsucker	.3	(150)	2.8	(212)	1.9	(146)
Varied thrush	5.0	(122)	9.2	(52)	9.3	(60)
Western flycatcher	15.4	(38)	12.8	(40)	15.3	(26)



Location of study sites.

Spring Bird Communities in the Oregon Cascade Range

Frederick F. Gilbert and Rochelle Allwine

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Abstract

Spring bird communities in the western Oregon Cascade Range were examined in 1984 and 1985 using point counts. Three locations in the northern (Mt. Hood), central (H.J. Andrews), and southern (Rogue River-Umpqua) portions of this physiographic region were studied in 1984; in 1985, only the central location was studied.

A total of 70 species was detected in 1984 in 56 Douglas-fir stands ranging in age from 30 to 450 years. Species richness values were similar for all locations in 1984 but increased slightly between years at H.J. Andrews to 62 species (from 56) in 1985. Numbers of bird species did not differ across the chronosequence (old, mature, young) or moisture gradient (dry, mesic, wet) in either year. The hermit warbler was the most common species encountered in 1984, and the winter wren the most common species at H.J. Andrews in both 1984 and 1985.

Locational differences were found for particular species, and the birds segregated out on the basis of elevation, latitude, and longitude and-where they shared the same environments-on the basis of resource utilization, Species associated with older stands, based on significant correlations with stand age or old-growth stands in the chronosequence, were the brown creeper, chestnut-backed chickadee, hairy woodpecker, rufous hummingbird, varied thrush, and winter wren. Two other species that were, with small sample sizes, significantly associated with old growth in 1984 were Vaux's swift and the olive-sided flycatcher; the red-breasted sapsucker was found only in old growth. In 1985, the evening grosbeak and western flycatcher were significantly associated with stand age, and Cooper's hawk, blue grouse, Hutton's vireo, red crossbill, and Vaux's swift were found only in old-growth stands.

In all, 17 species over the 2 years of study were significantly associated with either the dry or wet portion of the moisture gradient. Hutton's vireo and Swainson's thrush were found only in wet stands in 1985. At Andrews, however, 14 species changed their use of the moisture gradient from dry to mesic or wet between 1984 and 1985.

The variability found among locations and between years in bird detections suggested considerable flux in the way avian species selected habitats and that environmental factors and interspecific competition were important in modifying the relations of avian species to habitat but not necessarily to vegetative structure.

A few (5-6) species dominated the avifauna (>60 percent of all detections), and most were common in all age-classes. The only important old-growth associates may be some of the rarer species, such as Vaux's swift; spotted owl management prescriptions may accommodate the needs of these and other species.

The vegetative structure in the young stands studied, which were all fire-derived, had similar characteristics to that of the old-growth stands. Thus, our findings are probably not representative of the avifauna that might be found in managed stands of similar ages.

Introduction

The avifauna is the most visible component of the vertebrate community. As such, it frequently is used to define and thus indicate the total faunal support capacity of any given environment (see Graber and Graber 1976). Spring bird communities are the most stable and thus predictive because they normally are composed primarily of breeders. Breeding forest birds select and use habitat based on its structure (for example, Anderson and Shugart 1974; Crawford and others 1981; De Graaf and Chadwick 1987; Karr and Roth 1971; MacArthur and others 1962, 1966; Smith 1977). Although this relation to structure is generally accepted, some researchers disagree (for example, Tomoff 1974, Willson 1974). Old-growth Douglas-fir forests have structural characteristics that distinguish them from younger and managed forests (Franklin and others 1981; Franklin and Spies 1984; Spies and others, unpubl. manuscript). Theoretically, determining the structural components responsible for any given bird species' presence and abundance in old growth should be possible. Management prescriptions to ensure its continued existence could be developed or appropriate areas set aside, as is being attempted for the spotted owl (U.S. Department of Agriculture 1988a). Conceivably, these structural components, if known, could be provided in younger stands.

The objectives of this study were to document the spring bird communities in the Oregon Cascade Range and to relate particular species and associations of species to the age and structural characteristics of unmanaged Douglas-fir forests.

Materials and Methods

The study was conducted at three locations on the west side of the Oregon Cascade Range during 1984 (Mt. Hood, H.J. Andrews (Andrews), and Rogue River-Umpqua (Rogue-Umpqua)) and Andrews in 1985. In 1984,56 stands extending along a chronosequence of 35 to 500 years (appendix table 15) and dominated by a Douglas-fir overstory were sampled (see frontispiece). Although mesic stands dominated the young (30-80 years) and mature (80-200 years) categories, a moisture gradient (wet, mesic, and dry) was determined for the old-growth stands. Of the 56 stands, 46 were used for chronosequence analysis and 28 for the old-growth moisture-gradient analysis.

Birds were sampled using simple point counts (Vemer 1985). Twelve stations separated by 150 m and at least 75 m from the edge of the stand were established within each stand. Six surveys were run for each stand in 1984 with the direction being reversed for each survey (that is, 1 to 12, 12 to 1, 1 to 12 and so on) and observers were randomly assigned to minimize observer bias. Different crews were used at the three locations, so despite common training procedures, observer bias among locations was possible. Detections were summed among stations and reported as counts of species per stand. Only birds detected within 75 m of the station and species detected on at least two sample days in a stand and in more than one stand per location were included in the data analyses. This strategy reduced the number of species from 70 to 38, suggesting that 46 percent of the species detected were migrants, transients, or rare breeders at the three locations. For the purpose of analysis, *Empidonax* flycatchers denote dusky and Hammond's flycatchers. Seven surveys were done in 1985 in each of 15 stands at Andrews.

Vegetational data were collected for the forest floor, shrubs, and trees, and physical characteristics of the 56 stands were measured (appendix table 16). Each station was individually described using a nested plot design with 500-m^2 (13-m radius) and 2000-m^2 (25-m radius) sampling areas.

We used nonparametric analysis of variance (ANOVA) to test the hypotheses that abundance of birds and species richness did not differ among age- or moisture-classes or locations. We used detrended correspondence analysis (DCA) (Hill 1979a) to explore the relation between bird abundances and habitat-classes or environmental variables. Detrended correspondence analysis is an ordination technique that arranges a matrix of species' abundances (communities) by samples (stands) in low-dimensional space so that the communities occurring in each stand are represented in space along several axes. Thus, many components are reduced to a few important ones and variability is reduced. Communities with similar species composition and relative abundances occupy positions near each other within the space described by the first and second DCA axes. To determine whether stands grouped themselves with respect to age, moisture, or location categories, a plot of the DCA axis scores was examined to detect clustering of stands that might be caused by these factors.

To classify sites into community phases, two-way indicator species analysis (TWINSPAN) (Hill 1979b) was used. The analysis, based on a multilevel, two-way partitioning of the correspondence analysis axis scores, was used to classify avian species into categories related to location and to the stand age- and moisture-classes.

Bird species found to be associated with old-growth forests from the TWINSPAN analysis were correlated with the vegetational and environmental variables to examine the relation between individual bird species and individual environmental features.

Old-growth-associated species based on significant, positive Spearman rank correlations with stand age were examined in relation to the vegetative structure of the old-growth stands to identify which vegetational characteristics may have been important elements in effecting the observed association. Avian guilds were assembled (Manuwal and others 1987) to examine intraguild habitat use.

In 1985, only the Andrews location was studied. The procedures followed were identical to the previous year, but as noted earlier only 15 stands were sampled (appendix table 15). Data from 1984 were compared to those from 1985 in the same 15 stands. Because of differences in species richness and relative abundances between the 2 years, these data could not be combined for analysis. Chi-square analyses (Zar 1974) were used to examine differences between years. Statistical significance is reported at $P < 0.05$; means are presented with standard errors.

Results

1984

A total of 38 different bird species were considered in 1984, although the total data set consisted of over 18,000 detections of 70 different species. Using the restructured data set, an average of 15.8 species were detected per stand (range 10-23). ANOVA indicated that neither abundance of birds detected (57.8 per stand in old-growth, 55.9 in mature, and 52.4 in young) nor the species richness values were related to age or moisture (table 1). The mean numbers of species in old-growth, mature, and young stands were 16.4 ± 0.6, 16.5 ± 0.7 and 15.2 ± 0.6. Species numbers detected at the three locations were not different (Rogue-Umpqua, 18.2 ± 0.9; Andrews, 15.0 f± 0.7; Mt. Hood, 14.3 ± 0.7). The most frequently detected species for all three sites combined was the hermit warbler, although the winter wren was the most frequently detected species at Andrews.

Nineteen species exhibited significant location effects by being predominantly found at only one or two of the three locations (table 2). More birds were detected at Rogue-Umpqua than at Andrews (average 62.5 ± 2.7 vs 52.7 ± 3.9 birds per stand per visit) ($P < 0.05$).

Table l-Analysis of variance for bird abundance and species richness values compared to age and moisture conditions, Oregon Cascades, 1984

Factors	DF	F- value	***Prob>F***
Species richness x age	2	0.01	0.9876
Species richness x moisture	2	0.26	0.7728
Bird abundance **x** age	2	0.67	0.5163
Bird abundance x moisture	2	0.33	0.7191

Seven species were positively associated ($P < 0.05$) with stand age and three negatively associated (table 3), based on Spear-man rank correlations. ANOVA showed the chestnut-backed chickadee to be significantly associated with old-growth compared to young stands, and Steller's jay and the western flycatcher detections approached significance ($P < 0.06$ and < 0.07, respectively). Two species with small sample sizes significantly associated with old growth were Vaux's swift and the olive-sided flycatcher.

TWINSPAN analysis distinguished two groups of birds (table 4), as indicator species. The first group was somewhat associated with stands that were old and mature, and the second with stands that were young and mature. Correlations of individual environmental components with DCA axis scores showed 10 significant physical variables correlated with DCAl (table 5). Foremost were elevation, latitude, and the two fern-height categories. More (20) physical variables were significantly correlated with DCA2, but only slope, large-diameter, and medium-height snags of decay-class 4, berry-producing and deciduous shrubs, and needle-leaved evergreen trees in the lower to midstory had r values ≥ 0.50 (table 6). Plots of DCAl versus DCA2 showed that age and moisture stands did not cluster, although location did (figs. l-3).

The most commonly detected species were represented similarly in the different-aged stands (table 7).

Species with old-growth associations differed considerably in relation to vegetative and physical factors of the environment. Spearman rank correlations showed that the varied thrush occurred significantly more than expected at locations with little exposed soil or fine organic litter, few tree pits but good ground cover by logs of decay-class 3 ($R = 0.42$; $P = 0.01$). This species was found predominantly in western hemlock ($R = 0.52$-0.67; $P < 0.001$) and, to a lesser extent, in stands of very large western redcedars ($R = 0.39$; $P < 0.03$) and Douglas-firs ($R = 0.32$; P c 0.02). The associations with deciduous tree species were generally negative although small alders ($R = 0.28$; $P = 0.03$) and maples ($R = 0.34$; $P = 0.01$) were used preferentially.

Table 2—Bird species showing significant (*P* c 0.05) association with location (based on ANOVA), Oregon Cascades, 1984

Species	F-value	*P*	Location influence[a]	
Brown creeper	3.73	0.031	RRU>HJA	
Black-headed grosbeak	5.42	0.007	RRU>MTH	
Chestnut-backed chickadee	13.59	0.0001	RRU>MTH	HJA>MTH
Red-breasted nuthatch	41.62	0.0001	RRU>MTH	RRU>HJA
Hermit thrush	11.80	0.0001	RRU>MTH	RRU>HJA
Townsend's solitaire	5.93	0.005	RRU>MTH	RRU>HJA
Nashville warbler	8.53	0.0006	RRU>MTH	RRU>HJA
Yellow-rumped warbler	5.41	0.007	RRU>MTH	RRU>HJA
Western tanager	6.71	0.003	RRU>MTH	RRU>HJA
Pine siskin	11.05	0.0001	RRU>MTH	RRU>HJA
Dark-eyed junco	9.17	0.0004	RRU>MTH	RRU>HJA
Hermit warbler	3.46	0.039	HJA>MTH	
Winter wren	14.26	0.0001	HJA>RRU	MTH>RRU
Band-tailed pigeon	4.41	0.017	Only at MTH	
Empidonax flycatchers	18.35	0.0001	MTH>HJA	RRU>HJA
Western flycatcher	20.48	0.0001	MTH>HJA	MTH>RRU
Varied thrush	19.67	0.0001	MTH>HJA	MTH>RRU
Golden-crowned kinglet	21.16	0.0001	MTH>HJA	RRU>HJA
Wilson's warbler	13.52	0.0001	MTH>HJA	MTH>RRU
Swainson's thrush	4.06	0.023	MTH>RRU	

[a] RRU = Rogue River-Umpqua National Forest; HJA = H.J. Andrews Experimental Forest; MTH = Mount Hood National Forest.

Table 3—Significant associations of bird species with stand age, Spearman rank correlations, Oregon Cascades, 1984

Species	Correlation coefficient	Probability
Hairy woodpecker	0.439	0.0009
Varied thrush	0.410	0.0021
Western flycatcher	0.384	0.0041
Rufous hummingbird	0.356	0.0082
Steller's jay	0.304	0.0255
Brown creeper	0.297	0.0293
Winter wren	0.276	0.0430
American robin	-0.449	0.0007
Evening grosbeak	-0.323	0.0170
Hermit warbler	-0.266	0.0520

Table 4—Bird species sorting out by stand age, TWINSPAN analysis, Oregon Cascades, 1984

Species generally associated with older stands:
- Northern flicker
- Pileated woodpecker
- Hairy woodpecker
- Common raven
- Brown creeper
- Varied thrush
- Pine siskin

Species generally associated with younger stands:
- Blue grouse
- American robin
- Swainson's thrush
- Nashville warbler
- Black-throated gray warbler
- Townsend's warbler
- Wilson's warbler
- Western tanager
- Black-headed grosbeak

The western flycatcher was detected primarily in areas with down logs of decay-classes 3 and 4 ($R = 0.34\text{-}0.41$; $P < 0.01$), substantial fern cover ($R = 0.43$; $P =$ O.OOl), deciduous shrubs in the understory ($R = 0.32\text{-}0.57$), and with an overstory dominated by western hemlocks ($R = 0.30\text{-}0.40$; $P < 0.02$) and very large western rcdcedar ($R = 0.27$; $P < 0.05$).

The hairy woodpecker was detected at sites with very large Douglas-firs ($R = 0.43$; $P = 0.001$), large and very large western redcedars ($R = 0.30\text{-}0.32$; $P < 0.02$), large and very large western hemlocks ($R = 0.30\text{-}0.32$; $P = 0.02$), and large Pacific madrones ($R = 0.31$; $P = 0.02$). The winter wren was associated with western hemlocks of all size-classes ($R = 0.44\text{-}0.54$; $P < 0.006$) and very large western redcedars ($R = 0.30$; $P = 0.02$). The rufous hummingbird was found at sites with large and very large western hemlocks ($R = 0.07\text{-}0.32$; $P < 0.04$).

Table 5—Physical and vegetative variables significantly associated with DCA1 (DECORANA) bird species, Oregon Cascades, 1984 (Spearman rank correlations)

Factor	*R* value	*P*
Elevation	0.57	<0.0001
Latitude	–0.73	<0.0001
Short snags, decay-class 3	0.30	0.024
Medium-tall snags, decay-class 5	–0.39	0.003
Fern (0-0.5-m tall)	–0.51	<0.0001
Evergreen shrub (0-0.5-m tall)	0.29	0.032
Fern (0.5-2-m tall)	–0.54	<0.001
Needle-leaved evergreen trees (super canopy)	0.44	0.0008
Logs, decay-class 2	–0.32	0.018
Logs, decay-class 3	–0.37	0.005

Table 6—Physical and vegetative variables significantly associated with DCA2 (DECORANA) bird species, Oregon Cascades, 1984 (Spearman rank correlations)

Factor	*R* value	*P*
Stand age	0.33	0.015
Latitude	0.27	0.045
Slope	–0.50	<0.0001
Number of very large trees (0-0.5 m)	0.38	0.004
Number of very large trees (0.5-2 m)	0.29	0.038
Number of very large trees (2 m-midstory)	–0.39	0.003
Medium-diameter, medium-tall[a] snags, decay-class 5	0.27	0.041
Medium-diameter, tall snags, decay-class 4	0.34	0.009
Medium-diameter, tall snags, decay-class 5	0.30	0.023
Large-diameter, medium-tall snags, decay-class 3	0.45	0.0005
Large-diameter, medium-tall snags, decay-class 4	0.50	<0.0001
Large-diameter, medium-tall snags, decay-class 5	0.30	0.024
Berry-producing shrubs (0-0.5 m)	0.62	<0.0001
Evergreen shrubs (0-0.5 m)	–0.37	0.005
Deciduous shrubs (0-0.5 m)	0.67	<0.0001
Needle-leaved evergreen trees (2 m-midstory)	0.52	<0.0001
Deciduous shrubs (all height-classes combined)	0.58	<0.0001
Logs, decay-class 3	0.35	0.008
Logs, decay-class 4	0.42	0.001
Logs, decay-class 5	0.35	0.008

[a] Medium tall means 5-15 in height.

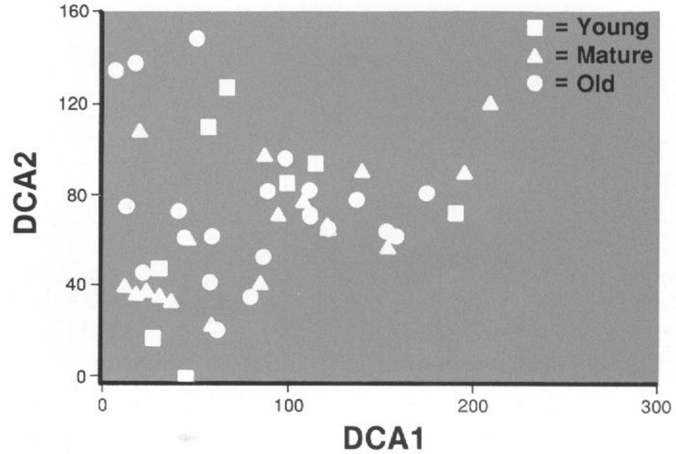

Figure 1—Plot of detrended correspondence analysis axis scores for 1984 Oregon Cascades bird data with stand age (old, mature, and young Douglas-fir stands).

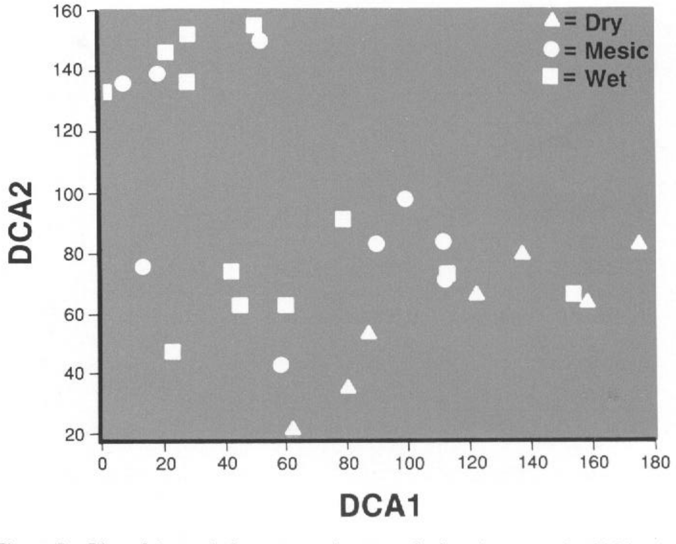

Figure 2—Plot of detrended correspondence analysis axis scores for 1984 Oregon Cascades bird data with stand moisture condition (wet, mesic, and dry old-growth Douglas-fir stands).

Clear segregations of habitat associations occurred within two guilds, the aerial insectivores (western and *Empidonax* flycatchers) and tree-seed eaters (evening grosbeak and pine siskin). Pine siskins were positively associated with sites with grand fir trees, and evening grosbeaks were negatively associated (table 8). *Empidonax* flycatchers were detected at sites with deciduous trees and medium-large Douglas-firs, tree types either avoided or having no significant association with the western flycatcher based on Spearman rank correlations (table 9).

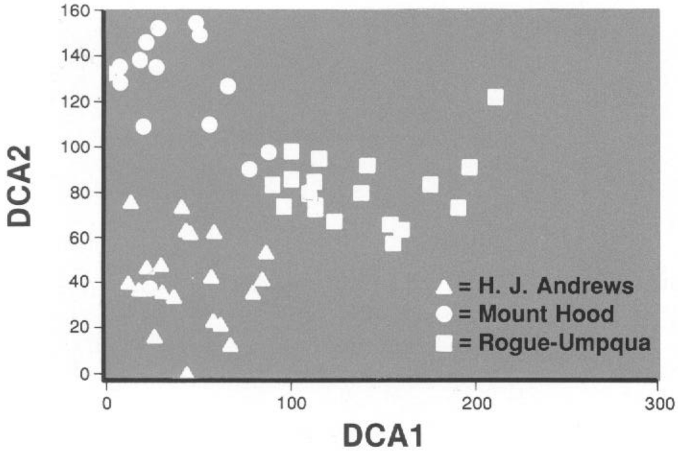

Figure 3—Plot of detrended correspondence analysis axis scores for 1984 Oregon Cascades bird data with location (MTH = Mt. Hood National Forest, HJA = H.J. Andrews Experimental Forest, RRU = Rogue River-Umpqua National Forest).

Table 7—The 6 most frequently detected bird species (combining Hammond's and dusky flycatchers as *Empidonax* flycatchers) by stand age, Oregon Cascades, 1984

Rank	Old-growth	Mature	Young
1.	Winter wren	Hermit warbler	Hermit warbler
2.	Hermit warbler	Winter wren	Winter wren
3.	Chestnut-backed chickadee	*Empidonax* flycatchers	Chestnut-backed chickadee
4.	*Empidonax* flycatchers	Chestnut-backed chickadee	*Empidonax* flycatchers
5.	Western flycatcher	Red-breasted nuthatch	Western flycatcher
6.	Varied thrush	Western flycatcher	Red-breasted nuthatch

Other guilds—for example, understory-ground insectivores and bark insectivores—were separately related to tree species and size-class. The only overlap in significant Spearman rank correlations for bark insectivores was for small sugar pine with the red-breasted nuthatch and the red-breasted sapsucker (table 10). The large understory-ground insectivore guild showed more overlap, but clear separations of habitat association were evident between the hermit thrush and Swainson's and varied thrushes, and between Wilson's warbler and the winter wren and three other smaller members of the guild (tables 11-12).

Table 8—The tree-seed-eater guild and the significant Spearman rank correlations for tree species and size-classes, Oregon Cascades, 1984 (correlation coefficient with probability in brackets)

Tree species and size	Evening grosbeak	Pine siskin
Medium Douglas-fir	+0.37 (0.004)	–0.10 (0.48)
Small grand fir	–0.36 (0.007)	+0.59 (0.0001)
Medium grand fir	–0.37 (0.006)	+0.60 (0.0001)
Large grand fir	–0.31 (0.02)	+0.53 (0.0001)
Very large grand fir	–0.10 (0.48)	+0.44 (0.0007)
Small golden chinkapin	–0.08 (0.55)	+0.26 (0.05)
Medium golden chinkapin	+0.05 (0.73)	+0.34 (0.01)
Small incense-cedar	–0.29 (0.03)	+0.50 (0.0001)
Medium incense-cedar	–0.29 (0.03)	+0.47 (0.0002)
Large incense-cedar	–0.27 (0.04)	+0.47 (0.0003)
Very large incense-cedar	–0.19 (0.16)	+0.44 (0.0007)
Large western white pine	–0.10 (0.48)	+0.36 (0.007)
Small sugar pine	–0.18 (0.19)	+0.29 (0.03)
Medium sugar pine	–0.24 (0.07)	+0.35 (0.008)
Large sugar pine	–0.28 (0.03)	+0.50 (0.0001)
Very large sugar pine	–0.23 (0.09)	+0.47 (0.0002)
Small California red fir	–0.05 (0.69)	+0.27 (0.05)
Small hazel	–0.13 (0.35)	+0.46 (0.0004)
Small red alder	+0.42 (0.001)	–0.22 (0.10)

Table 9—Significant Spearman rank correlations of the aerial insectivore guild with tree species and size-classes, Oregon Cascades, 1984 (correlation coefficient with probability in brackets)

Tree species and size	Western flycatcher	*Empidonax* flycatchers
Medium Douglas-fir	–0.28 (0.04)	+0.27 (0.05)
Large Douglas-fir	–0.37 (0.005)	+0.28 (0.04)
Very large redcedar	+0.27 (0.05)	–0.07 (0.60)
Small western hemlock	+0.30 (0.02)	–0.23 (0.09)
Medium western hemlock	+0.32 (0.02)	–0.33 (0.01)
Large western hemlock	+0.40 (0.002)	–0.28 (0.03)
Very large western hemlock	+0.40 (0.002)	–0.46 (0.0004)
Small bigleaf maple	–0.04 (0.75)	+0.28 (0.04)
Medium bigleaf maple	+0.04 (0.79)	+0.30 (0.03)
Small golden chinkapin	–0.15 (0.26)	+0.35 (0.01)
Medium golden chinkapin	–0.21 (0.13)	+0.31 (0.02)
Medium red alder	–0.05 (0.70)	+0.27 (0.05)
Small Pacific dogwood	–0.21 (0.13)	+0.54 (0.0001)
Medium Pacific dogwood	–0.18 (0.19)	+0.46 (0.0004)

Table 10—Significant Spearman rank correlations with tree species and sizes for members of the bark insectivore guild, Oregon Cascades, 1984

Tree species and size	Hairy woodpecker	Pileated woodpecker	Red-breasted nuthatch	Red-breasted sapsucker
Small Douglas-fir	—	—	+.40	—
Medium Douglas-fir	–.41	—	—	—
Large Douglas-fir	+.43	—	—	—
Small Pacific madrone	—	—	+.33	—
Medium Pacific madrone	—	—	+.36	—
Large Pacific madrone	+.31	—	—	—
Small grand fir	—	—	+.57	—
Medium grand fir	—	—	+.66	—
Large grand fir	—	—	+.60	—
Medium western redcedar	—	—	-.30	—
Large western redcedar	+.32	—	—	—
Very large western redcedar	+.30	—	—	—
Small western hemlock	—	—	–.52	—
Medium western hemlock	—	—	–.58	—
Large western hemlock	+.32	—	–.38	—
Very large western hemlock	+.30	—	–.36	—
Small Pacific yew	—	+.32	—	—
Medium Pacific yew	—	+.29	—	—
Small red alder	—	—	–.33	—
Medium red alder	–.34	—	—	—
Small sugar pine	—	—	+.35	+.36
Medium sugar pine	—	—	+.55	—
Large sugar pine	—	—	+.63	—
Very large sugar pine	—	—	+.63	—
Small golden chinkapin	—	—	+.51	—
Medium golden chinkapin	—	—	+.48	—
Small incense-cedar	—	—	+.69	—
Medium incense-cedar	—	—	+.65	—
Large incense-cedar	—	—	+.61	—
Very large incense-cedar	—	—	+.54	—
Large bigleaf maple	—	—	–.27	—
Small vine maple	—	—	–.37	—
Small hazel	—	—	+.39	—

1985

More than 6500 detections of 62 species were made. Although the most species (40) were found in old growth, the differences (30 in mature and 35 in young) were not significant. Only 40 species were used in the other analyses, and, for this data set, 21.0 ± 2.4 species were found in old-growth, 19.7 ± 4.4 in mature, and 21.0 ± 4.2 in young stands. Mean detections per stand did not differ between young, mature, and old-growth (24.0 ± 7.0, 27.0 ± 15.1, 33.2 ± 6.9).

Species associated with old growth based on significant positive Spearman rank correlations with stand age were the evening grosbeak ($R = 0.54$, $P < 0.04$) and the western flycatcher ($R = 0.55$, $P < 0.04$). Five other species, Cooper's hawk, blue grouse, Hutton's vireo, red crossbill, and Vaux's swift, were found only in old-growth stands.

ANOVA indicated no significant associations with old growth. Similar analyses for these same stands in 1984 showed only that the brown creeper was associated with old-growth stands though not significantly (ANOVA, $P < 0.08$). No significant differences were found based on the moisture gradient in either abundance or species richness values in 1985.

We found 21.5 ± 4.7 species in wet stands, 20.5 ± 4.5 in mesic stands, and 20.7 ± 4.7 in dry stands; 37.3 ± 11.8 individuals were detected per stand in wet stands, 31.6 ± 21.3 in mesic, and 28.7 ± 10.8 in dry. Blue grouse, ruffed grouse, and rufous hummingbirds were found only in the dry portion of the moisture gradient, and Hutton's vireo and Swainson's thrush were found only in the wet portion. None of these species was significantly (ANOVA) associated with the moisture gradient, however. Based on Spearman rank correlations, five species were significantly associated with older stands at Andrews in 1984: the brown creeper ($R = 0.77$; $P = 0.0001$), hairy woodpecker ($R = 0.60$; $P = 0.006$), pileated woodpecker ($R = 0.52$; $P = 0.02$), western flycatcher ($R = 0.46$; $P = 0.04$) and Steller's jay ($R = 0.49$; $P = 0.03$).

The hairy woodpecker selected both mesic and wet stands, the hermit thrush and pileated woodpecker selected mesic stands, and the winter wren selected dry stands (ANOVA).

The five most abundant species in 1985 represented 65.9 percent of the detections. When the *Empidonax* flycatchers were added, 72.2 percent of the detections were accounted for, which compared with 76.1 percent for these same species in 1984 in the same stands (table 13).

The hairy woodpecker and hermit thrush were the only species that showed any differences in their use of vegetative structure and physical environment between years—that is, changed from three or more positive or negative relationships to the opposite (Spearman rank correlations).

Fourteen species had significant (chi-square) differences in relation to the moisture gradient in 1985 when compared to 1984. The hairy woodpecker and winter wren shifted from the wet to dry portion of the gradient, and the numbers of the northern flicker, pileated woodpecker, and western tanager increased in either dry and wet stands when they had been most common in mesic stands in 1984. Nine other species shifted from dry to wetter stands in 1985 compared to 1984 (table 14). The majority of the species showed consistent patterns of chronosequence and moisture-gradient use. The *Empidonax* flycatchers were a good illustration of this consistency (figs. 4-7).

Table 11—Significant conifer associations for larger members of the low understory-ground insectivore guild, based on Spearman rank correlations, Oregon Cascades, 1984

Tree species and size	American robin	Hermit thrush	Northern flicker	Swainson's thrush	Varied thrush
Small Douglas-fir	—	+.31	—	—	–.30
Medium Douglas-fir	+.50	—	—	—	–.34
Very large Douglas-fir	–.34	—	—	—	+.32
Small grand fir	—	+.46	—	–.46	–.38
Medium grand fir	—	+.49	—	–.40	–.46
Large grand fir	—	+.47	+.27	–.32	–.54
Small western hemlock	—	—	—	+.29	+.52
Medium western hemlock	—	—	—	+.38	+.57
Large western hemlock	–.34	–.29	—	—	+.67
Very large western hemlock	–.42	–.33	—	+.31	+.66
Small western redcedar	–.29	—	—	—	—
Medium western redcedar	–.27	—	—	—	—
Large western redcedar	–.28	—	—	—	—
Very large western redcedar	—	—	—	—	+.39
Small sugar pine	—	—	—	–.27	–.30
Medium sugar pine	—	+.32	—	–.32	–.46
Large sugar pine	—	+.42	—	–.47	–.49
Very large sugar pine	—	+.42	—	–.36	–.43
Small Pacific yew	–.39	—	—	—	—
Medium Pacific yew	–.35	—	+.27	—	—
Small incense-cedar	—	+.55	—	–.49	–.55
Medium incense-cedar	—	+.48	—	–.49	–.54
Large incense-cedar	—	+.46	—	–.46	–.51
Very large incense-cedar	—	+.44	+.26	–.35	–.35

Table 12—Significant conifer associations for smaller members of the low understory-ground insectivore guild, based on Spearman rank correlations, Oregon Cascades, 1984

Tree species and size	Dark-eyed junco	MacGillivray's warbler	Townsend's solitaire	Wilson's warbler	Winter wren
Small Douglas-fir	+.53	—	—	–.30	–.49
Large Douglas-fir	+.28	—	—	—	—
Small grand fir	+.43	+.32	+.41	–.42	–.54
Medium grand fir	+.43	—	+.51	–.35	–.50
Large grand fir	+.39	—	+.35	—	+.45
Very large grand fir	—	—	+.46	—	—
Small western hemlock	–.41	—	–.36	—	+.51
Medium western hemlock	–.49	–.27	–.43	—	+.54
Large western hemlock	–.35	—	–.26	—	+.44
Very large western hemlock	–.28	—	—	+.37	+.51
Small western redcedar	—	—	–.36	—	—
Medium western redcedar	—	—	–.27	—	—
Large western redcedar	—	—	–.31	—	—
Very large western redcedar	—	—	—	—	+.30
Small sugar pine	+.37	+.48	—	—	–.52
Medium sugar pine	+.27	+.28	—	–.32	–.47
Large sugar pine	+.32	+.28	—	–.38	–.55
Very large sugar pine	+.31	+.35	—	–.30	–.51
Small Pacific yew	—	—	—	–.38	—
Medium Pacific yew	—	—	—	–.30	—
Small incense-cedar	+.42	+.37	—	–.45	–.56
Medium incense-cedar	+.41	+.33	—	–.44	–.56
Large incense-cedar	+.44	+.35	—	–.42	–.60
Very large incense-cedar	+.31	+.42	—	–.36	–.44

Table 13—The 5 most common bird species plus the *Empidonax* flycatchers detected at Andrews in 1984 and 1985 by point counts, Oregon Cascades (values are percentages of total detections)

Species	1984	Rank	1985	Rank
Winter wren	18.9	2	18.4	1
Hermit warbler	23.7	1	17.2	2
Chestnut-backed chickadee	17.7	3	11.1	3
Golden-crowned kinglet	0.4	—	10.8	4
Red-breasted nuthatch	1.4	10	8.4	5
Empidonax flycatchers	14.0	4	6.3	6
Western flycatcher	5.6	5	—	—

Table 14—Bird species that changed their use of the moisture gradient from dry to wet between 1984 and 1985, H.J. Andrews, Oregon Cascades

Species	Chi-square
Western flycatcher	($P < 0.002$)
Chestnut-backed chickadee	($P = 0.06$)
American robin	($P < 0.002$)
Hermit thrush	($P < 0.0001$)
Swainson's thrush	($P < 0.0001$)
Black-throated gray warbler	($P < 0.001$)
Townsend's warbler	($P < 0.0001$)
Hermit warbler	($P < 0.0001$)
Wilson's warbler	($P < 0.002$)

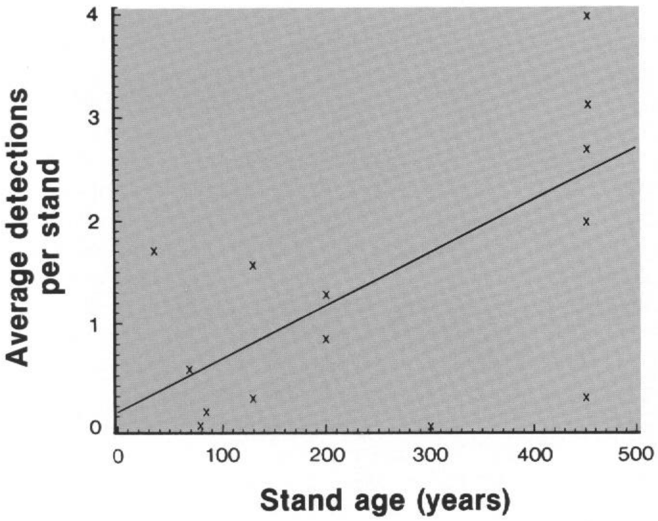

Figure 4—Average detections per stand of *Empidonax* flycatchers compared to the age of the stand, H.J. Andrews Experimental Forest, 1985.

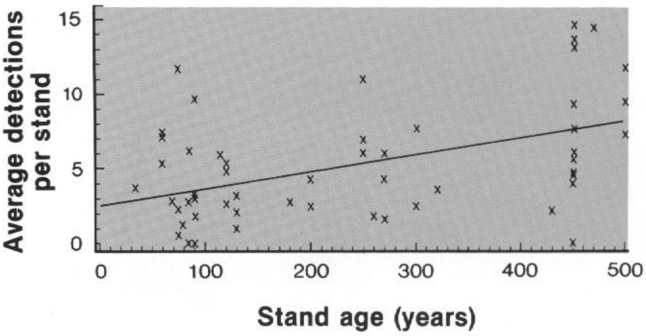

Figure 5—Average detections per stand of *Empidonax* flycatchers compared to the age of the stand, Oregon Cascades, 1984.

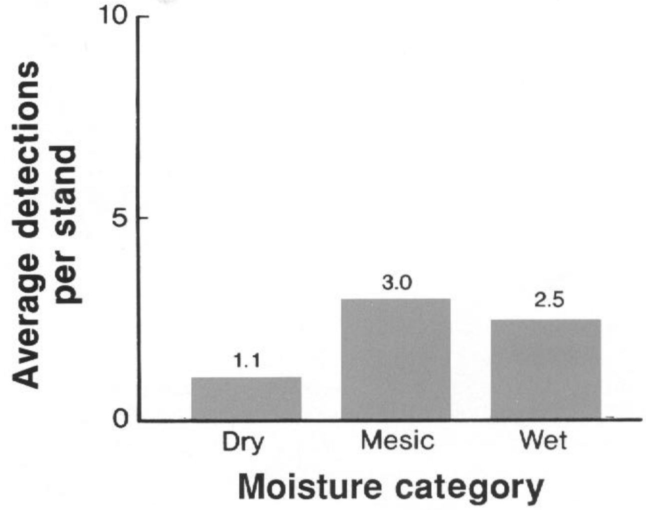

Figure 6—Average detections per stand of *Empidonax* flycatchers compared to the moisture condition of old-growth stands, H.J Andrews Experimental Forest, 1985.

Discussion

The similarity in species richness values and bird abundances along the chronosequence parallels findings in the Oregon Coast Range (Carey and others, this volume), northern California (Ralph and others, this volume; Raphael and Barrett 1984), and southern Washington (Manual, this volume; Manuwal and Huff 1987). The very similar stand physiognomies probably accounted for this. The young and mature stands had considerable coarse woody debris both standing (snags) and on the ground (logs) (see Spies and others 1988). Most of the stands studied were fire-derived rather than a result of logging. Therefore, our findings do not answer the concerns of Harris and others (1982) that long-term declines in species richness might be expected if truncation of seral development occurs at 80 to 100 years. Even in naturally regenerated stands, large-diameter snags would be gone after the harvest unless specific provision was made for them in the stand prescription, or uneven-aged

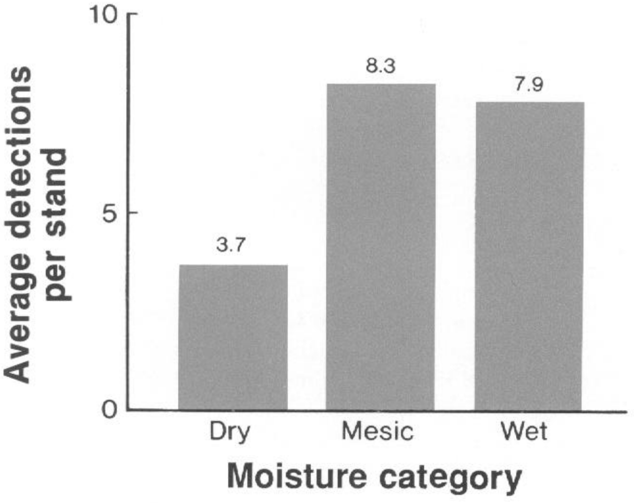

Figure 7—Average detections per stand of *Empidonax* flycatchers compared to the moisture condition of old-growth stands, Oregon Cascades, 1984.

management was used. Nyberg and others (1987) discuss the implications of such management activities to provide old-growth components in younger stands.

Many authors, including De Graaf and Chadwick (1987), Johnson and Landers (1982), Kessler and Kogut (1985), Manuwal and Huff (1987), and Wetmore and others (1985), have shown the changes in bird species and populations that can be expected from logging or changing the sizes of trees in a stand. But few long-term studies provide information on whether old-growth-associated species such as those in our study would persist 100 to 200 years from now in commercial forests without management intervention. The cavity nesters are the most vulnerable, but models are available that should ensure even their existence (Davis and others 1983, Thomas and others 1979).

Breeding bird communities in the Oregon Cascade Range were dominated by a few, relatively abundant species. Odum (1971) suggests that a more stable environment tends to have dominance shared among more species. Stand age appeared to have little effect on the dominance values, possibly because Douglas-fir forests in the western Oregon Cascades are a seral stage on the way to a western hemlock climax. Spies and others (1988) postulate that such forests may not reach an equilibrium state until they are 1000 years old. The implication is that many of the avian species present are generalists rather than specialists in the still-evolving landscape, and the species have not had the opportunity to segregate into niches of more equal size (see Orians and Willson 1964, Slobodkin and Sanders 1969). Huff and others (1985), however, found only four dominant species in a 515-year-old hemlock stand on the Olympic Peninsula of Washington State; they noted that more species reached their highest populations in this forest compared to younger stands.

Rufous hummingbird, brown creeper, chestnut-backed chickadee, hairy woodpecker, western flycatcher, varied thrush, and winter wren were associated with older stands and showed a positive selection for sites with very large trees. Western hemlock, western redcedar, and sugar pine were as important as Douglas-fir, however. The rufous hummingbird is normally associated with forest edges, and the numerous small openings in the older stands probably created suitable edge conditions. The counting stations were at least 150 m from edges in the young and mature forests, so fewer rufous hummingbirds were counted in these younger age-classes. The brown creeper, chestnut-backed chickadee, and the hairy woodpecker are foliage or bark insectivores and thus exploited the surfaces of the large trees for foraging. The western flycatcher, as an aerial-sallying insectivore, has a feeding behavior that requires open space beneath, or in the canopy, which is best met in the older stands. The varied thrush is an understory-gleaning insectivore, and the complex understory characteristics of old-growth stands probably favored this species. The particular patterns observed suggested that resource partitioning was occurring within guilds. More niche overlap was evident in the larger guilds, such as the low understory-ground insectivore guild, but species still separated out, with bird size an obvious factor.

Noon and others (1980) found considerable consistency in habitat preferences of Eastern forest birds despite acknowledging that local population-genetic differences, changes in habitat availability, or changes in the competitive environment could theoretically result in selection of different habitats. Those species that shifted between dry stands in 1984 and wet stands in 1985 continued to use stands of similar structure. Thus, predictability of stand vegetative and physical characteristics was possible between years for these birds. The importance of weather cannot be overestimated. The winter of 1983-84 was long, with deep snow cover, especially in the southern portion of the Oregon Cascades. Spring was late and wet in 1984 and insect populations may have been low, resulting in fewer nesting pairs. This weather may have been responsible for the greater use of the dry portion of the moisture gradient in 1984 at Andrews.

Two species (hairy woodpecker and hermit thrush) at Andrews used very different habitats between the two years. At the same time, population size of other species apparently changed (an order of magnitude in a few cases), with 10 more species meeting the abundance criteria for analysis in 1985 than did so in 1984. Some changes in field personnel occurred between years, and although training techniques were equivalent, observer variability might have accounted for the major differences in detection rates (Verner and Milne 1989).

The cold, wet spring of 1984 may have depressed breeding activity by some species. The hairy woodpecker may have been influenced competitively in 1985 because other species in its guild (pileated woodpeckers, red-breasted nuthatches, red-breasted sapsuckers, and northern flickers), which compete either for foraging locations or nesting sites (Bull and others 1986a), were much more abundant or participated more in breeding in 1985.

What are the implications for Douglas-fir forest management other than the obvious ones already mentioned? The variety of vegetative structure in old-growth Douglas-fir stands favors a few rare species, such as the Vaux's swift, that comprise a small component of the total community. These species may never be common even in stands aged 1000 years or more. Instead of concentrating on old growth in unmanaged stands, perhaps we should examine much more closely such factors as moisture, where obvious relations, if not dependencies, exist. Old-growth trees are impressive to the human observer but most bird species apparently make little discrimination between trees 200 years old and trees 450 years old. The chronosequence can therefore end at the point where sufficient vegetative diversity and structural elements generate coarse woody debris and microhabitats for the rarer species. Large tracts of old growth may not be necessary for such mobile species as birds. Work is needed on minimum viable population sizes for these rarer species and the extent of habitat needed for their support. Intuitively, we suspect the minimum area sizes for most species will be less than those projected for the spotted owl (Anon. 1988), so that the spotted owl habitat conservation areas may accommodate the needs of these other birds. If that proves true, selection of the spotted owl as an indicator species may have been fortuitous, despite the current controversy.

Acknowledgments

The Oregon Cascades study was made possible by the contributions of many people, including U.S. Forest Service peronnel. Effective field supervision was given by Wynn Cudmore, and crew leaders Jim Reichel and Troy Cline at Rogue River-Umpqua, Kathleen Fulmer at H.J. Andrews, and Jeff Picton at Mount Hood in 1984. The 1985 crew leader was Tony Fuchs. John Teburg, Dick Gilbert, Rich Alldredge, and Betsy Piersone all assisted in data entry and analysis. The hard-working field crews, primarily made up of Washington State University wildlife students, were essential to successful completion of the work.

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Appendix

Table 15-Douglas-fir stands in the Oregon Cascade Range examined for vertebrate communities, Spring 1984 (age and moisture condition of stand given where appropriate)

Type[a]	Stand	Forest-Ranger District	Section	Township	Range	Elev	Lat	Long	Age	Moisture
Mt. Hood										
OG	5001	Mt. Hood-Columbia Gorge	8	T1S	R7E	610	45.490	121.980	470	Wet
OG	5005	Mt. Hood-Columbia Gorge	2	T1S	R6E	641	45.510	122.030	450	Wet
OG	5009	Mt. Hood-Columbia Gorge	4 & 9	T1S	R7E	907	45.490	121.980	450	Wet
OG	5017	Mt. Hood-Columbia Gorge	22	T1N	R6E	940	45.550	122.050	500	Mesic
OG	5019	Mt. Hood-Columbia Gorge	27	T1N	R6E	937	45.560	122.050	500	wet
OG	5020	Mt. Hood-Columbia Gorge	29 & 32	T1S	R6E	557	45.420	122.080	450	Mesic
OG	5031	Mt. Hood-Columbia Gorge	29	T1S	R6E	580	45.430	122.070	450	Mesic
OG	5033	Mt. Hood-Columbia Gorge	26	T1N	R6E	980	45.560	122.020	500	Wet
OG	5039	Mt. Hood-Columbia Gorge	19 & 30	T1S	R8E	1081	45.450	121.850	320	Wet
M	5041	Mt. Hood-Columbia Gorge	3	T2S	R5E	326	45.400	122.200	90	
M	5052	Mt. Hood-Columbia Gorge	29	T1S	R6E	—	45.300	122.070	—	
M	5048	Mt. Hood-Zig Zag	18	T3S	R6E	717	45.300	122.110	85	
Y	5050	Mt. Hood-Zig Zag	33	T3S	R8E	928	45.260	121.810	75	
M	5066	Mt. Hood-Zig Zag	3	T4S	R7E	677	45.260	121.930	85	
Y	5067	Mt. Hood-Columbia Gorge	34	T1N	R6E	871	45.520	122.030	60	
Y	5061	Mt. Hood-Columbia Gorge	14	T1S	R6E	552	45.480	122.020	75	
H.J. Andrews[b]										
OG	I L w	Willamette-Blue River	32	T16S	R5E	560	44.220	122.240	450	Mesic
OG		Willamette-Blue River	25	T15S	R5E	815	44.220	122.150	450	Wet
OG	E	Willamette-Blue River	30	T15S	R5E	975	44.220	122.150	450	Wet
OG	1015[c]	Willamette-Blue River	14 & 23	T15S	R5E	793	44.250	122.170	450	Wet
OG	1124[c]	Willamette-Blue River	25	T15S	R5E	862	44.220	122.160	450	Wet
OG	1019	Willamette-Blue River	15	T15S	R5E	902	44.250	122.180	450	Mesic
OG	1029	Willamette-McKenzie	25 & 26	T16S	R5E	700	44.150	122.150	200	Dry
OG	1083[c]	Willamette-McKenzie	25 & 26	T16S	R5E	950	44.130	122.150	300	Dry
OG	1133	Willamette-McKenzie	26	T16S	R6E	819	44.230	122.060	200	Dry
M	1035[c]	Willamette-Blue River	14 & 11	T16S	R5E	1000	44.260	122.170	130	
M	1111	Willamette-Blue River	3	T17S	R5E	610	44.100	122.290	130	
M	1037	Willamette-Blue River	15	T16S	R3E	490	44.160	122.430	90	
M	1038	Willamette-Blue River	24	T16S	R3E	535	44.160	122.420	90	
M	1036	Willamette-Blue River	13	T15S	R5E	—	44.260	122.150	130	
M	1065	Willamette-Blue River	15	T16S	R3E	708	44.170	12.430	90	
M	1066	Willamette-Blue River	14	T16S	R3E	—	44.165	122.435		
M	1093[c]	Willamette-Blue River	7	T17S	R6E	600	44.100	122.150	90	
Y	1086[c]	Willamette-Blue River	2	T15S	R5E	909	44.290	122.170	79	
Y	1048	Willamette-Blue River	2	T15S	R5E	1073	44.290	122.150	69	
Y	1089[c]	Willamette-Blue River	14	T16S	R4E	520	44.160	122.300	35	
Rogue River-Umpqua										
OG	6006	Umpqua-Tiller	23	T29S	R1W	437	43.030	122.810	300	Wet
OG	6001	Rogue River-Prospect	23	T32S	R4E	1199	42.770	122.310	260	Wet
OG	6003	Rogue River-Prospect	24 & 25	T30S	R2E	1284	42.940	122.510	270	Mesic
OG	6021	Umpqua-Tiller	13	T28S	R1W	566	43.050	122.780	250	Mesic
OG	6028	Umpqua-Tiller	31	T28S	R1W	920	43.090	122.850	450	Mesic
OG	6017	Rogue River-Prospect	25	T30S	R2E	1189	42.930	122.550	270	Dry
OG	6031	Rogue River-Prospect	31	T30S	R3E	1123	42.900	122.510	430	Dry
OG	6032	Rogue River-Prospect	36	T30S	R2E	1110	42.910	122.510	270	Dry
OG	6039	Umpqua-Tiller	12	T29S	R1W	642	43.060	122.760	250	Dry
OG	6046	Umpqua-Tiller	27	T28S	R2E	737	43.100	122.560	250	Mesic

See *footnotes* on next page.

Table E-continued

Type[a]	Stand	Forest-Ranger District	Section	Township	Range	Elev	Lat	Long	Age	Moisture
M	6052	Umpqua-Tiller	26	T28S	R1W	943	43.080	122.850	120	
M	6040	Rogue River-Prospect	26	T30S	R3E	1092	42.930	122.430	90	
M	6041	Umpqua-Tiller	32	T28S	R1W	840	43.090	122.830	115	
M	6044	Rogue River-Prospect	27	T31S	R4E	1478	42.850	122.330	90	
M	6047	Umpqua-Tiller	23	T28S	R2E	698	43.100	122.590	180	
M	6050	Umpqua-Tiller	25	T28S	R2W	1052	43.090	122.860	120	
M	6051	Umpqua-Tiller	5	T29S	R1W	831	43.080	122.840	120	
Y	6063	Umpqua-Tiller	1 & 12	T30S	R1W	924	42.980	122.760	60	
Y	6069	Umpqua-Tiller	5	T30S	R1W	1072	42.980	122.780	60	
Y	6099	Rogue River-Prospect		T32S	R4E	1428	42.820	122.350	75	

[a] OG = old-growth, M = mature, Y = young.
[b] Andrews stands studied in 1985 are underlined.
[c] Andrews stands sampled for small mammals and amphibians with new pitfall grids in 1985.

Table M-Vegetation and site measurements for stations used in the point count bird surveys

Measurements on a 500-m^2 area (13-m radius) centered at station).

Forest floor
1. Cover of logs by decay class (%) (>10-cm diameter).
2. Cover of forest floor by various substrates: exposed bare rock, exposed bare mineral soil, fine organic litter (10-cm diameter), coarse organic litter (>10-cm diameter), moss, lichen (Total = 100%.)

Vegetation characteristics
3. Cover of foliage by height interval and life form
    a. Height intervals:
        1. 0-0.5 m (500-m^2 area)
        2. 0.5-2.0 m (500-m^2 area)
        3. 2.0 through midstory (trees and shrubs not entering main canopy) (measured on 2000-m^2 area)
        4. Canopy trees forming main canopy layer (2000-m^2 area)
        5. Super canopy trees (crowns extending well above main canopy layer) (2000-m^2 area)

    b. Life forms
        1. Herbs
        2. Graminoids
        3. Ferns
        4. Berry-producing ericaceous shrubs
        5. Evergreen shrubs (including those in no. 4)
        6. Deciduous shrubs (including those in no. 4)
        7. Deciduous trees
        8. Broad-leaved evergreen trees
        9. Needle-leaved evergreen trees

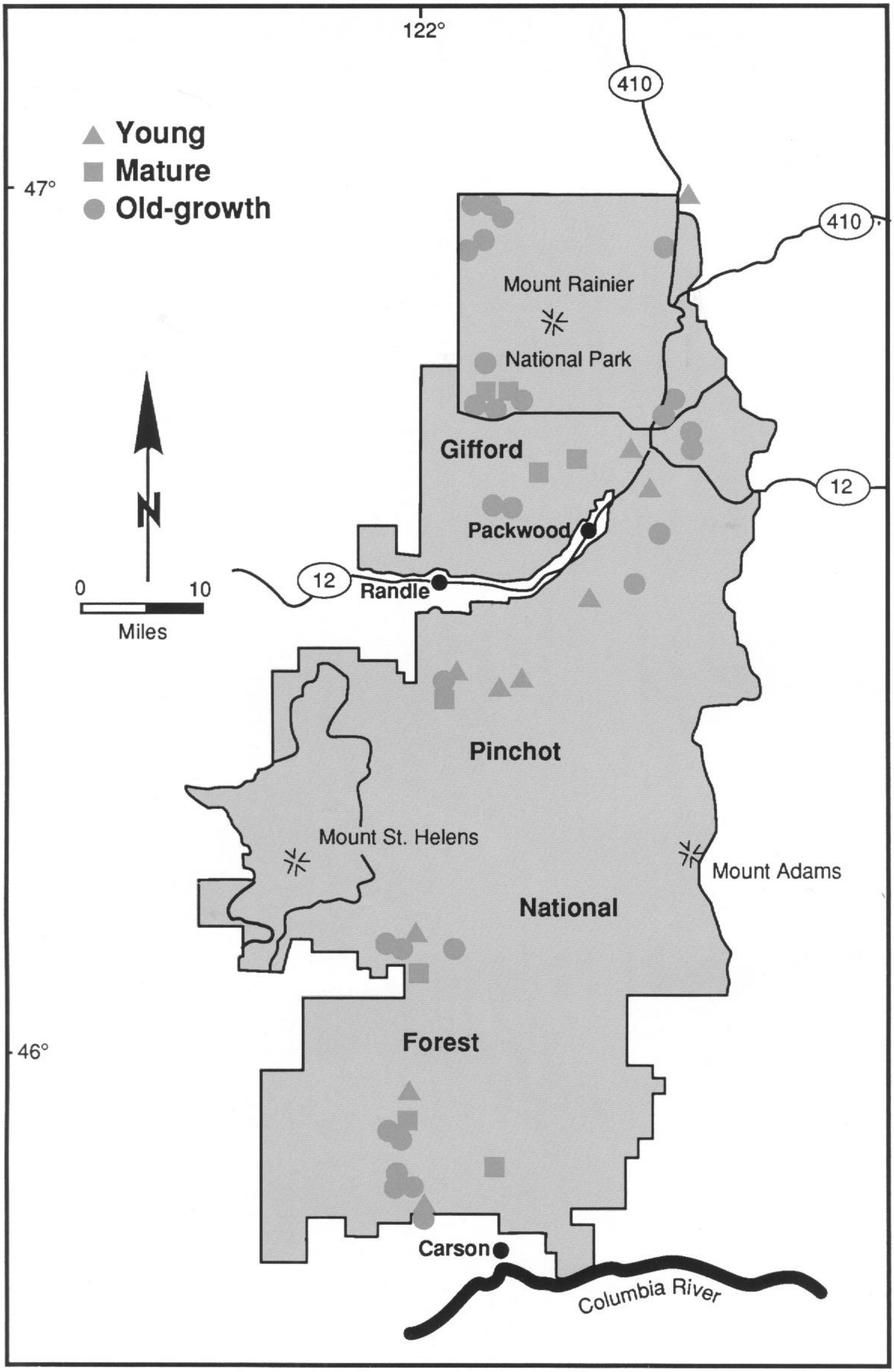
Stand characteristics
4. Number and species of small-diameter live trees (1-10 cm d.b.h.).
5. Number and species of medium-diameter live trees (10-50 cm d.b.h.).
6. Number by decay class of short snags (any d.b.h., 1.5-5 m tall).
7. Number by decay class of medium-diameter, medium tall snags (10-50 cm d.b.h., 5-15 m tall).
8. Numbers by decay class of large-diameter, medium tall snags (50 cm d.b.h. and 5-15 m tall).
9. Number of recent tree-fall mounds or pits with exposed tree roots or mineral soil.

Table H-continued

Measurements on a 2000-m^2 area (25-m radius centered at counting station)

A. Site characteristics
   10. Surface water (presence/absence).
   11. Type of water: I (intermittent stream); P (perennial stream); S (seep); 0 (pool/pond).
   12. Rock outcrop (% of area) (presence/absence).
   13. Exposed talus (% of area) (presence/absence).
   14. Aspect
   15. Slope (%)

B. Stand characteristics
   16. Average height of dominant canopy trees.
   17. Number and species of large, live trees (50-100 cm d.b.h.).
   18. Number and species of very large, live trees (>lOO cm d.b.h.).
   19. Number by decay-class of medium-diameter, tall snags (l0-50 cm d.b.h. and 15 m).
   20. Number by decay-class of large-diameter, tall snags (>50 cm d.b.h. and 15 m tall).



Location of study sites.

Continue

Spring Bird Communities in the Southern Washington Cascade Range

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Abstract

Spring bird populations were studied in 1984 and 1985 in 46 Douglas-fir forest stands in the southern Washington Cascade Range. Stands were classified into young (55-80 years), mature (95-190), and old-growth (250-700) age-classes and varied in elevation and latitude. Birds were surveyed by the point-count method, and detection rate (birds/visit) was used as an index of abundance. All birds detected within 75 m of a count station were included in the analysis. Thirty-four species were detected in the study areas. Mean bird species richness varied from 13.6 to 16.4 per stand and differed significantly among age-classes in 1985 but not in 1984, although mean richness was not significantly different between years. Mean richness showed a weak negative relation to increasing elevation and latitude. The nesting avifauna typically consisted of a core group of nine common species and about five uncommon species. Highest pooled detection rates occurred in old-growth wet and old-growth dry sites; lowest rates were in mature and young stands. The five most abundant species in decreasing order of abundance were winter wren, golden-crowned kinglet, hermit/Townsend's warbler, chestnut-backed chickadee, and western flycatcher. Total avian abundance showed a weak negative relation to gain in elevation and latitude. A correlational analysis was made of vegetation variables associated with bird abundance. Cluster analysis revealed two major groups of forest stands that differed in elevation and latitude. Among birds in which significant relation to vegetation variables were found, live trees and snags typical of late-successional forests were negatively correlated with abundance of the blue grouse and evening grosbeak. These same factors were positively correlated with abundance of the varied thrush, winter wren, and western flycatcher. All but 3 of 17 species analyzed were most abundant in old-growth compared to younger forests. Although many species were most abundant in old growth, the Vaux's swift appears to be the only diurnal bird that may depend on old growth for its continued survival. Cavity nesters and birds that feed on the forest floor may suffer drastic declines in intensively managed monocultures. Bird populations may be most affected by changes in forest structure and fragmentation in the nesting range and by winter habitat availability. The relatively large percentage of permanent residents in Douglas-fir forests makes winter habitat particularly important to their survival.

Introduction

Until recently, few accounts have been published on bird community studies in naturally occurring, coniferous forests of the Washington Cascade Range. Manuwal and Huff (1987) described spring and winter bird populations in a subset of the stands reported in this paper. Manuwal and others (1987) discussed the characteristics of subalpine bird communities in the Washington Cascades. The widespread conversion of remaining old-growth coniferous forests of the Pacific Northwest to younger, more intensively managed forests may have an impact on forest bird communities. Sound management of forests to protect bird species richness and rare species is possible only with an understanding of bird communities in natural systems as a baseline.

This report summarizes a study of spring bird populations in different age- and moisture-classes of unmanaged Douglas-fir forests on the west slope of the southern Washington Cascade Range during 1984 and 1985. Objectives of the study were to determine the abundance and species composition of bird populations over a range of forest stand-age and site conditions in the Douglas-fir forests of the southern Washington Cascades; to examine the relation of bird presence to vegetative characteristics at bird-survey locations; and to identify bird species that may depend on old-growth forests for their continued existence.

Methods

Field

We surveyed birds by the point-count method (Verner 1985): observers counted all birds detected during an 8-minute count period beginning within 30 minutes of official dawn at each of 12 stations (points) spaced 150 m apart We did this in 46 stands located from Mount Rainier to the Columbia River (see frontispiece and table 1). Birds were not surveyed during periods of rain, snow, or strong winds. We visited each stand six times from 15 April to 30 June in 1984 and 1985. The abilities of observers to identify birds by both sight and sound and to estimate horizontal distances to within 10 percent of the actual distance were tested. During a given year, most stands were surveyed by more than one observer. Most stands were surveyed in 1985 by different observers from those of the previous year to avoid as much bias as possible. Because of logistical constraints, some stands were surveyed by only one observer during a particular year, so some interstand variability may have resulted from observer differences.

All vegetation sampling was done at all 12 bird-count stations located in each stand. At each station, trees or snags were counted, depending on diameter at breast height (d.b.h.), in either a 13-m-radius (0.05 ha) or a 25-m-radius circular plot (0.2 ha). The total area sampled in a stand was 0.6 ha for 13-m-radius plots and 2.4 ha for 25-m-radius circular plots. In the 13-m plots, small trees (l-10 cm d.b.h.), medium trees (11-50 cm d.b.h.), large trees (51-100 cm d.b.h.), and small snags (l0-19 cm d.b.h.) were counted. In the 25-m-radius-plots, very large (>l00 cm d.b.h.) live trees, and medium (20-49 cm d.b.h.) and large (>50 cm d.b.h.) snags were counted. Density estimates were then calculated for each species by diameter-class. Snags were classified into five decay-classes; class 1 was a hard snag and class 5 a soft, highly decayed snag (Cline and others 1980).

Table 1-Mean elevation, latitude, and age of 46 Douglas-fir stands studied in 1984 and 1985 in the southern Washington Cascades

			Old growth		
	Young	Mature	wet	Mesic	Dry
Number of stands	10	8	9	12	7
Mean elevation (meters)	757	784	762	736	838
Mean latitude (degrees)	43.39	46.23	46.76	46.35	46.41
Mean age (years)	68	133	520	439	336
Range of age (years)	55-80	95-190	300-730	250-700	210-440

Data Analysis

Detection rate (birds per visit) was used as an index of abundance. A visit represented the mean number of birds detected at 12 counting stations on a particular day. Detections were used to compare relative abundance of species among age-classes and environmental gradients, assuming that detectability of a given species did not differ among stands and age-classes, observers were equivalent in their ability to detect birds, and all species had the same probability of detection. Several stands were surveyed by two observers instead of one during a particular spring. Furthermore, observers were trained to estimate distances to detected birds to within 10 percent of actual distances and periodically retested themselves to remain accurate. In the gradient analyses, I used bird detection rates and species richness data from all detections within 75 m of a counting station. For the Vaux's swift, all detections of flying birds (within 150 m) judged by the observer to be associated with the stand being surveyed were used. Furthermore, all species detected less than twice during a season were omitted from the analysis because they were probably associated with other habitats. In assessing the relation of birds to vegetation, birds detected <l50 m from the counting stations were used.

I used Student's t test to compare differences in mean species richness and abundance between years, and the Mann-Whitney U Test (Siegel 1956) to compare differences between two means of small samples. For comparing mean richness and total detection rates among age-classes, I used one-way analysis of variance. Differences in abundance among age-classes for individual bird species were tested by using either analysis of variance or the nonparametric Kruskal-Wallis test (Siegel 1956), depending on whether or not the data were normally distributed. I calculated the

Pearson correlation coefficient *(r)* or Spearman's rank correlation coefficient *(r_s)* to evaluate responses of birds to latitude and elevation and preliminary bird-vegetation relationships.

Associations between habitat variables and counts of each bird species were examined in two different, but related ways. First, Spearman rank correlation coefficients (SPSS, Inc. 1986) were computed to look for significant correlations between tree and snag densities and counts of each bird species. For this analysis, vegetation data were first summarized into the seven most common tree species (or groupings), with four diameter-classes of live trees (l-10 cm, 11-50 cm, 51-100 cm, >l00 cm) and three diameterclasses (l0-19 cm, 20-49 cm, >50 cm) and decay-classes (hard, composed of classes 1 and 2; and soft, composed of classes 3,4, and 5) of snags.

The large number of variables was reduced to a subset of 22 (appendix table 12) by examining highly significant correlations among vegetation variables. Any pair of variables with correlations of >0.50 (thus explaining >25 percent of each other's variances) was either combined into one, or the more ecologically interpretable variable was retained. Thus variables such as all live trees >l00 cm d.b.h., or live western hemlock ≤ 50 cm d.b.h., were created.

In computing a large number of correlations, Type I errors may cause some to be judged statistically significant (that is, $P < 0.05$) simply because of random sampling error. Therefore, we focused on those correlations that 'occurred with the the same sign (positive or negative) in both years and emphasized those that were significant at the $P < 0.01$ level. Conflicting results, such as correlations that were positive one year and negative the next, were considered as possible evidence of Type I errors. (Marcot 1984, Meslow and Keith 1971). Even where correlations are consistently significant, however, they demonstrate only numerical association and do not necessarily imply some biologically meaningful cause.

Second, associations between bird abundance and tree and snag densities were investigated by stepwise multiple linear regression (Kleinbaum and Kupper 1978) with SPSSX (SPSS, Inc. 1986). This approach generated equations explaining each bird species' abundance from vegetation variables and was used for descriptive, rather than predictive purposes. The stepwise procedure evaluates each variable to be entered while controlling for variables already in the equation. Because of the sample size (*n* = 46 stands) and some remaining intercorrelations, a new, smaller set of uncorrelated vegetation variables was generated using factor analysis (Afifi and Clark 1984). The initial factors, each of which was a linear combination of all 22 original variables and explained a known amount of the total variance in vegetation data, were extracted by principal components analysis and rotated with Varimax rotation to ease interpretation. We interpreted the factors with a minimum eigenvalue of one (Battacharyya 1981) by examining the relative sizes of correlations ("loadings") between the factors and original variables.

Bird counts and vegetation variables were first log-transformed [$\log_{10}(x+10)$] for regression analyses to more closely meet underlying distributional assumptions. Transformed bird counts were regressed on vegetation factor scores separately for 1984 and 1985 data. Because of the large number of equations generated and time limitations, we were unable to search for better fits with polynomial and interaction terms, which may explain some species' distributions more fully (Meents and others 1983). The accuracy of each regression was evaluated by the adjusted coefficient of determination (adjusted R^2), an unbiased measure of the percentage of total variation in bird abundance explained by the equation (Zar 1984:336).

Cluster analysis (Afifi and Clark 1984) was used to describe assemblage-level patterns of the similarities of bird species' relative abundances (or simple occurrence). Bird communities were classified with total count data for the spring of 1985 by means of hierarchical, agglomerative cluster analysis. This classification groups species into clusters based on their stand-specific relative abundances and distributions. The properties common to a group of species in a cluster are then used to describe that set of species as a whole. More detailed descriptions of cluster analysis and its applications can be found in Afifi and Clark (1984), Cormack (1971), Gauch (1982) and Sneath and Sokal(l973). Because each distance or similarity measure, as well as each clustering technique, imposes a "structure" on the data, I searched for obvious clusters in the data by comparing results from several of them. Two separate sets of analyses were run. For the first, I converted total counts of the 28 most commonly occurring bird species to presence-absence data and compared sets of clusters formed by several similarity or dissimilarity measures and clustering techniques. I did cluster analyses using similarity measures of presence-absence bird data described by Mueller-Dombois and Ellenberg (1974) and Dice (1945), and the simple-matching equation of Sokal and Michener (1958). The second set of analyses was performed on total bird counts by using squared euclidean distance, After reviewing all the analyses, I decided to present only results from the measures that gave the most definite classification patterns--the simple-matching and squared euclidean measures. They are discussed briefly below:

Simple-matching (Sokal and Michener 1958)

$$S(x,y) = a + b / a + b + c + d,$$

where

a = number of stands in which species x occurred,
b = number of stands in which species y occurred;

c = number of stands in which both species occurred; and
d = number of stands in which neither species occurred.

Squared euclidean:

The second set of analyses was performed on stand-specific total counts of birds. Only birds detected during 8-minute station counts, at distances less than 150 m, and associated with a given stand were counted for these analyses. Bird counts were first log-transformed to reduce the controlling influence of the more abundant species on classification patterns. The formula for the squared euclidean distance is:

$$D\,(x,y) = \sum_{k=1}^{p} (x_{ik} - y_{jk})^2\,;$$

I clustered stands by means of average (between groups) and complete linkage techniques for both distance measures and also by Ward's method on the squared euclidean distance. As with the presence-absence data, I compared clusters obtained in all these runs to elucidate apparent clusters.

Results

Stand and Age-Class Characteristics

Live trees—Highest mean densities of live trees occurred in young stands with very high numbers of western hemlock saplings (1-10 cm d.b.h.) and 11- to 50-cm-d.b.h. Douglas-firs (fig. 1). Not surprisingly, highest densities of the largest diameter trees (>100 cm d.b.h.) were found in old-growth stands, but nearly equal densities of 51- to 100-cm-d.b.h. Douglas-fir were found in young stands. Also, many young stands had some very large (>100 cm) Douglas-fir, hemlock, and western redcedar that had survived previous fires. These trees apparently made the stands more old-growth-like in structure than if the stands were even aged. Although stands varied considerably, old-growth stands had higher densities of hardwood trees than other age-classes.

Among old-growth stands, wet sites had the highest densities of western hemlock and Pacific silver fir, but mesic sites had the highest densities of vine maple and miscellaneous conifers. Highest densities of the largest live trees—particularly western redcedar—occurred on old-growth wet sites.

Deadwood—In general, snag composition reflected past successional dynamics of the stands. Stem competition in the pioneer species Douglas-fir resulted in early mortality after canopy closure. These trees resulted in relatively high snag densities among boles less than 49 cm d.b.h. in young and mature stands (fig. 2). As western hemlock became more common in the understory and later in the canopy, the number of hemlock snags also increased. Pacific silver fir snags also become more prevalent in later stages of succession. The opposite trend appeared for western white pine, which was present in low densities in all age-classes but did not reach maturity because of blister rust. Highest densities of western white pine snags were in young stands and continued to decrease with stand age. The highest density of snags occurred in young stands where 70 percent of all snags were Douglas-fir and over 40 percent of them were in the small diameter-class (10- 19 cm). The 6.2 large snags per ha in young stands reflected the fire history of the stands and probably represented a significant biological resource for cavity-nesting birds and mammals. Predictably, old-growth stands had the highest densities of very large snags. Those of Douglas-fir and western hemlock were most common. Large hardwood snags, primarily bigleaf maple and cottonwood, were most abundant in mature stands.

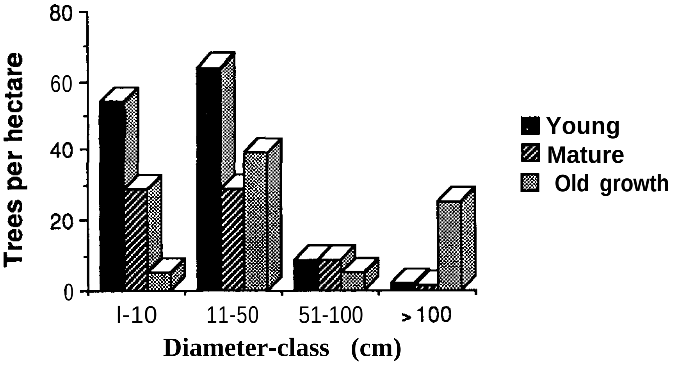

Figure. 1—Density of live trees in three diameter-classes among young, mature, and old-growth Douglas-fir forests in the southern Washington Cascades.

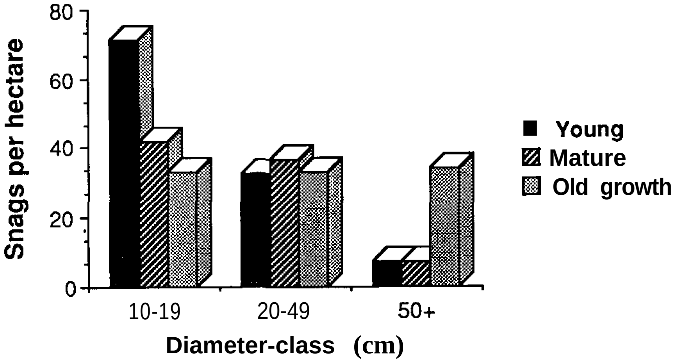

Figure 2—Density of snags in three diameterclasses among young, mature, and old-growth Douglas-fir forests in the southern Washington Cascades.

Snag abundance varied considerably among stands, presumably reflecting fire history and vagaries of successional patterns. Nevertheless, on an age-class basis, the outcome of tree competition followed a predictable pattern (see Cline and

Table 2—Stand variation in bird species richness in Douglas-fir forests of the southern Washington Cascades

					Old growth					
	Young		Mature		Wet		Mesic		Dry	
	1984	1985	1984	1985	1984	1985	1984	1985	1984	1985
Total species	27.0	28.0	22.0	23.0	24.0	22.0	26.0	26.0	25.0	23.0
Mean richness	15.2	17.2	13.2	14.0	13.9	13.3	15.1	14.8	15.0	17.7
SD	2.8	3.8	4.1	3.3	2.9	2.1	2.8	3.4	2.1	1.4

Table 3—Number of species of flycatchers, thrushes, and warblers detected in the 7 lowest and the 7 highest elevation Douglas-fir stands in the southern Washington Cascades in 1985

				Bird group		
Stand	Age	Elevation	Latitude	Flycatchers	Thrushes	Warblers
302	500	500	46.10	4	3	2
316	500	506	46.09	3	3	2
317	500	529	46.10	3	4	2
340	130	586	46.07	1	5	2
401	500	617	46.99	3	3	1
423	250	644	46.72	2	4	3
365	75	704	46.64	2	3	5
Mean	351	584	46.39	2.6	3.6	2.4
418	550	1037	46.91	2	3	2
332	600	1049	46.67	2	4	3
419	320	1072	46.93	1	3	2
346	190	1124	46.40	2	3	1
468	65	1164	46.98	0	2	1
303	600	1168	46.69	2	2	3
432	300	1217	46.94	1	2	1
Mean	375	1119	46.79	1.4	2.7	1.9

others 1980, Franklin and Dyrness 1973) in Douglas-fir forests. Most stands had five to seven conifer species and two to four hardwood species . The large snags (>50 cm d.b.h.) were primarily Douglas-fir, western hemlock, western redcedar, Pacific silver fir, and western white pine. All other species combined usually comprised less than 5 percent of the total snag population.

Avian Species Composition and Richness

General—In this analysis, I used 27,156 bird detections of 34 species in the study stands. Bird groups in natural Douglas-fir forests (between the ages of 55 and 700 years old) with the largest number of species were the woodpeckers, thrushes, flycatchers, corvids, warblers, and finches. Mean bird species richness was not significantly different between years (in 1984, 14.5, SD = 2.8; in 1985, 15.3, SD = 3.4 (t = 1.17, P = 0.24).

Effect of forest age and moisture—Mean species richness was 16.2 species per visit in young stands, 13.6 in mature stands, and 15.0 in old-growth stands. It was not significantly different among age-classes in 1984 (F = 0.25, P = 0.91) but it was significantly different in 1985 (F = 2.63, P < 0.05). Along the moisture gradient, mean species richness was 14.1 in old-growth wet, 14.8 in old-growth mesic, and 16.4 in old-growth dry (table 2). Mean richness was not significantly different along the old-growth moisture gradient in 1984 (F = 0.01, P = 0.98), but it was significantly different in 1985 (F = 5.67, P < 0.01).

Effect of elevation—Bird species richness declined with increasing elevation of study sites in both years (r = –0.32; P > 0.05). The lowest seven stands had a mean of 15.4 species, and the highest seven stands, 12.9 species. The difference was not significantly different. Among groups, significantly fewer species of flycatchers (t = –2.41, P = 0.03) and thrushes (t = 2.57, P = 0.02) but not warblers (t = 2.07, P = 0.06) were found in the high-elevation stands compared with low-elevation stands (table 3).

Effect of latitude—Richness showed a weak negative relation to latitude (1984: r = –0.36, P = 0.013; 1985: r = –0.41, P = 0.005). Species richness was highest in the Wind River area and lowest near Mount Rainier. When all 46 stands are considered, however, stand elevation increased with latitude (r = 0.63, P < 0.001), so the two factors were interrelated. Nevertheless, the latitudinal effect was probably a real one.

Avian Abundance

General—A core group of species nesting in natural Douglas-fir forests between the ages of 55 and 700 years old typically consisted of about ten common and widely distributed species, with frequencies of occurrence of at least 85 percent, and four less-common species, with frequencies of occurrence of 46 to 54 percent (table 4). A third group contained an additional 19 relatively rare species. The Vaux's swift was not included in this analysis because of its wide-ranging foraging behavior. In addition to these 34 species detected within 75 m of the counting points, other species,

Table 4—Frequency of occurrence of birds in 46 Douglas-fir stands in the southern Washington Cascades, 1984 and 1985

	Percentage of stands in which species[a] was recorded		
Species	1984	1985	Mean[b]
Group 1			
Golden-crowned kinglet	100	100	100
Chestnut-backed chickadee	100	100	100
Winter wren	100	100	100
Varied thrush	100	96	98
Brown creeper	93	98	96
Dark-eyed junco	93	89	91
Western flycatcher	91	89	90
Red-breasted nuthatch	91	89	90
Hermit/Townsend's warbler	89	89	89
Gray jay	87	83	85
Group 2			
Hermit thrush	40	67	54
Pine siskin	41	61	51
Hairy woodpecker	52	48	50
Steller's jay	48	43	46
Group 3			
American robin	36	35	36
Rufous hummingbird	30	39	35
Wilson's warbler	41	26	34
Swainson's thrush	33	26	30
Hammond's flycatcher	15	35	25
Western tanager	26	17	22
Evening grosbeak	15	22	19
Pileated woodpecker	20	9	15
Blue grouse	13	9	11
Red crossbill	11	9	10
Black-throated gray warbler	7	11	9
MacGillivray's warbler	4	11	8
Band-tailed pigeon	11	0	6
Yellow-rumped warbler	7	2	5
Olive-sided flycatcher	0	7	4
Northern flicker	4	4	4
Red-breasted sapsucker	2	4	3
Common raven	4	0	2
Hutton's vireo	0	2	1

[a] Vaux's swift not included because of its wide-ranging habits; it was found in 72 percent of the stands.

[b] Numbers rounded to nearest whole number.

Table 5—Mean number of birds detected per visit in Douglas-fir forests in the southern Washington Cascades in 1984 and 1985 (feeding guilds[a] are shown in parentheses)

			Old-growth		
Species	Young	Mature	Wet	Mesic	Dry
Blue grouse (LUHI)	0.20	0.48	0.28		
Band-tailed pigeon (TS)	.04	.10	.02		
Vaux's swift (AI)	.23	.36	2.56	1.73	0.52
Rufous hummingbird (N)	.11	.22	.19	.35	.36
Red-breasted sapsucker (BI)		.02	.04		
Hairy woodpecker (BI)	.19	.22	.51	.34	.22
Northern flicker (BI)			.04	.03	
Pileated woodpecker (BI)	.09	.11	.07		
Olive-sided flycatcher (AI)	.03				
Hammond's flycatcher (AI)	.06	.25	.13	.27	.43
Western flycatcher (AI)	4.49	3.65	5.28	5.26	3.75
Gray jay (OS)	.94	.83	1.21	1.46	1.31
Steller's jay (OS)	.39	.14	.87	.34	.19
Common raven (OS)			.02		
Chestnut-backed chickadee (TFI)	3.31	3.47	6.51	5.43	3.84
Red-breasted nuthatch (BI)	2.39	1.53	1.67	3.48	4.71
Brown creeper (BI)	1.49	2.88	2.12	3.23	2.10
Winter wren (LUHI)	6.98	8.00	19.45	10.94	8.24
Golden-crowned kinglet (TFI)	6.20	7.27	8.86	6.52	9.02
Swainson's thrush (LUHI)	.18	.15	.22	.43	.36
Hermit thrush (LUHI)	.90	.28	.27	.58	.76
American robin (LUHI)	.24	.17	.48	.16	.28
Varied thrush (LUHI)	2.72	2.48	5.71	4.10	4.68
Hutton's vireo (TFI)	.03				
Yellow-rumped warbler (TFI)	.04	.02	.06	.23	
Black-throated gray warbler (TFI)	.19	.02		.06	
Hermit/Townsend's warbler (TFI)	7.90	5.61	1.59	2.11	6.23
MacGillivray's warbler (LUHI)		.06	.02	.02	.05
Wilson's warbler (LUHI)	.19	.13	.49	.22	.34
Western tanager (TFI)	.25	.22	.06	.06	.13
Dark-eyed junco (LUHI)	3.71	2.28	1.59	2.30	5.30
Red crossbill (TS)	.06	.11	.10	.60	.03
Pine siskin (TS)	1.29	.54	.55	.78	2.03
Evening grosbeak (TS)	.47	.49		.07	.04
Total	45.31	42.09	60.97	51.10	54.92

[a] Guild abbreviations: AI = air-insect, BI = bark insectivore, LUHI = low understory herbivore-insectivore, N = nectarivore, OS = omnivore-scavenger, TFI = timber-foliage-insectivore, TS = timber-seed eater.

such as raptors and grouse with large territories, were rarely detected within 75 m but were nevertheless members of the avifauna associated with the study stand.

Effect of forest age and moisture—Significant differences occurred in mean counts/visit among forest age-classes (1984: $F = 13.2$, $P < 0.01$; 1985: $F = 2.50$, $P = 0.06$) and along the moisture gradient (1984: $F = 18.3$, $P < 0.01$; 1985: $F = 3.30$, $P = 0.05$) (table 5, fig. 3). Highest detection rates were in old-growth wet and old-growth dry sites, and lowest detection rates were in mature and young sites. The higher numbers in

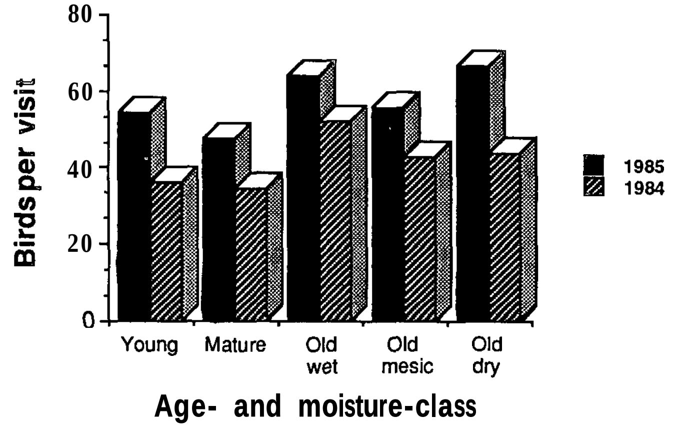

Figure 3-Mean number of bids per visit in young, mature, and old-growth Douglas-fir stands in the southern Washington Cascades.

Table 6—The 5 most abundant bird species in Douglas-fir forests in the southern Washington Cascades in 1984 and 1985

	Birds per visit					
	1984			1985		
Species	Mean	SD[a]	CV[b]	Mean	SD	CV
Chestnut-backed chickadee	24.9	12.1	48.5	30.9	17.0	55.1
Golden-crowned kinglet	42.8	19.6	45.7	47.6	20.3	42.7
Hermit/Townsend's warbler	19.2	17.5	90.9	37.3	34.8	93.1
Western flycatcher	23.3	15.2	65.1	32.5	21.4	65.9
Winter wren	55.3	29.9	54.1	77.0	45.1	58.6

[a] Standard deviation.
[b] Percent coefficient of variation (100 SD/$\bar{x}$).

old-growth wet sites were due to large counts of Vaux's swifts, winter wrens, chestnut-backed chickadees, and western flycatchers.

Effect of elevation and latitude-Although total avian abundance declined with gain in elevation, the relation was not significant and not all species showed a decline. Among the five most abundant species, only the western flycatcher showed a strong relation to elevation (r = -0.58, P = 0.0001). The response of other species was less obvious: golden-crowned kinglet (r = 0.42, P = 0.004); chestnut-backed chickadee (r = 0.35, P = 0.019); hermit/Townsend's warbler (r = 0.13, P = 0.951); winter wren (r = -0.03, P = 0.344). Pooled counts of all species did not change with increase in latitude.

Between-year variation-The mean detection rate was significantly lower in 1984 than 1985 (t = -6.65, P < 0.01). The largest differences occurred in young and old-growth dry stands (fig. 3). Of the five most abundant species, only the golden-crowned kinglet was not significantly more abundant in 1985 then in 1984 (table 6). The winter wren and hermit/Townsend's warbler showed the largest differences between years.

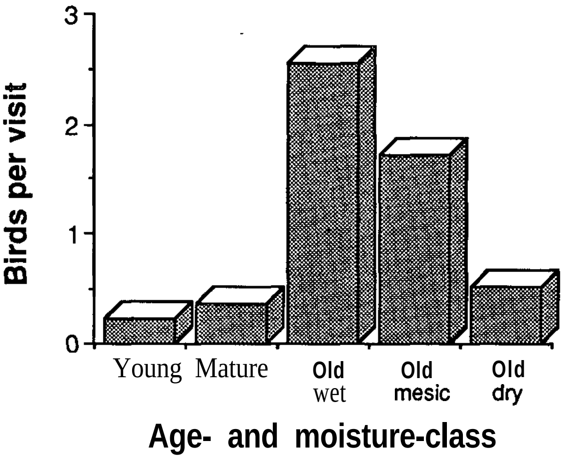

Figure 4-Mean detection rates of the Vaux's swift in young, mature, and old-growth Douglas-fir stands in the southern Washington Cascades, 1984 and 1985 combined.

Species and species-group abundance patterns-The data indicate that the Vaux's swift is the only diurnal bird species that may depend on old-growth forests. This species was significantly more abundant in old-growth compared with other age-classes (that is, 7.0 and 4.4 times more abundant in old-growth than in young or mature forests, respectively) (fig. 4). Among the picids, the hairy woodpecker was the most abundant and was found in virtually every stand. It did not show a strong trend in abundance along the age gradient. The northern flicker was missing or uncommon in all stand types. This species uses edges primarily, and apparently found the Douglas-fir forests to be marginal habitat. The red-breasted sapsucker was uncommon and was recorded only in mature and old-growth wet stands, but the sample size was very small. We detected both the red-breasted and yellow-breasted color morphs, the red being by far the most common. About the same number of pileated woodpeckers were found in all age-classes. The rufous hummingbird was substantially more abundant in old-growth mesic and dry stands.

Of the three species of flycatchers, the western was overwhelmingly the dominant one. It was found in all stands and comprised 93 percent of all flycatcher observations. It was most common in old-growth wet sites. The Hammond's flycatcher, the second most commonly detected flycatcher, was found primarily in old-growth mesic and old-growth dry stands.

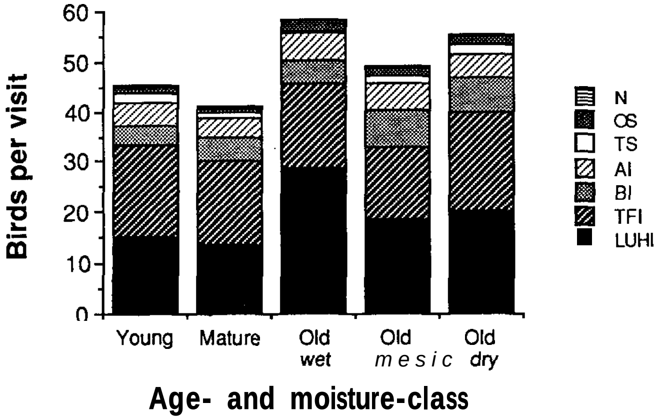

Figure 5-Avian feeding-guild structure based on mean detection rate for 1984 and 1985 in young, mature, and old-growth Douglas-fir forests in the southern Washington Cascades. Guild codes: AI, air-insect; BI, bark insectivore; LUHI, low understory herbivore-insectivore; N, nectarivore; OS, omnivore-scavenger. TFI, timber-foliage insectivore; and TS, timber-seed eater.

Among the corvids, the gray jay was slightly more common than the Steller's. Both species were detected less in mature stands than in either young or old-growth types. Steller's jays were significantly less common at higher than lower elevations. No such change was found for the gray jay. No trends in abundance with environmental gradients were detected for the common raven.

The only parid found in Douglas-fir forests was the chestnut-backed chickadee. This species was significantly more abundant in old-growth sites, particularly old-growth wet, than in younger stands.

The hermit warbler (and hermit/Townsend's hybrids) was by far the most abundant of the six species of warblers. It was the predominant upper canopy warbler in all stands where it occurred. Other upper canopy warblers included the Townsend's and yellow-rumped, but they were far less abundant and had relatively low frequencies of occurrence. The second most abundant warbler was the Wilson's, which was the dominant understory species. The black-throated gray warbler was uncommon but was most often found in young stands with a large broadleaved tree component. MacGillivray's warbler seemed to be associated with edges or patches of broadleaved shrubs growing in tree-fall gaps. The most abundant finches were the pine siskin, evening grosbeak, and red crossbill. The siskin and grosbeak tended to be more abundant in young and mature stands, but the crossbill was more often detected in old-growth stands. The siskin and grosbeak, however, were much commoner than the crossbill.

Foraging guild structure---The two dominant foraging guilds in all stand types were the low understory herbivore-insectivore and the timber-foliage insectivore (fig. 5). The principal species in the low understory guild were the winter wren, varied thrush, and dark-eyed junco. Birds in this guild were most abundant in old-growth and least abundant in mature stands, except for the junco, which was most common in young and old-growth dry stands. The primary birds in the timber-foliage guild were the chestnut-backed chickadee, golden-crowned kinglet, and hermit warbler. The chickadee was most common in old-growth stands. The golden-crowned kinglet did not show a strong trend among age-classes, but the winter wren was clearly most abundant in old-growth. Hermit/Townsend's warblers clearly preferred younger forests and responded negatively to moisture. Another obvious difference in guild structure across the age and moisture gradients was that the aerial insectivores were more abundant in old-growth wet and mesic sites than in other stand types because of the high densities of the western flycatcher and Vaux's swift.

Habitat Characteristics Associated With Avian Abundance

Correlational analysis between primary live-tree and snag variables (tables 7, 8; appendix table 12) and six non-cavity-nesting species showed a significant response to at least one of the six vegetation factors both years of the study. A similar analysis of cavity-nesting species is presented elsewhere in these proceedings (Lundquist and Mariani, this volume).

The six factor scores were correlated with stand-age and moisture values. Factors 1 (r_s = 0.55) and 4 (r_s = 0.55) were positively correlated, and factor 6 (r_s = -0.30) was negatively correlated with stand age ($P \leq 0.05$). Factor 1 (r = 0.50) was positively correlated with moisture, but factor 4 (r = -0.68) was negatively correlated.

For the blue grouse, the most significant positive relationships (obtained from initial regression analysis) were with vine maple and other hardwoods, and density of small live Douglas-firs. Negative responses were to all very large live trees (>100 cm d.b.h.) and density of true firs (l-10 cm d.b.h.). Blue grouse tended to be negatively correlated with most true fir characteristics. Blue grouse were negatively correlated with factor 1. The evening grosbeak was also negatively correlated with factor 1, but the varied thrush and winter wren were positively correlated. Factor 2 was significantly correlated with the varied thrush, western flycatcher, and western tanager.

Bird Habitat and Community Classification

Analysis of stands-Two distinct clusters of stands were produced by the simple matching clustering technique using the 1985 presence-absence data (fig. 6). Two other but similar clusters were produced by using 1985 bird-detection data (squared euclidean distance) (table 9). No distinct clustering

Table 7—Description of vegetation variables comprising 6 factors derived by factor analysis

Factor	Vegetation variable	Eigenvalue	Percent of variation
Factor 1	Live Douglas-fir <100 cm d.b.h. Douglas-fir snags 20-49 cm d.b.h. All live trees >100 cm d.b.h. Live true firs <100 cm d.b.h. All soft snags	6.65	31.7
Factor 2	Hardwood snags 1-49 cm d.b.h. Western hemlock snags 20-49 cm d.b.h. Western hemlock snags ≥50 cm d.b.h. True firs snags 20-49 cm d.b.h. Live western hemlock 51-100 cm d.b.h.	3.06	14.6
Factor 3	Live western redcedar 1-50 cm d.b.h. Live western redcedar 51-100 cm d.b.h. Western redcedar snags 20-49 cm d.b.h. Western redcedar snags ≥50 cm d.b.h.	2.68	12.8
Factor 4	Other live conifers <100 cm d.b.h. Western white pine snags 20-49 cm d.b.h. Western white pine snags ≥50 cm d.b.h. Hard Douglas-fir snags ≥50 cm d.b.h.	1.56	7.4
Factor 5	Soft Douglas-fir snags ≥50 cm d.b.h.	1.30	6.2
Factor 6	Live western hemlock ≤50 cm d.b.h. Stumps and stubs	1.15	5.5

Table 8—Results of stepwise multiple linear regression of mean total bird counts[a] with vegetation factor[b] analysis scores

Species and year	Step	Factor	Multiple R	Adjusted R^2	Significance
Blue grouse					
1984	1	1	-0.46	0.19	0.001
1985	1	1	.36	.11	.013
Evening grosbeak					
1984	1	1	–.39	.13	.007
1985	1	1	.30	.07	.046
Varied thrush					
1984	1	1	.31	.08	.034
1985	1	1	.35	.10	.019
1984	3	2	.52	.22	.040
1985	2	2	.50	.21	.002
Western flycatcher					
1984	2	2	–.53	.25	.001
1985	2	2	–.52	.24	.001
1984	3	5	.62	.35	.000
1985	1	5	.40	.14	.006
1984	1	6	–.38	.13	.008
1985	3	6	–.60	.32	.000
Western tanager					
1984	1	2	.35	.11	.015
1985	4	2	.72	.47	.000
Winter wren					
1984	1	1	.47	.20	.001
1985	1	1	.40	.40	.006

[a] Bird counts and tree and snag densities were. log-transformed.

[b] Vegetation variables comprising the vegetation factors are in table 7.

occurred with the 1984 data. Cluster analysis verified the previous conclusions on the importance of elevation, latitude, and forest structural characteristics. Stands that were lower in elevation and more southerly had higher bird species richness and abundance than lower elevation stands in northern sites of the study area (table 9).

Although I did not analyze all bird species in each cluster, differences in bird abundance between clusters were apparent. For example, the flycatchers (U = 0, P = 0.0001) were significantly more abundant in low-elevation, lower latitude stands than elsewhere (table 9), but the winter wren was not (U = 32.5, P = 0.45). Old-growth wet stands tended to be clustered together in one of the two larger clusters (fig. 6). Stands 401, 403, 410, 411, and 302 were strongly associated with each other. In other words, the bird assemblage associated with each-of those stands was similar. This pattern presumably indicates that the stands themselves were similar and provided nearly equivalent habitat. Stand 402, despite being adjacent to stands 401 and 403, was consistently classified in a different cluster; no reasons for this difference are apparent, although 402 had fewer birds detected. It had hermit warblers, and the others did not, it did not have Wilson's warblers and it had only the western flycatcher, but 401 and

Table 9—Some characteristics of stand clusters created by the squared euclidean technique using 1985 bird detections

	Cluster 1	Cluster 2
Number of stands	26	17
Stand classification		
Young	7	2
Mature	6	2
Old-growth wet	1	7
Old-growth mesic	5	5
Old-growth dry	7	1
Mean elevation	885.5	600.1
Mean latitude	46.6	46.2
Mean age	261.5	350.0
Total detections	454.9	653.4
Total warbler detections	60.0	50.9
Total flycatcher detections	27.1	72.4
Total winter wren detections	71.9	121.6

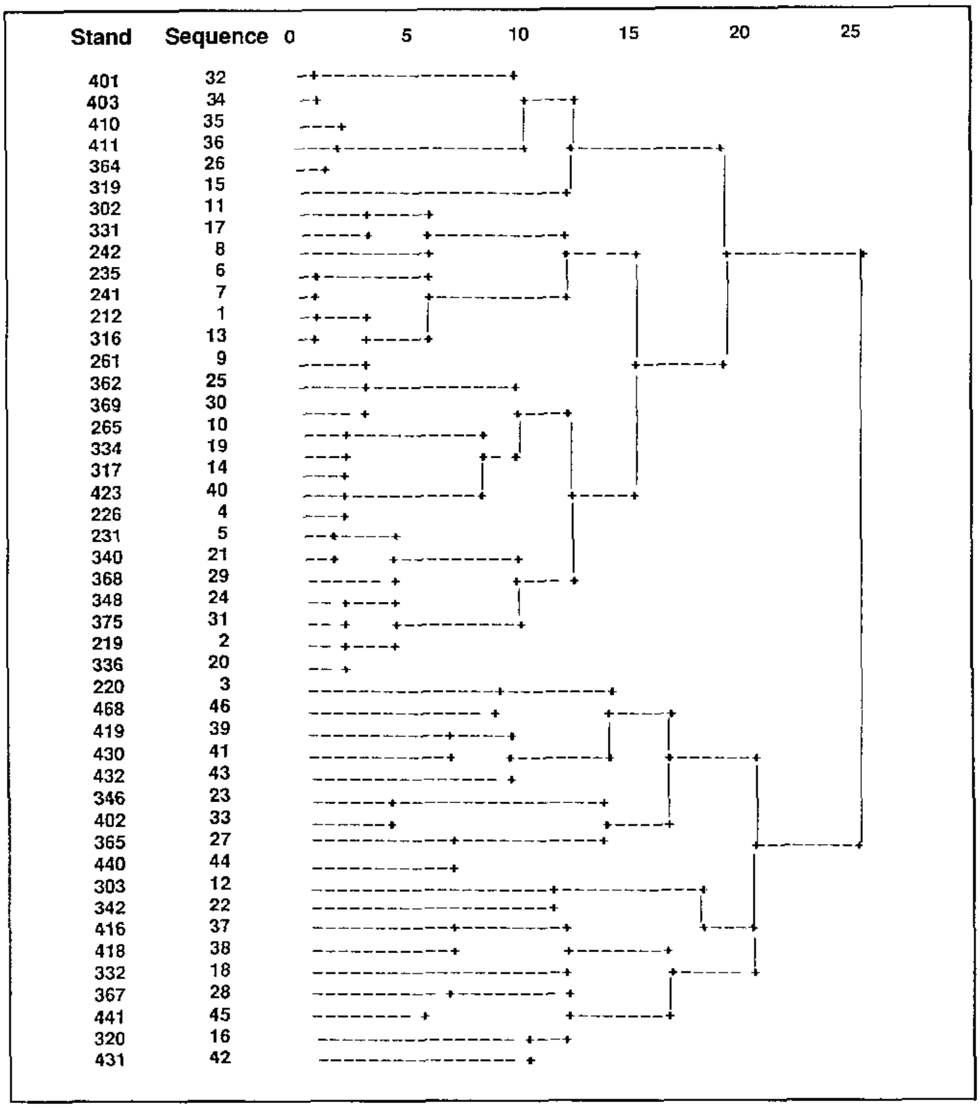

Figure 6—Cluster analysis dendrogram of birds found in 46 Douglas-fir stands derived from the simple-matching technique.

403 had small numbers of Hammond's flycatchers in addition to the westerns. Cluster 1 was also typified by young, mature, and old-growth dry stands. Birds particularly associated with these stands were the red-breasted nuthatch, hermit/Townsend's warbler, dark-eyed junco, and pine siskin.

Analysis of bird composition—Cluster analysis revealed that at least one major group of species was identifiable based on either presence-absence or abundance data (fig. 6). Depending on the particular metric used, 8 to 10 bird species consistently clustered together. This group was somewhat analogous to the core group to which I referred earlier. Why this group of species so consistently clustered together is difficult to determine. They did not all share the same feeding or nesting strategies, but they all (except the western flycatcher, which did not occur in stand 468) were detected on each visit to all 46 stands and were abundant species. My tentative conclusion is that birds in cluster 1 simply were abundant and widespread. They were particularly well adapted to resources found in natural Douglas-fir forests over the complete range of environmental conditions that exist. Even though a few other species had high frequencies of occurrence, they were much less abundant (except the hermit/Townsend's warbler) than those species in cluster 1. Much more in-depth analysis of the response of birds to vegetation variables would be required to determine what factors might cause the particular clustering patterns shown in fig. 6.

Discussion

Because this was only a 2-year study, drawing conclusions on some aspects is difficult. For example, species richness was significantly different among forest age-classes in 1985 but not in 1984. The same was true along the moisture gradient. The 1984 spring was colder and wetter than average (data from U.S. Department of Commerce), and most observers that contributed to this study during both years believed that the cold wet weather depressed bird singing and activity, thus preventing detection. The large difference in abundance between 1984 and 1985 seems unlikely to be because of differences in actual populations. The pilot study year of 1983 was similar to 1985. The spring of 1985 was typical for the southern Washington Cascades, so the relationships exhibited in 1985 probably more accurately reflected ecological relationships than those in 1984.

Abundance patterns were consistent between years even though total bird abundance was significantly lower in 1984 than in 1985. Bird abundance was significantly higher in late-successional forests both years, as was the response of birds to the moisture gradient. The primary reason was the consistently higher numbers of Vaux's swifts, winter wrens, chickadees, and western flycatchers in old-growth wet stands. The high numbers of wrens and chickadees might have been due to the large amounts of standing and forest-floor woody debris common in most wet stands. Those stands were the oldest and more likely to have snags, logs, and canopy openings (tree-fall gaps) that could also have been more conducive to flycatcher foraging.

Elevation gain is ecologically similar to gain in latitude, so presumably similar ecological forces are at work on mountain slopes. The finding that species richness declines with increasing elevation agrees with the study by Able and Noon (1977) in the northeastern United States. Although the reasons for this decline are unclear, some combination of climate, habitat structure, and competition probably shape the response of birds to these gradients. Emlen and others (1986) showed that the abundance of 12 of 41 bird species in the northern Midwest responded significantly to latitude. The remaining species were affected by habitat factors or competition effects. They attributed the latitudinal effect to breeding season length and hours available for adult feeding and feeding of young. I found that some bird species increased with elevation, but others decreased or showed little change, a phenomenon similar to that found by Emlen and others (1986) for latitude.

The analysis of vegetation characteristics associated with bird abundance was inconclusive for all but six species, probably because of inadequate sample size for some uncommon species, complex interactions among habitat variables, and bird response to forest characteristics that were not measured. Significant bird responses were related only to variables normally associated with late-successional stages (factors 1,2, and 5) or with earlier succession (factor 6). Of particular significance may be the large leaf surface area associated with late-successional forests. The most significant variables in factor 1 included all live Douglas-fir, live true firs ~100 cm d.b.h., and all live trees >100 cm d.b.h. This association implies that birds may have responded to large amounts of foliage, which attract insects. Net primary production tends to increase with leaf surface area (Gholz 1982). Studies by Grier and Logan (1977) indicate that greater leaf biomass may allow an increase in insect abundance. Because virtually all songbirds are insectivorous in the spring, they would presumably be more abundant in forests with high insect populations.

I believe that the fact that the mean stand age was not significantly different between groups of stands derived from cluster analysis verified our earlier observations that many young and mature stands had remnant very large live trees and snags that apparently made stand characteristics similar to old-growth sites. Further analysis of the vegetation in these stands might give clues to some of the important habitat features to which some birds responded.

Birds Finding Optimal Habitat in Old-Growth Douglas-Fir Forests

This study was largely based on conventional correlational analyses. Such analyses do not necessarily show causal relationships between avian abundance or occupancy and habitat types or features (Wiens and Rotenberry 1981). Nevertheless, the extensive data set enables us to describe the general relationships between bird abundance and habitat types. Ideally, reproductive success and subsequent information on survival of offspring would be necessary to ascertain whether a particular habitat was optimal for breeding species (Van Home 1983). Such data were unavailable, so avian abundance was used as an indicator of habitat suitability with the knowledge that some stand types may have acted as either source or sink segments of some populations (Wiens and Rotenberry 1981).

Old growth was optimal habitat for all but 3 of 17 species (table 10). These species reached maximum abundance in old growth but were also relatively common in other age-classes. I was unable to assign optimum habitat for other species because the data were either inadequate or no peak in abundance in any stand type was recognizable. Old-growth, particularly old-growth wet stands, appeared important to many species of birds, however.

Table M-Optimum habitat types for selected bird species nesting in Douglas-fir forests of the southern Washington Cascades

Bird species	Standtype
Vaux's swift	Old growth[a]
Hairy woodpecker	Old growth (wet)
Pileated woodpecker	Old growth
Hammond's flycatcher	Old growth
Western flycatcher	Old growth (wet)
Gray jay	Old growth
Steller's jay	Old growth (wet)
Chestnut-backed chickadee	Old growth (wet)
Red-breasted nuthatch	Old growth (dry)
Winter wren	Old growth (wet)
American robin	Old growth (wet)
Varied thrush	Old growth (wet)
Hutton's vireo	Young
Black-throated pray warbler	Young
Hermit warbler	Young
Wilson's warbler	Old growth (wet)
Red crossbill	Old growth

[a] Old-growth category means that no trend was evident among the 3 moisture categories.

[b] Includes Townsend's warbler and hybrids between them.

Birds Potentially Dependent on Old-Growth Douglas-Fir Forests

Birds potentially dependent on old-growth Douglas-fir forests are those found almost exclusively in old-growth and that rely on habitat features found primarily in old-growth forests. The Vaux's swift nests colonially in very large, hollow snags-a habitat feature occurring mainly in old-growth forests. Because swifts are aerial insectivores, their food or forest structure are unlikely to have an important bearing on survival-unless, of course, the insects on which they feed depend on old-growth forests. Even though the feeding ecology of this species is poorly known, the nest site is likely to be the critical limiting resource for this species and the species may depend on old-growth for its continued existence.

Other researchers (see Gutierrez and Carey 1985) have tentatively concluded that the northern race of the spotted owl is potentially dependent on old-growth forests for continued survival. Our data, collected opportunistically along with regular bird survey work, also suggest the close association between old growth and spotted owls. We detected five spotted owls in mature and seven in old-growth stands over the 3 years (1983-85). We also detected one barred owl in a young stand and four in old-growth stands. The potential impact of the barred owl on the spotted owl is a concern to many biologists.

Ramifications of Changes in Forest Structure and Fragmentation

Changes in forest structure-Many habitat variables such as density of trees or shrubs of various species are correlated with the presence or abundance of some bird species. A more extensive analysis might uncover yet more significant relations. These results support the basic premise that avian diversity, abundance, and species composition are strongly influenced by habitat patchiness. Recent research by Blake and Hoppes (1986), Brokaw (1985), Hartshome (1978), Martin and Karr (1986), Runkle (1981), Whitmore (1978), Willson and others (1982) indicates that canopy gaps are important patches for forest birds. Most research on this topic has been done in tropical forests or in eastern North American hardwood forests, but similar phenomena are likely to exist in Douglas-fir forests. Old-growth Douglas-fir forests often have tree-fall gaps similar to those described by the cited authors. The general conclusions they draw are that these canopy openings provide food or food-getting resources in greater abundance than the forest interior in general. Blake and Hoppes (1986), in particular, have documented the increase in fruit and insect abundance in tree-fall gaps in an Eastern deciduous forest, coincident with an increase in birds and a change in species composition in those areas.

The fundamental differences in canopy structure between young and old-growth Douglas-fir forests undoubtedly account for some of the differences in the avifauna between these age-classes. The vegetation variables in this study were not specifically designed to measure canopy structure, but those that were measured probably gave an indirect measure of some dimensions of the canopy. The different tree species have different geometric shapes and leaf types. These attributes probably affect both resource abundance (mostly insects) and the ability of birds to exploit those resources. Forests composed of different tree species and tree age-classes would presumably differ somewhat in resource availability. If these resources were limiting, differences in avifaunal response would be expected. In fact, such differences apparently existed in Douglas-fir forests, but they appeared to have more impact on winter birds than summer birds (Manuwal and Huff 1987). Even-aged management of Douglas-fir reduces canopy and understory heterogeneity, the same heterogeneity characteristic of natural stands of older Douglas-fir. The primary aspects of heterogeneity reduced by even-aged management will be canopy and understory patchiness and standing and forest-floor dead wood. Bird species affected by these changes are cavity-nesters and birds associated with the forest floor, where coarse woody debris provides habitat for insect prey. The magnitude of these effects in Douglas-fir forests is unknown but may be strongly influenced by effects of fragmentation.

Table 11—Comparison of the major wintering areas for birds of the Washington Cascades and those from sites in Eastern hardwood forests[a]

	Permanent residents		Low elevation or Southern United States		Mexico		Central and South America[b]	
	N	%	N	%	N	%	N	%
Washington Cascades	24	42	11	19	7	12	15	26
Eastern hardwoods	14	31	6	15	6	15	16	39

[a] From 3 studies in the Appalachians (Crawford and others 1981), eastern Tennessee (Anderson and Shugart 1974), and West Virginia (Maurer and others 1981).

[b] South of Mexico to South America.

Fragmentation of nesting habitat—The effects of forest fragmentation result from many factors, such as the size, dispersion, and structure of the patches, and the natural history characteristics of the birds. The intent here is merely to mention the problem that fragmentation may have on birds in Douglas-fir forests. Birds that have large home ranges or those that are found only in the forest interior are those most affected by fragmentation (Martin 1981, Robbins 1980, Robbins and others 1989, Rosenberg and Raphael 1986, Whitcomb and others 1981). The Douglas-fir forests of the southern Washington Cascades are becoming increasingly fragmented (Morrison 1988). New studies similar to that conducted by Robbins and others (1989) are now needed to understand the relation of patch size and shape to the population size and persistence of birds.

The combined effects of forest fragmentation and simplification of forest structure through even-aged management will probably result in substantial declines in some bird species. Species or groups likely to show declines are all cavity-nesting birds (woodpeckers, nuthatches, chickadees, brown creeper, small owls) and species that are closely associated with the forest floor (winter wren, thrushes) or vertical habitat layering (warblers, chestnut-backed chickadee).

Fragmentation and changes in winter habitat—Reductions in breeding bird populations may not result from changes in the nesting habitat. Factors operating outside the nesting season may have consequences during later nesting seasons. Recently, ecologists have become alarmed at the amount of habitat being lost through harvesting of neotropical forests (Powell and Rappole 1986), although many temperate long-distance migrants reach maximum abundance in tropical second growth (Hutto 1989). A substantial percentage (38-44 percent) of North American nesting birds spend the winter in neotropical forests (table 11). Typical neotropical migrants include the flycatchers, swallows, thrushes, tanagers, vireos, and many species of warblers. The percentage of neotropical migrants in Douglas-fir forests is relatively low compared with other regions of the United States, and a relatively high percentage of permanent residents live in the Cascades Douglas-fir forests (table 11).

One obvious consequence of the large percentage of permanent residents in the Pacific Northwest is the importance of winter habitat. The effects of fragmentation and simplification of forest structure will not only affect breeding birds but also the permanent residents. The ecological bottleneck that so often affects northern temperate wildlife may be more severe if the forest lacks suitable resources to allow birds to survive the winter. Changes in forest structure and reduction in patch (stand) size would be expected to reduce the winter carrying capacity of forests. Previous studies (Manuwal and Huff 1987; Huff and others, this volume) suggest that old-growth forests, with their complex canopy structure and rich tree-species diversity, provide substantially better winter habitat for many bird species than do younger stands. Old growth may actually provide habitat in which a much larger percentage of birds survive the winter than survive in younger stands and therefore are able to replenish stands unable to support winter populations at numbers adequate to maintain the resident population. Studies of the response of birds to intensively managed Douglas-fir forests are now urgently needed, so that new silvicultural prescriptions can be developed to reduce the loss of birds from massive changes in forest structure. More information is particularly needed on habitat needs of permanent residents in the Pacific Northwest.

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Appendix

Table 12-Stem count variables for bird and vegetation correlation and regression analyses

Code	Description
Coarse variables	
LT4	Live trees >l00 cm d.b.h.
TSTP	Stumps and stubs (snags <5 m tall, >l0 cm d.b.h.)
SS	AU small snags l0-19 cm d.b.h.
Species-specific variables	
DFD13	Live Douglas-fir l-100 cm d.b.h.
WHD12	Live western hemlock l-50 cm d.b.h.
WHD3	Live western hemlock 51-100 cm d.b.h.
RCD12	Live western redcedar l-50 cm d.b.h.
RCD3	Live western redcedar 51-100 cm d.b.h.
ABD13	Live true firs l-100 cm d.b.h.
CPD13	Live other conifers l-100 cm d.b.h.
VMD12	Live vine maple l-50 cm d.b.h.
HDD13	Live other hardwoods l-100 cm d.b.h.
DFS34	All Douglas-fir snags 20-49 cm d.b.h.
DFS5	Hard Douglas-fir snags ≥ 50 cm d.b.h.
DFS6	Soft Douglas-fir snags ≥ 50 cm d.b.h.
WHS34	All western hemlock snags 20-49 cm d.b.h.
WHS56	All western hemlock snags ≥ 50 cm d.b.h.
RCS34	All western redcedar snags 20-49 cm d.b.h.
RCS56	All western redcedar snags ≥ 50 cm d.b.h.
ABS34	All true fir snags 20-49 cm d.b.h.
WPS34	All western white pine snags 20-49 cm d.b.h.
WPS56	All western white pine snags 550 cm d.b.h.

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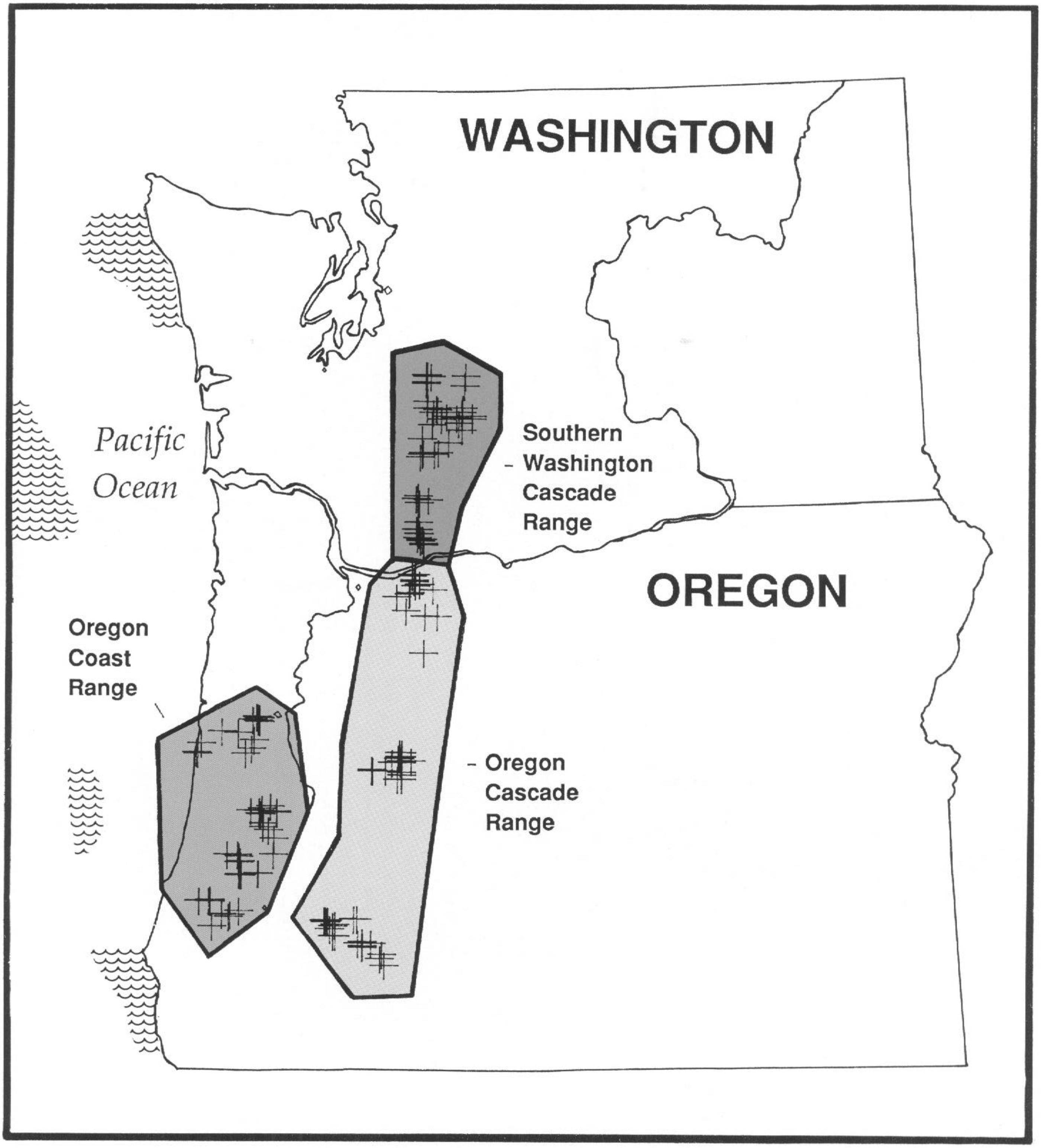

Location of study sites within the three physiographic provinces.

Regional Patterns of Diurnal Breeding Bird Communities in Oregon and Washington

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Abstract

Breeding bird communities surveyed in 132 natural fire-regenerated Douglas-fir forest stands were examined for differences in species richness and abundance among forest stand age-classes: young, 35 to 79 years old, n = 27; mature, 80 to 190 years old, n = 37; and old-growth, 200 to 730 years old, n = 68, and among physiographic provinces: Oregon Coast Range (1985 and 1986, n = 45); Oregon Cascade Range, 1984 and 1985, n = 48 and 15, respectively; and southern Washington Cascade Range, 1984 and 1985, n = 39. Stands were surveyed six times each spring using 8-minute counts at 12 counting stations spaced 150 or 100 m apart. More than 115,000 birds were detected. We counted 41 species that regularly used Douglas-fir forests >40 years old, after the exclusion of raptorial, nocturnal, and poorly detected species. The most widespread and abundant species were chestnut-backed chickadee, western flycatcher, winter wren, hermit and Townsend's warblers, and golden-crowned kinglet. All bird species significantly more abundant in forests >80 years old in at least two of three regions at $P \leq 0.10$ were hole or bark nesters: red-breasted sapsucker, brown creeper, chestnut-backed chickadee, red-breasted nuthatch, and Vaux's swift.

Results suggested that patterns of bird abundance were regionally distinct, even though the study design differed between regions. Total bird abundance, species richness, and bird abundance in four spatial-foraging guilds (aerial, bark, canopy, and understory) were significantly higher in the Oregon Coast Ranges than in the southern Washington or Oregon Cascade Range. Aerial and bark guilds showed strong differences among ageclasses: the aerial guild reached its highest abundance in young and old growth and the bark guild was least abundant in young and highest in old growth. Vegetation characteristics used for multiple linear regression models predicted only a small proportion of the variance in bird abundance.

Introduction

Douglas-fir is the primary tree species of the densely forested slopes of western Oregon and Washington. Old-growth Douglas-fir forests (>200 years old), which once covered large land areas throughout the region (for example, Dodwell and Rixon 1902), are rapidly becoming scarce (Marcot and others, this volume). Most old-growth Douglas-fir forests have been cut on private and industrial holdings; consequently, those that remain are almost exclusively on Federal lands (DeBell and Franklin 1987, Franklin and others 1981).

To meet Federal laws, land managers must decide which old-growth forests to cut and which to preserve, yet the amount of information available to make these decisions as they relate to wildlife populations is often inadequate (Carey 1984).

Converting large forested regions from older to younger age-classes poses specific problems for interpreting and predicting the relation of birds to their habitats. Difficulties arise from, for example, high variability in interregional habitat characteristics (Hamel and others 1986) and scale of measurement, which influences how habitat occupancy by birds is interpreted (Wiens 1981a, Wiens and Rotenberry 1981b). Bird movements resulting from rapid liquidation of old-growth forests, exceeding 20,000 ha per year on Federal land in the Pacific Northwest (Torrence 1986), are poorly understood and could be misleading if bird dispersal from potentially optimal into suboptimal habitat *(sensu* Pulliam 1988) is widespread.

In Finland, where bird populations have been surveyed relative to forestry practices over several decades, researchers found that, in general, species associated with edge and brushy habitats have increased proportionally with the creation of forest openings from cutting (see Stjernberg 1979), but other species closely associated with older coniferous forests have decreased (see Jarvinen and Vaisanen 1978). Similarly, birds associated with mature and old-growth forests in northwestern California have likely declined from the presettlement period to the present because of extensive logging, and especially over the last 20 to 30 years, but ground-brush-foraging birds have increased substantially during the same period (Raphael and others 1988). Species projected to be most significantly affected by rapid and widespread changes in forest composition and structure are those with relatively restricted ranges and habitat requirements (Raphael and others 1988).

In Pacific Northwest forests, 58 percent of the vertebrate fauna consists of bird species (Harris 1984), but, only a few of them regularly use the interior of coniferous forests (Carey 1988, Wiens 1975). Even though birds strongly associated with old-growth Douglas-fir forests seem to be many *(sensu* Brown 1985), the spotted owl and Vaux's swift are suggested as being the most closely associated (Carey 1985, Lundquist 1988, Manuwal and Huff 1987, Meslow and others 1981).

We compared bird species richness and abundance along a forest sere within a large geographic area, throughout the Oregon Coast Ranges and the Oregon and Washington Cascade Ranges, to determine which species consistently are most abundant in old-growth Douglas-fir forests; if old-growth forests have distinct faunal associations; which abundance trends are consistently related to forest age between and within the study regions; and which vegetative characteristics help to explain the patterns of bird abundance among the study regions. We examined only bird communities of unmanaged, fire-regenerated stands. Wherever plausible, we speculated on how our results might be applied to forested areas intensively managed for timber production.

Methods

Study Area

Breeding bird communities were surveyed in Douglas-fir stands of three physiographic provinces, the southern Washington Cascade Range, Oregon Cascade Range, and Oregon Coast Ranges (see frontispiece). The three provinces were divided into subprovinces: three each in the southern Washington and Oregon Cascade Range and two in the Oregon Coast Ranges. A subprovince consisted of study stands within about 60 km of one another and isolated from other subprovinces by varying latitude (see frontispiece). Stands were selected to encompass the range of variation within Douglas-fir forests of each subprovince (table 1).

A study stand was defined as an area relatively homogeneous in structure, disturbance history, vegetational composition, physiography, and soil. Unmanaged, naturally regenerated stands were selected to represent a chronosequence of forest development (young, 35 to 79 years; mature, 80 to 190; and old-growth, 200 to about 730 years). Stand elevation was restricted to the range in which Douglas-fir was a dominant overstory species (see Franklin and Dyrness 1973) and varied substantially within and among provinces (see frontispiece). Although the experimental design called for stands of. at least 40 ha to avoid edge effects, not all stands in the Oregon Coast Ranges met this criterion because few large tracts of unmanaged forest remained. Median size of study stands in the Oregon Coast Ranges was 29 ha, ranging from 14 to 62 ha (Carey and others, this volume).

Avian surveys were done in 151 Douglas-fir stands; 19 stands were excluded from our analysis because they exhibited moisture conditions (either extremely wet or extremely dry) that were outside the range of the young and mature stands sampled. Of the 132 stands suitable for bird community analysis, 39 were in the southern Washington Cascades, 48 in the Oregon Cascades, and 45 in the Oregon Coast Ranges. Because no stand vegetational data were collected from two mature stands in the Oregon Cascades, only 130 stands were analyzed.

Rugged mountains, steep valleys, and high annual precipitation (800 to 3000 mm), which increases rapidly from low to high elevations, characterize the three provinces (Franklin and Dyrness 1973; Spies and Franklin, this volume). Although

Table 1—Means and range (in parentheses) of environmental variables for young, mature, and old-growth stands sampled in 3 physiographic provinces (n = sample size)

Variable	Young n = 8	Mature n = 10	Old growth n = 25	All stands n = 43
Oregon Coast Ranges:				
Latitude	43.7 (43.2-44.3)	44.0 (43.0-44.5)	43.7 (43.1-44.5)	43.8 (43.0-44.5)
Longitude	123.7 (123.5-124.0)	123.7 (123.3-124.1)	123.6 (123.3-124.1)	123.6 (123.3-124.1)
Elevation (m)	307.0 (86-473)	487.0 (260-1022)	401.0 (153-909)	403.0 (86-1022)
Percent slope	48.0 (16-73)	50.0 (26-75)	48.0 (19-82)	48.0 (16-82)
Aspect[a]	.96 (.05-1.67)	.84 (.04-1.71)	1.00 (.10-1.89)	.95 (.04-1.89)
Stand age (yr)	59.0 (40-72)	102.0 (80-120)	314.0 (200-525)	213.0 (40-525)
	n = 9	n = 17	n = 22	n = 48
Oregon Cascades:				
Latitude	44.2 (42.8-45.5)	43.9 (42.9-45.4)	43.8 (42.8-45.6)	43.9 (42.8-45.6)
Longitude	122.3 (121.8-122.8)	122.4 (121.9-122.9)	122.4 (122.1-122.9)	122.4 (121.8-122.9)
Elevation (m)	920.0 (520-1428)	812.0 (326-1478)	848.0 (437-1284)	849.0 (326-1278)
Percent slope	42.0 (16-71)	40.0 (3-90)	44.0 (15-80)	43.0 (3-90)
Aspect[a]	1.18 (.07-1.91)	.70 (.03-1.84)	.93 (.02-1.95)	.90 (.02-1.95)
Stand age (yr)	65.0 (35-79)	108.0 (84-180)	355.0 (200-500)	213.0 (35-500)
	n = 10	n = 10	n = 19	n = 39
Southern Washington Cascades:				
Latitude	46.4 (45.8-47.0)	46.3 (45.9-46.8)	46.3 (45.8-47.0)	46.3 (45.8-47.0)
Longitude	121.9 (121.5-123.0)	121.9 (121.7-122.0)	121.8 (121.5-122.0)	121.9 (121.5-123.0)
Elevation (m)	728.0 (476-1168)	749.0 (483-1124)	759.0 (420-1049)	748.0 (420-1168)
Percent slope	41.0 (13-66)	46.0 (19-73)	35.0 (9-80)	39.0 (9-80)
Aspect[a]	1.27 (.29-1.97)	1.02 (.08-1.96)	.89 (.02-1.99)	1.02 (.02-1.99)
Stand age (yr)	67.0 (55-75)	127.0 (80-190)	418.0 (210-700)	253.0 (55-700)

[a] Transformed aspect = cosine (aspect - 45 degrees) + 1.

Douglas-fir dominates the study region, the climax species are western hemlock and Pacific silver fir (Spies, this volume). Forests begin displaying old-growth characteristics at about 200 years, yet rarely approach climax because catastrophic fires occur before shade-tolerant species completely replace the long-lived Douglas-firs (Franklin and Spies 1984, Franklin and others 1981).

Sampling Methods

Birds—Birds were surveyed in each province for two consecutive breeding seasons: 1984 and 1985 in the southern Washington Cascades (Manuwal, this volume), 1984 and 1985 (only 32 percent of the 1984 stands in 1985) in the Oregon Cascades (Gilbert and Allwine, this volume b), and 1985 and 1986 in the Oregon Coast Ranges (Carey and others, this volume). Birds were sampled by using the variable circular plot technique (Reynolds and others 1980). Twelve counting stations were spaced at 150-m intervals in a rectangular pattern placed no closer than 75 m from the edge of the stand. Stands were surveyed six times from April 26 to July 7. Because the Coast Ranges stands were small, the spacing between stations was reduced to 100 m. Six stands in the Oregon Coast Ranges had fewer than 12 stations: one stand with 7 stations, one stand with 10 stations, and three stands with 11 stations. Additional surveys were done to make the total sample time at these six stands comparable to all other stands. All surveys began no later than 15 minutes after sunrise and were completed within 4 hours. All birds seen or heard during each 8-minute count at each counting station were recorded. Field observers, trained to estimate horizontal distances, recorded horizontal distance for each detection.

Vegetation—Vegetation data on snags, logs, live trees, shrubs, and herbaceous vegetation were collected in each stand in five nested, systematically established plots (Spies and Franklin, this volume; Spies and others 1988). Our objective in using this data set was to quantitatively describe the structure and composition of the stand as a whole, rather than specific points associated with the bird counts as reported in this volume by Manuwal, Gilbert and Allwine, and Carey and others.

Sampling Biases

Verner (1985) describes five sources of bias in bird counts: observer, habitat, birds, study design, and weather. During this study, attempts to minimize some of these biases included using trained observers, avoiding weather conditions that would interfere with locating and identifying birds, spacing counts throughout the breeding season, and, where possible, rotating observers in each stand. Robbins and Stallcup (1981) suggested rotating observers among plots to help compensate for observer variability. Observers were rotated in all stands surveyed in the Oregon Cascade and Coast Ranges, but logistical problems prevented rotation in more than half of the stands in the southern Washington Cascades. Over all provinces, observers were rotated in 77 percent of the stands surveyed. In general, different observers were used between survey years.

Only birds detected within 50 m of the counting station-representing half of the shortest distance between the stations-were used in the main analysis. Detection distances were truncated so that the ares searched would be comparable among stands, and to minimize biases associated with counting the same birds twice. Additionally, we believe that truncating detection at 50 m should help to reduce other biases inherent in bird surveys. Richards (1981) describes three environmental acoustic factors that are distance- and frequency-dependent, and affect the ability of an observer to detect and accurately identify a singing bird in forested habitats: attenuation, the decrease in intensity of sound with distance; random fluctuations in the received level of sound resulting from wind and thermal conditions; and scattering and reverberation of sound by trees, foliage, and the ground. Selecting trained observers can minimize these factors (Richards 1981), but reducing the distance searched further minimizes them as well as differences among observers.

To evaluate whether detectability of bird species changed with location, we compared mean detection distance (60 m radius of the counting station) within each forest age-class among the three physiographic provinces by the Kruskal-Wallis procedure (Zar 1984). We selected 10 common species to evaluate the relative magnitude of differences among the three provinces (table 2). Within young stands, few strong differences were found among the provinces. More strong differences among provinces were found within mature and old-growth stands, as indicated by the P-values, but the mean values were well within the 50-m cut distance and differences among mean values were generally small (<5 m).

Table 2-For each forest age-class, mean detection distance for 10 common bird species and significance level of Kruskal-Wallis comparisons among 3 provinces

	Mean detection distance (m)			
Bird species	Oregon Coast Ranges	Oregon Cascades	Southern Washington Cascades	*P-value*
Young forests:				
Brown creeper	24.0	20.8	24.1	0.5541
Chestnut-backed chickadee	22.9	24.0	24.1	.5619
Dark-eyed junco	21.4	27.6	27.2	.7819
Golden-crowned kinglet	22.0	21.0	22.7	.7143
Hermit thrush	32.6	31.8	32.0	.8135
Hermit/Townsend's warbler	34.2	32.5	34.1	.3142
Red-breasted nuthatch	35.0	34.3	39.6	.0067
Varied thrush	34.8	35.7	31.7	.2018
Western flycatcher	30.1	32.1	31.5	.6390
Winter wren	29.7	29.5	30.8	.4933
Mature forests:				
Brown creeper	25.4	24.4	29.0	.1050
Chestnut-backed chickadee	23.0	23.6	29.2	.0039
Dark-eyed junco	30.6	28.8	26.2	.4058
Golden-crowned kinglet	22.6	21.5	27.4	.0015
Hermit thrush	36.4	27.8	33.0	.0718
Hermit/Townsend's warbler	35.7	33.8	35.1	.1938
Red-breasted nuthatch	35.6	32.0	39.5	.0007
Varied thrush	34.0	33.6	35.7	.6007
Western flycatcher	30.4	32.3	32.8	.4485
Winter wren	30.3	30.8	35.4	.0059
Old-growth forests:				
Brown creeper	24.3	23.1	28.7	.0011
Chesmut-backed chickadee	22.0	23.4	27.3	.0003
Dark-eyed junco	29.4	27.8	26.7	.1880
Golden-crowned kinglet	21.4	21.7	25.6	.0027
Hermit thrush	31.9	34.6	31.5	.4478
Hermit/Townsend's warbler	35.5	33.0	36.4	.0002
Red-breasted nuthatch	37.7	32.3	36.3	.0000
Varied thrush	35.7	32.8	34.1	.1099
Western flycatcher	28.5	29.4	32.8	.0000
Winter wren	29.4	30.9	32.5	.0002

Major biases in the sample design and data collection occurred during this study. First, elevation was not controlled for when study stands were selected; consequently, the degree and magnitude of variation is different within and among provinces. The three provinces were not surveyed during the same two sample years, and in no year were all stands in all provinces surveyed. Also, some stands were surveyed in only one sample year instead of two. The data from these stands represent a mean based on one sample year, whereas data from the remaining stands represent a mean of two sample years. Five stands in the Oregon Coast Ranges had fewer than 12 counting stations (one stand had 7, one had 10, and three had 11 stations). Analyses were conducted to evaluate the effect of fewer counting stations, and differences with and without the five stands were negligible. Finally, observers were different among the three provinces and generally

Continue

between the two sample years. We did not evaluate observer bias directly because it is evaluated and discussed elsewhere in this volume (see Manuwal, Gilbert and Allwine b, and Carey and others). Potential effects of sampling biases on the results are evaluated in the discussion.

Analytical Methods

This study was designed to be exploratory, thus no a priori hypotheses were identified. In light of this objective, the statistical tests were used to elucidate trends and consistent patterns of **variation** in the data rather than for testing specific hypotheses. We report exact P-values to evaluate the strength of the patterns, except where we needed to define a level of significance to proceed with further analyses. The exceptions were using a P-value of <O.05 to indicate a significant main effect or an interaction between main effects of two-way analysis of variance before we proceeded with appropriate planned comparisons, and using a P-value of <0.151 with the Kruskal-Wallis procedure to identify which bird species showed strong differences in abundance among forest age-classes in at least two of the three provinces.

Bird abundance was calculated as the number of birds detected per survey per stand for each of the two sample years, where one survey day equals 12 counting stations x 8 minutes. We calculated species richness as the number of unique species detected in a stand over all surveys during one year. Only detections estimated to be ≤ 50 m from the counting station were used. Nocturnal and raptor species were poorly sampled by the counting technique and were not included in the analysis. To remove vagrants and species detected in few stands, we used two criteria: a species was included in the count for a particular stand if it was detected during at least two surveys in that stand, and, to be included, a species had to be detected in >8 percent of the stands within a subprovince. Thus, rare species (that is, species detected in low numbers) were included in the analysis if detection criteria were met at the stand and subprovince level. This procedure removed species that commonly occurred in habitats substantially different from ones dominated by Douglas-fir (for example, red-winged blackbird, northern oriole, belted kingfisher, mourning dove). We did not distinguish between hermit and Townsend’s warblers (hereafter, hermit warbler) or between dusky and Hammond’s flycatchers (hereafter, Empidonax flycatchers) during our analyses because these species were difficult to distinguish in the field.

Because our primary objective was to evaluate regional patterns of species composition and abundance, and not yearly variation, we used the mean of the two sample years in our analysis. Thus, mean bird species richness and mean abundance values represent the average of two sample years. Mean abundance values were calculated for individual bird species, all species combined, all resident species, all migrant species, and for each of four spatial-foraging guilds: bark, aerial, canopy, and understory foragers (see appendix table 8 for list of species associated with each group).

Table W-values for 3 planned comparisons when limiting experimental error rates to 5, 10, 15, and 20 percent

Experimental error rate (percent)	P-value for 3 planned comparisons’
5	0.017
10	.035
15	.053
20	.072

[a] a' = l- (1-a)l/K, where a’ = significance level of each individual comparison for an experimental error rate of a, and *K* = the number of comparisons (Sokal and Rohlf 1981).

Province and age comparisons-To evaluate whether bird abundance or number of species differed among forest age-classes, species richness values and mean abundance values for all species combined, residents, migrants, and the four foraging guilds were analyzed by a two-way analysis of variance (ANOVA) for unbalanced designs (Wilkinson 1988). For all ANOVA’s, stand age (that is, young, mature, old-growth) and province (that is, southern Washington Cascades, Oregon Cascades, Oregon Coast Ranges) were used as the independent factors (the main effects). Normality and homogeneity of variance of richness and abundance values were improved by performing a square-root transformation before the ANOVA.

Multiple comparisons were planned; thus, we used F-tests to determine differences among age-classes and among provinces (Sokal and Rohlf 1981). Because the planned comparisons were nonorthogonal (that is, lacked independence), we used the Bonferroni procedure (Klockars and Sax 1986, Wilkinson 1988) to reduce the probability of interpreting a difference as related to ages and provinces when in fact the patterns were a result of random variation. Given that the interaction between the main effects was not significant, we tested three planned comparisons per main effect (Sokal and Rohlf 1981). Instead of setting a specific experimental error at 5 percent, for example, we reported the exact P-value for each comparison, and provide a list of what the acceptable P-values are for experimental errors of 5, 10, and 15 percent (table 3).

Abundance patterns of individual bird species-Species were categorized into four groups based on general knowledge of territory size, percentage of all detections that were ≤ 50 m versus >50 m from the counting station, and consistency of detection within a stand (see appendix table 8).

Group 1 species were detected more often 150 m of a counting station and, typically, were the ones detected most consistently and often on the surveys. To determine their abundance, we used all detections 150 m from a counting station, the same criteria used for calculating abundance throughout this study. Species included in groups 2 and 3 were detected more often >50 m from a counting station and detected less often than group 1 species. Group 3 species were more difficult to detect than group 2 species. Group 3 species have large territories and were detected less consistently within a stand. If single occurrences accounted for >30 percent of the stands in which a species was detected, then that species was put in group 3. Detections ≤ 150 m from a counting station were used for calculating abundance of both group 2 and 3 species. Group 2 species had to be detected ≥ 2 times within a stand but group 3 species only once. If a species was detected in <3 percent of the stand counts, it was placed into group 4 and no abundance was calculated. We gauged our interpretation of the results according to the reliability of the count data. We assumed group 1 was the most reliable abundance data and group 3 the least.

Within each province, mean abundance of individual species was compared between stand age-classes by the Kruskal-Wallis procedure. Experimental error rates were evaluated by comparing the number of significant comparisons to the total number of comparisons made. Of all the species evaluated, 16 had P-values that were <0.151 in at least two of the three provinces. Because of their strong trends among forest age-classes, these species were discussed in further detail.

Ordination of bird data-We used detrended correspondence analysis (DECORANA or DCA), an ordination procedure, to describe differences in bird communities of the sampled stands. DECORANA uses species composition and abundance data to determine a sample’s position in relation to all **other** samples (Gauch 1982, Hill 1979a). Thus, samples (that is, stands) that are similar are close together and dissimilar samples are far apart To simplify interpretation, we removed the effects of abundance differences between stands and provinces by relativizing the data, so that species abundances totaled 100 in each stand (Mohler 1987). We plotted the position of each stand using DECORANA scores for the first and second axes, where the scores represented the position of a stand along some identifiable environmental gradients (that is, each axis represents an environmental gradient). Median scores for age-class and province categories were calculated, and the position of each age-class and province category was plotted such that the boundaries included at least 90 percent of the stands. Spearman rank (r_s) correlations and scatterplots were used to evaluate relations between all DECORANA scores for the first and second axes, and environmental (elevation, latitude, stand age) as well as biological (species richness, bird abundances) variables.

Relation to habitat-Of the vegetation and site characteristic variables measured by Spies, we selected 143 as potentially important to our analysis. Variables selected included 58 live-tree, 13 stand-condition, 32 snag, 25 log, and 15 understory-plant variables (see appendix table 9). Each variable was tested for normality by the Kolmogorov-Smimov test (Zar 1984), and, if necessary and useful, transformations were applied. No one transformation worked well on all variables; thus, we used three: log (X + l), square root (X + 0.375), and arcsine (square root X) on some of the percentage variables (see appendix table 9).

We used all possible subsets multiple regression (Dixon 1985) to evaluate which vegetation variables explained the most variation in species richness, total bird abundance, abundance of resident and migrant species, and abundance of each of the four foraging guilds. The analysis was approached from two levels. Multiple regressions were performed using data from all three provinces together, and then on each province individually. Pearson correlations of vegetation and bird abundance variables were done as a first step before regression analysis. This analysis determined which variables were most associated with bird abundance; variable selection was based on strength of the correlations with dependent variables; and the correlations were generally low so that any variable with an absolute value >0.200 was considered; low intercorrelations with other vegetation variables; and ease of measurement and applicability to management decisions. Vegetation variables that were intercorrelated but were highly correlated with the dependent variable were not removed at this stage because of their potential importance to the total equation. No intercorrelated variables were selected in the final regression equations.

The ‘best’ multiple regression equation was selected from all possible subsets by evaluating which group of variables explained the most variance (adjusted R), low inter-correlation among vegetation variables, and ease of interpretation. The number of independent variables in an equation (see Johnson 1981) was limited to no more than four for the within-province regressions, and no more than six for the all-stands regressions.

Results

Over 115,000 birds were detected during more than 16,000 station counts in the three physiographic provinces. Ninety-three bird species were detected. We detected 41 species that regularly used’ Douglas-fir forests >40 years old, after the

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[1] This term refers to the analysis criteria established for this study: bird species within a province detected ≤ 50 m from a counting station on ≥ 2 sample days per stand in >3 stands (>8 percent).

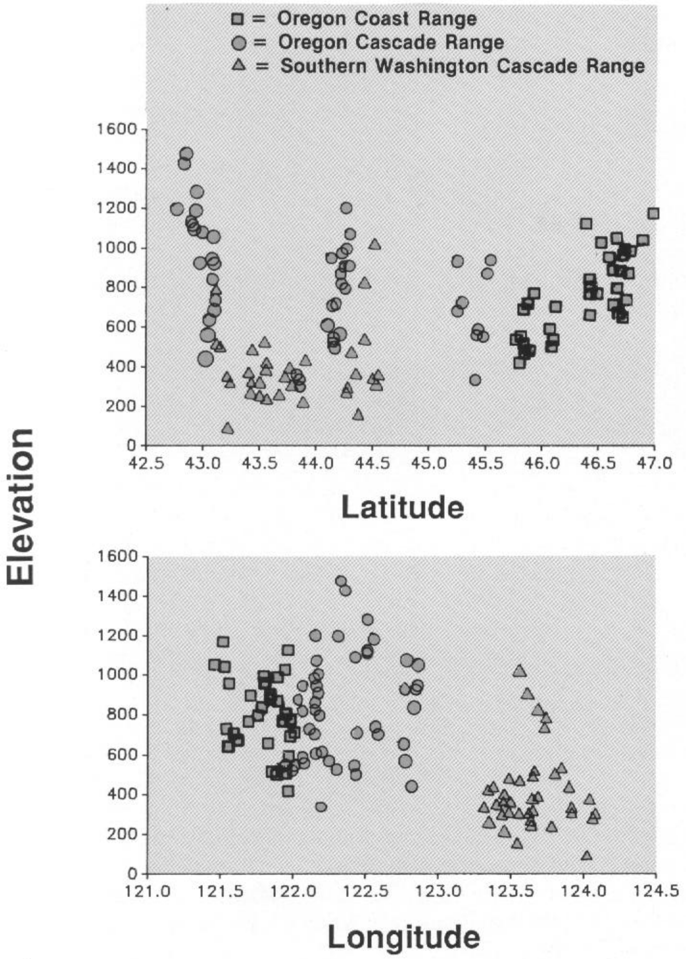


Figure 1—Scatterplots of latitude, longitude, and elevation by province.

exclusion of raptorial, nocturnal, and poorly detected species. Of these 41 species, 56 percent regularly used all three provinces, and 73 percent regularly used two provinces. Six species regularly used only the Oregon Coast Range: the black-capped chickadee, wrentit, purple finch, rufous-sided towhee, song sparrow, and orange-crowned warbler. The Townsend's solitaire regularly used only the Oregon Cascades. The red crossbill and Vaux's swift regularly used only the southern Washington Cascades.

Elevation, Latitude, and Longitude

Stand elevation varied with latitude and longitude within and between provinces (fig. 1). Study stands low and high in elevation tended to be in the Oregon Coast Ranges and Oregon Cascades, respectively. Total bird abundance was correlated negatively with elevation and latitude and correlated positively with longitude (fig. 2).

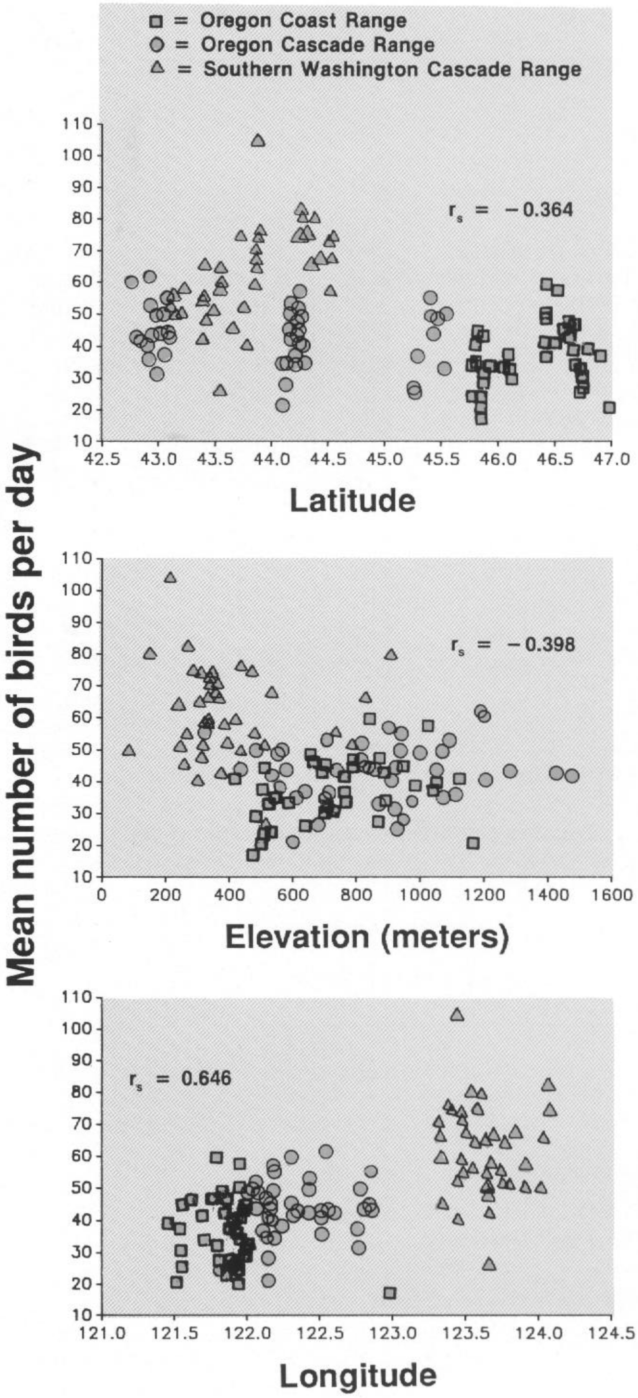


Figure 2—Scatterplots and Spearman rank correlation coefficients of latitude, longitude, and elevation with total bird abundance.

Table 4—The percentage of young, mature, and old-growth stands in which 16 species were detected that showed abundance differences in at least 2 of the 3 provinces

Bird species	Oregon Coast Ranges			Oregon Cascades			Southern Washington Cascades		
	Young	Mature	Old growth	Young	Mature	Old growth	Young	Mature	Old-growth
Group 1:[a]									
Black-throated gray warbler	63	20	37	33	24	41	50	20	5
Brown creeper	100	100	96	100	100	100	90	100	100
Chestnut-backed chickadee	100	100	100	100	100	100	100	100	100
Gray jay	50	40	19	33	41	55	80	60	95
Hermit/Townsend's warbler	100	100	100	100	100	100	100	100	100
Red-breasted nuthatch	88	90	96	78	71	100	100	80	100
Western flycatcher	100	100	100	100	82	100	90	90	100
Group 2:									
American robin	100	100	74	89	82	59	80	70	53
Evening grosbeak	75	90	37	67	65	36	100	90	95
Hairy woodpecker	75	80	93	33	65	68	70	80	84
Hermit thrush	88	60	78	100	76	95	100	80	95
Steller's jay	100	100	100	78	100	100	80	90	84
Group 3:									
Northern flicker	50	70	93	78	76	82	80	70	84
Pileated woodpecker	50	80	96	67	71	91	60	50	84
Red-breasted sapsucker	50	40	89	33	35	68	0	40	58
Vaux's swift	0	0	4	11	12	41	40	60	100

[a] Group 1 refers to species which were evaluated using detections ≤50 m from a count station, species that were detected at least twice in any particular stand and in at least 10 percent of the stands within a subprovince. Group 2 refers to species evaluated using detections ≤150 m from a count station, and a species had to be detected at least twice in any particular stand. Group 3 indicates those species evaluated using detections ≤150 m from a count station even if a species was only detected once.

Table 5—Number and percentage (in parentheses) of bird species with significantly different abundances among age-classes at *P*-values of 0.05, 0.10, 0.15, and 0.20

P-value	Southern Washington Cascades	Oregon Cascades	Oregon Coast Range
0.05	7 (21%)	5 (15%)	18 (51%)
0.10	9 (27%)	7 (21%)	20 (57%)
0.15	14 (42%)	9 (26%)	26 (74%)
0.20	16 (48%)	11 (32%)	26 (74%)
Total number of species[a]	33	34	35

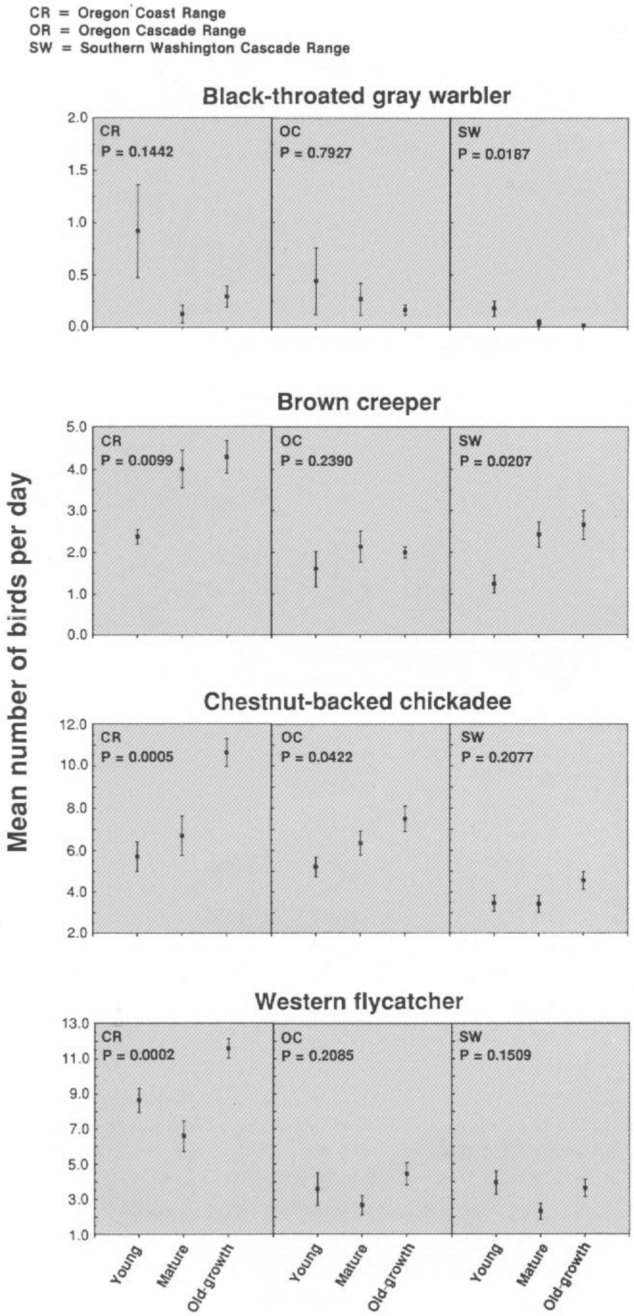
[a] Number of species detected in ≥7 stands within each province.

Abundance Patterns of Individual Bird Species

Chestnut-backed chickadees and hermit warblers, detected in all 132 study stands, and winter wrens, western flycatchers, and golden-crowned kinglets, detected in >95 percent of the study stands, were the most abundant species over all three provinces (table 4).

Bird abundance differences among stand age-classes were detected for 29 species at $P \leq 0.151$. Twice as many species had differences in abundance at $P < 0.050$ among stand age-classes in the Oregon Coast Ranges than in the southern Washington Cascades or Oregon Cascades (table 5).

Sixteen species showed abundance differences in at least two of the three provinces at $P \leq 0.151$ (figs. 3-5, table 4), yet despite the large sample size, patterns were not similar for any species in all three provinces. Abundance of all sixteen species, except Vaux's swift, showed age-class differences in the Oregon Coast Ranges. Six hole nesters—the chestnut-backed chickadee, red-breasted nuthatch, hairy woodpecker, pileated woodpecker, red-breasted sapsucker, and Vaux's swift—were most abundant in old-growth stands in at least two provinces (figs. 3-5). Brown creeper abundance was highest in old-growth and mature stands (fig. 3), but western flycatcher (fig. 3) and hermit thrush (fig. 4) were most abundant in old-growth and young stands. Black-throated gray and hermit warblers tended to be most abundant in young stands (fig. 3). Evening grosbeak and American robin abundance was highest in young and mature stands (fig. 4). No clear pattern was observed for gray jay, Steller's jay, and northern flicker (figs. 3-5). Abundance of only the red-breasted sapsucker differed in all three provinces at $P \leq 0.151$ (fig. 5).



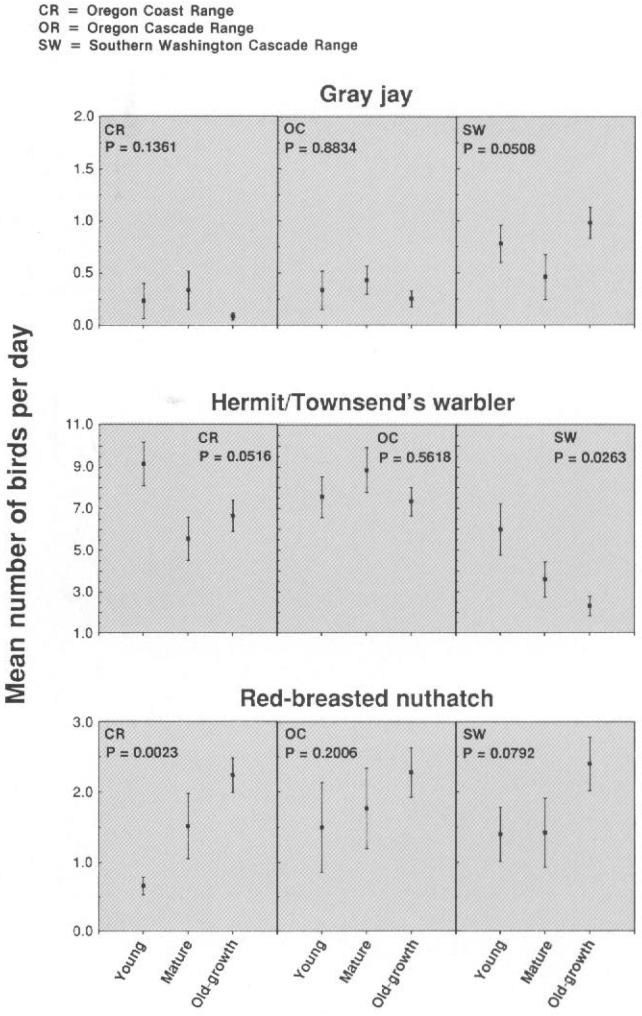


Figure 3—Results of Kruskal-Wallis one-way analyses on mean abundance (using detections ≤50 m from count station) of seven bird species from group 1 by age-classes for each province, with plots of means and standard errors: Oregon Coast Ranges (n = 45), Oregon Cascades (n = 48), and southern Washington Cascades (n = 39); young (n = 27), mature (n = 37), old growth (n = 68).

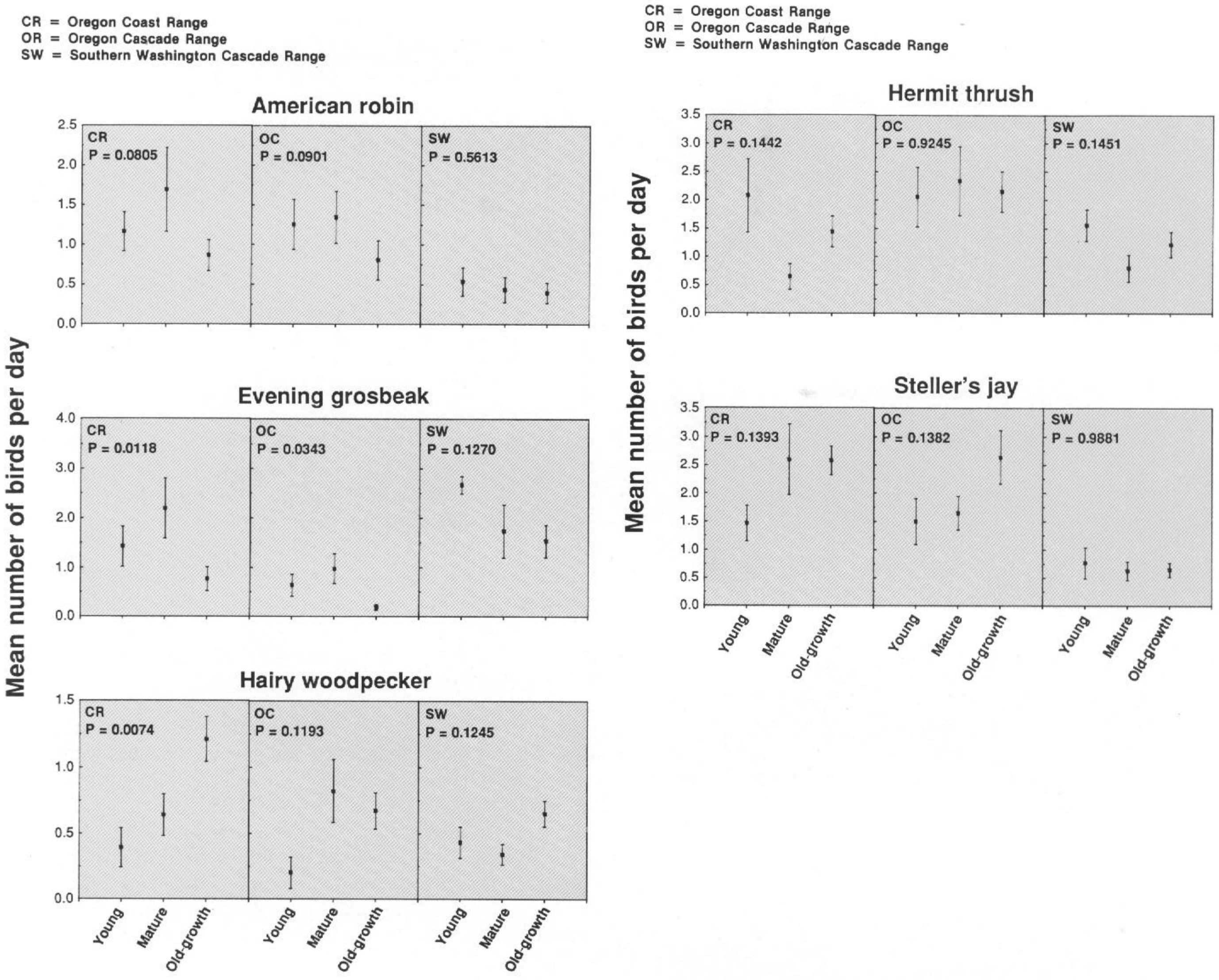
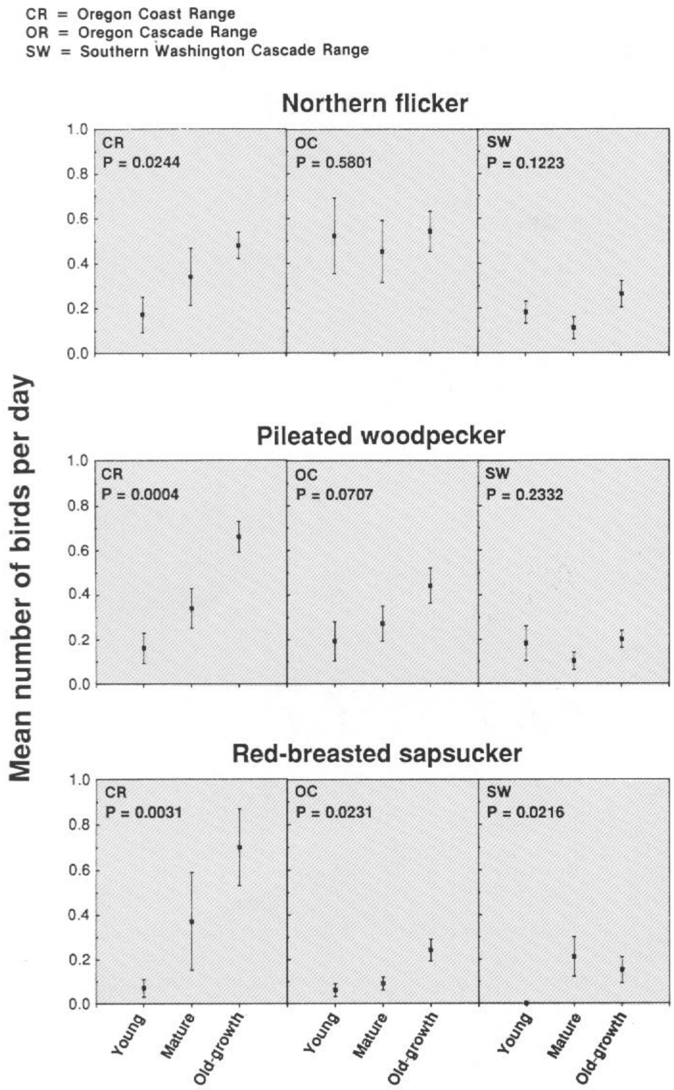


Figure 4—Results of Kruskal-Wallis one-way analyses on mean abundance (using detections ≤150 m from count station, and a species had to be detected ≥2 times in a stand) of five bird species from group 2 by age-classes for each province, and plots of means and standard errors: Oregon Coast Ranges (n = 45), Oregon Cascades (n = 48), southern Washington Cascades (n = 39); young (n = 27), mature (n = 37), old growth (n = 68).



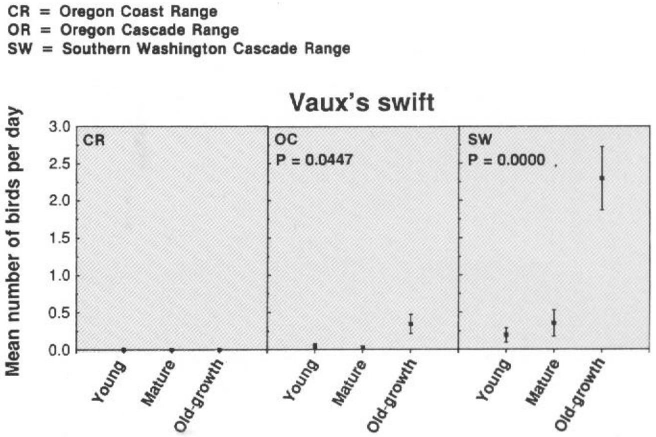


Figure 5—Results of Kruskal-Wallis one-way analyses on mean abundance (using all detections ≤150 m from count station even if a species was only detected once within a stand) of four bird species from group 3 by age-classes for each province, and plots of means and standard errors: Oregon Coast Ranges (n = 45), Oregon Cascades (n = 48), southern Washington Cascades (n = 39); young (n = 27), mature (n = 37), old growth (n = 68).

Province and Age Comparisons

Interaction and main effects—No province x age interaction effects were detected in the eight two-way ANOVA tests at $P < 0.146$, except for the comparison of migrant species ($P = 0.060$) (figs. 6-13). The main effect of province was different in all ANOVA tests at $P < 0.010$. Only half the tests on stand age—namely, total abundance and abundance of resident species, bark foragers, and aerial foragers—were different at $P < 0.050$ (figs. 6-13). All other stand age comparisons were different at $P > 0.250$.

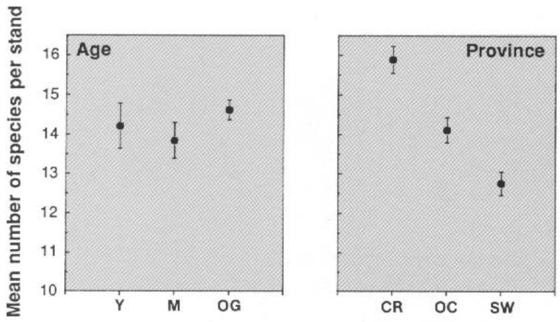
Pairwise comparisons of province—All multiple pairwise comparisons of mean abundance and species richness were higher in the Oregon Coast Ranges than in the Oregon and southern Washington Cascades at $P < 0.050$ (figs. 6-13). Bird abundance was generally higher in the Oregon than southern Washington Cascades, except for resident species and understory foragers, which were more abundant in the southern Washington Cascades, and bark foragers, whose abundance did not differ between the two provinces (figs. 6-13).

Pairwise comparisons of stand age—Stand-age pairwise comparisons showed that total abundance and abundance of resident species and bark foragers were highest in old-growth stands (figs. 7, 8, 10). Abundance of aerial foragers was highest in young and old-growth stands (fig. 11). The only substantial and consistent increase with stand age-class was the abundance of bark foragers (fig. 10). In six of the eight ANOVA comparisons, mean abundance and richness were lowest in mature stands (figs. 6-13). No comparisons were lowest in old growth.

A

Source	Degrees of freedom	Sums of squares	Mean sums of squares	F-ratio	P
Province x age	4	32.545	8.136	1.738	0.146
Age	2	12.999	6.500	1.388	0.253
Province	2	207.959	103.979	22.209	0.000
Error	122	571.183	4.682		

B



C

Source	Degrees of freedom	Mean sums of squares	F-ratio	P
Province:				
CR vs OC	1	75.444	16.114	0.000
CR vs SW	1	206.248	44.053	0.000
OC vs SW	1	39.100	8.351	0.005

Y = Young
M = Mature
OG = Old-growth

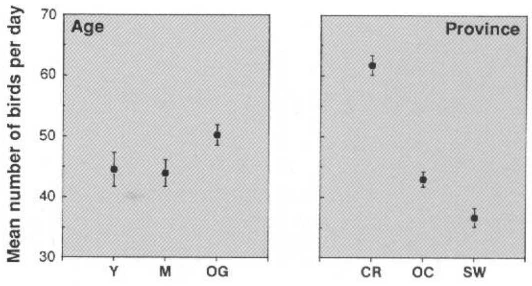
CR = Oregon Coast Range
OC = Oregon Cascade Range
SW = S. Washington Cascade Range

Figure 6—Results of two-way analysis of variance for unbalanced designs on mean bird species richness (A), with means and standard errors for age-classes and provinces (B), and results of planned comparisons using *F* tests (C).

A

Source	Degrees of freedom	Sums of squares	Mean sums of squares	F-ratio	P
Province x age	4	1.721	0.430	0.810	0.521
Age	2	4.031	2.015	3.795	0.025
Province	2	61.322	30.661	57.730	0.000
Error	121	64.264	0.531		

B



C

Source	Degrees of freedom	Mean sums of squares	F-ratio	P
Age:				
Y vs M	1	0.113	0.212	0.646
Y vs OG	1	1.743	3.282	0.073
M vs OG	1	3.437	6.472	0.012
Province:				
CR vs OC	1	31.649	59.592	0.000
CR vs SW	1	57.821	108.870	0.000
OC vs SW	1	5.277	9.937	0.002

Y = Young
M = Mature
OG = Old-growth

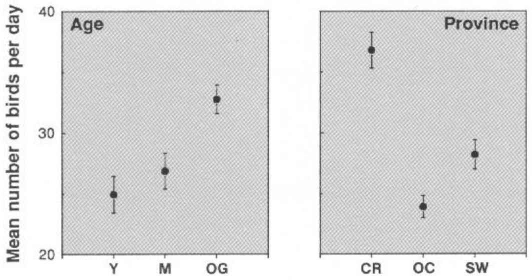
CR = Oregon Coast Range
OC = Oregon Cascade Range
SW = S. Washington Cascade Range

Figure 7—Results of two-way analysis of variance for unbalanced designs on mean total bird abundance (A), with means and standard errors for age-classes and provinces (B), and results of planned comparisons using *F* tests (C).

A

Source	Degrees of freedom	Sums of squares	Mean sums of squares	F-ratio	P
Province x age	4	1.688	0.422	0.850	0.496
Age	2	10.186	5.093	10.265	0.000
Province	2	20.339	10.169	20.496	0.000
Error	122	60.532	0.496		

B



C

Source	Degrees of freedom	Mean sums of squares	F-ratio	P
Age:				
Y vs M	1	0.970	1.955	0.165
Y vs OG	1	8.835	17.807	0.000
M vs OG	1	4.169	8.401	0.004
Province:				
CR vs OC	1	20.119	40.549	0.000
CR vs SW	1	7.699	15.517	0.000
OC vs SW	1	2.635	5.311	0.023

Y = Young
M = Mature
OG = Old-growth

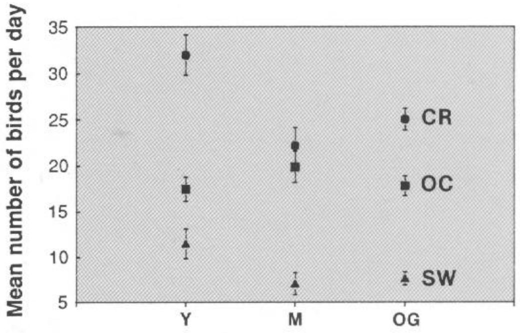
CR = Oregon Coast Range
OC = Oregon Cascade Range
SW = S. Washington Cascade Range

Figure 8—Results of two-way analysis of variance for unbalanced designs on mean abundance of resident species (A), with means and standard errors for age-classes and provinces (B), and results of planned comparisons using *F* tests (C).

A

Source	Degrees of freedom	Sums of squares	Mean sums of squares	F-ratio	P
Province x age	4	4.335	1.084	2.324	0.060
Age	2	4.223	2.112	4.528	0.013
Province	2	89.428	44.714	95.884	0.000
Error	123	57.360	0.466		

B

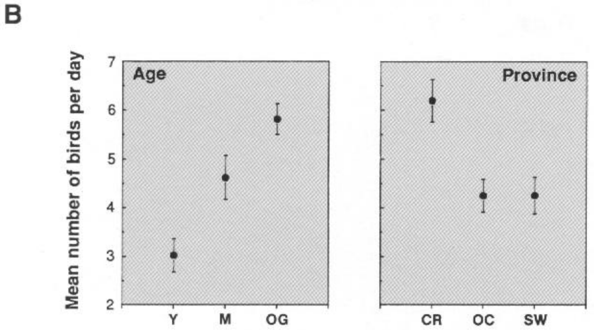


Y = Young
M = Mature
OG = Old-growth
CR = Oregon Coast Range
OC = Oregon Cascade Range
SW = S. Washington Cascade Range

Figure 9—Results of two-way analysis of variance for unbalanced designs on mean abundance of migrant species (A), with means and standard errors for age-classes and provinces (B).

A

Source	Degrees of freedom	Sums of squares	Mean sums of squares	F-ratio	P
Province x age	4	0.416	0.104	0.364	0.834
Age	2	7.169	3.584	12.540	0.000
Province	2	2.598	1.299	4.544	0.013
Error	123	35.156	0.286		



C

Source	Degrees of freedom	Mean sums of squares	F-ratio	P
Age:				
Y vs M	1	2.150	7.521	0.007
Y vs OG	1	7.085	24.788	0.000
M vs OG	1	1.231	4.306	0.040
Province:				
CR vs OC	1	2.057	7.198	0.008
CR vs SW	1	1.911	6.684	0.011
OC vs SW	1	0.000	0.000	0.999

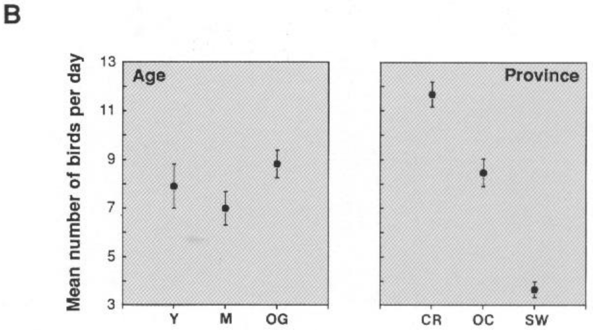
Y = Young
M = Mature
OG = Old-growth

CR = Oregon Coast Range
OC = Oregon Cascade Range
SW = S. Washington Cascade Range

Figure 10—Results of two-way analysis of variance for unbalanced designs on mean abundance of bark foragers (A), with means and standard errors for age-classes and provinces (B), and results of planned comparisons using *F* tests (C).

A

Source	Degrees of freedom	Sums of squares	Mean sums of squares	F-ratio	P
Province x age	4	1.092	0.273	0.804	0.525
Age	2	2.227	1.113	3.280	0.041
Province	2	39.491	19.745	58.180	0.000
Error	121	41.065	0.339		



C

Source	Degrees of freedom	Mean sums of squares	F-ratio	P
Age:				
Y vs M	1	1.259	3.709	0.056
Y vs OG	1	0.001	0.003	0.954
M vs OG	1	2.045	6.025	0.016
Province:				
CR vs OC	1	4.174	12.298	0.001
CR vs SW	1	37.697	111.076	0.000
OC vs SW	1	18.133	53.430	0.000

Y = Young
M = Mature
OG = Old-growth

CR = Oregon Coast Range
OC = Oregon Cascade Range
SW = S. Washington Cascade Range

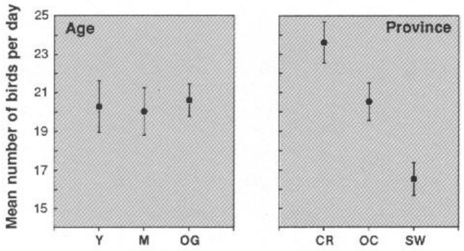
Figure 11—Results of two-way analysis of variance for unbalanced designs on mean abundance of aerial foragers (A), with means and standard errors for age-classes and provinces (B), and results of planned comparisons using *F* tests (C).

Continue

A

Source	Degrees of freedom	Sums of squares	Mean sums of squares	F-ratio	P
Province x age	4	0.886	0.221	0.419	0.795
Age	2	0.159	0.080	0.151	0.860
Province	2	10.109	5.055	9.567	0.000
Error	122	64.457	0.528		

B



C

Source	Degrees of freedom	Mean sums of squares	F-ratio	P
Province:				
CR vs OC	1	2.082	3.940	0.049
CR vs SW	1	10.032	18.988	0.000
OC vs SW	1	3.484	6.594	0.011

Y = Young
M = Mature
OG = Old-growth

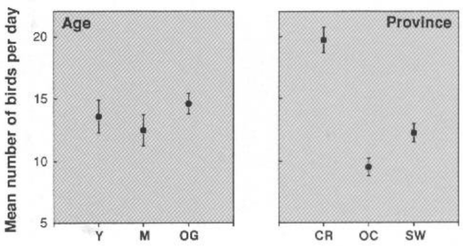
CR = Oregon Coast Range
OC = Oregon Cascade Range
SW = S. Washington Cascade Range

Figure 12—Results of two-way analysis of variance for unbalanced designs on mean abundance of canopy foragers (A), with means and standard errors for age-classes and provinces (B), and results of planned comparisons using *F* tests (C).

A

Source	Degrees of freedom	Sums of squares	Mean sums of squares	F-ratio	P
Province x age	4	2.296	0.574	1.017	0.402
Age	2	0.681	0.340	0.603	0.549
Province	2	38.807	19.404	34.362	0.000
Error	123	69.455	0.565		

B



C

Source	Degrees of freedom	Mean sums of squares	F-ratio	P
Province:				
CR vs OC	1	37.221	65.916	0.000
CR vs SW	1	18.440	32.656	0.000
OC vs SW	1	2.752	4.873	0.029

Y = Young
M = Mature
OG = Old-growth

CR = Oregon Coast Range
OC = Oregon Cascade Range
SW = S. Washington Cascade Range

Figure 13—Results of two-way analysis of variance for unbalanced designs on mean abundance of understory foragers (A), with means and standard errors for age-classes and provinces (B), and results of planned comparisons using *F* tests (C).

Ordination of Bird Data

Geographic and stand-age patterns—DCA ordination of bird species' abundances from all 132 stands produced low eigenvalues of 0.16 and 0.13 for the first two axes, respectively. Stand scores organized by geographic location separated into relatively distinct groups, but scores organized by stand age-classes overlapped extensively (fig. 14B, C). Additional ordinations of each province separately, although not shown, produced similar results: distinct clusters of stands could be identified easily by geographic location (that is, by subprovince) and not by stand age-class.

Bird communities that separate along DCA axis 1 were in two groups: stands from the central and southern Oregon Cascades, and stands from the Oregon Coast Ranges, northern Oregon Cascades, and southern Washington Cascades (fig. 14B). Along axis 2, bird communities from the southern Washington Cascades were distinct from the Oregon Coast Ranges and Oregon Cascades. Bird communities within the three subprovinces of the Oregon Cascades showed the most intra-province variation; however, the geographic area sampled in this province was far more extensive than the other two provinces (see frontispiece and fig. 1; table 1). Bird communities in the north subprovince of the Oregon Cascades (fig. 14B; left dashed circle) were more similar in species composition and abundance to those of the southern Washington Cascades and Oregon Coast Range than in subprovinces of the central and southern Oregon Cascades.

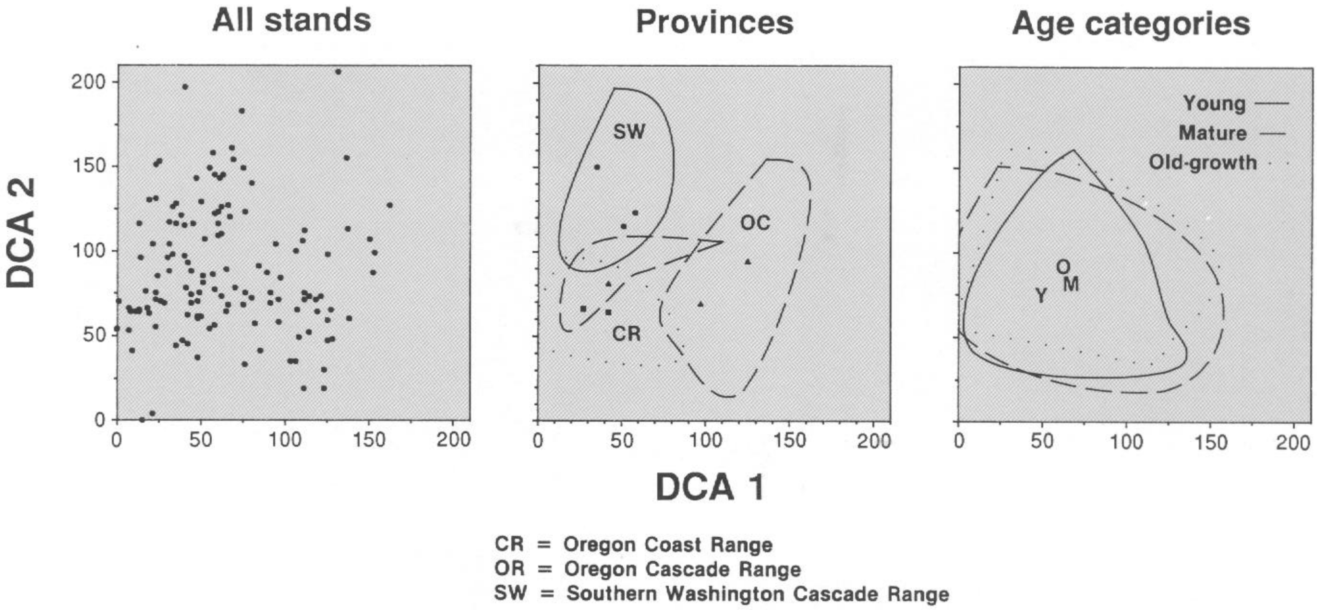


Figure 14—Results of detrended correspondence analysis (DECORANA) on all stands using bird abundance data, and DECORANA space occupied by at least 90 percent of the stands in each province and age-class. Stands were plotted by using DECORANA scores of the first (DCA 1) and second (DCA 2) axes. Median scores for subprovinces within each province and age-class are denoted as follows: squares = Oregon Coast Ranges (CR), triangles = Oregon Cascades (OC), circles = southern Washington Cascades (SW), Y = young, M = mature, O = old growth.

Table 6—Spearman rank correlations of DECORANA scores of axes 1 and 2 with environmental and biological variables

Variable	DCA Axis 1	DCA Axis 2
Latitude	–0.376	0.524
Longitude	–0.171	0.664
Elevation	0.455	0.568
Stand age	–0.213	0.153
Aspect	–0.127	0.009
Slope	0.034	–0.177
Understory vegetation DCA 1 (wet to dry[a])	0.310	–0.513
Understory vegetation DCA 2 (cool moist to warm moist[a])	–0.461	–0.604
Douglas-fir density	0.426	–0.165
Western hemlock density	–0.303	0.344
Bark-forager relative density	–0.051	0.375
Aerial-forager relative density	0.068	–0.659
Canopy-forager relative density	0.590	0.459
Understory-forager relative density	–0.740	–0.086
Resident relative density	–0.394	0.747
Migrant relative density	0.367	–0.734
Species richness	0.034	–0.273
Total abundance	–0.252	–0.389

[a] DCA ordination scores of cover of understory vegetation collected by T. Spies. Interpretation of environmental gradients for each axis were made by T. Spies (pers. comm.) and (Spies and Franklin, this volume).

Correlation and interpretation of the DCA axes—Fifty-five percent of the Spearman rank correlations between DCA axis 1 and the environmental and bird abundance variables were significant at $P < 0.001$ ($r_s > 0.283$ or < -0.283, $n = 130$) and 67 percent were significantly correlated with DCA axis 2 (table 6). In general, axis 2 yielded higher correlation coefficients than axis 1; however, no single strong association for either axis emerged from the variables measured (table 6). The complex patterns seemed to follow a temperature and moisture gradient, especially along axis 2, that was related to elevation, latitude, longitude, and understory vegetation (figs. 15, 16). Also strongly correlated with axis 2 were the abundance of resident and migrant species, in positive and negative directions, respectively (fig. 16). Abundance patterns along axis 1 were highly correlated with the abundance of understory-foraging species (fig. 15).

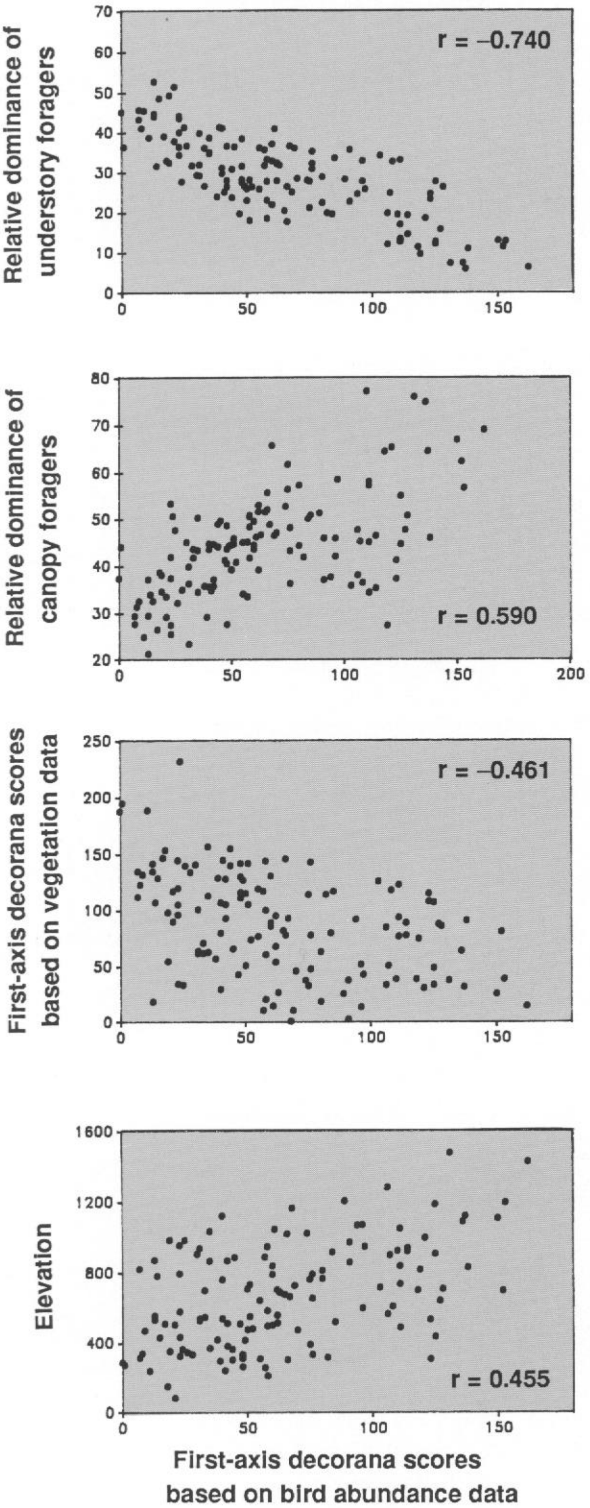


Figure 15—Scatterplots and Spearman rank correlations (r_s) of first-axis detrended correspondence analysis (DECORANA) scores for all stands, based on bird abundance data, with biological and environmental variables.

Relationships to Habitat

All 32 multiple regression equations of relationships to habitat, whether for all provinces combined or each separately, were significant at $P \leq 0.007$ (table 7, see appendix table 9). Yet, in general, the linear relationships were weak. Only 47 percent of the regression models had an $R^2 \geq 0.40$ and only 13 percent were ≥ 0.50. The linear relationships of all provinces combined and each separately were strongest for the understory foragers (range $R^2 = 0.36$ to 0.63 and mean $R^2 =$ 0.54) (table 7) and weakest for species richness (range $R^2 =$ 0.18 to 0.35 and mean $R^2 = 0.26$) (table 7). The lowest R^2 was 0.18 for species richness in the Oregon Coast Range (table 7) and highest was 0.65 for canopy foragers in the Oregon Cascades (table 7). In general, the proportion of variance explained by the regression equations tended to be lower in the Oregon Coast Ranges than the other provinces (table 7).

Fifty-two vegetation variables were selected for the 32 regression equations (table 7). The variables selected differed markedly between each province for each of the eight dependent variables. Only three vegetation variables were associated with the same dependent variable in more than one province: density of live deciduous trees was positively associated with abundance of migrant bird species (table 7); evergreen shrub cover was negatively associated with resident bird species (table 7); and fern cover was positively associated with understory foragers (table 7).

Live deciduous-tree variables—namely, density, basal area, and importance value—were selected in at least one regression model for every species-richness or abundance-dependent variable tested, except for the bark foragers (table 7). The live deciduous-tree variables were selected most frequently with the data sets of both the Oregon Coast Ranges and all provinces together and were always positively related to species-richness and bird abundance. Other variables selected often in the regression models were two dead-wood variables—mean snag diameter and density of snags 10 to 50 cm in d.b.h. and 5 to 15 cm tall—that were positively and negatively associated with the dependent variables, respectively.

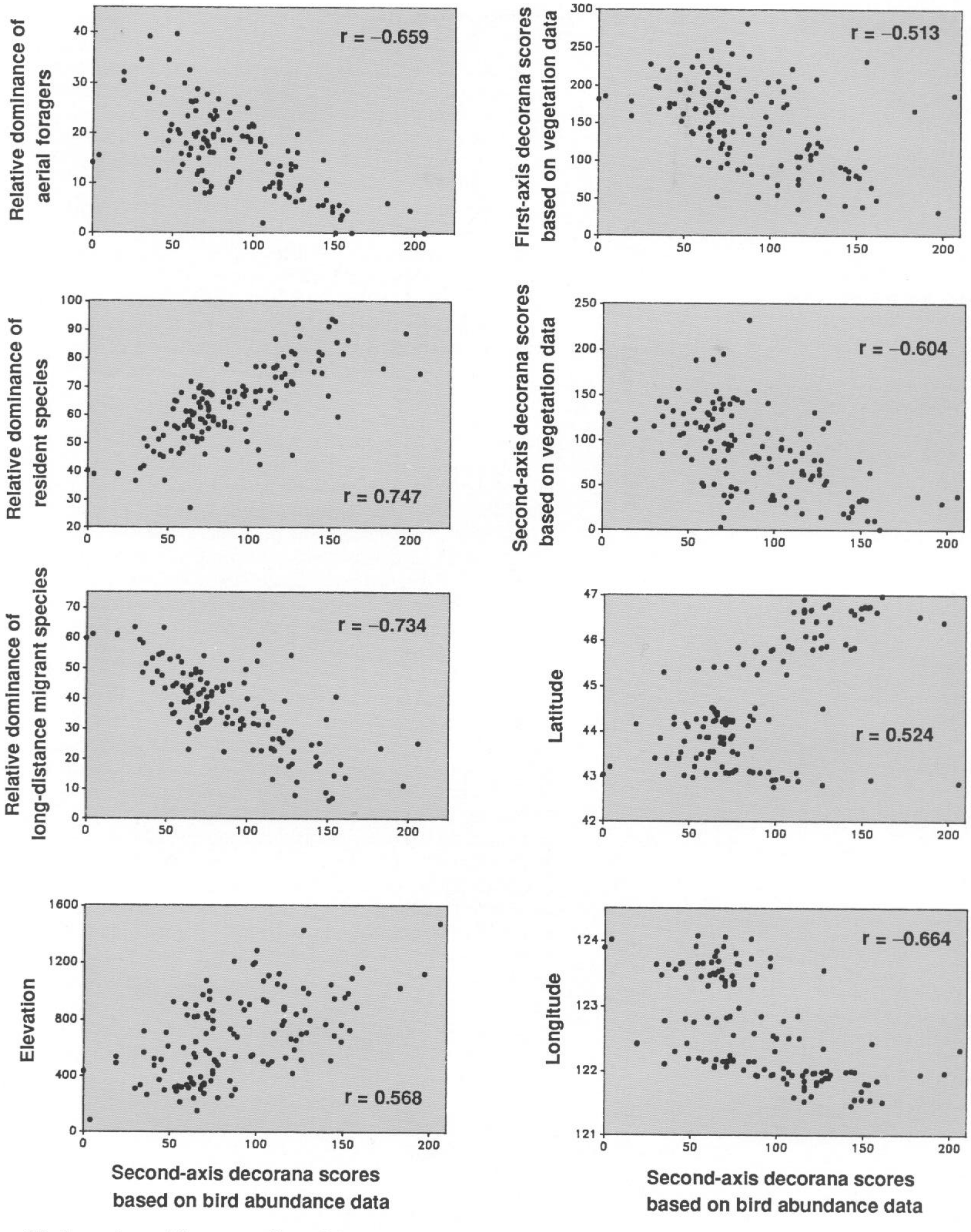


Figure 16—Scatterplots and Spearman rank correlations (r_s) of second-axis detrended correspondence analysis (DECORANA) scores for all stands, based on bird abundance data, with biological and environmental variables.

Table 7—Multiple regression using all possible subsets of independent vegetation variables with dependent variables of bird species richness, total abundance, abundance of residents and migrants, and abundance of bark, aerial, canopy, and understory foragers

Dependent variable/independent variables	Regression coefficient	T-statistic	Two-tailed significance	Contribution[a] to R^2
Species richness:				
All provinces (df[b] = 5, 117; R^2 [c] = 0.25; P[d] = 0.000)				
Intercept	12.996	13.15	.000	
Basal area of live deciduous trees	0.359	2.74	.007	.046
Percentage ground cover of moss	–0.025	–2.61	.010	.042
Importance value of live western redcedar[e]	–0.010	–2.5	.014	.038
Mean height of live dominant trees	0.047	2.38	.019	.035
Density of western hemlock snags >1.5 m tall	–0.017	–2.12	.036	.028
Oregon Coast Ranges (df = 2, 40; R^2 = 0.18; P = 0.007):				
Intercept	16.846	21.20	.000	
Density of decay-class-2 logs[f]	–0.338	–2.43	.019	.115
Basal area of live deciduous trees	0.245	2.01	.051	.079
Oregon Cascades (df = 4, 43; R^2 = 0.25; P = 0.002):				
Intercept	15.542	11.98	.000	
Percentage cover of ferns	–1.492	–2.34	.024	.088
Density of snags >50 m d.b.h. and 5-15 m tall	–0.569	–1.95	.057	.061
Density of live trees 50-99 cm d.b.h.	0.148	1.27	0.211	.026
Importance value of live western redcedar	–0.008	–1.20	0.235	.023
Southern Washington Cascades (df = 4, 34; R^2 = 0.35; P = 0.001):				
Intercept	14.059	6.33	.000	
Density of snags 10-50 cm d.b.h. and 5-15 m tall	–1.841	–2.28	.029	.089
Density of western hemlock snags >1.5 m tall	–0.022	–1.95	.059	.065
Importance value of live western redcedar	–0.010	–1.82	.078	.057
Density of live trees 25-49 cm d.b.h.	1.076	0.76	.455	.010
Total abundance:				
All provinces (df = 4, 118; R^2 = 0.41; P = 0.000):				
Intercept	6.952	35.61	.000	
Density of snags 10-50 cm d.b.h. and 5-15 m tall	–0.659	–5.78	.000	.162
Basal area of live bigleaf maple	0.303	3.87	.000	.073
Percentage cover of plants <0.5 m tall	0.008	2.06	.041	.021
Basal area of live pine trees	0.040	1.35	.179	.009
Oregon Coast Ranges (df = 4, 38; R^2 = 0.25; P = 0.004):				
Intercept	7.774	20.03	.000	
Basal area of live deciduous trees	0.125	2.88	.006	.148
Density of live incense-cedar	–0.035	–1.57	.125	.044
Volume of decay-class-5 snags	0.285	1.39	.172	.034
Density of live Douglas-fir	–0.032	–1.31	.198	.030

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Table 7—continued

Dependent variable/independent variables	Regression coefficient	T-statistic	Two-tailed significance	Contribution[a] to R^2
Oregon Cascades (df = 3, 44; R^2 = 0.24; P = 0.002):				
Intercept	5.251	9.18	.000	
Mean height of live dominant trees	0.032	2.88	.006	.134
Relative dominance of Douglas-fir snag volume	−0.008	−1.49	.142	.036
Density of live trees 50-99 cm d.b.h.	0.031	0.86	.396	.012
Southern Washington Cascades (df = 3, 35; R^2 = 0.30; P = 0.001):				
Intercept	3.194	2.28	.029	
Percentage cover of plants <0.5 m tall	0.014	2.16	.038	.086
Percentage cover of live deciduous trees ≤8 m tall	−0.114	−1.90	.066	.066
Mean d.b.h. of snags	1.599	1.85	.073	.063
Resident species:				
All provinces (df = 5, 117; R^2 = 0.42; P = 0.000):				
Intercept	3.328	3.36	.001	
Basal area of live deciduous trees	0.199	4.41	.000	.093
Density of snags 10-50 cm d.b.h. and 5-15 m tall	−0.375	−4.06	.000	.079
Percentage cover of evergreen shrubs	−0.089	−2.94	.004	.042
Biomass of decay-class-3 snags	0.368	2.43	.016	.028
Basal area of live needle-leaved evergreen trees	1.25	2.33	.022	.026
Oregon Coast Ranges (df = 4, 38; R^2 = 0.45; P = 0.000):				
Intercept	6.23	17.09	.000	
Importance value of live broad-leaved evergreen trees	−0.007	−3.22	.003	.134
Basal area of live deciduous trees	0.087	2.21	.033	.063
Importance value of live western redcedar	0.006	2.00	.053	.052
Density of live Douglas-fir	−0.033	−1.30	.200	.022
Oregon Cascades (df = 4, 43; R^2 = 0.42; P = 0.000):				
Intercept	4.735	9.65	.000	
Percentage cover of evergreen shrubs	−0.136	−3.86	.000	.185
Importance value of live western yew	0.005	2.34	.024	.068
Mean height of live dominant trees	0.021	2.30	.027	.065
Relative dominance of Douglas-fir snag volume	−0.006	−1.42	.164	.025
Southern Washington Cascades (df = 4, 34; R^2 = 0.47; P = 0.000):				
Intercept	4.87	14.06	.000	
Percentage cover of plants <0.5 m tall	0.016	2.97	.005	.124
Density of snags >50 cm d.b.h. and 5-15 m tall	0.244	2.59	.014	.094
Percentage cover of evergreen shrubs	−0.105	−2.18	.036	.067
Percentage cover of live deciduous trees ≤8 m tall	−0.068	−1.34	.191	.025

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Table 7—continued

Dependent variable/independent variables	Regression coefficient	T-statistic	Two-tailed significance	Contribution[a] to R^2
Migrant species:				
All provinces (df = 4, 118; R^2 = 0.44; P = 0.000):				
Intercept	4.69	26.86	.000	
Density of snags 10-50 cm d.b.h. and 5-15 m tall	–0.563	–5.15	.000	.123
Importance value of live Pacific silver fir	–0.008	–3.87	.000	.070
Relative frequency of western hemlock snags	–0.015	–2.73	.007	.035
Importance value of live deciduous trees	0.004	2.18	.031	.022
Oregon Coast Ranges (df = 4, 31; R^2 = 0.38; P = 0.001):				
Intercept	4.407	16.86	.000	
Density of live incense-cedar	–0.056	–3.39	.002	.205
Percentage cover of shrubs 0.5-2.0 m tall	0.091	1.88	.070	.063
Percentage ground cover of moss	0.010	1.64	.111	.048
Density of live deciduous trees	0.001	0.73	.471	.009
Oregon Cascades (df = 4, 43; R^2 = 0.24; P = 0.003):				
Intercept	3.95	14.17	.000	
Importance value of live Pacific silver fir	–0.008	–2.56	.014	.107
Density of live trees 50-99 cm d.b.h.	0.066	2.08	.043	.070
Density of decay-class-1 logs	–0.012	–1.83	.074	.054
Percentage cover of live deciduous trees ≤8 m tall	0.045	1.30	.200	.027
Southern Washington Cascades (df = 4, 34; R2 = 0.36; P = 0.001):				
Intercept	5.449	2.79	.009	
Density of snags 1.5-4.9 m tall	–0.009	–2.45	.020	.101
Relative frequency of Douglas-fir snags	0.017	2.36	.024	.094
Basal area of live needle-leaved evergreen trees	–1.878	–1.88	.069	.059
Density of live deciduous trees	0.011	1.51	.141	.038
Bark foragers:				
All provinces (df = 5, 124; R^2 = 0.31; P = 0.000):				
Intercept	0.869	1.04	.300	
Density of live trees 25-49 cm d.b.h.	–0.539	–3.37	.001	.060
Basal area of live bigleaf maple	0.085	3.14	.002	.052
Basal area of live needle-leaved evergreen trees	1.033	2.97	.004	.047
Basal area of live grand fir	0.050	2.43	.017	.031
Mean height of snags	0.584	2.01	.047	.021
Oregon Coast Ranges (df = 4, 38; R^2 = 0.40; P = 0.000):				
Intercept	1.114	0.89	.377	
Basal area of live bigleaf maple	0.070	2.52	.016	.090
Basal area of live needle-leaved evergreen trees	1.219	2.23	.031	.071
Density of live trees 25-49 cm d.b.h.	–0.512	–2.02	.051	.058
Density of live western redcedar	0.004	1.98	.055	.055

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Table 7—continued

Dependent variable/independent variables	Regression coefficient	T-statistic	Two-tailed significance	Contribution[a] to R^2
Oregon Cascades (df = 3, 44; R^2 = 0.38; P = 0.000):				
Intercept	0.967	1.13	.263	
Percentage cover of shrubs 2.0-4.0 m tall	–0.609	–3.43	.001	.155
Basal area of live needle-leaved evergreen trees	1.175	2.64	.011	.092
Relative dominance of Douglas-fir snags	–0.006	–1.66	.105	.036
Southern Washington Cascades (df = 2, 36; R^2 = 0.40; P = 0.000):				
Intercept	5.041	6.00	.000	
Density of live needle-leaved evergreen trees	–1.226	–4.20	.000	.278
Density of snags >50 cm d.b.h. and >15 m tall	0.194	2.80	.008	.123
Aerial foragers:				
All provinces (df = 4, 118; R^2 = 0.40; P = 0.000):				
Intercept	1.669	3.92	.000	
Density of snags 10-50 cm d.b.h. and 5-15 m tall	–0.497	–5.04	.000	.125
Mean height of snags	1.358	3.10	.002	.047
Percentage cover of ferns	0.355	2.50	.014	.031
Importance value of live broad-leaved evergreen trees	0.003	1.97	.051	.019
Oregon Coast Ranges (df = 3, 32; R^2 = 0.30; P = 0.002):				
Intercept	5.17	5.08	.000	
Density of live incense-cedar	–0.036	–2.83	.008	.160
Mean d.b.h. of live trees	–1.221	–2.00	.054	.080
Percentage cover of live evergreen trees ≤8 m tall	0.123	1.68	.103	.057
Oregon Cascades (df = 4, 43; R^2 = 0.32; P = 0.000):				
Intercept	1.159	1.68	.101	
Volume of Douglas-fir snags	0.645	3.28	.002	.157
Density of snags 10-50 cm d.b.h. and 5-15 m tall	–0.429	–2.77	.008	.112
Equitability index of tree basal area by height-classes[g]	0.537	1.81	.077	.048
Importance value of live grand fir	0.003	1.43	.160	.030
Southern Washington Cascades (df = 3, 35; R^2 = 0.40; P = 0.000):				
Intercept	1.800	15.56	.000	
Basal area of live western yew	0.280	3.52	.001	.197
Density of live deciduous trees	0.012	2.45	.019	.096
Density of live western redcedar	–0.003	–2.07	.046	.068

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Table 7—continued

Dependent variable/independent variables	Regression coefficient	T-statistic	Two-tailed significance	Contribution[a] to R^2
Canopy foragers:				
All provinces ($df = 4, 118$; $R^2 = 0.34$; $P = 0.000$):				
Intercept	4.647	35.51	.000	
Basal area of live deciduous trees	0.205	4.93	.000	.131
Percentage ground cover of moss	–0.011	–3.76	.000	.076
Basal area of live pine trees	0.072	2.88	.005	.045
Density of snags 1.5-4.9 m tall	–0.003	–1.76	.081	.017
Oregon Coast Ranges ($df = 3, 32$, $R^2 = 0.41$; $P = 0.000$):				
Intercept	5.975	11.36	.000	
Basal area of live deciduous trees	0.177	3.43	.002	.198
Equitability index of tree density by diameter-classes[d]	–0.455	–2.56	.015	.111
Percentage cover of berry (*Vaccinium* spp.) shrubs	–0.827	–2.29	.029	.088
Oregon Cascades ($df = 3, 44$; $R^2 = 0.65$; $P = 0.000$):				
Intercept	4.291	22.33	.000	
Percentage cover of grass, herbs, and ferns	–0.021	–6.53	.000	.319
Density of live trees 50-99 cm d.b.h.	0.129	5.30	.000	.211
Basal area of live pine trees	0.043	2.26	.029	.038
Southern Washington Cascades ($df = 4, 34$; $R^2 = 0.38$; $P = 0.000$):				
Intercept	4.383	18.88	.000	
Biomass of decay-class-5 snags	–0.982	–2.50	.017	.102
Percentage cover of live deciduous trees ≤8 m tall	–0.101	–2.25	.031	.082
Percentage cover of plants <0.5 m tall	0.011	2.13	.040	.074
Basal area of live western yew	–0.150	–1.56	.127	.040
Understory foragers:				
All provinces ($df = 5, 117$; $R^2 = 0.61$; $P = 0.000$):				
Intercept	1.388	1.99	.049	
Percentage cover of plants 0.5-2.0 m tall	0.175	6.07	.000	.117
Basal area of live deciduous trees	0.201	5.26	.000	.088
Mean d.b.h. of snags	1.784	4.79	.000	.073
Density of live pine trees	–0.034	–3.95	.000	.049
Mean number of live tree species	–1.715	–3.67	.000	.043
Oregon Coast Ranges ($df = 3, 32$; $R^2 = 0.36$; $P = 0.001$):				
Intercept	6.235	4.21	.000	
Percentage cover of ferns	0.643	2.50	.018	.115
Importance value of live incense-cedar	–0.012	–2.26	.031	.094
Basal area of live needle-leaved evergreen trees	–0.951	–1.72	.095	.055

Footnotes on page 200.

Table 7—continued

Dependent variable/independent variables	Regression coefficient	T-statistic	Two-tailed significance	Contribution[a] to R^2
Oregon Cascades (df = 4, 43; $R^2 = 0.63$; $P = 0.000$):				
Intercept	0.738	1.40	.168	
Percentage cover of ferns	0.575	3.76	.001	.110
Importance value of live pine trees	–0.007	–3.69	.001	.106
Mean height of live dominant trees	0.027	3.52	.001	.096
Biomass of logs	0.607	2.52	.016	.049
Southern Washington Cascades (df = 4, 34; $R^2 = 0.56$; $P = 0.000$):				
Intercept	1.439	1.55	.130	
Percentage cover of plants <0.5 m tall	0.016	3.65	.001	.155
Percentage cover of evergreen shrubs	–0.114	–3.01	.005	.105
Mean d.b.h. of snags	1.380	2.49	.018	.072
Percentage cover of live deciduous trees ≤8 m tall	–0.067	–1.66	.107	.032

[a] The contribution to R^2 is the amount by which R^2 would be reduced if that variable were removed from the regression equation.

[b] Degrees of freedom.

[c] Adjusted $R^2 = 1 - ((\text{residual sum of squares} / N - p - 1)) / (\text{total sum of squares} / (N - 1)))$, where N was the number of study sites and p was the number of independent variables in the equation.

[d] P-value.

[e] Importance value is the mean of relative density, basal area, and frequency.

[f] Decay-class of wood is ranked on a scale of 1 to 5; 1 was solid and recently dead, and 5 was punky or easily crumbled.

[g] Shannon-Wiener equitability index (see Whittaker 1975) was done on basal area by height-classes, and density by diameter-classes of live trees.

Discussion

Regional Patterns

Our results suggested that bird abundance patterns were regionally distinct (fig. 14B) and that abundance was substantially higher in the Oregon Coast Ranges than in the other two provinces (figs. 6-13), even though >70 percent of the bird species were detected in two or more provinces. Location of the study stands by latitude, longitude, and elevation; inconsistencies in sample design; and varying degrees of forest fragmentation appeared to be partly responsible for the differences among regions.

In the ordination analyses, regional abundance patterns (fig. 14B) were best explained by correlations with latitude, longitude, and elevation (table 6; figs. 15, 16). They were negatively associated with latitude and elevation and positively associated with an east-to-west longitudinal gradient (fig. 2). Elevation was essentially overlooked when stands were selected and varied substantially within and among provinces. Partial correlation using elevation as a constant was impractical for explaining abundance patterns. The southernmost stands in the Oregon Cascade Ranges were among the highest in elevation and generally had more birds than stands to the north, while stands in the Oregon Coast Ranges were generally the lowest in elevation but were higher in abundance than stands in the Cascade Ranges (table 1, fig. 1). Although we detected a relatively high correlation between longitude and abundance (fig. 2), we assumed longitude per se had little effect on bird abundance within one broad vegetation zone (see Hamel and others 1986). The increase in abundance from east (Cascade Range) to west (Oregon Coast Ranges) was likely more directly related to the moderate climate of the Oregon Coast Ranges relative to the colder Cascades, or to variation in elevation among the provinces.

Shortening the interstation distance to 50 m to accommodate the smaller stand sizes in the Oregon Coast Ranges may have resulted in higher bird counts than in stands with longer interstation distances. Field observers were trained not to count individual birds more than once on a given day; however, double counting was possible. We attempted to minimize these biases by using only detections ≤50 m from a counting station in all three provinces, except during the analysis specifically on individual species.

High species richness and abundance in Oregon Coast Range stands may also be a result of forest fragmentation that has increased the diversity of stand ages over the landscape and may have in turn increased the packing of individuals within

Continue

the residual stands ***sensu*** Lehmkuhl and others, this volume; Rosenberg and Raphael 1986) A long history of logging and high incidence of fires were primarily responsible for the much smaller stand sizes and more fragmented landscapes in the Oregon Coast Ranges (Agee, this volume; Carey and others, this volume; Spies and others 1988). As a result, edge habitats were probably more abundant and closer to stands in the Oregon Coast Ranges and exerted a stronger influence on richness and abundance than in other provinces. Quantifying the characteristics of fragmentation over the landscape and determining their effects across the provinces was beyond the scope of this study. Such analyses are available for the southern Washington Cascades (Lehmkuhl and others, this volume).

Our province comparisons are highly uncertain because not all the provinces were surveyed in the same year. Yearly variation and covariation in bird abundance are expected to be high at any one site and fluctuate more widely with the more abundant species (see Holmes and others 1986). Temporal sampling variation included fewer birds detected in the southern Washington Cascades during the cool and wet spring of 1984 compared to 198.5 (Manuwal and Huff 1987); birds not surveyed in 1984 in the Oregon Coast Ranges, but only in 1985 and 1986; and only 68 percent of the Oregon Cascade stands were sampled in 1985.

In summary, distinct provincial patterns were suggested, and bird abundance appeared to be higher in the Oregon Coast Ranges, although natural variability in avian communities seemed to be high within and among provinces. Significant differences between the provinces must be considered in relation to sample design problems-namely, the widely varying elevation and sampling frequency that limit extrapolation of results beyond the study areas sampled.

Stand-Age Patterns

No broad differences were found in bird abundance patterns related to forest age (fig. 14C). Bird communities of old-growth stands showed great overlap with those of young and mature stands. The vegetation in the old-growth stands was distinguished from younger forest by only a small set of structural attributes, such as tree density, mean stand diameter, and basal area (Spies and Franklin, this volume). General homogeneity of many stand attributes indistinguishable among stand age-classes may have discouraged the development of unique bird associations along the sere. Bird community patterns at this broad level of analyses, for example, were probably closely tied to plant species composition, which did not differ significantly between age-classes, except for a few minor species (Spies, this volume).

Significant age-class differences were detected for bark and aerial foragers (figs. 10, 11) and likewise for 16 bird species in at least two of three provinces (figs. 3-5). Seven of eight hole or bark nesters, six of which were bark foragers, reached their highest abundance in mature and old-growth stands. In northwestern California Douglas-fir stands, 12 bird species (excluding raptors) were positively correlated with stand age during spring (Raphael 1984), but only 2 of the 12 were hole or bark nesters. Only the chestnut-backed chickadee was positively associated with stand age in both northwestern California and in at least two of provinces in Oregon and Washington.

Bark-forager abundance in northwestern California, modeled now as being >30 percent below the historical (prelogging) populations, has been projected to return to near historical populations if forested landscapes, excluding reserves and stream-management zones, are managed at l00-year harvest rotations (Raphael and others 1988). If populations were modeled similarly for Oregon and Washington, bark-forager abundance seems unlikely ever to approach prelogging populations because bark-forager abundance was so much higher in older than younger Douglas-fir forests here compared to northwestern California. The strong association between bark-forager abundance and stand age in Oregon and Washington may be a function of the increase in large snags (>50 cm d.b.h.) as stands age (Spies and Franklin, this volume). Large snags have been identified as crucial for bark-foraging and hole-nesting bird species (see Davis and others 1983; Lundquist and Mariani, this volume; McClelland 1977; Zamowitz and Manuwal 1985). Generally more than a century is required to replace large snags once they are removed. Large snags would essentially disappear in forests managed on l00-year rotations, except in buffer strips, riparian corridors, and reserves. Therefore, we would expect bark-forager and hole-nester abundance to remain well below prelogging populations.

Most of the species detected in the study stands were habitat generalists with widespread geographic distribution and occupying a diverse array of habitats. Much fewer in number were those species with a distribution restricted primarily to the Pacific forest belt (sensu Raphael and others 1988). The birds in this group that reach their highest abundance in mature and old-growth forests were assumed to be the most sensitive to short-rotation management. This group included two resident species, the chestnut-backed chickadee (fig. 3) and the red-breasted sapsucker (fig. 5), and one migrant, Vaux's swift (fig. 5), which winters from Mexico south to Venezuela (American Ornithologists' Union 1983). The abundance patterns derived for Vaux's swifts and red-breasted sapsuckers, however, were based on limited data and from detection distances of $\leq$ 150 m. We advise interpreting and using these results judiciously.

Relations to Habitat

The study design was limited to an extensive approach (sensu Van Home 1986), observing repeatable patterns in the relation of birds to their habitat over a broad geographic area. The vegetation characteristics selected for multivariate regression models predicted only a small proportion of the variance of species richness, total abundance, and species grouped by residency and by foraging guild (table 7). Probable causes for the high degree of unexplained variability in this pattem-oriented approach are numerous (see Verner and others 1986: 207-258). The variability may be because of the effects of weather on bird populations and the interaction of weather, prey, predators, competitors, and parasites (O'Neil and Carey 1986); because species' abundances were not a good measure of habitat quality, were independent of stochastic variation, and were not measured consistently between observers (Rotenberry 1986, Van Home 1983, Verner 1985); because means were used to characterize within-habitat heterogeneity; or because of influences outside the stand that were not measured, such as alteration of distant wintering grounds or changes in the landscape nearby.

Understory foragers were most strongly related to the measured habitat variables (table 7). We suspect this may be a result of lower sampling error for the understory foragers than for other foraging guilds. The understory foragers used, for the most part, only the vertical strata within a few meters of the forest floor. The sampling error associated with estimating abundances in this stratum was probably lower than in strata much farther from the observer. Likewise, measuring habitat characteristics within strata used by understory foragers is considerably easier to measure than the vegetative attributes used by species in the canopy, on tree limbs and boles, or in canopy gaps.

Consistent prediction of habitat associations do not necessarily imply cause and effect (Rotenberry 1986). In some instances, the vegetation variables measured had little direct biological meaning for the bird populations being predicted. For example, the canopy foragers were positively and negatively associated with certain forest-floor variables, such as percentage cover of moss and percentage cover of plants <0.5 m tall (table 7). As indirect measures of habitat quality, these variables most likely are identified with a complex set of stand attributes that alone are highly variable and poor predictors. Nevertheless, the management applicability of indirect indicator variables needs to be tested.

The most positive association between bird abundance or richness, and vegetation or stand structure was with live deciduous-tree characteristics (for example, density, basal area, importance value). The deciduous-tree component, most strongly associated with young stands and long-distant migrants, was likely a result of natural reestablishment of the forest after fire. In intensively managed, short-rotation conifer plantations of Douglas-fir, deciduous trees are discouraged, or, if possible, eliminated during stand reestablishment. Based on results from naturally regenerated stands, maintaining a small component of deciduous trees (for example, bigleaf maple) on harvestable timberlands most likely would have a positive effect on bird populations.

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Appendix

Table g-Designations for residency and detectability of birds by foraging guild

Bird[a]	Residency[b]	Detectability[c]
Common raven		3
Northern pygmy-owl		3
Olive-sided flycatcher		3
Aerial foragers		
Dusky/Hammond’s flycatcher’	**M**	1
Vaux’s swift’	M	3
Western flycatcher	M	1
Bark foragers		
Brown creeper’	**R**	**1**
Hairy woodpecker[d]	**R**	**2**
Pileated woodpecker[d]	**R**	**3**
Red-breasted nuthatch[d]	**R**	**1**
Red-breasted sapsucker[d]	**R**	**3**
Canopy foragers		
Band-tailed pigeon	M	**4**
Black-capped chickadee[d]	R	**4**
Black-headed grosbeak	M	3
Black-throated gray warbler	M	1
Chestnut-backed chickadee[d]	R	1
Evening grosbeak	R	2
Golden-crowned kinglet	R	1
Gray jay	R	1
Hermit/Townsend’s warbler’	M	1
Nashville warbler	M	1
Pine siskin	R	1
Purple finch	R	1
Red crossbill	R	3
Steller’s jay	R	2
Western tanager	M	2
Yellow-rumped warbler	M	1
Understory foragers		
American robin	R	2
Blue grouse	R	3
Dark-eyed junco	R	1
Hermit thrush	M	2
Hutton’s vireo		1
MacGillivray’s warbler	M	1
Northern flicker[d]	R	3
Orange-crowned warbler	M	1
Rufous hummingbird	M	1
Rufous-sided towhee	R	4
Song sparrow	R	
Swainson’s thrush	M	4
Townsend’s solitaire	M	3
Varied thrush	R	2
Wilson’s warbler	M	1
Winter wren	R	1
Wrentit	R	1

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[a] Species mentioned in text but not part of the community data analysis were mourning dove, belted kingfisher, red-winged blackbird, northern oriole, and spotted owl.

R = year-long resident; M = long-distance migrant; blank = not included in residency analysis.

[c] Species were assigned to one of three detectability groups, as follows: 1 = majority of detections were within 50 m of the count station; 2 = the majority of detections were beyond 50 m, and species were detected at least twice in any particular stand, 3 = the majority of detections were beyond 50 m, species generally have large territories, and single occurrences (that is. a species was detected only once in a stand) accounted for >30 percent of all the stands in which a species was detected; 4 = species detected in <3 percent of the stand counts, no abundance was calculated.

[d] These birds are hole- or bark-nesting species.

[e] We did not distinguish between dusky and Hammond’s flycatchers or between hermit and Townsend’s warblers because they were difficult to identify in the field.

Table 9—Vegetation variables and type of data transformations performed (ARC = arcsine (square root (x)); LOG = log (x + 1); SQRT = square root (x + 0.375); SQRT' = square root (x); blanks indicate untransformed values)

Variable	Transformation
Live-tree variables:	
Mean number of tree species	LOG
Density	
Bigleaf maple	
Douglas-fir	
Golden chinkapin	
Grand fir	
Incense-cedar	
Pacific madrone	
Pacific silver fir	
Red alder	
Western hemlock	SQRT
Western redcedar	
Western yew	
Total tree density	LOG
Trees 5-9 cm d.b.h.	SQRT
Trees 10-24 cm d.b.h.	LOG
Trees 25-49 cm d.b.h.	LOG
Trees 50-99 cm d.b.h.	SQRT
Trees 100-149 cm d.b.h.	SQRT
Trees ≥150 cm d.b.h.	
Needle-leaved evergreen trees	LOG
Broad-leaved evergreen trees	
Deciduous trees	
Pine trees	
Basal area	
Bigleaf maple	
Douglas-fir	
Golden chinkapin	
Grand fir	
Incense-cedar	
Pacific madrone	
Pacific silver fir	
Red alder	
Western hemlock	SQRT
Western redcedar	
Western yew	
Total basal area	LOG
Needle-leaved evergreen trees	LOG
Broad-leaved evergreen trees	
Deciduous trees	
Pine trees	
Importance value[a]	
Needle-leaved evergreen trees	
Broad-leaved evergreen trees	
Deciduous trees	
Pine trees	
Bigleaf maple	
Douglas-fir	ARC
Golden chinkapin	
Grand fir	
Incense-cedar	
Pacific madrone	
Pacific silver fir	
Red alder	
Western hemlock	
Western redcedar	
Western yew	
Mean d.b.h. of live trees[b]	LOG
Mean height of dominant trees	
Equitability index	
Tree density by diameter classes[c]	
Tree basal area by height classes	
Stand condition variables:	
Density	
Trees with fire scars	
Trees with excavated cavities	
Trees with natural cavities	LOG
Trees with root cavities	LOG
Trees with small amount of moss/lichen	SQRT
Trees with moderate amount of moss/lichen	SQRT
Trees with heavy amount of moss/lichen	LOG
Percentage	
Trees with fire scars	
Trees with excavated cavities	
Trees with natural cavities	LOG
Trees with small amount of moss/lichen	ARC
Trees with moderate amount of moss/lichen	
Trees with heavy amount of moss/lichen	LOG
Snag variables:	
Density	
Decay-class-1 snags[d]	LOG
Decay-class-2 snags	LOG
Decay-class-3 snags	LOG
Decay-class-4 snags	LOG
Decay-class-5 snags	SQRT
Snags 1.5-5.0 m tall	
Snags 10-50 cm d.b.h. and 5-15 m tall	LOG
Snags 10-50 cm d.b.h. and >15 m tall	LOG
Snags >50 cm d.b.h. and 5-15 m tall	SQRT
Snags >50 cm d.b.h. and >15 m tall	SQRT
Douglas-fir snags >1.5 m tall	LOG
Western hemlock snags >1.5 m tall	

Table 9—continued

Variable	Transformation
Decay-class-1 snags	LOG
Decay-class-2 snags	LOG
Decay-class-3 snags	LOG
Decay-class-4 snags	LOG
Decay-class-5 snags	LOG
All snags	LOG
Volume	
Decay-class-1 snags	LOG
Decay-class-2 snags	LOG
Decay-class-3 snags	LOG
Decay-class-4 snags	LOG
Decay-class-5 snags	LOG
All snags	LOG
Douglas-fir snags	LOG
Western hemlock snags	
Relative frequency	
Douglas-fir snags[e]	ARC
Western hemlock snags	
Relative dominance	
Douglas-fir snags[f]	ARC
Western hemlock snags	
Mean height of all snags	LOG
Mean d.b.h. of all snags	LOG
Biomass of all snags	
Log variables:	
Density	
Decay-class-1 logs	
Decay-class-2 logs	SQRT
Decay-class-3 logs	SQRT
Decay-class-4 logs	SQRT
Decay-class-5 logs	SQRT
Logs <30 cm in diameter at large end	LOG
Logs 30-60 cm in diameter at large end	LOG
Logs >60 cm in diameter at large end	SQRT
All logs	LOG
Biomass	
Decay-class-1 logs	
Decay-class-2 logs	LOG
Decay-class-3 logs	LOG
Decay-class-4 logs	LOG
Decay-class-5 logs	LOG
All logs	LOG
Volume	
Decay-class-1 logs	
Decay-class-2 logs	LOG
Decay-class-3 logs	LOG
Decay-class-4 logs	LOG
Decay-class-5 logs	SQRT
Logs <30 cm in diameter at large end	LOG
Logs 30-60 cm in diameter at large end	LOG
Logs >60 cm in diameter at large end	SQRT
All logs	SQRT
Percentage cover of logs	LOG
Understory variables:	
Percentage cover by	
Moss	
Lichens	ARC
Ferns	LOG
Grasses	
Herbs	LOG
Evergreen shrubs	ARC
Deciduous shrubs	LOG
Deciduous trees ≤8 m tall	
Evergreen trees ≤8 m tall	SQRT
Berry (*Vaccinium* spp.) shrubs	LOG
Rubus species	ARC
Grasses, herbs, and ferns	
Plants <0.5 m tall	
Plants 0.5-2.0 m tall	SQRT
Plants 2-4 m tall	SQRT

---

[a] Importance value = sum of relative density, basal area, and frequency.

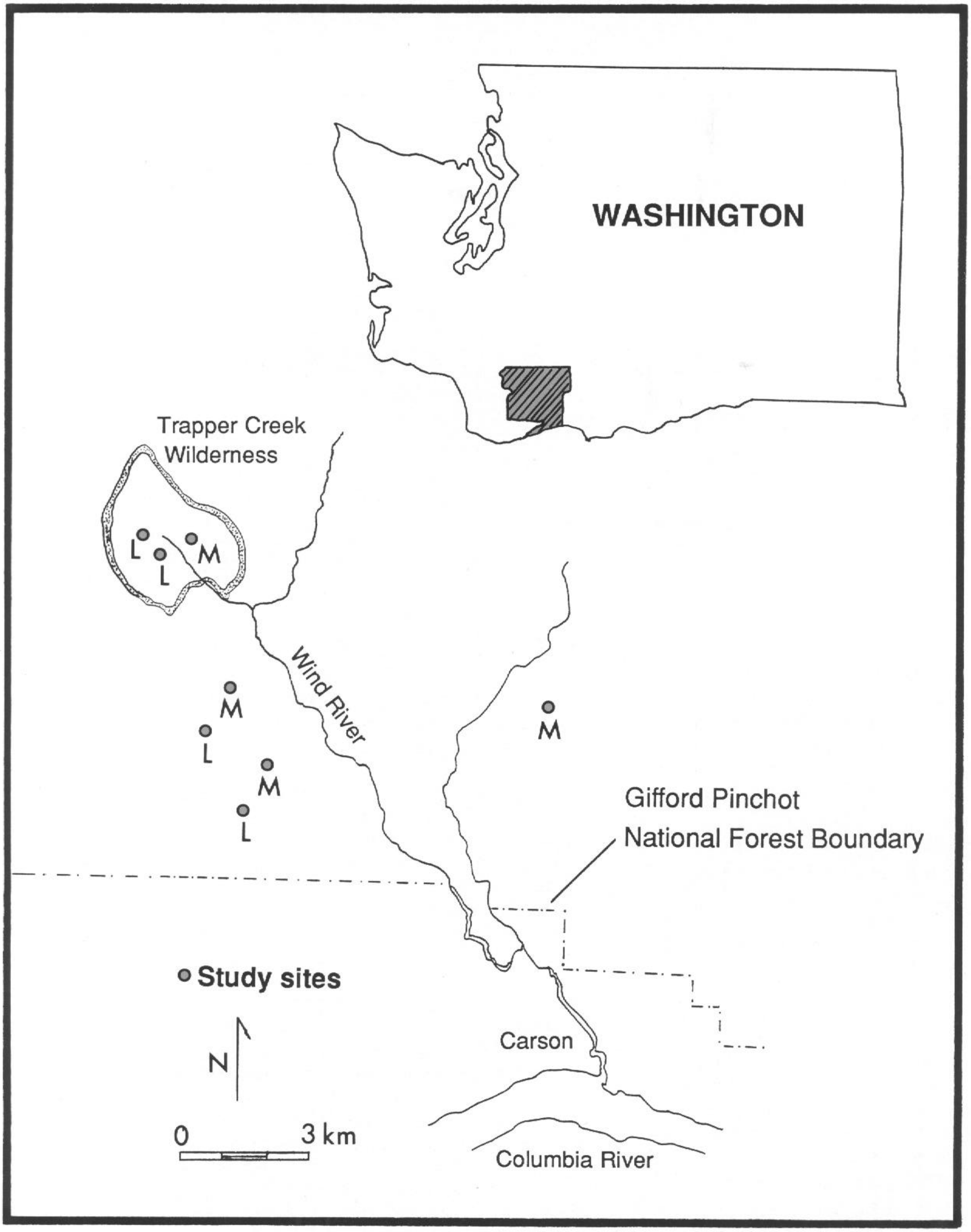
[b] D.b.h. = diameter at breast height in centimeters.

[c] Shannon-Wiener equitability index (see Whittaker 1975) was done on density by diameter-classes, and basal area by height-classes of live trees.

[d] Decay of wood ranked on a scale of 1 to 5, where 1 was solid-recently dead, and 5 was punky or easily crumbled.

[e] Relative frequency = density of a species as a percentage of total density.

[f] Relative dominance = volume of a species as a percentage of total volume.



Location of mid-seral (M) and late-seral (L) study sites.

Winter Bird Communities in the Southern Washington Cascade Range

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Abstract

Winter is a critical season for many resident bird species. Bird communities in eight Douglas-fir forest stands, four mid-seral(65-140 years old) and four late-seral(325-600 years old), were surveyed for three winters (9 December-19 March) from 1983-84 to 1985-86 in southern Gifford Pinchot National Forest. Birds in each stand were surveyed eight times each winter by using 8-minute counts at 12 counting stations 150 m apart along a line. For all three winters, median species richness and mean total abundance were substantially higher in late- than in mid-seral forests. Of the four major guilds exam&d-bark insectivores, canopy insectivores, understory seed-eaters and insectivores, and canopy seed-eaters-mean abundance was consistently higher in late- than mid-seral stands. Red crossbills, chestnut-backed chickadees, red-breasted nuthatches, and gray jays were strongly associated with late-seral stands in winter.

Introduction

Forests dominated by Douglas-fir are prevalent over the montane landscape west of the Cascade Range in Washington and Oregon (Franklin and Dyrness 1973). Although many aspects of Douglas-fir forests have been studied intensively-perhaps more than any other forest in the world-the distribution, abundance, and basic life-history characteristics of many animal species that inhabit these forests during the winter still need to be determined. The breeding success and persistence of resident species are undoubtedly linked to the winter season (see Fretwell 1972). The availability of food resources and habitat structural features that provide roost sites and thermal cover are crucial to the survival of animals active during the winter.

Manuwal and Huff (1987) reported on the abundance of spring and winter birds in 16 Douglas-fir forest stands in the southern Washington Cascade Range. They found that seasonal changes in abundance were greater in young (42- to 75-year-old) and mature (105- to 165-year-old) than in old-growth (250- to >500-year-old) stands, and bird species richness and total abundance were greater in old-growth than in younger stands during winter. Their data also suggest that old-growth forest stands provide better winter habitat for many species (such as gray jay, red-breasted nuthatch, brown creeper, and red crossbill) than did young or mature stands.

Our objectives were to compare winter bird species composition and abundance in old-growth forests to younger forests sampled for three consecutive winters within a small geographic area, to identify vegetative characteristics that explain the abundance patterns of birds in winter, and to provide a foundation for asking specific questions and making hypotheses about the distribution, abundance, and resource needs of birds in winter throughout the Douglas-fir region.

Met hods

Study Area

To sample winter birds, four mid-seral(65 to 140-year-old) and four late-seral(325 to >500-year-old) stands were selected subjectively from the Wind River Ranger District of the Gifford Pinchot National Forest (see frontispiece). Main selection criteria were easy access during winter and a wide range of interstand variability. The study stands were a subset of those reported in Manuwal and Huff (1987), and all were naturally regenerated after fire. Age of mid-seral stands was determined by increment coring at least five dominant Douglas-fir trees at breast height, adding 5 to 7 years for growth to breast height, and averaging the estimates (Spies and others 1988). Age of old-growth stands was determined by aging stumps in nearby clearcuts, along trails, or sometimes from increment cores on dominant trees (Spies and others 1988). Ages estimated for the old-growth stands are reliable to ± 50 years (T. Spies, pers. comm.).

A study stand was defined as an area with relatively homogeneous structure, disturbance history, vegetation composition, physiography, and soil (Manuwal and Huff 1987). The study stands ranged from 91 to 760 ha. ‘Differences in stand size between late-seral (x= 565 ha; SD = 292 ha) and mid-seral stands (x’= 408 ha; SD = 225) were assumed to be minor because all stands were generally large. Stand fragmentation resulting from clearcutting was minimal (J. Lehmkuhl, pers. comm.). Only one late-seral stand had evidence of past logging near the sample area, about 200 m away.

Sampling

Vegetation-Sampling and stand summaries of vegetation were provided by T. Spies (pers. comm.). Our primary objective for vegetation analysis was to determine and contrast the structure and composition of our mid- and late-seral stands. Spies measured about 300 vegetation and site variables at each stand. We subjectively identified about 100 variables to be used for further analyses based on their potential importance to birds in winter. These included variables related to plant species composition, abundance of live and dead woody vegetation, and stand structural characteristics.

Annual cone-crop ratings of Douglas-fir and western hemlock, obtained from a regional summary of forests of the southern Washington Cascades (Anon. 1983-85), were used to measure food resources available for seed-eating birds. Each year, the cone crop was subjectively rated by species by a scale of 1 to 5: absent/failure = 1, very light = 2, light = 3, medium = 4, and heavy = 5. Because cone-crop ratings were nearly identical for western hemlock and Douglas-fir from 1983-85, we averaged their ratings together. The cone crop of Douglas-fir and western hemlock was rated at each study stand during winter 1985-86. Using the same rating scale, cone crop was rated over a 20-m radius at each of 12 bird-counting stations and averaged for each stand.

Birds-We followed the protocol of field methods established for birds by the Old-Growth Forest Wildlife Habitat Program (Carey and Spies, this volume), with minor adjustments for winter sampling. Birds were surveyed by the point-count method (see Verner 1985) over three winters (9 December to 19 March) from 1983-84 to 1985-86. Surveys were done only during acceptable weather, avoiding rain, high winds, and snowstorms or other conditions that would seriously inhibit detecting birds. Each stand was surveyed eight times each winter using 8-minute counts at 12 stations spaced 150 m apart along a line. Survey lines, fitted into each stand to maximize efficiency and stand homogeneity (for example, similar slope), were generally rectangular (600 x 300 m) or linear (1650 m).

Each observer identified all bird species based on sight or sound and estimated the ground distance to the detection location. Birds flying through or over the canopy received different codes according to their vertical stratification rather than distance estimates. Birds in flocks-three or more birds using similar resources together-received one distance estimate based on the central location of the flock. Observers were trained not to record an individual bird more than once, although the interstand and intrastand movements of large flocks of birds increased the likelihood of double counting, and not to record birds that were outside the sampled stand.

During the first two winters (Manuwal and Huff 1987), two observers visited a stand on the same day, surveying birds simultaneously but taking opposite routes. Simultaneous surveys were deemed necessary because of limited funds and the additional safety it provided for observers traversing mountainous terrain during winter. Time elapsed between the two observers counting at the same station ranged from 4 hours to 15 minutes. We summed the counts from the 12 stations by each observer separately. In total, the two observers visited each stand four times, and abundance was reported as a mean of the eight visits to each stand each winter.

Surveys conducted during the third winter, 1985-86, did not use a simultaneous approach (two observers per day per stand); rather, one observer visited each stand each day. The eight total visits/stand were rotated between two observers.

Biases were introduced by our sample design; as a consequence, our results were interpreted cautiously. Verner (198 1) categorizes bird-survey biases into four general sources: observer, bird species, site selection, and sample schedule; a thorough discussion of these biases can be found in Ralph and Scott (198 1). Our comparisons between winters were assumed to be suspect because different observers were used between winters, and the sampling technique was modified for the 1985-86 surveys. Hence, we made few comparisons between winters and highlighted only the most extreme differences: those we subjectively assumed to be real and not a result of sampling error. On the contrary, we assumed within-winter comparisons between mid- and late-seral stands to be unaffected by the design problems.

The skill and experience of field observers to detect and identify birds, estimate flock sizes, monitor bird movements, and estimate detection distances accurately was crucial to minimizing the error associated with sampling birds. Although some differences between observers were to be expected, determining the exact magnitude to correct this error was too costly to measure and analyze. We took indirect measures to minimize interstand observer variability, however, by apportioning the eight samples per stand equally between the two observers for every stand. An unknown amount of disturbance by observers, either repelling or attracting birds, occurred during the surveys, however.

Some potential sampling errors related to species and sample schedule that could not be controlled in the experimental design included the rate of detectability during winter (bird present but not detected); the differential detectability between species and between stands; the rate of bird mortality between species and stands, and the effects of weather-especially temperature-over the season, on bird presence and cue emission. Unknown sample error related to site selection and survey design included potential differences in the total area sampled per stand resulting from differences in shape of survey routes, intersample area homogeneity, including the elevational change within and between stands; differences in stand history and stand age; and degree of landscape fragmentation surrounding the sample area, which was assumed to be minor.

Data Analysis

Limitations of the data-This study was designed as a simple survey of winter bird abundance. The data were exploratory in that stands were chosen subjectively, sample size was small, and some biases were uncontrolled. No hypotheses were tested and, consequently, no overall alpha level was designated. We reported P-values using nonparametric tests as a way of showing the trends in variation among the stands sampled. Because an a priori goal of this study was to identify which species and guilds are more abundant in old-growth forests than in younger forests, we reported P-values from one-tailed tests.

Vegetation-All comparisons between the four mid- and four late-seral stands of vegetation characteristics were made with the Mann-Whitney U test where $n_1 = 4$ and $n_2 = 4$ (Siegel 1956). Because no a priori goals were established for vegetation analysis, two-tailed tests were used to examine differences between mid- and late-seral stands. The association between different vegetation variables was measured by using Spearman rank correlation in which r_s was the coefficient of association. Vegetation variables were assumed to be correlated if r_s was 20.643 ($n = 8$; significance level for two-tailed test = 0.100).

Birds-Only birds detected 175 m from the counting station (half the distance between stations) and species detected during more than one survey (vagrants removed) at a given stand were included in the main analysis. A separate supplemental analysis using all bird detections was used for wide-ranging and nocturnal species, such as hawks and owls, which were poorly sampled by the point-count method, and for species not easily detected <75 m from a counting station.

Median bird species richness was determined as the median number of bird species per stand per winter. Distribution and abundance patterns combined from all three winters and all stands were plotted together to identify species patterns. The distribution categories, based on the proportion of stands in which a species occurred, were widespread, >67 percent; irregular, 33 to 66 percent; and local, <33 percent of the stands per winter Abundance categories were common, >8; uncommon, 2 to 8; and scarce, <2 birds detected of a given species per eight visits.

All comparisons of total abundance, species abundances, and abundance within avian guilds between the four mid- and four late-seral stands were made using the Mann-Whitney U test, where $n_1 = 4$ and $n_2 = 4$. The avian guilds, each identified by forest structure and spatial components and by preferred food, were canopy seed eaters; canopy insectivore; bark insectivores; and understory seed eaters and insectivores. Species were placed in a guild based on field observations and compiled literature (fig. 1). Nearly all the observed species could be categorized into one of the four guilds. Gray and Steller's jays, because of their low numbers and omnivorous diets, were not included in the guild comparisons. Some species regularly change or supplement their diets within and between seasons with several different resources that are not easily cross-categorized. Examples are chestnut-backed chickadees, identified as canopy insectivores, and red-breasted

CANOPY SEED EATERS Evening grosbeak Pine siskin Red crossbill White-winged crossbill	**CANOPY INSECTIVORES** Chestnut-backed chickadee Golden-crowned kinglet
BARK INSECTIVORES Red-breasted nuthatch Brown creeper Hairy woodpecker Pileated woodpecker Red-breasted sapsucker	**UNDERSTORY SEED EATERS AND INSECTIVORES** American robin Dark-eyed junco Song sparrow Varied thrush Winter wren

Figure 1—Bird species listed by guild as determined by variables of forest structure, spatial components, and preferred foods.

nuthatches, identified as bark insectivores; both species also rely on seeds in their diets during winter. Hence, we view the guild framework only as a general guide for ordering abundance patterns.

We compared our findings to a winter bird study of four mid- and four late-seral stands surveyed in 1984-85 and 1985-86 near Mount Rainier National Park; the study used the same field methods as we did (Manuwal and Huff 1987; K. Aubry and J. Putera, unpubl. data). We used a two-tailed, Mann-Whitney *U* test, where $n_1 = 4$ and $n_2 = 4$ unless stated otherwise, to compare late- and mid-seral stands.

Mean abundances of each species were paired by late- and mid-seral stands within each survey year and study area. Each pair was ranked by highest and lowest mean abundance and summed for mid- and late-seral stands. The continuity of the ranked distributions within and between winters were examined using the sign test (Siegel 1956).

Relation to habitat—Spearman rank correlation between vegetation variables and bird abundance (mean of the three winter surveys) was assumed to be associated if $r_s \geq 0.643$ ($n = 8$; significance level for two-tailed test = 0.1). All vegetation variables associated with bird abundance were examined for colinearity.

Results

Weather

Weather records from the Carson Fish Hatchery, near Carson, Washington, showed that the wettest of the three winters was 1983-84, but it also was the winter with the least snow (figs. 2, 3). More than twice as much snow fell in 1984-85 and 1985-86 than in 1983-84. In 1985-86, the winter of greatest snowfall, >65 cm of snow fell each month from November through February. December was the coldest month in the winters 1983-84 and 1985-86, while January was the coldest month of 1984-85 (fig. 4). The survey season, December through March, was coldest in 1985-86, averaging 0.4 °C, and warmest in 1983-84, averaging 1.8 °C (fig. 4).

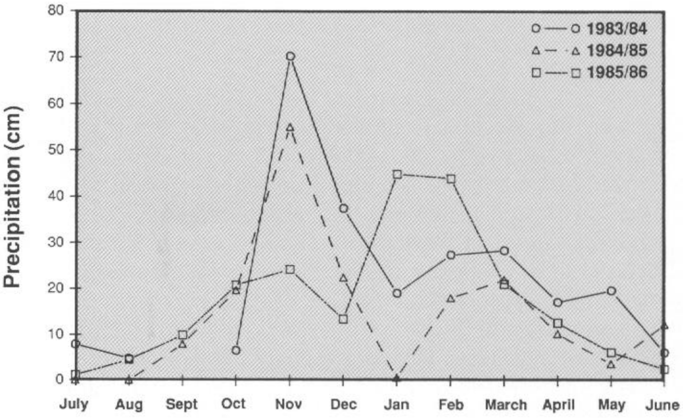


Figure 2—Monthly precipitation from July 1983 to June 1986 at the Wind River National Fish Hatchery near Carson, Washington.

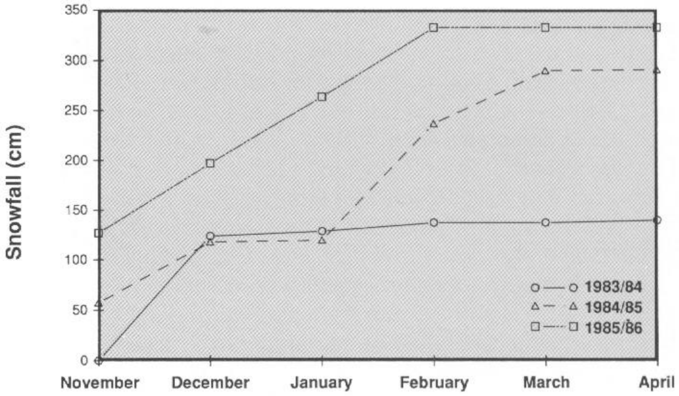


Figure 3—Cumulative snowfall over three winters at the Wind River National Fish Hatchery near Carson, Washington

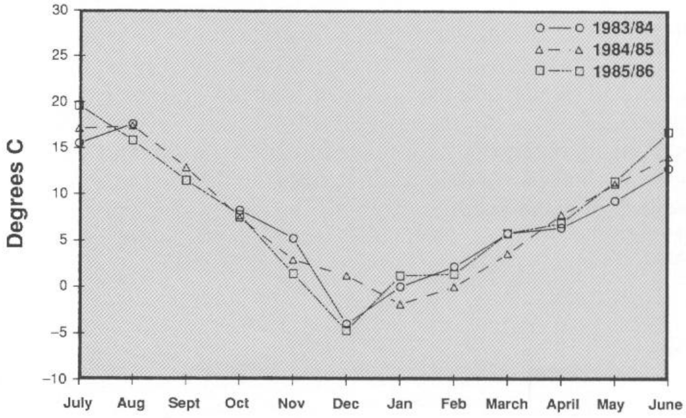


Figure 4—Monthly mean temperatures from July 1983 to June 1986 at the Wind River National Fish Hatchery near Carson, Washington.

Table 1—Means and standard deviations of vegetation variables within mid- and late-seral stands in the southern Washington Cascade Range

	Mid-seral		Late-seral			
Vegetation variable	Mean	SD	Mean	SD	U[a]	P[b]
Density (stems per ha):						
All live trees	712	588	375	96	7	>0.500
Live trees 5-9 cm d.b.h.	245	290	497	92	4	0.342
Live trees 10-24 cm d.b.h.	337	379	125	43	8	>0.500
Live trees 25-49 cm d.b.h.[c]	181	122	64	16	3	0.200
Live trees 50-99 cm d.b.h.	65	71	59	22	8	>0.500
Live trees >100 cm d.b.h.[c]	3	2	27	7	0	0.028
Live broadleaved deciduous trees	17	9	7	9	1	0.058
Live Douglas-fir[c]	544	430	36	14	0	0.028
Live western hemlock	98	128	172	47	4	0.342
Live Pacific silver fir[c]	4	8	96	78	0	0.028
Snags 10-49 cm d.b.h. and 5-15 m tall	59	36	8	5	0	0.028
Snags 10-49 cm d.b.h. and >15 m tall[c]	8	11	1	1	2	0.114
Snags >50 cm d.b.h. and >15 m tall[c]	2	2	11	5	0	0.028
Basal area (m^2 per ha)						
All live trees	53	13	72	11	2	0.114
Live deciduous trees[c]	0.4	0.5	0.1	0.1	3	0.114
Live Douglas-fir[c]	49	11	38	17	4	0.342
Live western hemlock[c]	2	2	27	8	0	0.028
Live Pacific silver fir	—[d]	—	3	2	0	0.028
Volume (m^3 per ha):						
All snags	123	92	284	99	2	0.114
All logs	150	69	299	45	0	0.028
Diameter (cm):						
All snags	30	6	62	21	0	0.028
Cover (percent):						
High shrub (0.5-2 m tall)	52	16	19	2	0	0.028
Low shrub (<0.5 m tall)	50	11	35	8	3	0.200
Deciduous shrub (0-2 m tall)	54	16	22	4	0	0.028

[a] Mann-Whitney U statistic.

[b] Two-tailed test.

[c] Vegetation variables highly correlated (Spearman rank) with mean abundance of one or more bird species.

[d] Less than 0.1.

Vegetation and Stand Structure

Mean total live-tree density was higher in mid- than late-seral stands but varied considerably between stands (table 1). In mid-seral stands, Douglas-fir and western hemlock averaged 76 percent and 14 percent of the total density, respectively. In late-seral stands, the shade-tolerant species, western hemlock and Pacific silver fir, averaged 72 percent of the total density, whereas Douglas-fir averaged only 10 percent of the total density. Broadleaved deciduous trees were a minor component of the stand composition, with only 3 and 2 percent of the total density in mid- and late-seral stands, respectively. Nevertheless, the higher density of broadleaved deciduous trees in mid-seral stands (table 1) was visually evident within the stands.

In contrast to total-tree density, mean total basal area was higher in late- than mid-seral stands (table 1). Douglas-fir, despite its low density in late-seral stands, contributed 53 percent of the total basal area, primarily large trees. In late-seral stands, western hemlock and Pacific silver fir comprised only 38 and 5 percent of the total basal area, respectively. Douglas-fir dominated the basal area in the mid-seral stands, with 93 percent of the total basal area.

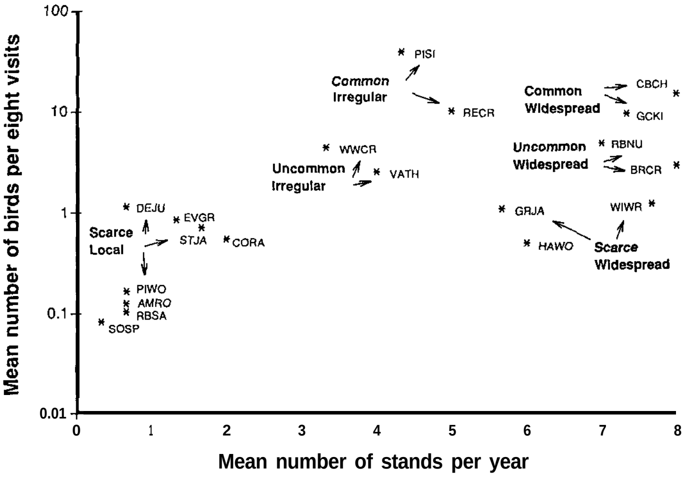


Figure 5-General distribution and abundance of the major bird species wintering in the study area, AMRO = American robin, BRCR = brown creeper, CBCH = chestnut-backed chickadee, CORA = common raven, DEJU = dark-eyed junco, EVGR = evening grosbeak, GCKI = golden-crowned kinglet, GRJA = gray jay, HAWO = hairy woodpecker. PISI = eine siskin, PIWO = pileated woodpecker. RBNU = red-breasted nuthatch, RBSA = red-breasted sapsucker, RECR = red crossbill, SOSP - song sparrow, STJA = Steller's jay, VATH = varied thrush, WTWR = winter wren, and WWCR = white-winged crossbill.

Late-seral stands generally had more trees in the 5- to 9-cm and >lOO-cm d.b.h.-classes; in mid-seral stands, density was substantially higher in the 25- to 49-cm size-class (table 1). Larger mean snag volumes and snag diameters were observed in late- than mid-seral stands (table 1). Very large snags, >50 cm d.b.h. and >15 m tall, were nearly six times more abundant in late- than mid-seral stands (table 1). Mean density of snags 10 to 49 cm d.b.h. and 5 to 15 m tall was eight times higher in mid- than late-seral stands. The volume of logs on the forest floor was substantially higher in late- than mid-seral stands (table 1).

Mean cover estimates of high (0.5 to 2 m) and low (<0.5 m) shrubs were higher in mid- than late-seral stands (table 1). Deciduous shrubs had about twice the cover in mid- than late-seral stands.

General Distribution and Abundance Patterns of Winter Birds

Over the three winters sampled, 27 bird species were recorded in the eight study sites. Nineteen of the 27 species were detected ≤ 75 m from a counting station and at least twice in a stand (fig. 5). The 11 species described below are "characteristic" of the study region in winter, based on their abundance and distribution. Canopy insectivores-the chestnut-backed chickadee and golden-crowned kinglet-were the most common and widespread species (fig. 5). Uncommon but widespread species were the bark-insectivores-red-breasted nuthatch and brown creeper, Also widespread but scarce were the winter wren, gray jay, and hairy woodpecker. Seed eaters-pine siskins and red crossbills-were detected irregularly but were common relative to most other species (fig. 5). Uncommon and irregular species were the white-winged crossbill and varied thrush. Eight species were classified as local and scarce because of their low detection rate and limited distribution (fig. 5), they were assumed to be a numerically minor component of the winter bird community.

Bird Species Richness

During all three winters, median bird species richness was higher in late- than mid-seral stands. The largest differences were detected in winters 1983-84 and 1984-85, when the median by year was 10 (range = 9 to 11) and 11 (range = 8 to 11) species in late-seral stands and 7 (range = 5 to 8) and 6 (range = 5 to 7) species in mid-seral stands. In 1985-86, the difference was less; median bird species richness was 11.5 (range = 10 to 14) species in late-seral and 10.5 (range = 9 to 14) species in mid-seral stands.

Total Abundance

In our study region (Wind River), mean total abundance was substantially higher in late- than mid-seral stands for all three winters (table 2). In 1983-84, nearly three times more birds were detected in late- than mid-seral stands (Mann-Whitney U [hereafter U] = 0; P = 0.014). In winters 1984-85 and 1985-86, late-seral stands had more than twice the number of birds than mid-seral stands (1984-85: U = 0; P = 0.014) (1985-86: U = 1; P = 0.029). Total abundance over the three winters averaged 48 and 113 birds per stand per visit in mid- and late-seral stands, respectively.

The largest differences in total abundance between winters were from 1984-85 to 1985-86 within both mid- and late-seral stands (table 2), when about 5- and 6-fold increases were detected, respectively. Although differences in total abundance between 1983-84 and 1984-85 were small relative to the high number of birds detected in 1985-86, nearly twice as many birds were detected in late-seral stands in 1983-84 than in 1984-85.

Guilds

Over the three winters, more birds were detected in the canopy seed-eater guild than the other three guilds examined, although marked differences occurred between winters (table 3). In 1983-84 and 1984-85, most of the detections were canopy insectivores, whereas in 1985-86, canopy seed eaters comprised nearly 70 percent of the birds detected (table 3). In all three winters, detections of bark insectivores were substantially fewer than of canopy insectivores; understory seed eaters and insectivores were detected in very low numbers (table 3).

Table 2—Means and standard deviations of total abundance of birds (mean number of detections/visit) in mid- and late-seral stands in the southern Washington Cascade Range

		Winter					
		1983-84		1984-85		1985-86	
Location	Seral stage	Mean	SD	Mean	SD	Mean	SD
Wind River	mid-	21	6	19	2	106	39
Wind River	late-	60	17	39	5	238	74
Mount Rainier	mid-	—[a]	—	14[b]	4	118[c]	17
Mount Rainier	late-	—[a]	—	23[b]	9	243[c]	61

[a] No survey in 1983-84.

[b] Data from Manuwal and Huff (1987).

[c] K. Aubry and J. Putera, unpubl. data.

Table 3—Percentages of birds in four guilds detected over 3 winters in the southern Washington Cascades

	Winter			
Guild	1983-84	1984-85	1985-86	Combined[a]
Canopy seed	23	16	69	55
Canopy insect	52	56	21	30
Bark insect	21	25	5	10
Understory insect/ seed	4	3	5	5
Total	100	100	100	100

[a] Data pooled across all three winters.

Table 4—Significance levels of one-tailed Mann-Whitney *U* tests of differences between late and mid-seral stand counts (mean number of birds detected/visit) by guilds and by years, with the *a priori* assumption that abundance was higher in late-seral stands

	Winter					
	1983-84		1984-85		1985-86	
Guild	*U*[a]	*P*[b]	*U*	*P*	*U*	*P*
Canopy seed	1	0.029	0	0.014	1	0.029
Canopy insect	1	0.029	3	0.100	4	0.171
Bark insect	2	0.057	0	0.014	4	0.171
Understory insect/ seed	1	0.029	5	0.243	7	0.443

[a] Mann-Whitney *U* statistic.

[b] One-tailed test.

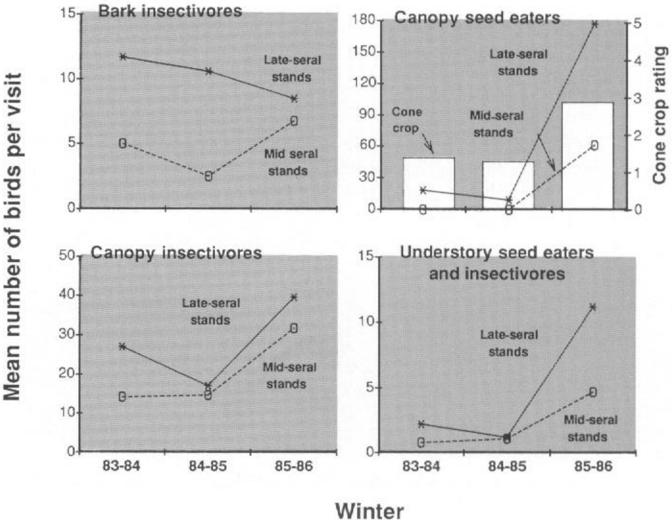
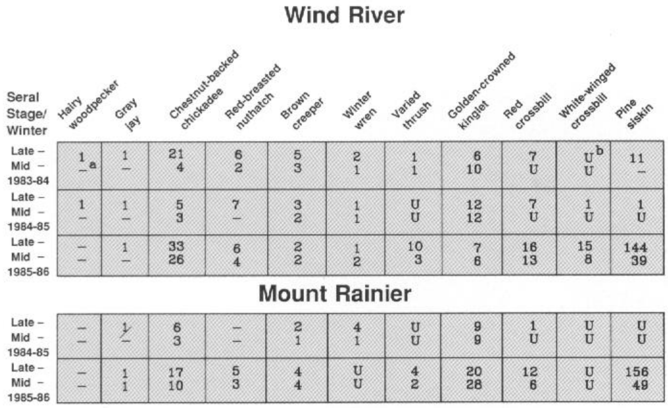


Figure 6—Abundance patterns (mean number of birds/visit) of four guilds in winter and histogram of cone-crop rating by year (absent/failure = 1, very light = 2, light = 3, medium = 4, heavy = 5).

Late-seral stands had consistently higher mean bird abundances than mid-seral stands for all four guilds examined (fig. 6). In winters 1983-84 and 1984-85, the canopy seed eaters were uncommon to common in late-seral stands, yet they were detected in low numbers or not detected (1984-85) in mid-seral stands (fig. 6, table 4). In winter 1985-86, seed eaters were relatively common in both mid- and late-seral stands, but were nearly three times more abundant in late-seral stands (fig. 6, table 4).



Wind River

Seral Stage/ Winter	Hairy woodpecker	Gray jay	Chestnut-backed chickadee	Red-breasted nuthatch	Brown creeper	Winter wren	Varied thrush	Golden-crowned kinglet	Red crossbill	White-winged crossbill	Pine siskin
Late – 1983-84	1	1	21	6	5	2	1	6	7	U[b]	11
Mid – 1983-84	–[a]	–	4	2	3	1	1	10	U	U	–
Late – 1984-85	1	1	5	7	3	1	U	12	7	1	1
Mid – 1984-85	–	–	3	–	2	1	U	12	U	U	U
Late – 1985-86	–	1	33	6	2	1	10	7	16	15	144
Mid – 1985-86	–	–	26	4	2	2	3	6	13	8	39

Mount Rainier

Seral Stage/ Winter	Hairy woodpecker	Gray jay	Chestnut-backed chickadee	Red-breasted nuthatch	Brown creeper	Winter wren	Varied thrush	Golden-crowned kinglet	Red crossbill	White-winged crossbill	Pine siskin
Late – 1984-85	–	½	6	–	2	4	U	9	1	U	U
Mid – 1984-85	–	–	3	–	1	1	U	9	U	U	U
Late – 1985-86	–	1	17	5	4	U	4	20	12	U	156
Mid – 1985-86	–	1	10	3	4	U	2	28	6	U	49

Figure 7—Abundance (mean number of birds/visit) of species by years and by mid- and late-seral stands in the study areas at Wind River and Mount Rainier ([a] <0.5 birds/visit; [b] undetected).

Table 5—Sign tests of the number of bird species with abundance (mean number of detections/visit) highest in late- compared to mid-seral stands over 3 winters at Wind River and 2 winters at Mount Rainier

	Winter					
	1983-84		1984-85		1985-86	
Study area	Ratio[a]	*P*[b]	Ratio	*P*	Ratio	*P*
Wind River	8:1	0.020	8:0	0.004	8:1	0.020
Mount Rainier	—[c]	—	5:0	0.031	5:1	0.109

[a] Ratio of number of species with mean abundance higher in late- compared to mid-seral stands.

[b] One-tailed sign test.

[c] No survey in 1983-84.

Mean abundance of bark insectivores over the three winters fluctuated from 2.3 to 4.0 to 1.3 times more abundant in late- than mid-seral stands (fig. 6, table 4). Generally, differences in abundance of understory insectivores and seed eaters and overstory insectivores between late- and mid-seral stands were less than the differences for other foraging guilds. In 1983-84, however, detections of overstory insectivores in late-seral stands substantially outnumbered those in mid-seral stands (fig. 6, table 4).

Species Patterns

Mean abundances of species detected in late- and mid-seral stands were compared over the three winters, and more species reached their highest mean abundance in late- than mid-seral stands (fig. 7, table 5). In 1983-84, the golden-crowned kinglet was the only species more abundant in mid- than late-seral stands (fig. 7). In 1984-85, all species had mean abundances either highest in late-seral stands or the same as mid-seral stands (fig. 7). In 1985-86, only the winter wren was more abundant in mid-seral stands (fig. 7).

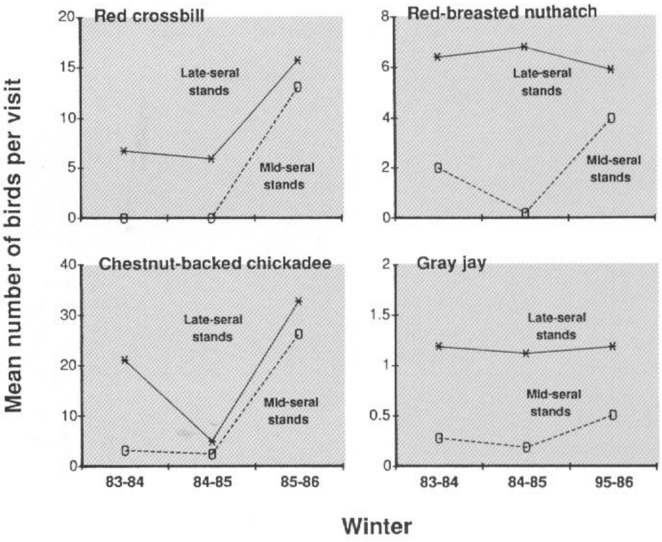


Figure 8—Abundance (mean number of birds/visit) of four species in mid- and late-seral stands over three winters.

Red crossbills were not detected in mid-seral stands in 1983-84 and 1984-85, yet substantial numbers of them were detected in late-seral stands (fig. 8) (1983-84 and 1984-85: $U = 0$; $P = 0.014$). In 1985-86, when detections of red crossbills were high in both late- and mid-seral stands, variability between stands was also high (fig. 8) ($U = 7$; $P = 0.443$).

Mean abundance of red-breasted nuthatches in late-seral stands varied little between 1983-84 and 1985-86 (fig. 8) but was substantially higher than mid-seral stands in 1983-84 ($U = 1$; $P = 0.029$) and 1984-85 ($U = 0$; $P = 0.014$). In 1985-86, differences in abundance between mid- and late-seral stands were noticeably less (fig. 8) ($U = 4$; $P = 0.100$). Counts of red-breasted nuthatches, using a 3-year average, were 13.5 times higher in late- than in mid-seral stands.

Mean abundance of chestnut-backed chickadees was consistently higher in late-seral stands in all three winters, but differences varied between winters (fig. 8). The most substantial difference between mid- and late-seral stands was in 1983-84 ($U = 0$; $P = 0.014$). Even though mean abundance of chestnut-backed chickadees was low in both mid- and late-seral stands in 1984-85, abundance was consistently higher in late-seral stands ($U = 0$; $P = 0.014$). Chestnut-backed chickadees, like red crossbills, were detected more often in 1985-86 than in previous winters, but variability between

Table 6—Means and standard deviations of the abundance (mean number of detections/visit) of seed eaters in mid- and late-seral stands over 3 winters, using all distances and distances ≤ 75 m

	Mid-seral stage				Late-seral stage			
	≤ 75 m		All distances[a]		≤ 75 m		All distances	
Species winter	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pine siskin:								
1983-84	—[b]		1	1	11	22	32	49
1984-85	u[c]	u	u	u	1	1	1	1
1985-86	39	33	60	34	144	44	190	64
Red crossbill:								
1983-84	u	u	2	2	7	5	47	49
1984-85	u	u	—		7	6	11	7
1985-86	13	6	27	4	16	6	28	9
White-winged crossbill:								
1985-86	8	3	19	1	15	15	30	13

[a] Includes birds detected flying in and above (but close to) the tree canopy.
[b] Uncommon = <0.5 detections/visit.
[c] Undetected.

Table 7—Percentage of detections/visit of seed-eaters in mid- and late-seral stands over 3 winters, using all distances and distances ≤75 m

	Mid-seral stage		Late-seral stage	
Species and winter	≤ 75m	All distances[a]	≤ 75m	All distances
Pine siskin:				
1983-84	1	3	99	97
1984-85	0	0	100	100
1985-86	21	24	79	76
Red crossbill:				
1983-84	0	4	100	96
1984-85	0	—[b]	100	98
1985-86	45	49	55	51
White-winged crossbill:				
1985-86	34	38	66	62

[a] Includes birds detected flying in and above (but close to) the tree canopy.
[b] Less than 0.5 percent.

mid- and late-seral stands was also higher ($U = 6$; $P = 0.343$). Using a 3-year mean, chestnut-backed chickadee abundance was 2.7 times higher in late- than mid-seral stands.

The gray jay, relatively rare in both mid- and late-seral stands (fig. 8), was 4.2 times commoner in late than in mid-seral stands. We detected substantially more gray jays in late- than mid-seral stands in 1983-84 ($U = 2$; $P = 0.057$) and 1984-85 ($U = 1$; $P = 0.029$) relative to 1985-86 ($U = 4$; $P = 0.171$).

Supplemental Analysis of Troublesome Species

By examining the data using no limit on the detection distance (see Methods, Data Analysis—Birds), we found four additional species, northern pygmy-owl, pileated woodpecker, common raven, and northern goshawk, with sufficient detections to at least identify some patterns. The northern pygmy-owl, a forest bird that has not been well studied in the Pacific Northwest, showed the most striking pattern: all 12 detections over the three winters occurred in late-seral stands. The three other species were detected in both mid- and late-seral stands but slightly more often in late-seral stands: pileated woodpecker had 58 percent of 43 detections in late-seral stands; common raven had 59 percent of 162 detections; and northern goshawk had 57 percent of 14 detections in late-seral stands.

The seed eaters, red and white-winged crossbills and pine siskin, were often detected in large numbers >75 m from a count station (table 6). Nevertheless, the proportion of detections within late- and mid-seral stands generally remained the same for either detections ≤75 m or all detections (tables 6 and 7).

Relations to Habitat

The abundance of eight bird species showed strong correlations with certain of the vegetation variables measured. Chestnut-backed chickadees, pine siskins, and red-breasted nuthatches increased in abundance as the density of Douglas-firs decreased (table 8). The abundance of red crossbills and brown creepers increased with western hemlock basal area. Low density of live Douglas-firs and high basal area of live

Table 8—Spearman rank correlations of vegetation variables highly correlated with mean abundance of birds in the southern Washington Cascade Range during the winter

Species	Vegetation variable	r_s[a]	P[b]
Hairy woodpecker	Live trees 25-49 cm d.b.h. (no. per ha)	-0.74	0.050
Gray jay	Deciduous trees (m^2 per ha[c])	-0.68	0.079
Chestnut-backed chickadee	Douglas-fir (no. per ha)	-0.88	0.010
Red-breasted nuthatch	Douglas-fir (no. per ha)	-0.95	0.001
Brown creeper	Western hemlock (m^2 per ha[c])	0.64	0.100
Golden-crowned kinglet	Douglas-fir (m^2 per ha[c])	-0.79	0.035
Red crossbill	Western hemlock (m^2 per ha[c])	0.74	0.050
Pine siskin	Douglas-fir (no. per ha)	-0.83	0.020

[a] Spearman rank correlation coefficient.

[b] Two-tailed test.

[c] Basal area.

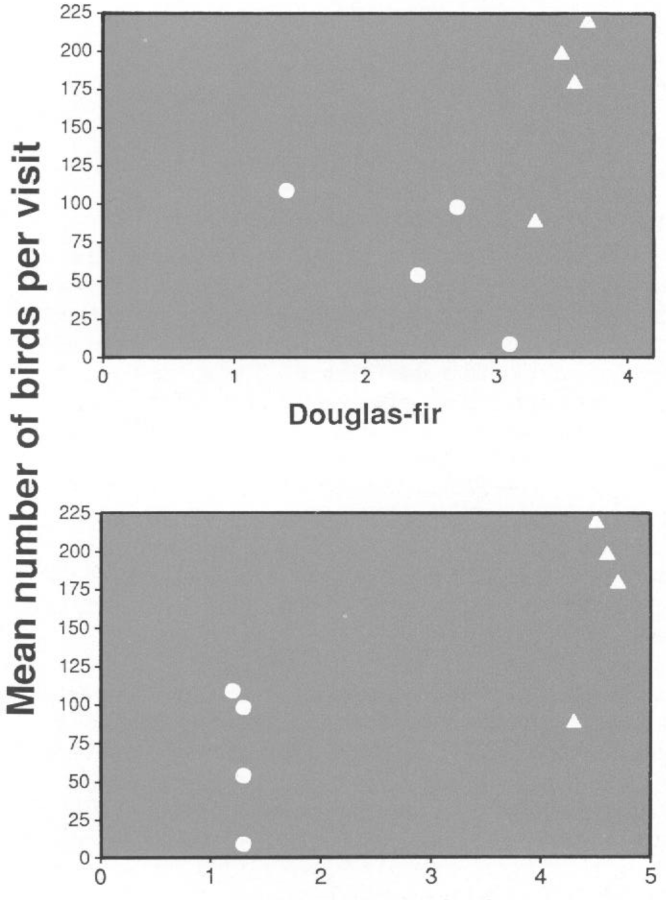


Figure 9—Abundance of seed eaters (mean number of birds/visit) in 1985-86 in mid-seral (circles) and late-seral (triangles) stands relative to cone-crop rating of Douglas-fir and western hemlock (absent/failure = 1, very light = 2, light = 3, medium = 4, heavy = 5).

western hemlocks were strongly associated with the late-seral stands (table 1). In addition, gray jay abundance was negatively associated with the basal area of live deciduous trees, and hairy woodpecker abundance decreased as density of medium-sized live trees (25 to 49 cm in d.b.h.) increased (table 8).

A poor cone crop was produced by western hemlock and Douglas-fir in the southern Washington Cascades before the 1983-84 and 1984-85 surveys, but a good cone crop was produced before the 1985-86 surveys (fig. 6). Seed-eater abundance, substantially higher in 1985-86 than in 1983-84 and 1984-85 (fig. 6), generally paralleled the annual variation associated with the cone crop.

The 1985 cone crop surveyed in the study stands during winter 1985-86 rated substantially larger in late- than mid-seral stands for both tree species (fig. 9) ($U = 0$; $P = 0.014$). Generally, seed eater abundance was high in stands with large cone crops of Douglas-fir and western hemlock (fig. 9).

Discussion

Results generally confirmed earlier studies showing that old-growth (late-seral) stands in general provide better winter habitat for most bird species than do younger forests (Manuwal and Huff 1987). For example, total bird abundance in late-seral stands was at least double that of mid-seral stands (table 2); nearly every major species detected in the study stands had higher mean abundances in late-seral stands (fig. 7); and seed-eating and bark-foraging species were conspicuously more abundant in late-seral stands (fig. 6). Gray jays, red-breasted nuthatches, and red crossbills appeared to prefer old-growth over younger stands. Only the brown creeper, previously identified by Manuwal and Huff (1987) as being significantly more abundant in old-growth forests, showed an unexplainable trend counter to earlier results (fig. 7).

During winters 1984-85 and 1985-86, our results were similar to those from near Mount Rainier: more birds were detected in late- than mid-seral stands (Mount Rainier, 1984-85: $U = 4$; $P = 0.342$) (Mount Rainier, 1985-86: nl = 3; n2 = 4; $U = 0$; $P = 0.028$); mean total abundance was higher in 1985-86 than 1984-85; and mean total abundance in 1985-86 was similar between the study regions (late-seral stands: $n_1 = 3$; $n_2 = 4$; $U = 6$; $P = >0.500$) (mid-seral stands: $U = 7$; $P \geq 0.500$) (table 2). Only in 1984-85 was mean total abundance different between regions (mid-seral stands: $U = 2$; $P = 0.228$) (late-se& $U = 0; P = 0.028$) (table 2).

At both Mount Rainier and Wind River, more species reached their highest mean abundance-in late- than in mid-seral stands. Overall, 71 percent of the comparisons between bird abundances in mid- and late-seral stages were highest in late-seral stands, 6 percent highest in mid-seral stands, and 23 percent the same. At Wind River, 77 percent of the mean abundance comparisons were highest in late-seral stands, but at Mount Rainier, 59 percent were highest in late-seral stands.

Species that were consistently more abundant in late-seral stands in four or more comparisons between winters and study areas were the chestnut-backed chickadee (sign test; $n = 5$, $x = 5$; $P = 0.031$), red crossbill ($n = 5$, $x = 5$; $P = 0.031$), gray jay ($n = 4$, $x = 4$; $P = 0.063$), and red-breasted nuthatch ($n = 4$, $x = 4$; $P = 0.063$) (fig. 7). Conversely, no species was consistently more abundant in mid-seral stands. In addition, pine siskins were notably higher in late-seral stands ($n = 4$, $x = 4$; $P = 0.063$). although few, they were not detected in 38 percent of the late- and 88 percent of the mid-seral stands in winters 1983-84 and 1984-85 (tables 6,7).

Pronounced fluctuations in abundance between years and seasons are typical of bird populations (for example, Hejl and others 1988, Holmes and others 1986, Smith 1982b). Not only were substantially more birds detected in 1985-86 than in the previous two winters (table 2), but abundance within all four guilds was higher in 1985-86 in both mid- and late-seral stands, except for bark insectivores in late-seral stands (fig. 5). Explaining the reasons for observed fluctuations between years is difficult, primarily because interactions within the environment are complex and difficult to measure thoroughly. Different observers between winters, a modification of the survey design in 1985-86, and differential detectability between winters potentially related to weather (figs. 2,4) could account for some or all of the differences. Because total abundance increased more than 5-fold from 1984-85 to 1985-86, more birds were likely present in 1985-86 than in previous winters, despite the potential biases and the fact that birds may have responded to availability of critical resources before and during the winter of 1985-86.

Variations in the number of birds detected between winters were exemplified by the seed eaters, namely red and white-winged crossbills and pine siskins. Detections of seed eaters increased 26-fold from 1984-85 to 1985-86 and accounted for 69 percent of the birds detected in 1985-86 (table 3). We believe that the abundance and movements of seed eaters, as reported elsewhere (for example, Benkman 1987, Bock and Lepthien 1976, Haapenen 1966), was closely associated with the type and size of conifer cone crop produced. During our 3-year study, the abundance of seed eaters closely tracked the cone crop of Douglas-fir and western hemlock within the southern Washington Cascades region (fig. 6).

Higher basal area of western hemlocks in late- than in mid-seral stands (table 1) is one of several factors that may explain the higher number of detections of seed eaters in late-seral stands (table 4, fig. 6). Western hemlock, a prolific seed producer, has heavy cone crops more regularly than does Douglas-fir and, unlike Douglas-fir, produces large quantities of seed even in dense-canopied stands (Fowells 1965). Furthermore, western hemlock releases its seed slowly throughout the winter, but 70 to 90 percent of Douglas-fir seeds can be dispersed before the end of October (Isaac 1943), possibly before many of the seed eaters arrive on their southward migration.

A possible explanation for the higher number of detections of bark foragers in late- than mid-seral stands (table 4, fig. 6) could be a shift in foraging activities and substrate use by resident bark foragers during the winter (Morrison and others 1985, Travis 1977), most likely in response to seasonal differences in insect prey location and availability (Connor 1979b). In a companion study in the southern Washington Cascades, bark foragers-such as red-breasted nuthatches-exhibited shifts in foraging behavior during the winter, most notably in old-growth stands, by significantly increasing their use of large-diameter Douglas-firs relative to their availability and by using a lower position on the tree bole away from tree branches (Lundquist and Manuwal 1990). They also found that bark-foraging species, except for the brown creeper, foraged primarily on trees >50 cm in d.b.h. in both spring and winter but used trees >50 cm in d.b.h. more frequently in winter than in spring.

The abundance of brown creepers and red-breasted nuthatches, which feed by probing bark crevices while searching for arthropods, may in part be related to the concentration of prey sites. Bark arthropod abundance and availability are positively correlated with tree size, bark characteristics, and possibly tree species (Morrison and others 1985, Nicolai 1986). In the southern Washington Cascades, bark furrows of Douglas-fir-used extensively by arthropods-increase in depth and surface area with increasing bole diameter

(Mariani and Manuwal 1990). We suspect that the higher number of large-diameter trees (>100 cm in d.b.h.) in late- than mid-seral stands (table 1), and the well-protected furrows they provide for overwintering arthropods may have resulted in higher counts of bark foragers in late-seral stands.

Chestnut-backed chickadees foraged on tree species in proportion to availability in late-seral stands during spring, but shifted during winter to western hemlock significantly more than it was available (Lundquist and Manuwal 1990). Western hemlock comprised 46 and 38 percent of the total tree density and basal area, respectively, in our late-seral stands and was nearly twice as dense and 13 times higher in basal area in late- than in mid-seral stands. This difference may explain why more chestnut-backed chickadees were detected in late- than in mid-seral stands (fig. 8), but the reasons they prefer western hemlock in winter are still not clear.

Based on the substantial differences in bird abundance between mid- and late-seral stands, we recommend that additional studies be done to substantiate the observed patterns over a wider geographic area.

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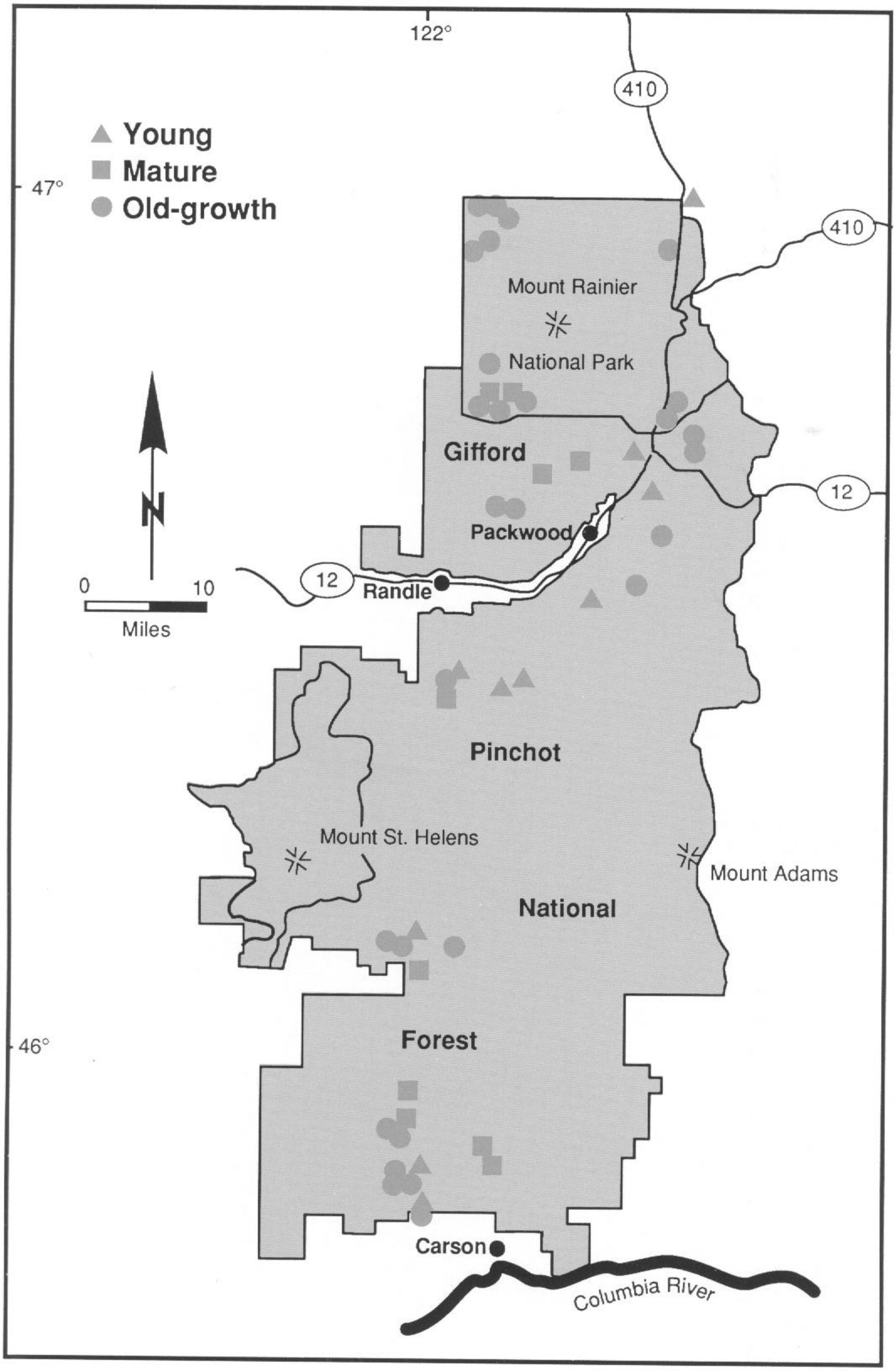

Location of study sites.

Continue

Nesting Habitat and Abundance of Snag-Dependent Birds in the Southern Washington Cascade Range

Richard W. Lundquist and Jina M. Mariani

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Abstract

We examined abundance patterns and nesting-habitat use of eight cavity-nesting bird species and the brown creeper, by using point-count data collected during the breeding seasons of 1984 and 1985 and nesting data collected from 1983 to 1986 in the southern Washington Cascade Range. Naturally regenerated Douglas-fir/western hemlock forest stands were sampled, representing one of three general age-classes: young (55-80 years), mature (95-190 years), and old-growth (210-730 years). Stands within the old-growth age-class also represented a variety of moisture conditions.

Woodpeckers showed no clear and consistent abundance patterns among forest age- and moisture-classes. Vaux's swifts were consistently more abundant in old-growth stands (all moisture-classes) in both 1984 and 1985. During both 1984 and 1985, chestnut-backed chickadees were most abundant in wet old-growth stands, red-breasted nuthatches were most abundant in dry old-growth stands, and brown creepers were most abundant in mesic old-growth stands. In general, counts of most of the bird species we studied were lowest and most variable in young and mature stands.

We found few consistent bird-habitat correlations, Numbers of both chestnut-backed chickadees and Vaux's swifts correlated most strongly with density of live trees >lOO cm in diameter at breast height (d.b.h.), and swift counts correlated with density of snags >50 cm d.b.h. Except for swifts, relative abundances of snag-dependent bird species were not well-predicted by densities of snags, perhaps because all forest stands sampled were naturally regenerated and contained numerous snags.

Except for chestnut-backed chickadees, few nests of any cavity-nesting species were found in young stands. Most of the chickadee nests found in young stands, however, were in old remnant snags, not in trees produced in the current stands. Cavity nesters disproportionally selected large, hard snags for nesting. In particular, selection of hard snags by hairy woodpeckers in this study area contrasted with findings of other studies in the Pacific Northwest, on which current management guidelines have been based. Woodpeckers and creepers used western white pine snags disproportionately, but chickadees and nuthatches nested primarily in Douglas-fir and western hemlock. Disproportionate use of certain tree species for nesting was probably closely related to their decay characteristics. Sample plots centered on nest trees of all species contained higher densities of large, hard snags than randomly sampled vegetation plots. Management recommendations for Douglas-fir forests of the Washington Cascades include retention of tall, hard snags ≥ 76 cm d.b.h. for all species. White pine snags are particularly important for woodpeckers and creepers, and Douglas-fir and western hemlook snags should be retained for chickadees and nuthatches. In designing snag-retention areas, managers should provide adequate snag distribution over large areas, live-tree replacement, and patches of older stands.

Introduction

Two of the goals of the Old-Growth Forest Wildlife Habitat Program were to identify species that may depend on or find optimum habitat in old-growth forests and to determine features of these stands that distinguish them as better habitat-particularly species that depend on elements lacking in managed forests. Snags are often removed, either because of safety or fire hazard, or because they are commercially useful (Lowery and others 1977, Snellgrove 1977, Snellgrove and Fahey 1977, USDA Forest Service 1976).

Several studies have shown the importance of snags to many wildlife species, especially birds, for nesting, feeding, shelter, communication, and resting (Balda 1975, Conner and others 1975, Haapanen 1965, Marcot 1983, McClelland 1977, Raphael and White 1984). Although cavity-nesting birds and snags have been studied in various locations in the Pacific Northwest (Bull 1980, Cline and others 1980, Madsen 1985, Mannan and others 1980, Zamowitz and Manuwal 1985), to date no study has examined habitat preferences in the productive Douglas-fir/western hemlock forests of the Washington Cascade Range. Because use of nesting and foraging habitat by cavity-nesting birds in these forests may differ from that in other regions of North America or other forest types in the Pacific Northwest, forest managers need specific local information to provide adequate habitat for these species in light of conflicting values placed on snags. In response to this need, we began our study in 1983. Our objectives were to compare relative abundance estimates of snag-dependent bird species across an array of Douglas-fir forest stands of different age- and moisture-classes; to examine the relation between bird abundance estimates and densities of live trees and snags in these stands; to characterize nesting sites of bird species in various stand age-classes and to evaluate use of forest habitat elements for nesting in relation to their availability; and to discuss management considerations for cavity- and bark-nesting birds in the Southern Washington Cascades Province.

Methods

Study Area

This study was done in the Southern Washington Cascades Province (Franklin and Dyrness 1973) west of the Cascade Crest in the Gifford Pinchot National Forest and in Mount Rainier National Park. Forty-eight forest stands represented young (55-80 years old, n = l0), mature (95-190 years old, n = l0), and old-growth (210-730 years old, n = 28) age-classes (see frontispiece). All stands originated from natural disturbance; that is, they have undergone no silvicultural manipulation. All stands were in the Western Hemlock Zone (Franklin and Dyrness 1973); because of limited availability of sufficiently large stands, particularly low-elevation old growth, eight stands (six old-growth, one mature, one young) were above 1000-m elevation at the upper end of the Western Hemlock Zone, where the transition to the Pacific Silver Fir Zone begins. Stands ranged from 404- to 1218-m elevation.

During spring and summer of 1986, cavity-nesting birds were studied on a subset of 17 stands in the Packwood and Randle Ranger Districts of the Gifford Pinchot National Forest and in the southern part of Mount Rainier National Park. Six stands were young, five were mature, and seven were old-growth.

The general study area is dominated by a maritime climate (Brubaker, this volume) characterized by cool, wet winters and warm, dry summers. Most precipitation occurs between October and April, but annual and monthly precipitation can vary greatly among years.

Vegetation Sampling

Vegetation and habitat characteristics were measured in nested circular plots (0.05 and 0.2 ha) centered on each of 12 bird count stations systematically located in each stand. We tallied live trees by species and diameter at breast height (d.b.h.) (l- to 10-, 11- to 50-, and >50-cm classes in the 0.05-ha plot plus a >lOO-cm class in the 0.2-ha plot). We counted snags by species, diameter-class (l0-19 cm in the small plot and 20-49 and 250 cm in the large plot), and decay-classes (1 to 4, from hardest to most decayed, modified from Cline and others 1980). Sampling criteria conformed with standard protocols established for other studies.

To obtain more detailed information on snag attributes and densities, snags (standing dead trees 210 cm in d.b.h. and 22 m tall) were also characterized, measured, and tallied in a 30-m-wide belt transect consisting of 11 l00-m-long segments along lines between bird counting stations in each stand. All snags 250 cm in d.b.h. and the first five snags in each of two smaller d.b.h.-classes (l0-19 cm and 20-49 cm) counted within each segment were characterized by species, diameter (cm), height (m), decay-class, number of limbs, bark remaining (percent), top condition (intact or broken), needle presence, presence and number of excavated cavities, and presence of woodpecker feeding sign. All subsequent snags in the two smaller diameter-classes in each segment were then tallied by decay- and height-class (2-5 m, >5 m).

Bird Abundance Counts

Bird populations were sampled on all stands during the spring breeding seasons of 1984 and 1985 by the point-count method. Verner (1985) and selected references in Ralph and Scott (1981) describe the technique in more detail. For a more detailed description of the sampling design and constraints, see Carey and Spies (this volume). In the southern Washington Cascades, each stand contained 12 count points systematically located 150 m apart and at least 75 m from roads or edges of adjacent habitat.

Each stand was visited six times between 25 April and 12 July 1984, and between 30 April and 28 June 1985. During each visit, detections of all bird species were recorded during 8-minute periods at each counting station after a l-minute pause on arrival at the station. To the extent possible, observers avoided double-counting of individual birds from multiple stations during each visit to a stand, particularly with wide-ranging species such as woodpeckers.

Observers were trained and tested in bird identification (both aural and visual cues) and distance estimation for 1 week beginning each sampling season to improve consistency among observers (Kepler and Scott 1981). Stands were assigned so that at least two observers visited each stand alternately during a given season (and across seasons) where possible. Limited time and resources and long distances between groups of stands prevented us from attaining a more optimal stand assignment as a way of limiting observer bias and variability. Fifteen observers assisted in the bird counts, of which three participated both years.

Nest- and Cavity-Tree Searches

In 1983-85, nests were most often discovered during routine bird counts. Stands were also searched after morning counts or on days when weather prohibited counting. In 1985, we devoted additional days exclusively to nest searches on a subset of stands.

In 1986, one observer systematically searched a subset of stands for nests between 22 May and 3 July. Each stand was visited twice: searches began in the early morning and continued until the entire stand was covered, usually by mid-afternoon. Only one stand was visited per day. Two field assistants briefly helped search two stands in each forest age-class. Search time was standardized as much as possible on all sites during all years. Because some areas were sampled more years than others (for example, Wind River pilot studies), however, total search time differed among stands that were not included in the 1985 and 1986 searches.

We confirmed activity at potential nest or roost trees following the criteria of McClelland (1977) except that for purposes of analysis, we treated active roost and active nest sites together as active trees. Where no adult was observed entering a cavity, the tree was termed simply a "cavity tree." We classified inactive cavities into the following categories based on general cavity size and shape (dimensions compiled from Bent 1964): pileated woodpecker (7.6-11 cm, oval); northern flicker (6.9-7.5 cm, round); unidentified small woodpecker, representing both hairy woodpeckers and red-breasted sapsuckers (3.8-5.1 cm, round); and unidentified nonwoodpeckers, representing chestnut-backed chickadees and red-breasted nuthatches (12.5 cm, irregularly shaped).

Characteristics recorded for each nest and cavity tree included the following: tree species, status (live or dead and top condition, after McClelland 1977), decay-class (after Cline and others 1980), diameter-class, and height (m); percentage of bark remaining; number of limbs >l m long remaining; origin of tree (current or previous forest stand) and presence of fire scar; and surface evidence of heartwood decay. Decay evidence was classified as in McClelland (1977). Additional nest characteristics included height of active nest above ground (m) and evidence of use by birds (either direct or indirect).

We sampled vegetation characteristics surrounding each nest and cavity tree in concentric 0.05-ha and 0.2-ha circular plots, centered on the nest tree, in a manner identical to that used for vegetation plots surrounding the bird-count stations.

Data Analysis

We used simple counts to analyze point-count bird abundance data. Raphael (1987a) showed that simple counts can provide as good an estimate of relative abundance as more complex techniques (Burnham and others 1980, 1981; Emlen 1971,1984; Reynolds and others 1980), when analyses are limited to within-species trends across similar (forested) habitats. Thus, for our analyses, we assumed equal detectability of each bird species among forest age- and moisture-classes.

Because all stands received equal sampling effort in both years, we report number of detections recorded during count periods per visit (total count at each stand divided by six visits) for each species and year. For wide-ranging and less frequently encountered species such as woodpeckers, we departed from the standard protocol by including detections beyond the 75-m limit. For the smaller woodpeckers, detection distances did not exceed 150 m, and for the larger species, none exceeded 250 m. In addition, Vaux's swifts were typically detected while foraging on the wing in or near the forest canopy. As a result, we included all detections of swifts that were apparently using the stand, even though no distance estimate could be made because of their movements.

Differences in bird species' abundances among forest age- and moisture-classes were tested by a series of one-way analyses of variance (ANOVA) and multiple range tests (Zar 1984). ANOVA is generally robust to small departures from normality and to moderate heterogeneity of variances when sample sizes are nearly equal (Sokal and Rohlf 1981). We log-transformed bird counts [$\log_{10}(x+1)$] before analysis to meet the underlying assumptions of normality and equality of variances more closely. The log transformation, as opposed to others, best approximated normality and made the means independent of variances. Based on Bartlett's test (Sokal and Rohlf 1981) on the log-transformed data, sample variances were sufficiently homogeneous ($P > 0.05$).

We should caution, however, that the inferential statistical procedures performed on our data should be viewed as exploratory, rather than as conclusive demonstrations of statistical significance. Although the study stands represent a wide range of geographic and environmental conditions in the region, they do not represent a random sample. Moreover, bird count stations were not sampled randomly. Therefore, conclusions on abundance patterns or relation to habitat should be viewed with caution.

We examined associations between counts of each bird species and habitat variables in two different but related ways. First, we computed Spearman rank correlation coefficients (SPSS, Inc. 1986) to look for significant correlations between tree and snag densities and counts of each bird species. For this analysis, we first summarized vegetation data into the seven most commonly occurring tree species (or groupings), with the four d.b.h. classes of live trees and two decay-classes (hard = classes 1 and 2, and soft = classes 3 and 4) of snags.

This large set of variables was reduced to 22 (appendix table 7) by examining highly significant correlations among vegetation variables. Any pairs of variables with correlations >0.50 (explaining >25 percent of each other's variances) were either combined into one, or the more ecologically interpretable variable was retained, whichever was appropriate. Thus, variables such as all live trees >100 cm d.b.h. or live western hemlock ≤ 50 cm d.b.h. were created.

In computing a large number of correlations, some may appear statistically significant (that is, $P < 0.05$) because of random sampling error. We therefore focused on correlations with the same sign (positive or negative) in both years, and emphasized those that were significant at $P < 0.01$. We considered conflicting results, such as correlations that were positive one year and negative the next, as possible evidence of Type I error (Marcot 1984, Meslow and Keith 1971). Even correlations that are consistently significant demonstrate numerical association only, not necessarily some biologically meaningful cause.

Second, we further investigated associations between bird-abundance counts and tree and snag densities by means of stepwise multiple linear regression (Kleinbaum and Kupper 1978, using SPSS, Inc. 1986). This approach generated equations explaining each bird species' abundance from vegetation variables and was used for descriptive, rather than predictive, purposes. The stepwise procedure evaluates each variable to be entered while controlling for variables already in the equation. Because of low sample size ($n = 48$ stands) and some remaining intercorrelations, we generated a new, smaller set of uncorrelated vegetation variables using factor analysis (Afifi and Clark 1984). The initial factors, each of which is a linear combination of all (22) original variables and explains a known amount of the total variance in vegetation data, were extracted by principal components analysis with the Varimax rotation to ease interpretation. We interpreted the factors with a minimum eigenvalue of 1.0 (Battacharyya 1981) by examining the relative sizes of correlations ("loadings") between the factors and original variables.

Bird counts and vegetation variables were first log-transformed for regression analyses to meet underlying distributional assumptions more closely. We regressed transformed counts of each bird species on vegetation factor scores separately for 1984 and 1985 data. Because of the number of equations generated and time limitations, we were unable to search for better fits with polynomial and interaction terms, which may explain some species distributions more fully (Meents and others 1983). We evaluated the accuracy of each regression equation by the adjusted coefficient of determination (adjusted R^2), an unbiased measure of the percentage of total variation in bird abundance explained by the equation (Sokal and Rolff 1981: 661; Zar 1984: 336) and by the standard error of estimate for the equation [(MSE), Kim and Kohout 1975: 331; Draper and Smith 1981: 20,34].

We also explored among-species variation in nest-tree characteristics by means of principal components analysis without rotation. Seven of the 11 nest-tree variables used in the analysis were entered as dichotomous variables, coded as 0 if the attribute was absent and 1 if it was present. These included top condition (broken, intact), tree condition (alive, dead), fire evidence (absent, present), and four tree species variables: Douglas-fir, western hemlock, western white pine, and other. A variable describing number of limbs (>1 m long) present was coded into intervals of 10 branches: 1 to 10 (coded 1), 11 to 20 (coded 2), and so on, or 0 if absent. We entered the other variables-tree diameter, tree height, and percentage of bark remaining (arcsine-transformed)-as continuous variables.

As with the regression analyses above and in other studies (Conner and Adkisson 1977, James 1971, Rotenberry and Wiens 1981, Whitmore 1977), principal components analysis is often used as a data reduction and ordination technique to describe habitat relationships among breeding bird species. For this analysis, however, it was used only as a first-order exploratory tool to identify attributes that accounted for much of the variation in nest trees.

For all nests except those of brown creepers, we used two-group linear discriminant function analysis (Lachenbruch 1975), using SPSSX (SPSS, Inc. 1986) to compare nest-site vegetation structure with samples representing general stand vegetation structure. We selected stand vegetation plots (those centered at bird-counting stations not containing nest trees) randomly from those stands where nests were found in two ways, and a separate analysis was done for each of them. The first sample was stratified so that the number of "random" plots equaled the number of nest-site vegetation plots in each forest age-class. This gave each age-class the same weight in both groups (nest site and random) and equalized the sample size of each group in the data set. The second sample was stratified to equalize the groups by stand to correct for disproportionately large numbers of nest plots on any given stand.

We included 15 variables in the analysis: percentage cover by logs (decay-class 1); percentage cover by deciduous shrubs or trees 0-2 m and 2-15 m tall; total canopy cover (>15 m tall) (all percentage-cover variables recorded on an octal scale); average height of dominant canopy trees (in 8-m intervals); total density of live trees 1 to 10 cm, 11 to 50 cm, 51 to 100 cm, and >100 cm in d.b.h.; total density of hard snags 10 to 19 cm, 20 to 49 cm, and ≥ 50 cm in d.b.h.; total density of soft snags 20 to 49 cm and ≥ 50 cm in d.b.h.; and density of stumps and stubs (snags <5 m tall and 210 cm in d.b.h.). All variables for the analysis were log-transformed. We recorded nest-site vegetation data for 58 of the active nests and for 23 of the trees with inactive cavities ("random" search data) for a total sample size of 81.

We performed the stepwise discriminant analyses using Wilks' method, and the single function derived was evaluated by the significance of the chi-square statistic based on Wilks' lambda (SPSS, Inc. 1986). We interpreted the discriminant function by examining the magnitude of the pooled within-group correlations between the discriminant score and the original variables (structure matrix) (Hull and Nie 1981, Raphael and White 1984, Williams 1981). We used classification techniques (SPSS, Inc. 1986) based on the same data set used to derive the discriminant function to assess the ability of the function to separate the groups effectively. The proportion of cases correctly classified according to actual group membership indicated the success of the between-groups separation. Further discussions of the theory and application of discriminant analysis can be found in Williams (1981, 1983) and Afifi and Clark (1984).

Where sample sizes permitted, we compared use of snag diameter-class, species, and condition for nesting with availability in the forest by means of log-likelihood G-tests, which are analogous to, and often preferred over, chi-square analysis (Sokal and Rohlf 1981: 704; Zar 1984: 52-53). We used Williams' (1976) correction to the G-statistic to obtain a better approximation to the chi-square distribution, even with only one degree of freedom. This correction appears to be superior to the Yates correction for continuity in such cases (Sokal and Rohlf 1981).

Because of small sample sizes for any one bird species, some pooling was necessary. Also, our samples were not large enough to analyze data comprehensively in multiway contingency tables and to search for interaction among the dimensions. Thus, we analyzed each tree attribute (diameter, species, decay-class) separately. Expected frequencies were calculated from the appropriate snag-density distributions on the stands from which the data came. Because the distribution of snags differed between forest age-classes, we evaluated the use of trees by nesting birds separately in each forest age-class, where possible. For most of the tests, however, small samples forced us to pool young with mature stands (hereafter termed "second growth"). Because live trees with nests or cavities constituted only a small fraction of the total, they were excluded from the tests.

Results

Bird Abundance Among Stand Types

Total counts of the four woodpecker species were generally too low and variable to detect significant differences among the five stand types in either 1984 or 1985 (table 1). All four were detected in all age- and moisture-classes, but not in all stands. Hairy woodpeckers were the most frequently detected, and red-breasted sapsuckers were relatively rare. Except for sapsuckers, total counts of woodpeckers were lowest in mature stands. Counts in old-growth stands varied substantially with moisture-class. Hairy woodpeckers were slightly more common in wet old-growth stands in both years; no consistent pattern was found among old-growth moisture classes between years for northern flickers or pileated woodpeckers.

The four nonwoodpecker species treated here were encountered more frequently than woodpeckers. Mean counts of these species were slightly lower in 1984, but the general

Table 1—Mean number[a] of snag-dependent bird species detected per census, based on point counts in the southern Washington Cascades, spring 1984 and 1985

		Forest type					
Species	Year	Young	Mature	Wet old-growth	Mesic old-growth	Dry old-growth	F[b]
Pileated woodpecker	1984	0.35	0.12	0.42	0.28	0.12	0.17
	1985	.30	.18	.15	.30	.20	.69
Northern flicker	1984	.22	.15	.13	.20	.52	1.43
	1985	.32	.08	.55	.42	.37	2.20
Hairy woodpecker	1984	.60	.37	1.07	.55	.57	2.01
	1985	.52	.65	1.32	.92	.65	1.78
Red-breasted sapsucker	1984	.08	.18	.07	.07	.07	.43
	1985	.05	.22	.17	.28	.07	.58
Chestnut-backed chickadee	1984	3.85	3.33	5.60	4.77	3.97	1.54
	1985	3.57 A[c]	3.85 A	9.77 B	5.58 A	4.15 A	6.35***
Red-breasted nuthatch	1984	3.62 AB	2.15 A	2.10 A	4.18 AB	5.03 B	2.72*
	1985	4.38	4.00	4.07	5.10	6.55	1.10
Brown creeper	1984	1.00 A	2.50 B	2.00 B	2.90 B	2.10 B	3.26*
	1985	2.40 AB	3.40 BC	1.80 A	4.70 C	2.30 AB	4.78*
Vaux's swift	1984	.17 A	.13 A	2.60 B	1.15 B	1.17 B	6.41***
	1985	.28 A	.58 A	2.65 B	2.42 B	2.70 B	11.68***

[a] Calculated as the mean number of birds detected per visit; all stands were visited 6 times each year, and each visit included 12 count periods (8-minute per count period).

[b] Based on 1-way analysis of variance among 5 groups. The significance of the test is indicated by the number of asterisks: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$. Counts were log-transformed for all analyses, but actual numbers are presented here for clarity.

[c] Within each row where the ANOVA was significant (indicated by asterisks), multiple range tests failed to find significant differences ($P < 0.05$) between groups of mean counts sharing the same letter (for example, "A" or "B").

patterns were similar in both years. Vaux's swift was the only cavity-nesting species with counts significantly higher in old growth (all moisture-classes) than in the other forest age-classes ($P < 0.001$) (table 1). Chestnut-backed chickadees were more common in wet old-growth stands, significantly so in 1985 ($P < 0.001$). Red-breasted nuthatches were generally more abundant in dry old-growth stands, significantly so in 1984 ($P < 0.05$). For nuthatches, however, multiple range tests failed to separate mean counts in dry old-growth stands from the other stand types, which may indicate that at least one "Type II" error was committed in the analysis; it can result from small sample sizes (causing a lack of statistical power) or highly variable counts within a given stand type (Zar 1984). On the other hand, the overall ANOVA result could have been a Type I error, but at least the trends were consistent between years.

Brown creeper counts differed significantly among the stand types in both years ($P < 0.05$). In 1984, creepers were significantly less abundant in young stands than all the other stand types. In 1985, multiple range tests failed to detect any significant differences among stand types. Although abundance patterns differed between 1984 and 1985, creeper counts were highest in mesic old-growth stands both years.

Bird Abundance in Relation to Tree and Snag Densities

Correlation analysis—Few bird-habitat correlations were consistently significant in both years. Chestnut-backed chickadee and Vaux's swift counts were most strongly (positively) correlated with density of total live trees >100 cm d.b.h. in both years (table 2). Chickadee numbers also correlated positively with live redcedars 51 to 100 cm in d.b.h. and redcedar snags >50 cm in d.b.h. Swift counts correlated positively with several other kinds of trees and snags that reached maximum densities in old-growth stands (all live *Abies* and other conifers up to 100 cm in d.b.h., live western hemlock 51 to 100 cm in d.b.h., and snags ≥50 cm in d.b.h.). Brown creeper counts correlated positively with densities of hard Douglas-fir snags >50 cm in d.b.h.

Red-breasted nuthatches correlated positively with densities of live vine maple and negatively with redcedar snags 20 to 49 and >50 cm in d.b.h. Hairy woodpecker counts correlated positively only with the density of live hemlocks 51 to 100 cm in d.b.h.; pileated woodpecker, northern flicker, and sapsucker counts did not correlate consistently with any of the vegetation variables tested.

Factor analysis of vegetation variables—Six factors were derived that had eigenvalues greater than 1.0, three of which explained at least 10 percent of the total variance (table 3).

Table 2--Spearman rank correlation coefficients between mean counts of snag-dependent birds and densities of live trees and snags

Bird species	Variable" (tree sizes in cm d.b.h.)	*Year*[a] 1984 (n = 47)	1985 (n = 46)
Pileated woodpecker	(none)		
Northern flicker	(none)		
Hairy woodpecker	Live TSHE[b]51-100	0.32*	0.34"
Red-breasted sapsucker	(none)		
Chestnut-backed chickadee	All live trees > 100	.30*	.40**
	Live THPL51-100	.30*	.40**
	Stumps and stubs	–.33*	–.35*
	THPL snags ≥50	.32*	.37*
Red-breasted nuthatch	Live ACCI 1-50	.43**	.46**
	THPL snags 20-49	–.41**	–.45**
	THPL snags ≥50	–.32*	–.40**
Vaux's swift	AU live trees l-100	.64***	.68***
	Live PSME 1-100	–.55***	–.56***
	Live *Abies I-100*	.39**	.41**
	Live "conifers" l-l 00	.53***	.46**
	Live TSHE 51-100	.43**	.63***
	Live THPL 51-100	.43**	.47**
	All snags IO-19	–.31*	–.37*
	Hard PSME snags ≥50	.30*	.38**
	All TSHE snags ≥50	.46**	.44**
Brown creeper	Hard PSME snags ≥50	.39**	.32*

[a] Only coefficients significant for both seasons and those significant at $P < 0.05$ are shown.
[b] Tree species codes are as follows: ACCI, vine maple; PSME, Douglas-fin TSHE, western hemlock, THPL, western redcedar; *Abies.* Pacific silver fir, grand fir. and noble fir; "conifers," all other conifers except those above.

Table 3-Factors derived by factor analysis on 22 vegetation variables, including percentage of total variation explained, highly associated variables, and factor loadings

Factor[a]	Percentage of total variation	Cumulative percentage variation	Highly associated variables[b] (tree sizes in cm d.b.h.)	Factor loadings
1	31.7	31.7	Live PSME[c] l-100	-0.87
			All PSME snags 20-49	-.82
			All live trees >lOO	.70
			Live ***Abies* 1-100**	.64
			All snags l0-19	-.57
2	14.6	46.3	Live hardwoods 1-100	-.77
			All TSHE snags 20-49	.74
			Live TSHE 51-100	.69
			All Abies snags 20-49	.66
			All TSHE snags 550	.60
3	12.8	59.0	All THPL snags 20-49	.82
			Live THPL 1-50	.80
			All THPL snags ≥50	.67
			Live THPL 51-100	.64
4	7.4	66.5	All PIMO snags ≥50	.87
			All PIMO snags 20-49	.71
			Live otherconif. 1-100	.66
			Hard PSME snags ≥50	.64
5	6.2	72.7	Soft PSME snags ≥50	.87
6	5.5	78.2	Stumps and stubs	.80
			Live TSHE l-50	.67

[a] Factors listed are those extracted by principal components analysis that had eigenvalues greater than 1.0.
[b] Variables listed for each factor are those most highly associated with it (that is, with high factor loadings), as determined by the varimax rotation.
[c] Tree species codes are as follows: PIMO, western white pine; PSME. Douglas-fir, TSHE, western hemlock, THPL, western redcedar; *Abies,* Pacific silver fir, grand fir, and noble *fir;* "conifers," all other conifers except those above.

Together they accounted for 78 percent of the total variance. Variables with high positive loadings on the first factor included densities of live trees > 100 cm in d.b.h. and live *Abies* ≤100 cm in d.b.h., both of which tend to be higher in cooler, moister old-growth stands. Variables with high negative loadings on factor 1 were those typically more abundant in younger stands: densities of live Douglas-fir ≤100 cm in d.b.h., Douglas-fir 20 to 49 cm in d.b.h., and all snags 10 to 19 cm in d.b.h. Thus, stands with high scores on the first factor tended to be older, wetter stands, and those with low scores tended to be younger stands.

The second factor (14.6 percent of the total variance) was highly positively associated with trees and snags that were most abundant in mesic old-growth conditions: densities of western hemlock snags, both 20 to 49 cm and ≥50 cm in d.b.h., live western hemlock 51 to 100 cm in d.b.h., and *Abies* snags 20 to 49 cm in d.b.h. The factor was also highly negatively associated with densities of live hardwoods 1100 cm in d.b.h. The third factor (12.8 percent of the variance) was highly positively associated with western redcedar: snags 20 to 49 cm and ≥50 cm in d.b.h. and live trees ≤50 cm and 51 to 100 cm in d.b.h.

Factors 4 (7.4 percent), 5 (6.2 percent), and 6 (5.5 percent) each accounted for much less of the total variance. Variables with high (positive) loadings on factor 4 were generally those most abundant in drier old-growth sites: western white pine snags 20 to 49 cm and ≥50 cm in d.b.h., live other conifers, including pines, ≤100 cm in d.b.h., and hard Douglas-fir snags >50 cm in d.b.h. Factor 5 was most strongly associated (positively) with soft Douglas-fir snags >50 cm in d.b.h., and factor 6 was most strongly associated with forest elements more abundant in younger stands: total stumps (natural) and stubs, as well as live western hemlock trees ≤50 cm in d.b.h.

Multiple regressions-The multiple regression equations of all bird species accounted for less than half of the observed variation in total counts (table 4). Except for Vaux's swifts and red-breasted nuthatches, the factors entering regression equations for all bird species were not consistent between years. Two factors (1 and 5) entered the equations for swifts

Table 4—Results of stepwise multiple linear regression of mean total counts[a] of snag-dependent bird species with vegetation factors derived from factor analysis of 22 live tree and snag variables (see table 3 for lists of variables highly associated with each factor)

Year, bird species	Step	Variable	Multiple R	Adjusted R^2	SEE[b]	P
Spring 1984:						
Pileated woodpecker	1	Factor 1				
		Constant	0.29	0.06	0.28	0.048
Northern flicker	1	(Factor 6)				
	2	(Factor 1)				
		constant	.45	.17	.26	.007
Hairy woodpecker		(none entered)				
Red-breasted sapsucker	1	(Factor 3)				
		constant	.32	.08	.21	.031
Chestnut-backed chickadee	1	Factor 5				
	2	(Factor 2)				
		constant	.51	.23	.21	.001
Red-breasted nuthatch	1	(Factor 3)				
		Constant	.36	.11	.34	.012
Vaux's swift	1	Factor 1				
	2	Factor 5				
		constant	.64	.38	.39	.000
Brown creeper		(none entered)				
Spring 1985:						
Pileated woodpecker		(none entered)				
Northern flicker		(none entered)				
Hairy woodpecker	1	Factor 5				
		constant	.38	.12	.29	.010
Red-breasted sapsucker		(none entered)				
Chestnut-backed chickadee	1	Factor 1				
		constant	.54	.27	.21	.000
Red-breasted nuthatch	1	(Factor 3)				
		Constant	.41	.15	.32	.004
Vaux's swift	1	Factor 1				
	2	Factor 2				
	3	Factor 5				
	4	Factor 4				
		constant	.67	.39	.43	.000
Brown creeper		(none entered)				

[a] Bird counts and stem densities were log-transformed for the analysis. See the methods section for a description of adjusted R^2.

[b] Values given are standard error of predicted (estimated) bird counts, based on the transformed counts. SEE values were computed as: SEE = $\sqrt{[SSres/(N-k-1)]}$, where SSres = the sums of squares of residuals, N is the number of stands for a given year, and k is the number of independent variables in the equation (Kim and Kohout 1975: 331; see also Draper and Smith 1981: 20 and 34, and Marcot 1984: table 12). Small prediction errors mean the abundance of a given bird species was tightly associated with the given habitat variables, but large prediction errors suggested a loose association.

each year, with factors 2 and 4 also entering the 1985 equation. Thus, high swift counts were associated with high densities of trees and snags abundant in old-growth stands, particularly live trees >100 cm in d.b.h., soft Douglas-fir snags, and, in 1985, also with western hemlock and white pine snags and live trees. Both equations for nuthatches included only factor 3, with a negative coefficient, so nuthatch counts were typically higher in stands with a smaller component of redcedar. This analysis therefore echoed the correlation analysis for both species.

Different factors entered each equation for chestnut-backed chickadees. Factor 5, reflecting a positive association with hard Douglas-fir snags, and factor 2 (with a negative coefficient) entered the 1984 equation, but only factor 1, reflecting

Table S-Active nests and roosts of 9 snag-dependent bird species 1983-86, by forest age-class

Bird species	Young (n = 10)	Mature (n= 10)	Old-growth (n = 28)	Total
	Forest age-class			
Pileated woodpecker	0		2	2
Northern flicker	1	0	2	3
Hairy woodpecker	3	1	14	18
Red-breasted sapsucker	0	2	2	4
Yellow-bellied sapsucker[a]	0	0	1	1
Chestnut-backed chickadee	12	3	6	21
Red-breasted nuthatch	1	3	15	19
Brown creeper	6	7	15	28
Vaux's swift	0	0	1	1
Total	23	16	58	97

[a] This nest was pooled with those. of the red-breasted sapsucker for statistical analyses.

an association with wet old-growth conditions (particularly live trees >100 cm in d.b.h.), entered the 1985 equation. For hairy woodpeckers, northern flickers, pileated woodpeckers, and red-breasted sapsuckers, the factors entered equations for only one of the years. No factors entered creeper equations either year, although in preliminary regression runs using individual variables rather than factors, density of hard Douglas-fir snags ≥50 cm in d.b.h. (with a positive coefficient) was the only variable that entered both years' equations (Mariani 1987).

Nest-Tree Characteristics

We found 109 active nests and roosts of 10 snag-dependent bird species in the southern Washington Cascades from 1983 to 1986. Most of these (n = 98) were on the study stands; the rest were in similar habitat types outside the study stand boundaries. The analyses presented here focus on 96 nests and roosts of the following eight species found on the study stands: pileated and hairy woodpeckers, northern flicker, red-breasted and yellow-bellied sapsuckers, chestnut-backed chickadee, red-breasted nuthatch, and brown creeper (table 5); the single Vaux's swift nest was excluded from the analyses. Restricting analysis to nests found on the study stands allowed for direct comparison between nest site and study site habitat characteristics.

Most (62 percent) of the active nests and roosts of woodpeckers, nuthatches, and creepers were found in old-growth stands (table 5). In contrast, most chestnut-backed chickadee nests were found in young stands. Of the additional 127 trees with cavities of uncertain use found in 1985 and 1986, 55 percent were also in old-growth stands but because 58 percent of our study stands were old-growth, average numbers of nests found per stand were similar for all forest age-classes.

Condition-Few active or inactive nests found on the study sites were in live trees. Although we did not specifically test for use of dead versus live trees for nests or roosts, these data suggest a disproportionate selection of dead trees. Most trees (85-87 percent) on our study sites were alive, but the vast majority of nest and cavity trees were dead. Furthermore, all live trees harboring nests had dead or broken tops.

Size-The mean diameter of all active nest trees found on the study sites was 76 cm, and the mean tree height was 25 m (table 6). Nest trees ranged from 18 to 167 cm in d.b.h. and from 3 to 60 m in height. Mean nest-tree diameters for all bird species were greater than 50 cm; trees with nests of northern flickers had the largest mean nest-tree diameter, and those of brown creepers had the smallest. Flicker nest trees averaged the tallest, and chickadee nest trees the shortest. Nuthatches tended to excavate cavities closest to the top of the nest tree (averaging less than 2 m from the top), and pileated woodpeckers nested farthest from the top (averaging 21 m).

Mean diameter for trees with inactive cavities closely paralleled those of the active nest trees for the respective species (or groupings), even though sample sizes were sometimes small (pileated woodpeckers and northern flickers). In particular, the mean diameter of cavity trees used by small woodpeckers was nearly identical to that of active hairy woodpecker and red-breasted sapsucker nests. The mean diameter of nonwoodpecker cavity trees was between those of active chickadee and nuthatch nests.

On average, trees with inactive cavities were generally shorter, and except for pileated woodpeckers, inactive cavities were also located closer to the ground than active nests (that is, nest-hole height was lower), but this difference may reflect observability bias because active nests higher in trees are easier to spot than inactive ones. Trees with inactive cavities of nonwoodpeckers resembled nest trees of chickadees more closely than those of nuthatches in terms of tree height and height of the cavity above ground. Thus most inactive nonwoodpecker cavities may have been inactive chickadee nests.

The majority of nest trees of both woodpeckers and nonwoodpeckers were >50 cm in d.b.h. (fig. 1). Only two nests (brown creepers) were found in trees <20 cm in d.b.h. Log-likelihood G-tests showed that all cavity-nesting species (grouped as woodpeckers and nonwoodpeckers) used large (>50 cm in d.b.h.) snags disproportionately in all forest age-classes, no matter whether tests included all nest and cavity

Table 6—Mean and standard deviation of diameter at breast height (d.b.h.), height, nest-hole height, and diameter at the nest of all active nest trees of snag-dependent birds on study sites

		Tree d.b.h. (cm)		Tree height (m)		Nest height (m)		Diameter at nest (cm)	
Bird species	*n*	Mean	SD	Mean	SD	Mean	SD	Mean	SD
Pileated woodpecker	2	88.0	19.8	40.0	4.2	19.0	4.2	57.5	24.7
Northern flicker	3	127.7	38.5	46.3	15.0	38.7	20.6	51.0^a	4.2
Hairy woodpecker	18	73.9	33.4	28.6	14.4	17.7	10.4	39.6	15.0
Red-breasted sapsucker	4	76.3	4.8	22.0^a	1.4	15.5	1.7	42.5^a	3.5
Yellow-bellied sapsucker	1	111.0	—	38.0	—	21.0	—	65.0	—
Chestnut-backed chickadee	21	94.0	35.7	17.7	8.6	13.3	8.3	54.5	21.4
Red-breasted nuthatch	19	71.1	31.5	25.3	9.5	23.0	9.9	32.3	15.2
Brown creeper	28	58.8	33.3	25.3	12.9	9.5	5.1	44.2	31.0
All species	96	75.8	35.7	25.3^b	12.7	16.0	10.5	43.8^c	23.2

^{a} Because of missing data, $n = 2$ for this variable.
^{b} Because of missing data, $n = 93$ for this variable.
^{c} Because of missing data, $n = 92$ for this variable.

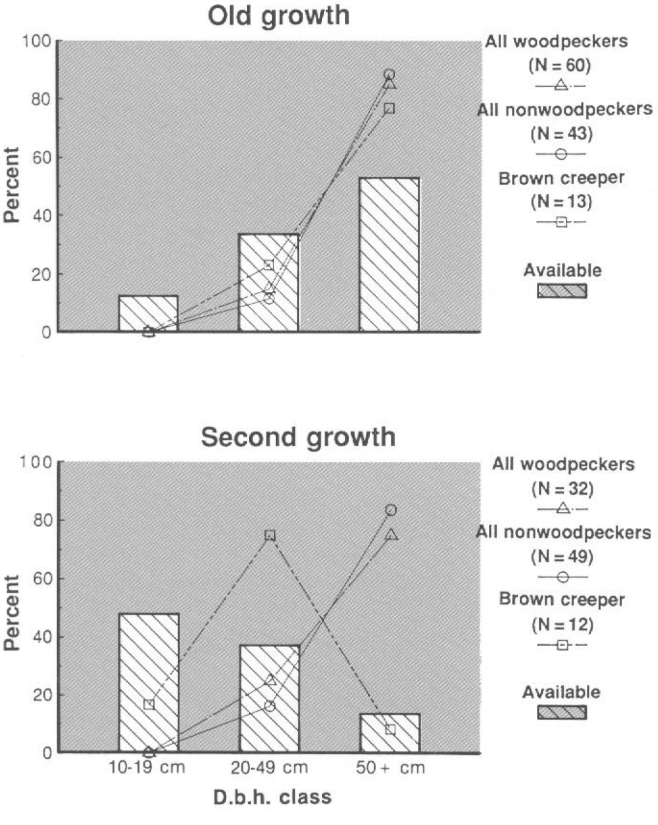

Figure 1—Availability and use of snag diameter-classes for nests and cavity trees by woodpeckers, nonwoodpeckers, and brown creepers.

trees (active and inactive) (*G*-tests, $P < 0.001$) or active trees alone ($P < 0.05$), or whether the smallest category (10-19 cm in d.b.h.) was included or not ($P < 0.05$).

Tests that examined use of snags by diameter-class by small woodpeckers (all but pileated woodpecker and northern flickers) revealed significant selection of snags (>50 cm in d.b.h. ($P < 0.005$), with one exception: active nest trees of small woodpeckers in old growth ($0.10 < P < 0.25$). Although not statistically significant, 14 of those 17 trees were >50 cm in d.b.h.

Brown creepers appeared more flexible than cavity nesters in their use of snag diameter-classes. Although creepers appeared to select large-diameter snags in old-growth stands ($P < 0.05$), no such pattern was apparent in second growth, where 20- to 49-cm-d.b.h. snags were used most often (fig. 1). The mean diameter of creeper nest trees, however, was slightly greater than 50 cm (table 6), and these analyses excluded three nests found in live trees, all >90 cm in d.b.h., two in Douglas-fir and one in a western redcedar.

Decay—The distribution of active nests among snag decay-classes differed somewhat from that of trees with inactive cavities. Of all active woodpecker nest trees, 92 percent (22 of 24) were in decay-classes 1 and 2, only 61 percent of all trees with inactive woodpecker cavities were in these classes. A similar trend held for nonwoodpecker trees: 59 percent (22 of 37) of the active trees and 36 percent (20 of 55) of the inactive trees were in decay-classes 1 and 2 (appendix table 8). This discrepancy may reflect the fact that some inactive trees had old holes with no conclusive evidence of

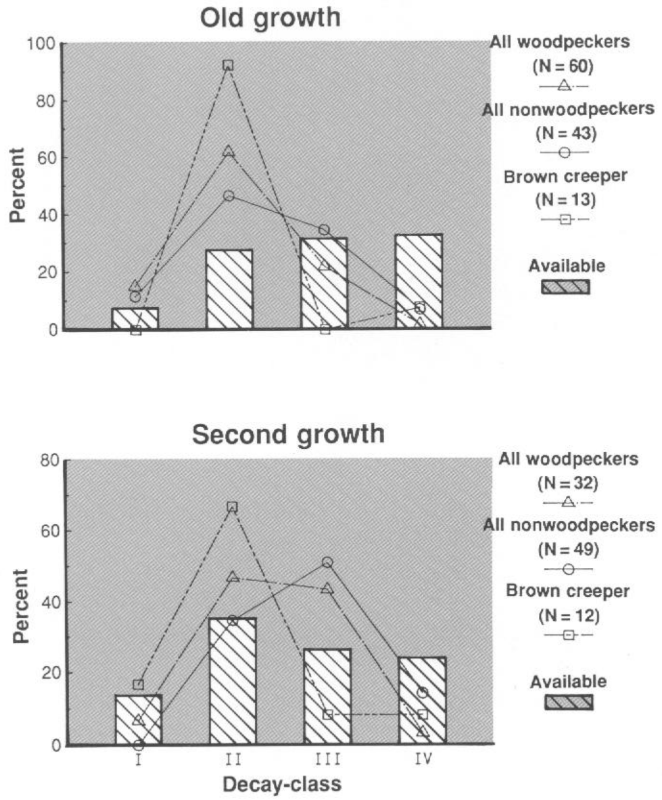

Figure 2—Availability and use of snag decay-classes for nests and cavity trees by woodpeckers, nonwoodpeckers, and brown creepers.

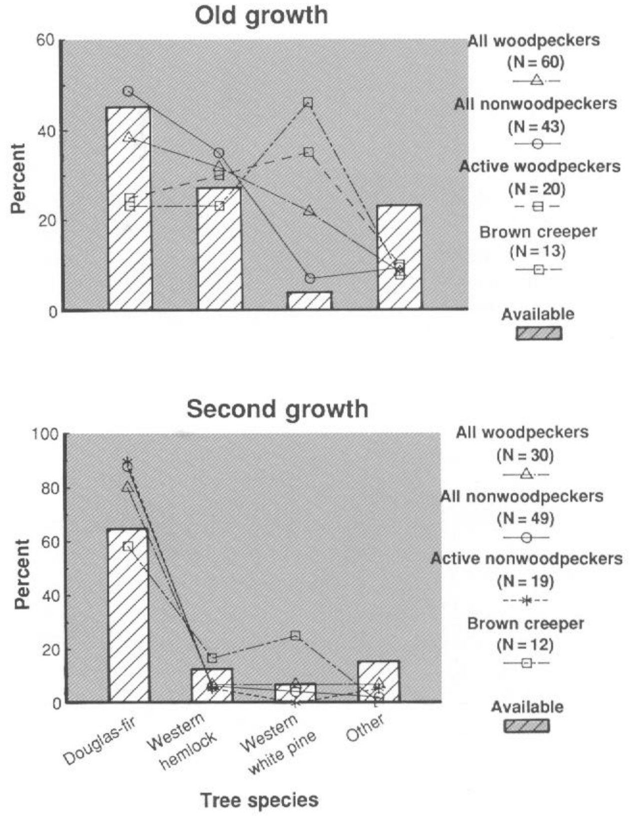

Figure 3—Availability and use of snag species for nests and cavity trees by woodpeckers, nonwoodpeckers, and brown creepers.

recent use. Because old or inactive brown creeper nests are difficult to detect, the sample includes only active creeper nest trees. The vast majority of creeper nest snags (80 percent, 20 of 25) were in decay class 2.

When use of snag decay-classes was compared to availability, small sample sizes again forced us to pool some decay-classes. Brown creepers nested in decay class 1 and 2 snags (pooled together for testing) more frequently than expected in all stand age-classes (*G*-tests, $P < 0.05$). Similarly, in old-growth stands, woodpeckers, chickadees, and nuthatches used snags in decay-classes 1 and 2 disproportionately, no matter whether we considered only active trees or included inactive trees as well ($P < 0.001$) (fig. 2).

In second-growth stands, woodpeckers used snag decay-classes 2 and 3 more frequently than expected ($P < 0.001$) (fig. 2), but the sample included both active and inactive nest trees. Active chickadee and nuthatch nests were found in snags in decay-classes 2 and 3 (pooled) more frequently than expected ($P < 0.025$), but trees with inactive cavities were found in decay-class 3 snags more than expected ($P < 0.001$) (fig. 2).

Tree species—Active nests of cavity-nesting birds were found most commonly in three tree species in the southern Washington Cascades: Douglas-fir, western hemlock, and western white pine. A wide variety of tree species held nests in old growth; most nests found in young and mature stands were in Douglas-fir.

In old growth, woodpeckers used western white pine more than expected (active nests, $P < 0.01$); active plus inactive trees, $P < 0.001$) (fig. 3A). Active nests of all woodpeckers in old growth were most commonly found in western white pine; inactive cavities were most commonly in Douglas-fir. Chickadees and nuthatches nested in western hemlock snags more frequently than expected in old growth, especially when considering only active nests, but not significantly so ($0.10 < P < 0.25$ in both tests).

In second-growth stands, woodpeckers used Douglas-fir snags slightly more than expected, but not significantly so ($0.10 < P < 0.25$) (fig. 3B). Too few active woodpecker nests were found in these stands to evaluate tree species use without including inactive trees. Nonwoodpeckers also used

Douglas-fir more than expected, but use differed from availability only when we included both active and inactive trees together ($P < 0.005$). In young stands alone, nonwoodpeckers (mostly chickadees) also nested in Douglas-fir more than expected ($P < 0.025$).

Like woodpeckers, brown creepers nested most frequently in western white pine snags in old-growth stands, and the proportional use of this species was greater than expected (based on availability) in second growth as well (fig. 3). Sample sizes were too small to test this selection in either forest age-class separately, but creepers used white pine snags significantly more than expected ($P < 0.05$) when tested over all stands combined.

Principal Components Analysis of Nest Tree Characteristics

Five principal component axes had eigenvalues greater than 1.0, four of which accounted for at least 10 percent of the total variance each. All five together accounted for 81 percent of the total variance. The first principal component (27 percent of the total variance) was most highly positively correlated with the number of limbs and most highly negatively correlated with Douglas-fir and with fire evidence. Thus, high values on this axis represented trees with more limbs (and generally less decay); low values corresponded to trees that had fire scars and were more likely to be Douglas-fir.

The second principal component, which accounted for nearly 20 percent of the total variance, was most highly positively correlated with tree height, diameter, and western white pine and most highly negatively correlated with western hemlock. Thus, nest trees with high values on this axis were taller, larger trees with intact tops likely to be western white pine, whereas trees with low values were more likely to be western hemlocks. Little additional insight was gained by interpreting the third and fourth components, each of which accounted for much less variation (13 percent and 11 percent, respectively).

A plot of mean (and standard error) principal component scores along the first two axes illustrates spatial relationships among bird species' nest-tree characteristics (fig. 4). Among the active nests, along axis 1, pileated and hairy woodpeckers, sapsuckers, red-breasted nuthatches, and brown creepers tended to nest in trees with more branches remaining than did northern flickers and chestnut-backed chickadees. The latter species tended to nest in Douglas-firs with fire evidence. The second axis further separated woodpeckers and creepers from chickadees and nuthatches. Woodpeckers and creepers tended to nest in taller, larger trees and more often in white pine. The exceptionally large standard error for sapsuckers was probably the result of a very small sample size ($n = 3$), together with a high degree of variability in nest-tree characters.

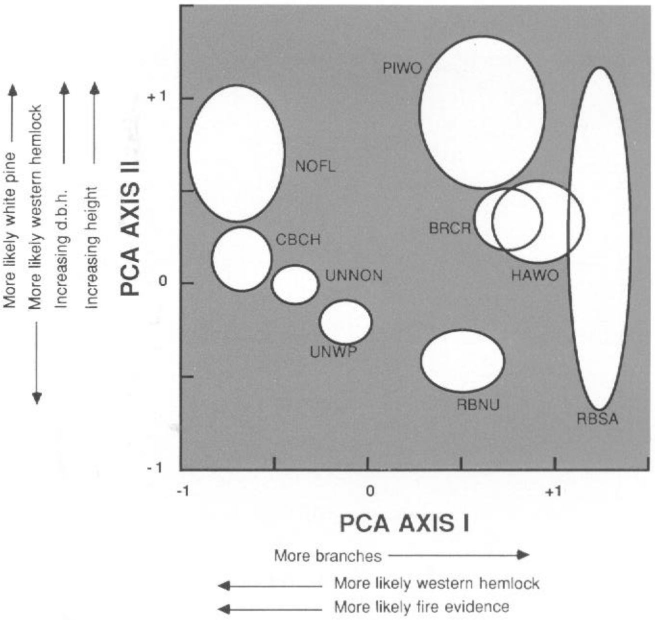

Figure 4—Principal components ordination of nest-tree characteristics of seven bird species and two categories of inactive trees on the first two principal component axes. Ellipses represent mean ± one standard error in principal component scores for each species or grouping. Codes are as follows: PIWO, pileated woodpecker; NOFL, northern flicker; HAWO, hairy woodpecker; RBSA, red-breasted and yellow-bellied sapsuckers; CBCH, chestnut-backed chickadee; RBNU, red-breasted nuthatch; UNWP and UNNON, trees with inactive cavities of woodpeckers and nonwoodpeckers, respectively.

Comparison of Nest-Site Vegetation With General Stand Characteristics

Both discriminant function analyses comparing nest-site vegetation plots with randomly sampled stand vegetation plots produced generally similar results. In both runs, higher proportions of nest sites (77-87 percent) were correctly classified by the discriminant functions than were random plots (72-74 percent).

Five variables entered discriminant equations in both runs: hard and soft snags >50 cm in d.b.h., stumps and stubs, and total canopy cover. The first variable entered, that which best distinguished nest sites from random plots, was either soft snags 20 to 49 cm in d.b.h. or hard snags >50 cm in d.b.h. Based on consistent early entry into the equations and on relatively high correlations with the canonical discriminant functions, the two latter variables, together with total density of stumps and stubs, were the most important variables discriminating nest sites from random plots. As a plot of mean and standard deviation discriminant scores for the two runs including active nest sites shows, nest sites generally had higher densities of hard snags >50 cm in d.b.h. and stumps and stubs, and lower densities of soft snags 20 to 49 cm in d.b.h., than did the random study-site samples (fig. 5).

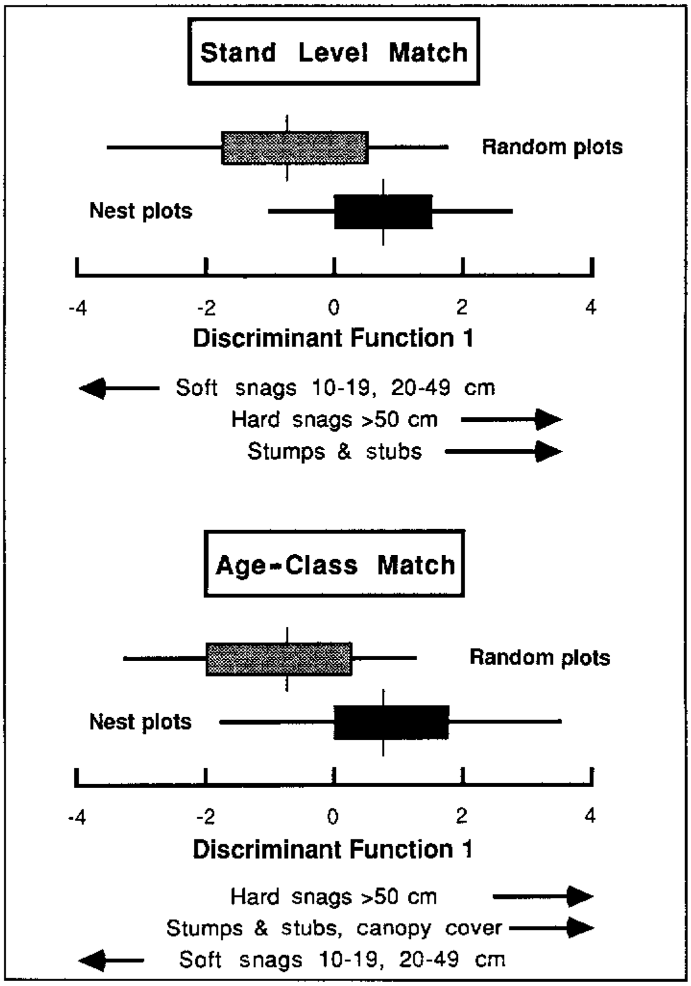

Figure 5—One-dimensional plot comparing mean (vertical bar), ± one standard error (thick horizontal bar), and range (thin horizontal bar) of discriminant scores for active nest-site vegetation plots (n = 81) and random samples (n = 81) of stand vegetation plots. All bird species' nest sites combined. Samples within each analysis were weighted equivalently at the stand level (top graph) and by age-class (bottom).

Discussion

Bird Abundance Among Stand Types

Only the Vaux's swift was significantly more abundant in old-growth stands (all moisture-classes) during both years. Although no other species showed such a strong association with old growth, mean counts of other species reached maximum abundance in one of the old-growth moisture-classes, and patterns were not always consistent between years. Few of these patterns were statistically significant, but the fact that counts of most species were often lowest or more variable in young or mature stands may suggest that these species find more consistently suitable conditions in a specific moisture-class of old growth (that is, chickadees in wet old growth, nut-hatches in dry old growth, and creepers in mesic old growth).

Merely to demonstrate significantly higher abundance in a particular habitat type does not necessarily mean that fitness, as defined by survival and reproductive success, is higher in that habitat (Van Horne 1983). The true evaluation of habitat quality can be made only by including such demographic data for comparison among sites (Wiens and Rotenberry 1981a).

In this study, gathering extensive demographic data on several bird species at once on study stands distributed over such a wide geographic range was impractical. Measures of variation in abundance, such as coefficients of variation (CV), however, may provide a way of evaluating habitat quality (Marcot 1984). This use is based on observations that in less preferred habitats, which were saturated only in high-density years, populations may fluctuate more than in preferred habitats, which were saturated except in lowest-density years (Krebs 1971; O'Connor 1981, 1986). Coefficients of variation varied greatly from year to year and from species to species, but the highest for each species were most often in mature stands. Although we did not test for statistical differences among coefficient of variation for any bird species, this comparison may suggest that mature stands were less suitable habitat than old growth for snag-dependent birds.

Several factors may have contributed to the observed lack of year-to-year consistency in bird abundance among stand types. For instance, harsh winter weather can affect populations of permanent-resident species (Gaud and others 1986, Graber and Graber 1979, Hejl and Beedy 1986, Hejl and others 1988, McClelland 1977) and may explain the generally lower mean counts we observed in 1984 than in 1985. The winter of 1983-84, although similar to long-term means, included periods of substantially higher precipitation and lower temperatures than either the next winter or those means. Several authors (Beedy 1982, Hejl and Beedy 1986, Hejl and others 1988, Raphael and White 1984) have found similar decreases in both permanent and summer resident species after harsh winters in coniferous forests in California.

In addition, observer bias or variability may have contributed to the lack of consistency in abundance patterns (or habitat associations) between years. Problems such as variation in different observers' training, experience, hearing ability, knowledge of local birds, and attentiveness can conceal patterns present in the system studied or cause spurious patterns to occur (see references in Ralph and Scott 1981). Although the effects of observer bias on our data are not known, we attempted to minimize it by conducting training sessions each season, having each stand visited by more than one observer during each year, and maintaining as much continuity of observers between years as possible.

The lack of clear, consistent abundance patterns of woodpeckers among forest age-classes may also be a problem of scale (Wiens 1981a). Woodpecker home ranges may be as large as the area encompassed by the array of count stations on each stand, and much larger for pileated woodpeckers (Bull and Meslow 1977, Mannan 1984b). Although we can assign some association or importance of one or more forest age-classes to wide-ranging species such as woodpeckers, the ability to evaluate habitat quality based solely on relative abundance patterns of these species is necessarily limited when the sampling unit (the stand) is small relative to home-range size. Evaluations of woodpecker occurrence or abundance over larger scale areas that encompass home ranges of many breeding pairs might provide better indices of habitat quality.

A related problem is that higher counts of the more wide-ranging species do not necessarily indicate the presence of nesting pairs. For example, pileated woodpecker counts were relatively high in young stands in both years. No nests or roosts of pileated woodpeckers were found in those stands during our study, but the stands had many snags with recent evidence of pileated feeding. Thus, young unmanaged stands may provide good feeding but not nesting habitat for pileated woodpeckers. This difference may be true for other woodpecker species, too, because few nest or roost trees of any woodpecker species were found in young (or mature) stands.

Other factors complicating the analysis of bird abundance patterns among the stand types are elevation and latitude. The study stands were, by design, distributed over a relatively wide geographic range and, by necessity, over a wide elevational range within this forest type in the southern Washington Cascades. Manuwal and others (1986) found that total bird abundance varied inversely with both elevation and latitude: counts were generally higher in stands lower in elevation and situated farther south in the study area, regardless of stand age. The same was true of the species we studied.

The bird count data were admittedly short term (only 2 years of data). Gaud and others (1986) argue that recommendations based on only 1 or 2 years' data may be inaccurate, and suggests a minimum of 5 years of study to adequately account for yearly fluctuations in bird abundance. The continuation of long-term monitoring on similar stands in the southern Washington Cascades will help clarify the relation of bird abundance patterns to forest stands of different age-classes.

Bird-Habitat Relationships

Relatively few correlations between cavity-nesting bird counts and snag and live-tree densities were consistent or interpretable. The significant correlations found between counts of woodpeckers or nuthatches and trees they were seldom observed using (or the negative associations) may be spurious, or the habitat variables may represent other features not sampled explicitly. The biological significance of the association between hairy woodpeckers and large, live hemlocks is not apparent, except that these trees may serve as future sources of potential nest trees (Zarnowitz and Manuwal 1985).

On the other hand, chestnut-backed chickadees, principally foliage-gleaners, correlated positively with densities of large overstory trees, which probably provide an optimum foraging environment. This correlation may be due to greater abundance of either insects or cones. Large, dominant conifers, particularly Douglas-fir, that are more exposed to the sun's rays are known to produce more cones than codominant trees (Fowells 1965). Similarly, Raphael and Barrett (1984) found that abundance of chickadees, which reached its maximum in old-growth stands in northwestern California, correlated with a principal component axis associated with higher densities of largest Douglas-fir (>90 cm in d.b.h.). In another study in California (Morrison and others 1987), chickadees were positively associated with mean canopy height, which clearly relates to the size of the largest trees.

The association of chickadees with very large western redcedars probably accounted for their greater abundance in wet old-growth stands, as densities of redcedars equaled or exceeded Douglas-firs of comparable size there. Because chickadee numbers were more consistently correlated with live trees than with snags, characteristics of foraging habitat may have been more important than nesting habitat in determining chickadee abundance, given that large, decayed snags and stubs suitable for nesting were relatively abundant in all stands.

Vaux's swifts correlated most strongly with the kinds of trees that provide suitable nesting habitat: very large live trees (mainly Douglas-fir, western hemlock, and western redcedar) and large snags (Douglas-fir and hemlock). Large, broken-topped trees (live or dead) with the trunks hollow at the top are known to harbor nests of Vaux's swifts (Baldwin and Zaczkowski 1963, Jewett and others 1953). During the 1983 pilot study, one swift nest was found in a broken-topped redcedar snag (77 cm in d.b.h., 10 m tall) in an old-growth stand. The need for large broken-topped trees probably accounts for the strong association of swifts with old growth, because these trees are most abundant there. The greater number of large, overstory trees and resulting broken, multilayered canopy in old growth, may however, also provide an optimum foraging environment for swifts, which are aerial foragers. Broken, multilayered canopies of old-growth stands may allow greater access to flying insects surrounding overstory trees than would closed, continuous canopies of younger stands.

Based on our regression analyses, abundance of cavity-nesting birds was not well predicted by live-tree and snag densities. Others (Marcot 1984, Morrison and others 1987, Raphael and Barrett 1984) have also found that habitat variables explain little of the variance in bird abundance. Morrison and others (1987) found their final regression models to predict presence or absence of bird species adequately, but the equations did not clearly track the variation in abundance between years (but see comments by Hejl and others 1988). Problems in elucidating bird-habitat relationships via correlation or regression analysis can result from a variety of factors, including, but not limited to, the following: nonlinear or nonmonotonic relationships; incomplete sampling of habitat gradients; variability in species' responses to habitat features; sampling scale; or not sampling the correct variables (Best and Stauffer 1986). Each is discussed briefly below.

The relation of bird abundance to habitat features can be linear, curvilinear, or otherwise nonmonotonic (Best and Stauffer 1986, Colwell and Futuyama 1971, Meents and others 1983). Some authors (Madsen 1985, Raphael 1980) have found the relation of cavity-nesting bird abundance to snag densities, particularly large snags, to be curvilinear. Meents and others (1983) found that although linear bird-habitat relationships were most common, polynomial variables increased the amount of variance explained by regression equations.

The lack of consistent associations between these bird species and snag densities (the kinds most often used for nesting) may also have been because all the stands were naturally regenerated and contained numerous snags or because they were all canopied stands. The lack may thus be viewed as a form of incomplete sampling of habitat gradients. Most recent studies that demonstrated stronger cavity nester and snag associations in western coniferous forests have included managed stands, where some or all snags have been removed (Balda 1975, Madsen 1985, Mannan and others 1980, Raphael and White 1984, Zamowitz and Manuwal 1985). On our study stands, snag densities may have been above a threshold (sensu Raphael 1980), so that other factors were more predictive of (and limiting to) snag-dependent bird populations. We suspect correlations would be stronger if managed stands or clearcuts lacking high densities of remnant snags were included in the analysis (Verner and Larson 1989).

Even if strong relationships are found, they may change, depending on whether or not the entire habitat gradient is examined (Colwell and Futuyama 1971, Wiens and Rotenberry 1981b). For example, Best and Stauffer (1986) found that snag density could be deemed to have little influence on habitat suitability for downy woodpeckers and house wrens if samples from areas of low snag-density were not analyzed. Examination of the entire gradient revealed not only increased suitability at higher snag densities (relative to low densities), but differences between the two species' suitability indices at lower densities.

A third factor concerns the relative abundance and detectability of the bird species under study. Some species are typically encountered less frequently than others, and the less frequently a species is encountered, the more variable its observed response to habitat features (Best and Stauffer 1986). Thus, in this study, the more wide-ranging woodpeckers may have been no less responsive to variation in snag densities than, say, swifts and chickadees, but the relative infrequency with which the woodpeckers were encountered may have made count data insufficient to detect possible relationships.

For species with large home ranges relative to the sampling array on each stand, low probability of encounter relates back to a problem of scale. As discussed above, sample stands may be too small to evaluate habitat relationships of woodpeckers. In addition, habitat variables and bird counts summarized as stand means may be too coarse to account for the possibility that some species may be using only small portions of each stand. Such patterns of use may contribute to the lack of significant correlations or cause spurious ones to appear.

Abundance of cavity-using birds is not necessarily correlated with or a function of densities of snags; other, unmeasured variables may be more important. Nevertheless, our findings, as well as those of others (Balda 1975, Madsen 1985, Mannan and others 1980, Raphael and White 1984, Zamowitz and Manuwal 1985), certainly attest to the importance of snags to cavity-using birds, particularly in terms of management for these species.

Nest Tree Characteristics

Size-Although a variety of kinds of trees harbored nests, our analyses clearly revealed disproportionate use of trees with certain attributes by cavity- and bark-nesting birds. Our findings agree with other studies that have demonstrated disproportionate use of large-diameter snags as nest trees (Madsen 1985, Mannan and others 1980, Raphael and White 1984, Zamowitz and Manuwal 1985). Mean nest-tree diameters in this study were generally larger than those reported from the Olympics of Washington (Zarnowitz and Manuwal 1985), but smaller than in the Oregon Coast Range (Mannan and others 1980, Nelson 1989). Hairy woodpeckers typically nested in snags of substantially larger diameter in this study area (and the Oregon Coast Range) than reported from studies in the northern Rockies (Harris 1982, McClelland 1977) the Blue Mountains of Oregon (Bull 1980), the east slope of the Cascades in northern Washington (Madsen 1985), or the Sierras of California (Raphael and White 1984). Unfortunately, because our data and those from the Oregon Coast Range were from natural stands, many of which were old growth, we could not assess the extent to which cavity-nesting birds can successfully use smaller snags where larger ones are not available, as was shown for white-headed woodpeckers in the Sierra Nevada (Milne and Hejl 1989). Future studies must specifically address that question.

Presumably, large-diameter trees offer better thermal insulation and more room to house larger clutches, thereby enhancing reproductive success (Karlsson and Nilsson 1977). Not surprisingly, nest trees of the largest bird species-pileated woodpeckers and flickers-were typically larger (at breast height and at cavity height) than the mean for all species. The smallest bird species, however-chickadees and nuthatches-likewise nested in large-diameter trees. Creepers, which typically nest under slabs of bark, showed more plasticity in nest-tree size-selection than the cavity nesters. Other factors, such as decay state, tree species, and bark characteristics, were more important in determining the suitability of potential nest trees for this species.

Decay-The disproportionate use of hard snags by woodpeckers, most commonly hairy woodpeckers, contrasts with the findings of Mannan and others (1980) in Oregon (but see Nelson 1989), who found nests of hairies most often in decay-class 3, although their data included only seven nests. The only exception among the woodpeckers in our study was the flicker, which nested most frequently in decay-class 3 snags, most of which in young stands were in fire-scarred, remnant snags.

Because they are less well-equipped for cavity excavation, chickadees and nuthatches might be expected to nest in trees in more advanced decay stages. In second growth, this was generally true, and, as with flickers, most nests were in remnant snags. In old growth, however, their disproportionate use of all hard snags may be explained partially by the observation that nest holes were near the tops of snags (or even live trees) where the wood was most severely decayed and resembled conditions in more rotten snags. The selection of decay-class 2 snags by creepers probably relates to the greater percentage of remaining bark, as well as relative firmness of the sapwood.

Tree species-Only three tree species contained active nests: Douglas-fir, western hemlock, and western white pine. The disproportionate use of white pine by. woodpeckers and creepers is important in that it is a relatively minor, but widely distributed, forest component throughout western Washington. White pine has a patchy distribution and has declined in this century since the introduction of the fungus *(Cronartium ribicola)* that causes white pine blister rust (Allen 1959, Fowells 1965, Boyd 1980).

Our findings differ, however, from other studies of cavity-nesting birds in Douglas-fir forests in the Northwest. In Oregon, all cavity nesters apparently used Douglas-fir more than expected, based on availability (Nelson 1989). In the Olympics of Washington, woodpeckers-mostly hairy woodpeckers-appear to nest primarily in western hemlock (Zarnowitz and Manuwal 1985). Thus, even within the Western Hemlock Zone in the Northwest, woodpeckers use tree species to different degrees in different areas.

Chickadees and nuthatches, nesting primarily in Douglas-fir and hemlock, were apparently less selective than woodpeckers as to nest-tree species. This analysis was complicated, however, by the fact that most of the nuthatch nests were found in old growth (in hemlocks), whereas most chickadee nests were found in young stands (in Douglas-firs). It is not clear why most chickadee nests were found in younger stands, given that chickadees were more abundant in old growth, except that nests may have been easier to see in young stands.

Selection of tree species by primary excavators probably relates to relative decay characteristics of trees, as well as the sizes of each tree species available (Conner and others 1976, Jackson 1977, McClelland 1977). The progression and rate of decay of snags results from the interaction of biotic and abiotic factors over time and varies with size and age of the tree at death, species, and geographic location (Kimney and Fumiss 1943). Because Douglas-fir snags decay more slowly than most other species (Buchanan and Englerth 1940, Cline and others 1980), and because decay usually proceeds from outside inward (Kimney and Fumiss 1943, Wright and Harvey 1967), this species is especially suitable for nests of the weaker excavators, chickadees, nuthatches, and flickers. These traits also underscore the importance of large, remnant Douglas-fir snags as the most suitable nest sites for chickadees in young stands, both in this area and in the Oregon Coast Range (Mannan and others 1980). Without these large, remnant snags, abundance of breeding chickadees probably would have been lower in young stands.

Western hemlock, a common snag species on the study stands, is much less durable than Douglas-fir and often harbors fungal heart rot while it is still living (Buchanan and Englerth 1940, Engelhardt 1957). The importance of fungal heart rot to woodpecker nesting is well known (Conner and others 1976, Jackson 1977, Kilham 1971, McClelland 1977, Shigo and Kilham 1968). The susceptibility of hemlocks to heart rot fungi probably makes them attractive to hairy woodpeckers and sapsuckers. Because hemlock snags remain standing a relatively short time, cavity nesters would have to use this species while the trees were still alive or within the first several years after death. These attributes undoubtedly contributed to the frequent use of hard hemlock snags, as well as occasional live trees, by cavity nesters.

Western white pine, compared to its relative rarity (≤ 5 percent of available snags), was the species most frequently used by woodpeckers for nesting. Although reasons for its decline are relatively well known, information relating to decay rates of dead trees is nearly lacking. The common infections of this species by fungal heart rots (Fowells 1965), its apparent resistance to uprooting (Cline and others 1980), and the durability of sapwood and major limbs (pers. obs.) probably account for the suitability of western white pine as woodpecker nest sites. McClelland (1977) and Madsen (1985) similarly attributed woodpecker selection of western larch in Montana and northcentral Washington, respectively, to decay of the heartwood in combination with relatively sound sapwood. The rarity of large white pine snags only underscores their importance to woodpeckers in this portion of the Washington Cascades.

Nest tree surroundings--Our finding that nest sites of cavity-nesting birds contained higher densities of large, hard snags-the kinds in which they typically nested-agrees with other studies that have reported nests of excavators in dense patches of snags (Bull 1980, Harris 1982, Madsen 1985, Raphael and White 1984). We do not know whether this observation implies selection of dense patches of snags by the birds, or whether it is simply an artifact of the patchy way in which trees are killed by insects or disease. Also, we do not interpret this observation to mean that isolated snags do not have value as nesting habitat. In fact, some nest trees that were used in successive years were not located within a group of snags.

Conclusions anld Magnagement Considerations

In recent years, much attention has focused on the specific problem of providing adequate numbers of suitable snags through time and space in intensively managed forests (Davis and others 1983; Neitro and others 1985; Thomas and others 1976, 1979). Our purpose here is not to rework these guidelines, but only to refine or augment them with information specific to Douglas-fir/western hemlock forests of the Washington Cascades.

Nest Sites

We concur with Evans and Conner (1979a), Raphael and White (1984), and Madsen (1985), among others, who argue for the use of mean nest-tree diameters as a guideline for snag management. Managing for minimum diameters of trees known to be used could cause a gradual decline in cavity-nesting bird populations (Conner 1979a). We therefore recommend managing for snags of at least 76 cm in d.b.h., the mean d.b.h. of all active nests, where possible in this area. This diameter is notably larger than those recommended by Thomas and others (1979) for the Blue Mountains or Neitro and others (1985) for westside forests, particularly for hairy woodpeckers and sapsuckers. Woodpeckers appear to nest in larger trees in Douglas-fir forests (Mannan and others 1980, Nelson 1989, this study, Zarnowitz and Manuwal 1985) than in eastside forests, though sample sizes are relatively small from most study areas. Snags no less than 50 cm in d.b.h. should be given top priority in managing for cavity- and bark-nesting birds because this broad size-class was used disproportionately for nesting by all bird species we studied. Emphasis should be placed on the largest snags available in a given area, because larger snags remain standing longer, retain bark longer, and support a larger variety of wildlife (Cline and others 1980, Conner 1979a, Evans and Conner 1979).

Managers **must** also consider the decay state of snags. Our study suggests that most woodpeckers (particularly hairy woodpeckers) prefer hard snags for nesting; softer snags were generally avoided. Neitro and others (1985: 144), however, assumed that hairy woodpeckers used primarily decay stages 4 and 5, in contrast to red-breasted sapsuckers, which used stages 2 and 3. Our results and those of Mannan and others (1980) and Nelson (1989) do not agree. The number of hard snags required for the most common woodpecker species in the western Cascades would be vastly underestimated if the guidelines of Neitro and others (1985: 145, table 9) are followed. On the other hand, weaker excavators, such as flickers, chickadees, and nuthatches, were more likely to nest in soft snags, as might be expected, but depending on the forest age-class and the characteristics of available snags, even these species nested frequently in harder snags and defective live trees.

The species of snag is also important. Given the species' relative rarity in the forest, large, hard western white pine snags should be retained wherever they occur in areas managed for woodpeckers. Retaining white pine snags for woodpeckers will benefit brown creepers as well. Chickadees and nuthatches, on the other hand, nested primarily in Douglas-fir and hemlock snags and were seldom found nesting in white pine. Obviously, comprehensive management schemes designed to provide for all cavity-nesting bird species must consider the needs of each species in the community. Meeting the snag requirements of one species will not necessarily meet the needs of other species (Mannan and others 1984).

Besides nesting in different types of snags than woodpeckers do, chickadees and nuthatches were not found to nest in old woodpecker holes, except in two instances. Although some birds may have fashioned their cavities from old woodpecker feeding holes or “false-start” cavities, most chickadee and nuthatch nests appeared to be solely the work of the nesting pair. These species chose trees of suitable species, size, and decay states and nested in locations appropriate to their abilities to excavate their own cavities. Suitable snags were sufficiently abundant in most of these natural stands to provide sites for nest cavities. Perhaps the presumed energetic efficiency of using old woodpecker holes was partially offset by possible fouling of holes caused by previous use or risk of predation in larger holes, thus making them less attractive or more harmful than newly excavated holes (Short 1979).

Conceivably, as snags--especially large ones-become scarcer in managed forests, noticeable changes in patterns of nest-site use from increased competition, because of lower snag availability, could occur. Possible changes include: smaller average diameter of nest trees (Milne and Hejl 1989); use of the smallest diameter portion of trunks (or limbs) capable of supporting nest-cavity dimensions (Short 1979); greater use of old woodpecker cavities by chickadees and nuthatches as more easily excavated sites became scarcer; greater use of defective live trees; or greater interference competition (Miller 1967) among bird species, which would effectively reduce the number of available (that is, unoccupied) snags. Pressures caused by the reduction of the snag resource, if sufficiently severe, could lower reproductive success of cavity-nesting birds or cause population declines outside of unmanaged areas or old-growth reserves. The list of possible changes could serve as hypotheses to test in examining responses of cavity nesters to changes in the snag resource under different management schemes.

Another important consideration is that, in the younger stands, very few nests were found in trees that arose from the current stands. The only species found nesting commonly in young stands, chestnut-backed chickadees, used remnant snags primarily. Thus, even under natural conditions, stands less than 80 years old have limited numbers of suitable nest trees for most cavity nesters. Stands initiated after clearcutting, with few, if any, remnant snags, would likewise contain few suitable nest trees. Given the target rotation ages of managed forests, roughly comparable to the young stands we studied, recommendations for retention of old growth where possible, strips of trees and snags along riparian corridors, patches of snags (and live trees) in clearcuts, as well as areas of longer rotations (Neitro and others 1985) become critical for maintaining populations of cavity-nesting birds. Modem silvicultural techniques have enabled foresters to produce larger trees that can serve as potential nest trees in shorter periods. Younger, faster-growing trees, however, tend to decay more rapidly after death than do older, slower-growing trees (Kimney and Furniss 1943), so the number of snags provided may have to be adjusted.

Foraging Sites

In managing for cavity- and bark-nesting birds, characteristics of foraging habitats should not be overlooked (Conner 1980). Birds may focus foraging activities on different species and sizes of trees from those used for nesting, and foraging activities may change seasonally (Conner 1981, Lundquist and Manuwal 1990). For example, in our study area, creepers, chickadees, hairy woodpeckers, and nuthatches foraged on large-diameter (>50 cm), live Douglas-fir more than expected based on availability, and chickadees appeared to shift to western hemlock in the winter (Lundquist and Manuwal 1990). Retention of large live trees, either in old growth or longer rotation patches, could also benefit species such as Vaux's swifts indirectly by serving as future sources of large snags (Mannan and Meslow 1984).

Implementing Snag Management

Harvest of old-growth forests, and shorter rotations, resulting in the prevalence of relatively young second-growth forests, will make the success of snag-management policies even more crucial for snag-dependent wildlife in the future. The Pacific Northwest Region (USDA Forest Service 1985) recommends managing dead and defective live trees to maintain viable populations of cavity-dependent wildlife at 40 percent of their population capacities on commercial forest lands. This policy was intended to set minimum standards and a baseline for managing Northwest forests. Although significant progress has been made in establishing and carrying out management programs in the last decade, Bull and ‘others (1986b) report considerable inconsistency in the numbers of snags being maintained on National Forest Districts. Nearly one-third-of the Districts surveyed reported fewer snags than necessary to maintain cavity-nesting bird populations (as defined by Thomas and others 1979). Similarly, Morrison and others (1986) concluded that although current guidelines for maintaining large snags in the Tahoe National Forest in California were appropriate, they were not being implemented effectively.

Recommendations that may help-attain snag-management goals in balance with human needs include retaining more snags than the minimum required to support targeted cavity-nesting bird populations. This recommendation allows for unforeseen losses, such as to windthrow or firewood cutters or uncertainties regarding natural fall rates of snags. It will also allow for removing trees that may pose safety threats while still maintaining enough trees for wildlife. Neitro and others (1985) discussed in detail innovative ways of selecting suitable types of snags compatible with logging safety regulations. In view of possible increases in demand for fuelwood (Force 1986), management plans should include ways to minimize impacts on snags provided for wildlife, such as restricting access to critical areas or limiting the size of snags cut. Producing large snags at high cost-either as direct or “opportunity” costs-and then leaving them unprotected from fuelwood cutters makes no sense, particularly where the number of snags is below stated goals (Bull and others 1986b, Morrison and others 1986).

Spatial distribution of snags is also important in designing management plans. Although our study and others (Bull 1980, Raphael and White 1984) have found cavity nesters in relatively dense patches of snags, lone snags may also provide suitable nest sites. Priority should be given to suitable snags (appropriate size, decay stage, and species) whether they occur in clumps or singly, to allow for adequate distribution over a large area. Adequate cover can be provided around lone snags in the form of live trees, which are also a source of future snags. Such flexibility in management will help prevent suitable snags of several cutting units from being crowded too close together to be usable.

Monitoring is essential to assess snag numbers and losses, their use by wildlife, and the implementation and effectiveness of snag-management programs. Given that the complete ecological and economic role of snags and cavity-dependent wildlife is not fully understood at present, management schemes must be carefully designed and flexible enough so that future management options are not lost. As new information and understanding are gained, programs can be modified as required to ensure the continued health of avian communities in managed forests.

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Appendix

Table 7-Stern count[a] variables and codes used in bird and vegetation correlation and regression analyses

Code	Description
Coarse variables:	
LT4	Live trees >100 cm d.b.h.
TSTP	Stumps and stubs (snags <5 m tall, >10 cm d.b.h.)
SS	All small snags 10-19 cm d.b.h.
Species-specific variables:	
DFD13	Live Douglas-fir 1-100 cm d.b.h.
WHD12	Live western hemlock 1-50 cm d.b.h.
WHD3	Live western hemlock 51-100 cm d.b.h.
RCD12	Live western redcedar 1-50 cm d.b.h.
RCD3	Live western redcedar 51 - 100 cm d.b.h.
ABD13	Live *Abies* spp. 1-100 cm d.b.h.
CPD13	Live other conifers 1-100 cm d.b.h.
VMD12	Live vine maple 1-50 cm d.b.h.
HDD13	Live other hardwood spp. 1-100 cm d.b.h.
DFS34	All Douglas-fir snags 20-49 cm d.b.h.
DFS5	Hard Douglas-fir snags (DC I-II) ≥ 50 cm d.b.h.
DFS6	Soft Douglas-fir snags (DC III-V) ≥ 50 cm d.b.h.
WHS34	All western hemlock snags 20-49 cm d.b.h.
WHS56	All western hemlock snags ≥ 50 cm d.b.h.
RCS34	All western redcedar snags 20-49 cm d.b.h.
RCS56	All western redcedar snags ≥ 50 cm d.b.h.
ABS34	All *Abies* spp. snags 20-49 cm d.b.h.
WPS34	All western white pine snags 20-49 cm d.b.h.
WPS56	All western white pine snags ≥ 50 cm d.b.h.

[a] All stem counts were converted to densities (number per hectare).

Table 8-Comparison of active nest trees and trees with inactive cavities of woodpeckers and nonwoodpeckers among decay classes by forest age-class

Hole-nester group/ tree-use status	Decay-class				
	I	II	III	Iv	Total
Woodpeckers/active					
Old-growth	7	12	1	0	20
Mature	0	0	1	0	3[a]
Young	1	2	0	0	3
Total	8	14	2	0	26
Woodpeckers/inactive					
Old-growth	2	25	12	1	40
Mature	1	7	4	0	12
Young	0	5	8	1	14
Total	3	37	24	2	66
Nonwoodpeckers/active					
Old-growth	4	10	4	0	18
Mature	0	5	1	0	6
Young	0	3	7	3	13
Total	4	18	12	3	37
Nonwoodpeckers/inactive					
Old-growth	1	10	11	3	25
Mature	0	6	4	1	11
Young	0	3	13	3	19
Total	1	19	28	7	55

[a] Includes two sapsucker nest snags with missing data.

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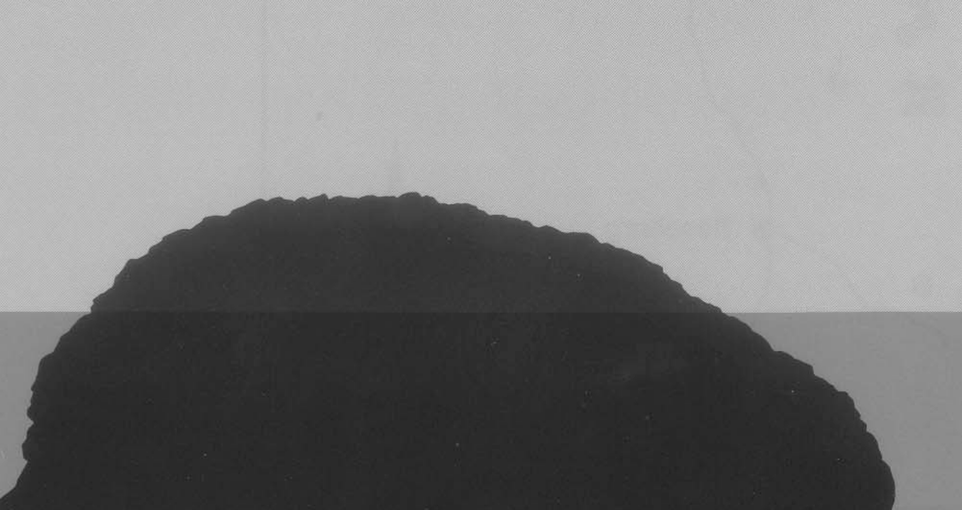
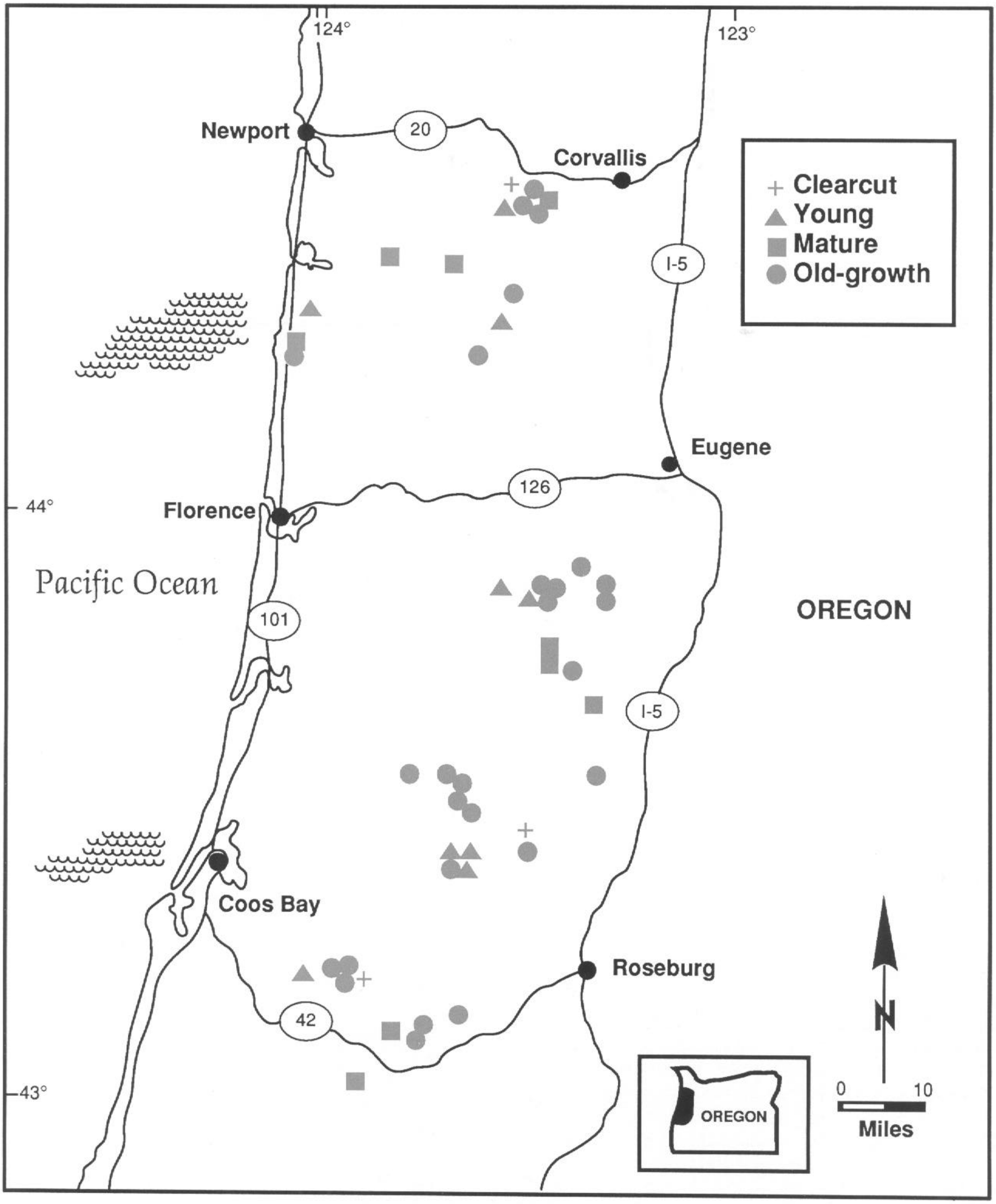


Part 5

Small Mammals of Oregon and Washington



Location of study sites.

Small Mammal Communities in the Oregon Coast Range

Paul Stephen Corn and R. Bruce Bury

Authors

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Abstract

We used pitfall trapping to sample small mammals in clearcut, young, mature, and old-growth forests in the Coast Ranges of Oregon in 1984 and 1985. Our objectives were to identify species or groups of species associated with old-growth forests and to identify structural components of the habitat associated with mammal abundance. Trowbridge's shrews, red-backed voles, and Pacific shrews were the most abundant species in forested stands; vagrant shrews, deer mice, and creeping voles were most abundant in clearcuts. Significantly more red tree voles were captured in old-growth stands than in mature and young stands, and Pacific shrews were significantly more abundant in mature stands than in either young or old-growth stands. No significant differences were found in the abundance of any species across a moisture gradient in old-growth stands. No strong correlations were found between habitat variables and the abundance of any mammals. Abundance and diversity of small mammals were greater in mature stands than in young stands, but abundance and diversity in old-growth stands broadly overlapped both mature and young stands. Diversity of small mammals did not display a U-shaped curve relative to stand age (high diversity in young and old-growth stands and low diversity in mature stands).

Introduction

The Pacific Northwest harbors one of the richest communities of small mammals in North America. Several species are endemic to the region, with their distributions restricted to forests west of the Cascade Range in California, Oregon, Washington, and British Columbia (Hagmeier and Stults 1964, Simpson 1964). These species include the Trowbridge's shrew, Pacific shrew, marsh shrew, shrew-mole, western red-backed vole, creeping vole, red tree vole, and white-footed vole (Ingles 1965, Maser and others 1981, van Zyll de Jong 1983). Because a majority of the forests west of the Cascade Range were old growth before logging began (Harris 1984, Spies and Franklin 1988), a logical hypothesis is that many of the unique small mammals of the region would reach their greatest abundance in old-growth forests. Early lists of vertebrates associated with old-growth forests included several small mammals (Franklin and others 1981, Meslow and others 1981), but data on habitat use were scarce for most of them.

Several habitat features of Douglas-fir forests when plotted against stand age have a U-shaped curve (high values in young forests, low values in mature forests, and the highest values in old-growth forests). These features include amount of coarse woody debris, heterogeneity of the understory, and plant species diversity (Spies and Franklin 1988). Because these features (particularly coarse woody debris) may be significant biological components of the habitat of forest mammals, Spies and Franklin (1988) hypothesized that species diversity of mammals follows the same U-shaped distribution with forest age. Raphael (1988c) did not find this distribution of mammals in northern California (diversity of mammals was highest in mature and old-growth forests), but few data existed relating species diversity to age of Douglas-fir forests in Oregon and Washington.

The Old-Growth Program was chartered, in part, to address the lack of information on the abundance of vertebrates and their habitat associations (Ruggiero and Carey 1984). Pilot studies were conducted in the Cascade Range in 1983 (Corn and others 1988), and, in 1984, vertebrate community studies were extended to the Coast Ranges in Oregon. The need for studies of old growth is most acute in the Coast Ranges. Because of fire and logging, little old growth remains (Spies and Franklin 1988), and it is distributed in small, scattered fragments (Harris 1984, Monthey 1984).

In this paper, we report the results of pitfall trapping of small mammals over a large area of the Coast Ranges in 1984 and 1985. Our objectives were to:

- Determine the relative abundance and diversity of small mammals in young, mature, and old-growth forests and across a moisture gradient in old growth;
- Compare the abundance of small mammals to physiographic features and vegetative characteristics important for maintaining diversity of small mammals; and
- Contrast differences in the abundance of small mammals between old-growth forests and clearcuts as a first step in comparing managed and natural forests.

Met hods

Study Areas

We studied 45 closed-canopy forest stands and 3 recently clearcut stands in the Coast Ranges of Oregon (see frontispiece). Three stands were near the coast in the vicinity of Cape Perpetua, but most stands were in the interior or on the eastern flank (valley margin) of the Coast Ranges. Most of the stands were south of Eugene on land managed by the Bureau of Land Management (BLM). One stand near Drain was on land owned by International Paper Company. Stands north of Eugene were on BLM land, the Siuslaw National Forest (including Cape Perpetua and Lost Creek Wilderness Areas), or land managed by the city of Corvallis (Marys Peak).

Stand Selection and Classification

Stands were selected initially to conform to a chronosequence of four categories beginning with 3 clearcut stands (less than 10 years old), 8 closed-canopy young stands (40-75 years), 10 mature stands (80-120 years), and 27 old-growth stands (150-525 years). Except for one young stand, the last three categories were all composed of naturally regenerated forests. Ages of stands were estimated a *posteriori* by increment coring of at least five dominant Douglas-fir trees per stand (young and mature stands), Ages of old-growth stands were estimated from increment cores and by examining stumps in adjacent clearcuts and roadsides (Spies and others 1988).

A moisture gradient (wet, moderate, and dry) was examined for old-growth stands. The initial position on the moisture gradient was determined largely by topographic position, for example, south- or west-facing ridges were generally dry, whereas stands on north-facing slopes were usually moist to wet. Later, a moisture classification was made based on a multivariate ordination of understory vegetation (Spies and Franklin, this volume). In the Coast Ranges, this resulted in five stands originally considered wet being reclassified as moderate, and one stand originally considered moderate being reclassified as dry. We used the revised classifications in this paper.

Pitfall Trapping

We installed 36 pitfall traps, 15 m apart in a square grid, in each stand in summer 1984. Each trap was constructed from two number-10 cans (3.2 1 volume), stacked and joined with duct tape (Bury and Corn 1987). A short plastic funnel (0.45kg margarine tub with the bottom cut out) nested in the top of the trap. Traps were buried flush with the ground and covered with a cedar shingle that was suspended 3 to 4 cm above the opening with twigs or small rocks. Between the time traps were installed and trapping began and at the end of each trapping season, traps were closed with a tight-fitting plastic lid.

Logistics of trapping 48 stands concurrently dictated placement of pitfall grids to some extent. The near comer of each grid was placed about 100 m from the edge of the stand. This distance was a compromise between the need to avoid edge effects and the need for a field crew to be able to check the grids in five to seven stands in one day.

We opened traps during the first week in October and trapped continuously for 50 days in 1984 and for 30 days in 1985. No water was put in traps because this has a deleterious effect on the preservation of amphibians, which were also sampled with pitfall traps (Corn and Bury, this volume b). In practice, most traps accumulated some water and most mammals drowned. Drowning is the method recommended by the American Society of Mammalogists (1987) when pitfall traps are used as kill traps. We checked traps about once a week; trapped animals were removed and any water that had accumulated was bailed out.

We determined sex and age and made standard measurements (total, tail, foot, and ear lengths, and mass) of mammals, which were then preserved whole in lo-percent formalin, or as skulls, skeletons, or skins and skulls. Specimens were deposited in the National Museum of Natural History, Washington, DC, where all species identifications were verified.

Vegetation Sampling

We sampled vegetation at nine points within the pitfall grid, with the center of each sampling plot equidistant from four pitfall traps. We measured or estimated physiographic, coarse woody debris, live tree, and ground-cover variables (appendix, table 6) in two nested circles. Percentage cover was estimated visually; all other variables were direct counts or were measured. Variables in the interior circle (5.6-m radius, 100 m^2) included slope, cover by down wood, numbers of small snags and small trees, and most ground-cover variables. Variables in the outer circle (15-m radius, 707 m^2) included the presence or absence of water, rock outcrops, or talus; the number of medium and large snags and trees, and cover by midstory and canopy trees. Count variables were converted to density (number per hectare). Because no single vegetation measurement was directly related to a single pitfall trap, we averaged the nine values for each variable to produce a single value for each pitfall grid.

Statistical Analyses

All statistical analyses were done on a microcomputer using SYSTAT. Analysis of the chronosequence was originally intended to exclude wet and dry old-growth stands, so comparisons among young, mature, and old-growth stands would not be influenced by the greater range of moisture conditions in old-growth stands (Carey and Spies, this volume). Mature and young stands had much greater variation on the moisture gradient than expected (Spies and Franklin, this volume), however, so only those old-growth stands that were outliers on the moisture gradient were excluded. In the Coast Ranges, all but two old-growth stands were' retained in the chronosequence analyses. Analysis of the moisture gradient was restricted to old-growth stands.

To facilitate comparisons between years and to reduce the effect of migration onto the trap grid, we used only animals captured during the first 32 to 34 days (the closest we could come to 30 days, because traps were not checked daily) in 1984 (but see below). We measured abundance as the number captured per 100 trap-nights. Analysis of the abundance of individual species depended on numbers captured. "Common" species were captured in more than 50 percent of the stands and with more than 50 total captures. "Rare" species occurred in less than 50 percent of stands with less than 50 but more than 10 captures. For some species-for example, flying squirrels-abundance data may reflect bias from the trapping technique rather than the actual density of the species. Differences on the age and moisture gradients for common species were analyzed by analysis of variance (ANOVA) of log-transformed data ($\log_e$ of abundance + 1). We used Tukey's honestly significant difference for unplanned multiple comparisons (Sokal and Rohlf 1981). Because of the low sample sizes, we used all captures of rare species in both years. Differences in numbers captured among age- and moisture-classes were tested using the G-test (log likelihood ratio) for goodness of fit (Sokal and Rohlf 1981).

Physiographic and vegetative variables--Variables measuring percentage cover were arcsin-transformed (Sokal and Rohlf 1981) before analysis. Count variables had large variances which were log-transformed. We computed Pearson product-moment correlation coefficients between the abundance of common species and each physiographic and vegetation variable. For these six species, we performed multiple regression on subsets of physiographic and vegetative variables. We first eliminated highly intercorrelated variables, then chose variables for each regression model using a stepwise procedure with a significance level of 0.10 to add or remove variables. For rare species, we compared mean values of physiographic and vegetation variables between stands where each species was present or absent. We also performed a principal components analysis with a subset of eight vegetation variables (table 1): LOGS (the sum of DLOGSA, DLOGSB, and DLOGSC), LSNAG, DECSNAG, CTREEL, MCTREE, CCTREE, FERN, AND ESHRUB. These variables represent characteristics used in ecological definitions of old-growth Douglas-fir forests (Franklin and Spies 1984, Morrison 1988, Spies and Franklin 1988). The variables were transformed but not standardized because the scales were generally equivalent after transformation. We used factors produced by the principal components analysis with eigenvalues greater than 1 to examine whether the vegetation variables we measured were reflecting differences among habitat types.

Mammal community structure-We examined the relations among stands in small mammal fauna by using nonmetric multidimensional scaling. By using a matrix of similarities among stands, multidimensional scaling analysis computes the coordinates of a set of stands in a few dimensions (usually 2 to 3), so that the distances between pairs of stands fit as closely as possible to their measured similarities (Wilkinson 1988). We measured similarity as the Euclidean distance between pairs of stands using the abundance (number per 100 trap-nights) of Trowbridge's shrews, Pacific shrews, vagrant shrews, marsh shrews, shrew-moles, and red-backed voles. We chose these six species as most likely to have been sampled in an unbiased manner by pitfall traps. Abundance was not standardized, because we were interested in the relative contributions of each species. To interpret the axes produced by multidimensional scaling analysis, we correlated them with the abundance of each species, total abundance (the sum of the six species), species diversity (Berger-Parker index, Magurran 1988), and physiographic and vegetative variables.

We used the abundances of the six species above and the K-MEANS procedure of SYSTAT to generate a specified number of non-overlapping pools (clusters, see Pielou 1984) of stands. We generated five pools because of the *a priori* classification of stands into five habitat types. The stands belonging to each pool were then plotted against the axes generated by the multidimensional scaling analysis to see if any patterns could be identified in the mammal community.

Results

Abundance of Small Mammals

We captured 3047 individuals of 20 species of small mammals in both years (table 1). Total numbers captured in each year were very similar: 1514 in 1984 and 1533 in 1985. Precipitation may affect capture rates of small mammals (Bury and Corn 1987), so we examined data from eight weather stations in the Coast Ranges (U.S. Department of Commerce, Climatological Data). Mean precipitation was slightly higher in 1984 (19.9 cm) than in 1985 (16.6 cm), but patterns of rainfall were similar in both years. The first region-wide rain was recorded 4 October in 1984 and 7 October in 1985, and rain was recorded almost daily in the second half of October in both years.

Deer mice were captured more frequently in 1985 than 1984 ($P < 0.001$), but no significant differences were found between years for any other species. All further analyses used the combined abundance (1984 + 1985) of each species. Six common species (Trowbridge's shrew, Pacific shrew, shrew-mole, coast mole, western red-backed vole, and deer mouse) had 55 to 1690 total captures (62-64 trap days). Four other rare species (marsh shrew, vagrant shrew, red tree vole, and flying squirrel) had 17 to 31 total captures (80 trap days). Ten other species had fewer than 10 captures, which was too few for meaningful analysis of differences in habitat types. These included species not well-sampled by pitfall traps (Townsend's chipmunk, Douglas' squirrel, and ermine), species from adjacent grassland habitats (Townsend's mole and California vole), and species most common in riparian habitats (white-footed vole and western jumping mouse).

Table 1-Total numbers of small mammals captured by pitfall grids in 45 forest stands in the Oregon Coast Ranges in 1984 and 1985

Species	1984[a]	1985	Total
Insectivores:			
Trowbridge's shrew[b]	896	794	1690
Pacific shrew[b]	187	153	340
Vagrant shrew[c]	12	14	26
Marsh shrew[c]	7	10	17
Shrew-mole[b]	45	41	86
Coast mole[b]	27	28	55
Townsend's mole[d]	2	1	3
Rodents:			
Western red-backed vole[b]	282	359	641
Red tree vole[c]	5	8	13
White-footed vole[d]	0	2	
Creeping vole[d]	2	7	9
California vole[d]	2	0	2
Long-tailed vole[d]	0	1	
Townsend's vole[d]	0		1
Deer mouse[b]	29	90[e]	119
Western jumping mouse[d]	1	4	5
Northern flying squirrel[c]	11	14	25
Townsend's chipmunk[d]	0	4	4
Douglas' squirrel[d]	0	2	2
Carnivores:			
Ermine[d]	6	0	6
Total (all mammals)	1514	1533	3047
Number of species	14	19	20

[a], Only captures from the first 32 to 34 trap days are listed.

Common species were captured in more than 50 percent of the stands and with more than 50 total captures.

[c] Rare species occurred in less than 50 percent of stands with less than 50 but more than 10 captures. Analyses of abundance used all captures (50 trap days in 1984).

Abundance of species not analyzed.

[e] Trap rate was higher in 1985 than 1984 ($P < 0.001$).

Sixty-two percent of the Trowbridge's shrews, 61 percent of the Pacific shrews, and 64 percent of the western red-backed voles captured were male. Because the home ranges of small mammal males are usually larger than those of females (Hawes 1977, Van Home 1981), males may have a higher probability of encountering traps. Habitat use by small mammals may not be constant among sex and age groups (Van Home 1981), but our data showed little variation in the proportions of adult male, adult female, and juvenile Trowbridge's shrews, Pacific shrews, and western red-backed voles among young, mature, and old-growth stands (fig. 1). All further analyses did not differentiate among sex and age groups.

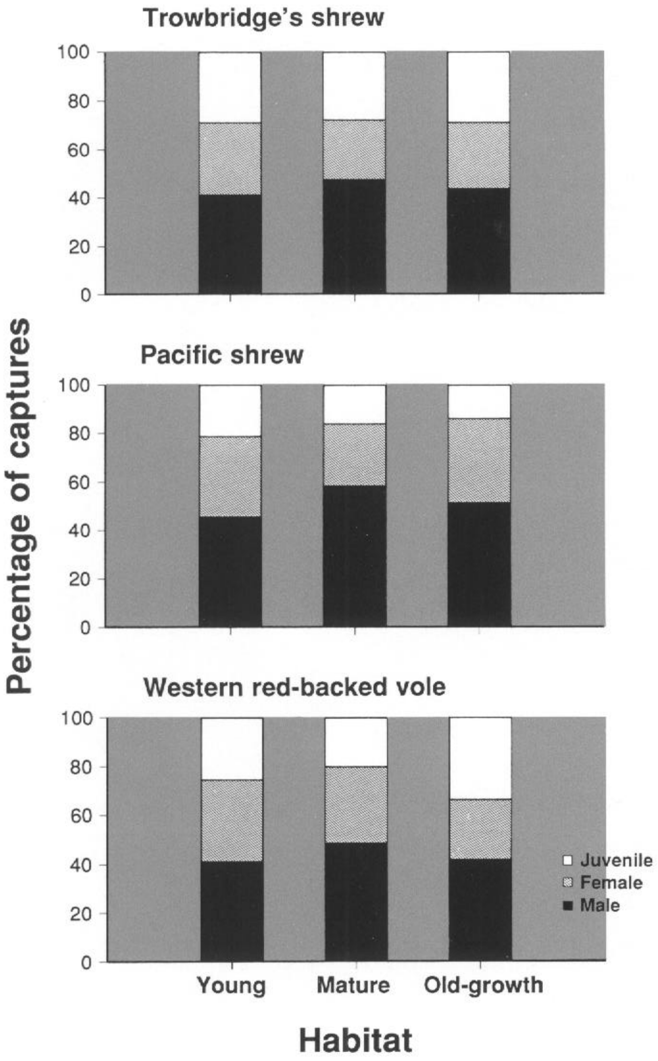

Figure 1—Mean percentage of adult male, adult female, and juvenile Trowbridge's shrews, Pacific shrews, and western red-backed voles captured in young, mature, and old-growth stands.

Table 2—Mean abundance, mean relative abundance,[a] and occurrence of common[b] small mammals in different forest types in the Oregon Coast Ranges

		Stand type (N)		
Species	Measure	Old-growth (25)	Mature (10)	Young (8)
Trowbridge's shrew	Number/100 TN[c]	1.660	1.907	1.350
	Relative abundance	57.0	54.2	61.4
	Percentage of stands	100	100	100
Pacific shrew	Number/100 TN	.256	.596*	.251
	Relative abundance	8.4	15.3	10.1
	Percentage of stands	96.0	100	100
Shrew-mole	Number/100 TN	.099	.079	.049
	Relative abundance	3.3	2.3	1.9
	Percentage of stands	68.0	70.0	62.5
Coast mole	Number/100 TN	.060	.040	.044
	Relative abundance	2.1	1.4	1.9
	Percentage of stands	64.0	60.0	37.5
Western red-backed vole	Number/100 TN	.668	.741	.449
	Relative abundance	21.7	21.7	17.7
	Percent of stands	100	100	100
Deer mouse	Number/100 TN	.138	.053	.132
	Relative abundance	4.6	1.5	5.2
	Percentage of stands	96.0	60.0	75.0

* Denotes significant difference among stand ages at $P < 0.05$.

[a] Relative abundance = the percentage of captures contributed by each species in each stand.

[b] Common species were captured in more than 50 percent of the stands and with more than 50 total captures.

[c] TN = trap-nights.

Variation with stand age—We calculated the mean abundance, relative abundance (percentage of total captures within a stand), and the frequency of occurrence of the six most abundant species in each age-class (table 2). Only Pacific shrews varied significantly among stand types in abundance ($F = 4.86$, $P = 0.013$). This species was more abundant in mature stands than either old-growth ($P = 0.024$) or young ($P = 0.052$) stands. The two most abundant species, Trowbridge's shrew and the western red-backed vole, were also more abundant in mature stands, but the differences were not statistically significant. Frequency of occurrence was high for all six species in all stand types, ranging from coast moles and deer mice detected in 60 percent of mature stands, to Trowbridge's shrews and western red-backed voles detected in all stands. Relative abundance of these six species was similar in old-growth and young stands; species ranks in order of abundance were: Trowbridge's shrew > western red-backed vole > Pacific shrew > deer mouse > shrew-mole > coast mole. In mature stands, the order was the same, except that shrew-moles were more abundant than deer mice. This minor variation is probably not significant, because pitfall traps do not sample deer mice well (Bury and Corn 1987).

Two rare species were not distributed evenly on the chronosequence (fig. 2). All but one red tree vole were captured in old growth (old growth versus mature plus young: $G = 9.58$, $P < 0.01$), and significantly more vagrant shrews were captured in mature stands than in old-growth and young stands ($G = 29.8$, $P < 0.001$). Captures of flying squirrels and marsh shrews were evenly distributed among age-classes. Of nine creeping voles captured in forested stands, five were in

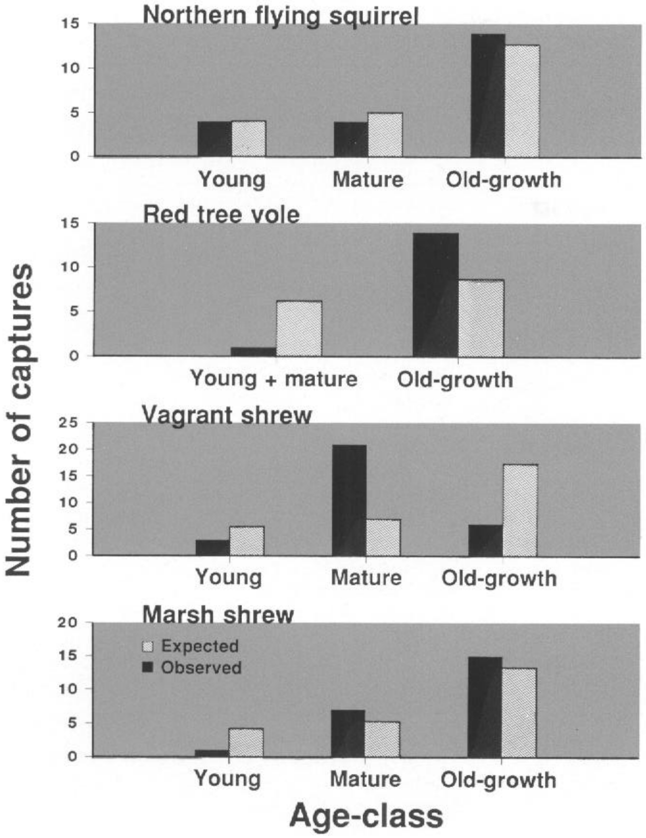

Figure 2—Total captures and expected values of marsh shrews, vagrant shrews, red tree voles, and northern flying squirrels captured in young, mature, and old-growth stands.

Table 3—Mean abundance, mean relative abundance,[a] and occurrence of common[b] small mammals on the moisture gradient in old-growth forests in the Oregon Coast Ranges

Species	Measure	Stand type (N) Wet (5)	Moderate (14)	Dry (8)
Trowbridge's shrew	Number/100 TN[c]	1.591	1.513	1.928
	Relative abundance	57.8	55.1	60.2
	Percentage of stands	100	100	100
Pacific shrew	Number/100 TN	.324	.256	.226
	Relative abundance	11.3	9.2	6.1
	Percentage of stands	100	100	87.5
Shrew-mole	Number/100 TN	.140	.073	.112
	Relative abundance	5.2	2.5	3.2
	Percentage of stands	80.0	64.3	62.5
Coast mole	Number/100 TN	.044	.066	.067
	Relative abundance	1.8	2.5	1.8
	Percentage of stands	60.0	71.4	62.5
Western red-backed vole	Number/100 TN	.467	.692	.678
	Relative abundance	14.2	23.8	20.8
	Percentage of stands	100	100	100
Deer mouse	Number/100 TN	.141	.117	.167
	Relative abundance	5.2	3.9	5.2
	Percentage of stands	100	92.9	100

[a] Relative abundance = the percentage of captures contributed by each species in each stand.

[b] Common species were captured in more than 50 percent of the stands and with more than 50 total captures.

[c] TN = trap-nights.

old-growth stands and four were in mature stands. Three white-footed voles were captured in forested stands, and one each in old-growth, mature, and young stands.

Variation on the moisture gradient—Neither abundance of the common species (table 3) nor number of captures of the rare species (fig. 3) varied significantly across the moisture gradient (only seven vagrant shrews were captured in old growth, too few for analysis on the moisture gradient). The relative abundances suggest some differentiation of the mammal community in wet stands, however. Pacific shrews and shrew-moles contributed a greater percentage of captures and red-backed voles a lower percentage of captures in wet stands than in moderate or dry stands.

Clearcuts versus old growth—We captured nine species in three clearcuts ($\bar{x} = 5.7$ per stand) and 10 species in three adjacent old-growth stands ($\bar{x} = 6.0$ per stand). Total abundance was also not significantly different ($\bar{x} = 2.26$ per 100 trap-nights in old growth; $\bar{x} = 1.95$ per 100 trap-nights in clearcuts), but the species composition of the small mammal fauna was considerably different between clearcuts and old-growth stands. The four small mammals with the greatest mean relative abundance in clearcuts were vagrant shrews, Trowbridge's shrews, deer mice, and creeping voles, but, in the three old-growth stands, the four most abundant species were Trowbridge's shrews, red-backed voles, Pacific shrews, and shrew-moles (fig. 4). Red tree voles, marsh shrews, and ermines were captured in at least one old-growth stand and not in any clearcuts. Creeping voles, pocket gophers, and white-footed voles were captured in at least one clearcut and not in any of the three old-growth stands. White-footed voles and creeping voles were captured in other old-growth stands, however.

Habitat Associations

Physiographic features—None of the physiographic variables we measured varied among the forested stands (table 4). We compared the abundance of common species or the occurrence of rare species to these variables plus latitude, longitude, and stand age, but we observed only six weak associations. Abundance of Trowbridge's shrews was weakly correlated with latitude ($r = 0.37$, $P < 0.05$). Abundance of

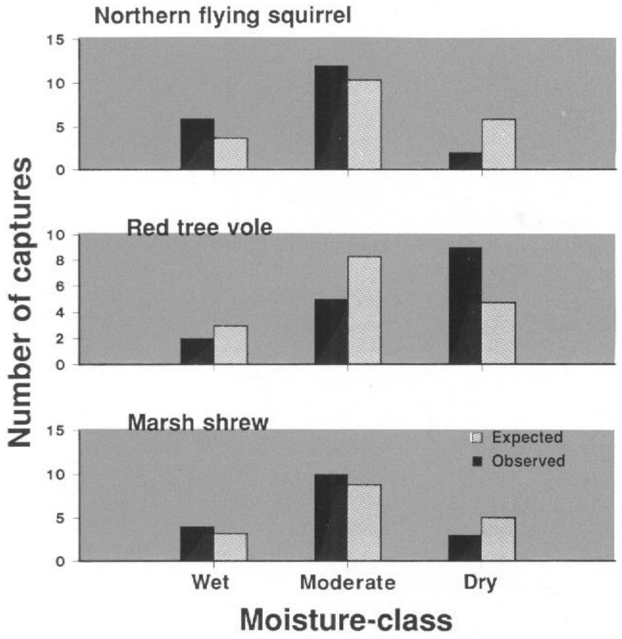

Figure 3—Total captures and expected values of marsh shrews, red tree voles, and flying squirrels captured in wet, moderate, and dry old-growth stands.

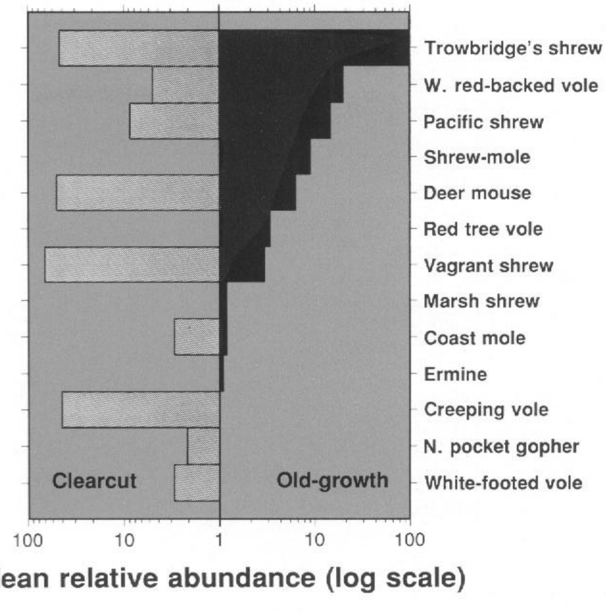

Figure 4—Mean relative abundance (log scale) of small mammals in three old-growth stands and three adjacent clearcuts.

Pacific shrews was weakly correlated with longitude ($r = 0.32$, $P < 0.05$) and negatively correlated with aspect ($r = -0.32$, $P < 0.05$; abundance was lower on southwest-facing slopes). Mean age of 13 stands where red tree voles were present was 294 years; 32 stands without red tree voles averaged 188 years old ($F = 6.75$, $P = 0.013$). Abundance of red-backed voles was 0.67 per 100 trap-nights in 39 stands without surface water and 0.36 per 100 trap-nights in 6 stands with surface water ($F = 4.19$, $P = 0.047$).

Vegetative characteristics—Only a few of the vegetation variables varied significantly ($P < 0.05$) among age-classes of forest stands (table 4). Small and medium-sized snags were most numerous in young stands. Densities of small and large coniferous trees were highest in old-growth stands, but medium-sized conifers were densest in young stands. Cover by broadleaf trees in the midstory was highest in young stands, but cover by conifers in the midstory was highest in old growth. Old-growth stands had the lowest canopy cover by coniferous trees.

Abundances of common species were correlated with few of the vegetation variables. Trowbridge's shrews were negatively correlated with percentage cover of class 3 and 4 down wood (DLOGSB; $r = -0.35$, $P < 0.05$) and cover by conifers in the midstory (MCTREE; $r = -0.30$, $P < 0.05$); they were positively associated with cover by ferns (FERN; $r = 0.32$, $P < 0.05$). Pacific shrews were correlated with the density of medium-sized snags (MSNAG; $r = 0.30$, $P < 0.05$) and cover by berry shrubs (BSHRUB; $r = 0.40$, $P < 0.01$). Coast moles were negatively correlated with canopy cover by broadleaf evergreens (CBTREE; $r = -0.31$, $P < 0.05$). Western red-backed voles were negatively correlated with cover by moss (MOSS; $r = -0.32$, $P < 0.05$) and positively correlated with cover by berry shrubs ($r = 0.33$, $P < 0.05$). Abundances of two species, shrew-moles and deer mice, were not significantly correlated with any vegetative variables.

Similarly, only a few vegetative variables varied between stands with rare species present or absent. In the 18 stands where marsh shrews were captured, mean canopy cover by conifers (CCTREE) was lower (41.3 percent versus 50.4 percent, $P = 0.009$) than in the 27 stands where they were not captured. Mean density of all deciduous trees and broadleaf evergreen trees (BTREES+BTREEM+BTREEL) was lower (45 per ha versus 145 per ha, $P = 0.002$) in 13 stands where vagrant shrews were collected versus 32 stands without vagrant shrews. In 13 stands where we captured red tree voles, there were more large coniferous trees (CTREEL: 34 per ha versus 17.4 per ha; $P = 0.014$) than in 32 stands where we did not capture this species. In 15 stands where flying squirrels were caught, mean density of large snags (LSNAG) was greater (9.2 per ha versus 4.9 per ha, $P = 0.032$), mean cover by fine litter (FLITTER) was greater (71.6 percent versus 58.6 percent, $P = 0.005$), but mean cover by moss (MOSS) was lower (19.2 percent versus 33.2 percent, $P = 0.005$) than in 30 stands without flying squirrels.

Table 4—Mean values of physiographic and vegetative variables (standard deviations in parentheses) measured at pitfall grids in the Oregon Coast Ranges[a]

		Stand type (N)			
Variable	Units	Old-growth (27)	Mature (10)	Young (8)	*P*
Physiographic:					
TRASPECT		1.03 (.62)	1.25 (.40)	1.20 (.70)	
SLOPE	Percent	38.4 (19.2)	46.1 (22.4)	32.1 (23.0)	
WATER	Percent present	22.2	0	0	
OUTCROP	Percent present	14.8	20.0	25.0	
TALUS	Percent present	48.2	50.0	50.0	
Coarse woody debris:					
DLOGSA	Percentage cover	1.9 (1.55)	2.3 (2.23)	1.8 (1.19)	
DLOGSB	Percentage cover	4.7 (2.65)	4.0 (3.38)	3.5 (2.10)	
DLOGSC	Percentage cover	1.5 (1.48)	1.6 (1.77)	1.4 (1.42)	
STUMP	Number/ha	20.6 (22.6)	61.1 (57.4)	62.5 (100.2)	
SSNAG	Number/ha	62.1 (79.5)	68.9 (74.4)	154 (91.3)	0.047
MSNAG	Number/ha	37.0 (38.0)	131 (129)	146 (66.3)	.001
LSNAG	Number/ha	7.2 (5.44)	6.7 (6.2)	2.9 (2.13)	
DECSNAG	Number/ha	8.4 (16.8)	22.6 (22.7)	14.1 (19.5)	
Live tree:					
CTREES	Number/ha	531 (644)	260 (344)	81.9 (106)	.012
CTREEM	Number/ha	271 (138)	321 (156)	501 (198)	.007
CTREEL	Number/ha	32.8 (13.1)	8.0 (6.73)	4.3 (9.31)	<.001
BTREES	Number/ha	30.0 (39.3)	109 (187)	86.1 (86.0)	
BTREEM	Number/ha	58.9 (50.8)	30.0 (39.0)	94.0 (71.1)	
BTREEL	Number/ha	.1 (.30)	.3 (.99)	.2 (.56)	
MDTREE	Percentage cover	8.2 (9.1)	4.3 (6.90)	4.7 (5.86)	
MBTREE	Percentage cover	.8 (1.61)	.8 (2.20)	3.9 (5.32)	.048
MCTREE	Percentage cover	22.3 (11.1)	10.5 (13.3)	5.1 (2.54)	<.001
CDTREE	Percentage cover	.6 (1.08)	.6 (1.90)	1.4 (3.27)	
CBTREE	Percentage cover	.1 (.30)	.1 (.23)	.3 (.65)	
CCTREE	Percentage cover	41.4 (8.38)	52.4 (13.5)	57.9 (6.98)	<.001
Ground cover:					
LITDEPTH	cm	3.6 (2.98)	6.0 (7.74)	3.1 (1.22)	
SOIL	Percentage cover	2.2 (2.12)	3.1 (6.48)	2.1 (1.92)	
ROCK	Percentage cover	.4 (.46)	1.5 (3.98)	.3 (.42)	
FLITTER	Percentage cover	65.9 (11.8)	56.3 (22.9)	61.2 (10.5)	
MOSS	Percentage cover	26.5 (13.4)	31.6 (24.9)	31.8 (12.4)	
FORB	Percentage cover	4.3 (4.41)	6.4 (7.1)	3.8 (7.86)	
GRASS	Percentage cover	.4 (.62)	1.0 (1.33)	.2 (.12)	
FERN	Percentage cover	28.1 (25.5)	18.1 (27.1)	5.8 (3.74)	
ESHRUB	Percentage cover	23.8 (19.8)	22.2 (31.4)	36.6 (20.4)	
DSHRUB	Percentage cover	7.5 (8.5)	5.5 (5.93)	7.8 (6.93)	
BSHRUB	Percentage cover	1.9 (3.02)	4.6 (5.19)	5.1 (9.31)	
MSHRUB	Percentage cover	16.4 (15.6)	9.2 (8.82)	12.1 (8.9)	

[a] Where a significant difference occurred among age-classes, solid lines indicate pairs of age-classes that were not significantly different at $P = 0.05$.

Multiple regression models of abundance of common species on vegetative variables usually included the same variables that were significant in the simple correlations plus one or two additional variables, but the predictive power of the models was low (table 5). Shrew-moles and deer mice, which did not have any significant simple correlations, both had multiple-regression models that contained four variables, but each model accounted for only about a third of the variance

Table 5-Stepwise multiple regression of the abundance of common[a] species on vegetative variables

Species and variable	Coefficient	SE	t	Multiple r^2	SE of the estimate	F	P
Trowbridge's shrew				0.428	0.163	5.845	<0.001
constant	1.124	0.126	8.902				
DLOGSB	-1.639	.408	-4.015				
FERN	.272	.082	3.310				
SLOPE	-.308	.112	-2.753				
LITDEPTH	.129	.053	2.444				
MDTREE	.313	.154	2.024				
Pacific shrew				.331	.170	4.951	.002
constant	-.142	.105	-1.361				
DECSNAG	.049	.020	2.404				
FERN	.203	.088	2.289				
SHRUB[b]	.157	.088	1.783				
BSHRUB	.480	.273	1.756				
Shrew-mole				.324	.076	4.802	.003
constant	.232	.057	4.093				
HERB	.355	.111	3.192				
DECSNAG	-.030	.010	-2.942				
MOSS	-.173	.068	-2.544				
MDTREE	-.149	.077	-1.939				
Western red-backed vole				.395	.177	6.531	<.001
constant	.479	.117	4.080				
BSHRUB	.909	.275	3.311				
MOSS	-.444	.148	-3.012				
TRASPECT	-.059	.027	-2.165				
CTREEL	.038	.022	1.728				
Deer mouse				.366	.084	5.767	.001
Constant	.381	.068	5.638				
DLOGSC	-.949	.255	-3.722				
SLOPE	-.186	.060	-3.123				
BSHRUB	-.297	.125	-2.371				
TRASPECT	-.024	.013	-1.858				

[a] Common species were captured in more than 50 percent of the stands and with more than 50 total captures.

[b] ESHRUB+BSHRUB.

in abundance. Most of the variables that were included in the regression models reflected ground cover at or below the shrub layer (less than 2 m above the ground). Abundance of Trowbridge's and Pacific shrews appeared to be associated with denser growth of shrubs and ferns, but the abundance of shrew-moles was associated with herbaceous vegetation, which indicates a more open shrub layer.

Multivariate analyses-A principal components analysis of eight vegetation variables with no rotation of factors produced three factors with eigenvalues greater than 1.0; these accounted for 67.6 percent of the variance. We interpret factor 1 (33.1 percent of the variance) as describing the structure of live trees; it was positively correlated with cover by conifers in the midstory, numbers of large conifers and large snags, and negatively correlated with cover by conifers in the canopy. Factors 2 (19.3 percent) and 3 (15.2 percent) together accounted for only about one-third of the variance. Factor 2 appears to represent coarse woody debris. It was positively correlated with numbers of well-decayed snags and cover by down wood. Factor 3 was associated with the shrub layer. It was positively correlated with cover by evergreen shrubs and negatively correlated with cover by ferns.

Young stands differed from old-growth stands mainly on factor 1 (fig. 5), which would be expected, because young stands lacked large Douglas-fir trees and a well-developed midstory layer. Most young stands had Factor 1 scores less than zero, and most old-growth stands had scores greater than zero. Factor 1 scores for mature stands, however, overlapped young and old-growth stands, so the three age-classes did not form discrete groups.

Mammal Community Structure

Multidimensional scaling of the similarity of 45 stands and K-MEANS clustering based on the abundance of six species of small mammals revealed differences among stands that do not fall in a simple gradient from young forests to old growth (fig. 6). The first multidimensional scaling axis (dimension 1) was strongly correlated with the abundance of Trowbridge's shrews ($r = 0.96$), Pacific shrews ($r = 0.60$), and with the sum of the abundance of all six species ($r = 0.93$, fig. 7). The second multidimensional scaling axis (dimension 2) was strongly correlated with the abundance of red-backed voles ($r = 0.80$) and the Berger-Parker index of species diversity ($r = 0.86$, fig. 8). This index measures dominance (Magurran 1988), so in stands with a low value, Trowbridge's shrews were a high proportion of captures. Stands with higher diversity indices had relatively fewer captures of Trowbridge's shrews and greater contributions from other species. Dimensions 1 and 2 define a gradient in the complexity of the mammal community. Stands with low abundance and species diversity (less complex) had low scores on both dimensions, and stands with high abundance and species diversity (more complex) had high scores on both dimensions.

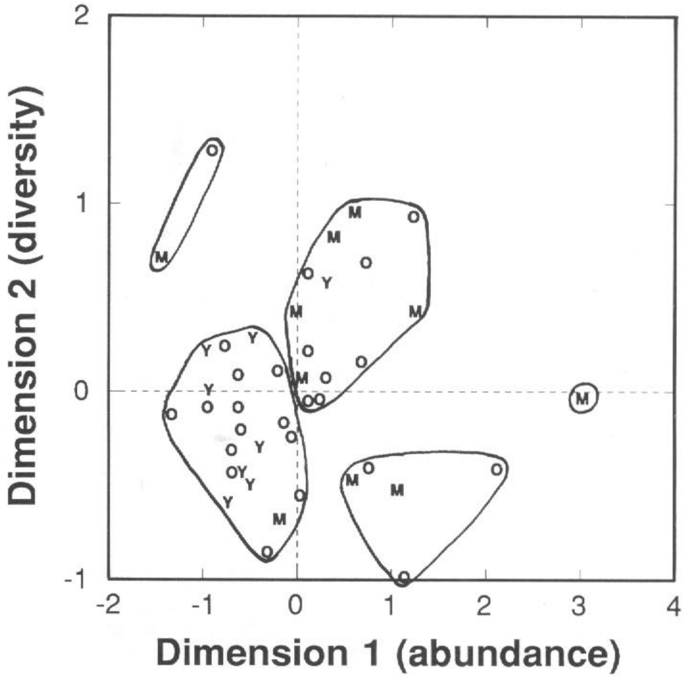

Figure 6—Multidimensional scaling of Coast Range stands based on abundance of six species of mammals (see text). Lines enclose non-overlapping clusters of stands, and symbols indicate habitat type (O = old-growth, M = mature, Y = young).

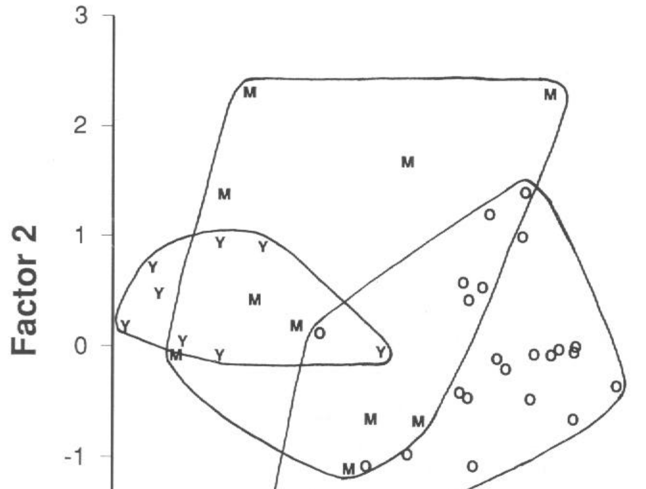

Figure 5—Position of different forest stands on the first two factors of a principal components analysis of eight selected vegetation variables. Habitat types are identified by O (old-growth), M (mature), and Y (young).

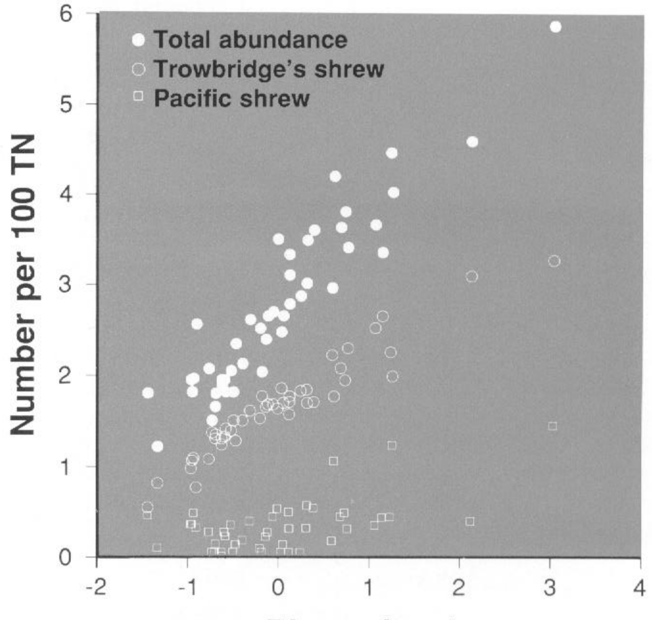

Figure 7—Total abundance of six small mammals and abundance of Trowbridge's and Pacific shrews versus multidimensional scaling axis 1.

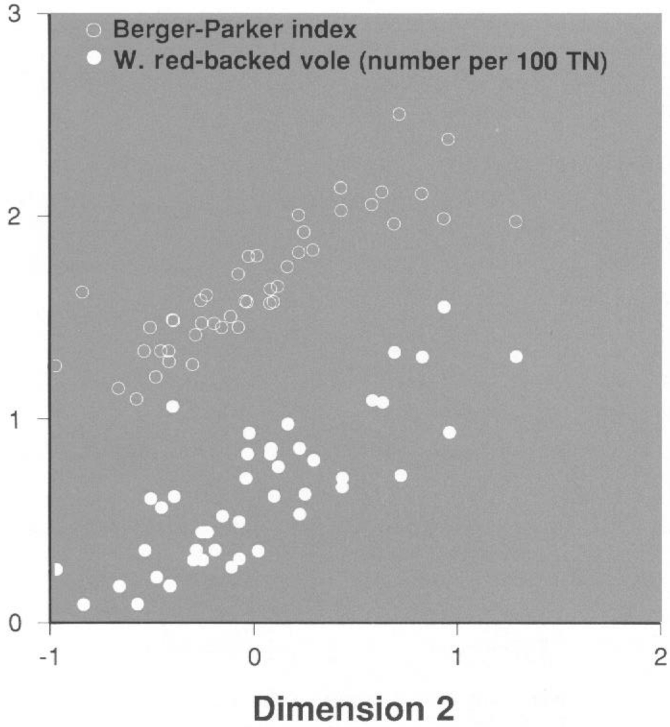

Figure 8—Abundance of western red-backed voles and species diversity (Berger-Parker index) versus multidimensional scaling axis 2.

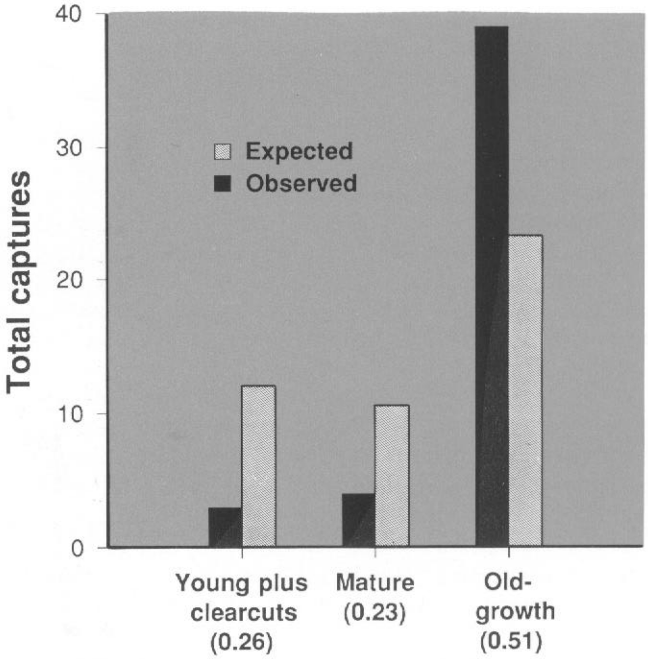

Figure 9—Total captures of red tree voles in the Oregon Cascade Range and Coast Ranges during old-growth community studies, 1983-85. The proportion of the total trapping effort in each age-class is listed in parentheses.

Nonhierarchical clustering generated pool 1 containing 23 stands, pool 2 containing 14 stands, pool 3 containing 5 stands, and two outlying pools with 2 and 1 stands (fig. 6). Pools 1 and 2 orient on the gradient from lower to higher complexity. Membership in pools 1 and 2 was not random with respect to age-class ($G = 7.93$, 2 df, $P = 0.02$). Old-growth stands were evenly distributed between pool 1 and pool 2, but seven of eight young stands were in pool 1 and five of six mature stands were in pool 2. The remaining four mature stands were in pools with either high diversity or high abundance.

No strong correlations were found between dimensions 1 and 2 and any of the physiographic or vegetation variables. Dimension 1 was weakly correlated with latitude ($r = 0.32$, $P < 0.05$), and dimension 2 was weakly correlated with longitude ($r = 0.38$, $P < 0.05$).

Discussion

Species Associated With Old-Growth Forests

One species, the red tree vole, was significantly more abundant in old-growth forests than in young or mature forests in the Oregon Coast Ranges. This small, arboreal rodent was seldom captured on the ground until we began using large numbers of pitfall traps (Corn and Bury 1986). Red tree voles are an important prey of spotted owls (Forsman and others 1984), and they were listed as a species potentially dependent on old-growth forests (Meslow and others 1981). Anecdotal reports have long indicated an affinity for large Douglas-fir trees (Bailey 1936, Howell 1926, Maser and others 1981), and we found greater density of large conifers in stands where we caught red tree voles. Recent searches for nests of red tree voles support the notion that old-growth trees are preferred as nest sites (Gillesberg and Carey, this volume); Meiselman and Doyle, in press), although nests have also been observed occasionally in young second-growth trees (Carey 1989, Maser 1966).

The 17 red tree voles we trapped in the Coast Ranges constitute a small sample, but since 1983, 46 red tree voles have been trapped in the Coast and Cascade Ranges of Oregon by old-growth researchers (this study; Corn and Bury 1986; Gilbert and Allwine, this volume a). Most (39) were captured in old-growth stands (fig. 9), and, because the trapping effort was about evenly split between old-growth stands and younger stands, a significant excess of captures was in old growth ($G = 24.0$, 2 df, $P < 0.001$). Raphael (1988c) captured an additional 19 red tree voles in pitfall traps in Douglas-fir forests in northwestern California. Although the difference in relative abundance among stand age-classes was not significant, most red tree voles were captured in stands older than 100 years. Meiselman and Doyle (in press) located several nests of red tree voles in northwestern California, and a statistically significant majority were in old-growth forests. These results indicate that red tree voles are strongly associated with old-growth Douglas-fir forests.

Aside from red tree voles and Pacific shrews (most abundant in mature stands), no statistically significant relations were found between stand age and the abundance of small mammals. Our results agree with other old-growth research from Oregon and Washington that found few species of terrestrial small mammals associated with older forests (Anthony and others 1987; Corn and others 1988; Gilbert and Allwine, this volume a; West, this volume).

The lack of strong correlations between habitat features and mammal abundance was somewhat surprising, considering that studies of insectivores (Hawes 1977, Terry 1981). earlier studies from the old-growth program (Corn and others 1988), and studies in California (Raphael 1988c, Raphael and Barrett 1984) found several significant habitat associations. One possibility is that by trapping only in the fall, we were sampling populations composed of high proportions of subadult animals (Sullivan 1979, Van Home 1981), which might be transients in habitat of lower quality. Abundance data, then, would give a misleading indication of habitat quality (Sullivan 1979, Van Home 1983). Our data did not reveal any marked differences in the proportions of subadult Trowbridge's and Pacific shrews and red-backed voles among young, mature, and old-growth forests. Hawes (1977) found that home ranges of subadult vagrant and montane shrews in British Columbia were smaller subsets of the areas they occupied when breeding the next spring. This finding suggests that subadult shrews have the narrowest habitat requirements and that trapping in the fall would reveal important habitat associations.

A more likely explanation for finding few habitat associations is that threshold values for critical habitat features to small mammals are exceeded in naturally regenerated forests after the canopy is reestablished (West, this volume). Understory plant communities in Douglas-fir forests are resilient and rapidly return to the composition found in old growth after disturbance (Halpern 1988). In the Coast Ranges, structural features likely to be associated with terrestrial mammals did not differ among different ages of stands. For example, no difference was found in the Coast Ranges in the percentage cover by down wood among young, mature, and old-growth stands (Spies and others 1988). Different age-classes of naturally regenerated forest represent a single habitat type for most small mammal species. This conclusion is supported by the observation that neither abundance nor diversity of small mammals displayed the predicted U-shaped pattern (Spies and Franklin 1988) when compared to stand age. No decline occurred in abundance or diversity in mature stands in the Cascade Range (Gilbert and Allwine, this volume a; West, this volume). In the Coast Ranges, the trend was opposite of the prediction; abundance and diversity of six species of mammals were greater in mature stands. These studies provide little support for a U-shaped pattern of diversity of small mammals.

Managed Forests

Many studies have examined the effects of logging on small mammals in the Pacific Northwest, and they have documented major changes in the composition of the mammal community. In general, populations of deer mice, creeping voles, vagrant shrews, and Townsend's chipmunks increase after logging, while red-backed voles and Trowbridge's shrews decline (Anthony and Morrison 1985; Corn and others 1988; Gashwiler 1959, 1970b; Hooven and Black 1976; Raphael 1988c; Sullivan and Krebs 1980; Tevis 1956; West, this volume). Some of these changes represent increased abundance by species adapted to open habitats, but for other species, clearcuts may act as dispersal sinks and the increased abundance is transitory (Sullivan 1979).

Species composition of mammal communities in clearcuts is less predictable than that of old-growth forests. Considering both this study and the earlier study in the Oregon Cascades (Corn and others 1988), Trowbridge's shrews (76 percent of captures in forested stands) and vagrant shrews (71 percent of captures in clearcuts) had similar relative abundances in forests and clearcuts, respectively. But while Trowbridge's shrews were always the most abundant insectivore in forested stands, vagrant shrews were the most abundant insectivore in only three of six clearcuts. Abundance of creeping voles and deer mice also varied widely among clearcuts. The low predictability of mammal populations in clearcuts may be related to the rapid succession occurring in the plant communities (Halpern 1988, Schoonmaker and McKee 1988), which may generate greater variability in food resources and microclimates than is found in closed-canopy forests.

The apparent low habitat quality and unpredictibility of clearcuts for many mammal species means that, as naturally regenerated forests are converted into managed forests, the long-term survival of many species will depend on whether managed forests provide essential habitat features. For example, modem logging practices greatly reduce both the amount of coarse woody debris carried over into a stand after harvest and the amount accumulated before the next harvest (Spies and Franklin 1988, Spies and others 1988). The results of our studies, however, provide little insight into this question. We did not investigate managed stands after closure of the canopy, and the range of variation of habitat variables in naturally regenerated stands is probably insufficient to make predictions about habitats and small mammal communities in intensively managed forests.

Recommendations

The studies of old-growth forests reported in this volume have provided baseline data on the occurrence of vertebrate species in natural Douglas-fir forests in the Pacific Northwest. In general, however, more questions have been created than answers supplied. We offer the following suggestions for high-priority research in the Coast Ranges of Oregon:

Determine the abundance of red tree voles in old-growth, mature, young, and managed forests. The data collected so far suggest that this species may depend on old growth, but the sample size is small. The red tree vole is probably the most difficult small mammal in the Pacific Northwest to study, but recently developed techniques (Gillesberg and Carey, this volume; Meiselman and Doyle, in press) show promise.

Compare small mammal populations in naturally regenerated and intensively managed forests. The changes in forest structure predicted between managed and natural forests are of a much greater magnitude than we measured in a natural sere. Although we found few differences among different-aged forests, the same prediction cannot be made for a comparison of managed and natural forests. Some work along this line has begun; more is needed.

Determine the effects of forest fragmentation on small mammal populations. We did not deal with fragmentation in this paper, and, currently, little evidence indicates that small-mammal populations are strongly influenced by stand size or degree of fragmentation (Raphael 1984, Rosenburg and Raphael 1986). Few data have been collected so far on the effects of fragmentation in western forests, however, and any effects are likely to be severe in the Coast Ranges, where most old growth exists as small, isolated patches (Harris 1984, Monthey 1984, Spies and Franklin 1988).

The lack of a unique community of small mammals in old-growth forests does not reduce the value of these habitats. Old growth is a nonrenewable resource (Schoen and others 1981) with numerous other intrinsic assets. In the Coast Ranges, our results suggest that the biological integrity of isolated blocks of old growth may be enhanced if tracts of younger, naturally regenerated forest are contiguous.

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Appendix

Table 6-Vegetative variables measured at 9 points within pitfall grids

Variable	Description
Physiographic:	
TRASPECT	Transformed aspect (cosine transformation [NE=O, SW=2])
SLOPE	Percent slope
WATER	Presence or absence of open water (seeps, ponds, permanent or intermittent streams) on grid
TALUS	Presence or absence of exposed talus on grid
Coarse woody debris:	
DLOGSA	Percentage cover by decay class 1 and 2 down wood
DLOGSB	Percentage cover by decay class 3 and 4 down wood
DLOGSC	Percentage cover by decay class 5 down wood
STUMP	Number of stumps per hectare
SSNAG	Number of small snags (<10 cm d.b.h.) per hectare
MSNAG	Number of medium snags (l0-50 cm d.b.h.) per hectare
LSNAG	Number of large snags (>50 cm d.b.h.) per hectare
DECSNAG	Number of well-decayed (class 4 and 5) medium and large snags per hectare
Live tree:	
CTREES, CTREEM, CTREEL	Number of small (<l0 cm d.b.h.), medium (≥ 10 cm and <l m d.b.h.), and large (>1 m d.b.h.) coniferous trees per ha
BTREES, BTREEM, BTREEL	Number of broadleaf trees (same size-classes) per ha
MDTREE	Percentage cover by deciduous midstory trees
MBTREE	Percentage cover by broadleaf evergreen midstory trees
MCTREE	Percentage cover by coniferous midstory trees
CDTREE	Percentage canopy cover by deciduous trees
CBTREE	Percentage canopy cover by broadleaf evergreen trees
CCTREE	Percentage canopy cover by coniferous trees
Ground cover:	
LITDEPTH	Depth (cm) of organic litter layer
SOIL	Percentage cover by bare soil
ROCK	Percentage cover by exposed rock
FLITTER	Percentage cover by fine organic litter
MOSS	Percentage cover by moss
HERB	Percentage cover by forbs
GRASS	Percentage cover by grasses
FERN	Percentage cover by ferns
ESHRUB	Percentage cover by evergreen shrubs
DSHRUB	Percentage cover by deciduous shrubs
BSHRUB	Percentage cover by ***berry*** shrubs ***(Rubus*** spp. and ***Vaccinium*** spp.)
MSHRUB	Percentage cover by midstory shrubs (>2 m high)

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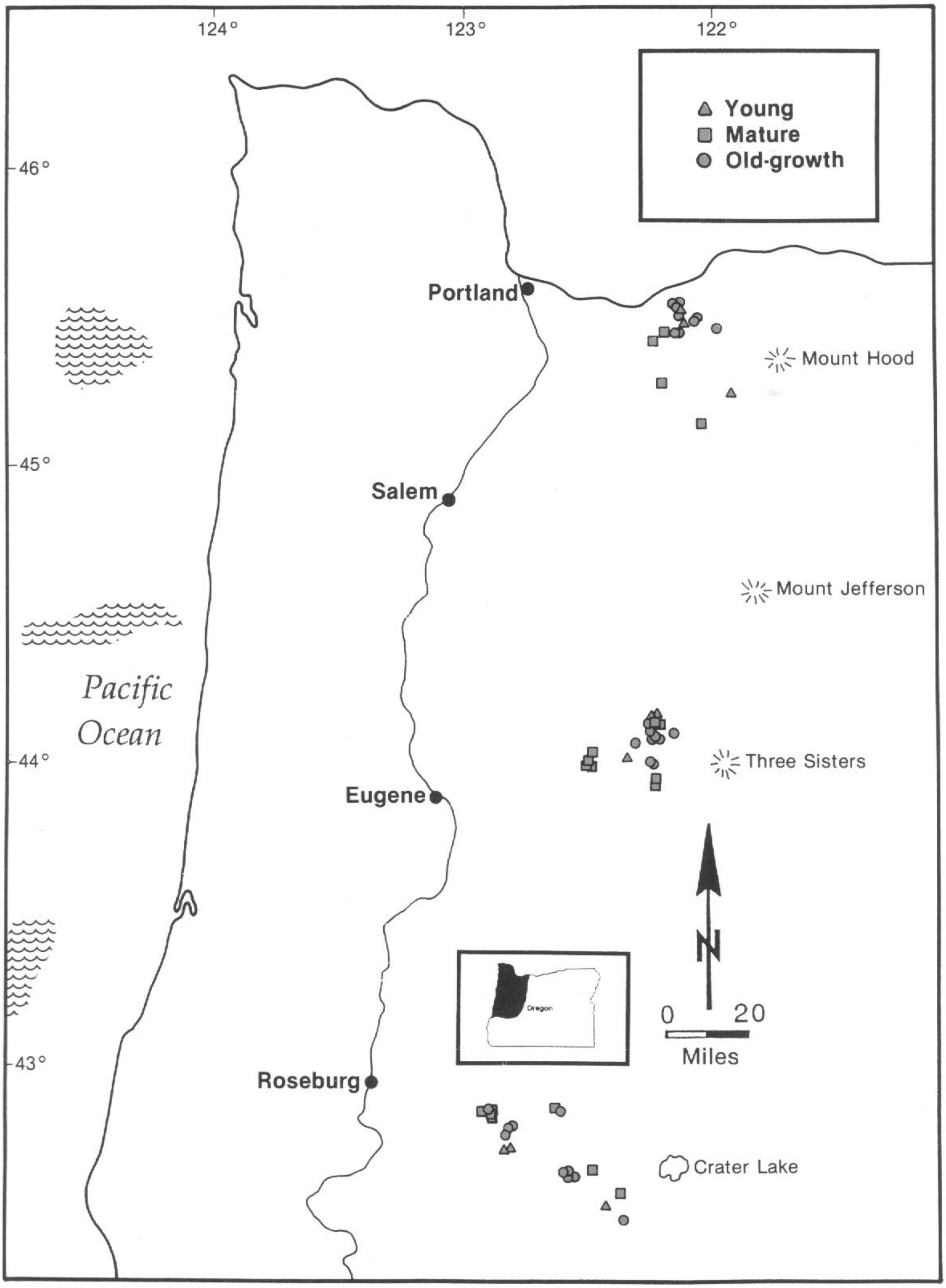

Location of study sites.

Small Mammal Communities in the Oregon Cascade Range

Frederick F. Gilbert and Rochelle Allwine

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Abstract

Pitfall and snap-trapping of small mammals in the western Oregon Cascade Range in 1984-85 revealed no significant differences in species richness among young, mature, and old-growth Douglas-fir stands. Trowbridge's shrew was the most abundant small mammal captured, accounting for about half of all captures. Species showing some association with older stands included Trowbridge's shrew, the shrew-mole, the deer mouse, and the red tree vole. The coast mole was found only in mature and old-growth stands in 1985. These species' associations with vegetational and physical characteristics indicated temporal and spatial differences in habitat use. The tree squirrels (Douglas' squirrel and northern flying squirrel) showed strong positive correlations with snags. The Soricidae segregated themselves on latitudinal, elevational, and moisture gradients.

Results from this study need to be treated with some caution: the young and mature stands contained many characteristics of old-growth stands because they had been naturally regenerated (usually after fire) and thus did not represent conditions that might be expected in stands managed for timber production.

Introduction

The effects of forest fragmentation or general loss of habitat are seldom immediately visible in small mammal communities. Studies in the western National Parks, though, support the contention that declines in species richness are likely over time with insularization of habitat (Weisbrod 1976). Harris and others (1982), Raphael (1988c), and Rosenberg and Raphael (1986) suggest that the long-term reduction of old-growth forests will negatively affect small mammal populations. Comparisons of species occurrence and abundance in different-aged stands may provide insight into the effects of truncation of seral development on existing faunal communities. The objectives of the current study were to assess the small mammal communities of young, mature, and old-growth Douglas-fir stands in the Oregon Cascade Range and and determine which environmental factors might be responsible for any differences observed.

Materials and Methods

Three locations on the western slopes of the Oregon Cascades were studied in 1984. Twenty stands were selected in the Rogue River and Umpqua National Forests (Rogue-Umpqua), 20 near the H.J. Andrews Experimental Forest (Andrews) and 16 in the Mount Hood region (Mt. Hood). These stands were selected to represent young, mature, and old-growth Douglas-fir forests and a moisture gradient (wet, mesic and dry) in the old-growth stands (Gilbert and Allwine, this volume b: see appendix table 15). In addition, a few stands were selected to represent either a mature-age moisture gradient or managed stands. Final analyses were done for fewer than 56 stands to assure comparison between mesic, unmanaged stands of the three age-classes (22 old-growth, 17 mature, and 9 young); 28 old-growth stands were in the moisture-gradient analysis (7 dry, 9 mesic, 12 wet).

Trapping Methods

Pitfall grids (6 x 6) were established in each stand and checked during September and October 1984. One pitfall trap consisting of 2 number 10 cans taped together and lined with plastic margarine tubs was buried within 2 m of each grid station. A cedar shake was placed above the opening to minimize rain and snow accumulation in the cans. Water was removed at each check. The traps were opened in early September and checked every 5 to 7 days for at least 50 days. In 1985, 15 stands at the Andrews were studied; the old pitfall grids were used in all stands, and new grids were established in 8 of them (Gilbert and Allwine, this volume b: see appendix table 15). Results from the old and new pitfall grids were compared to determine whether the previous year's trapping had affected the resident populations. Chi-square testing was used to examine species captured and number of individuals of each species in the eight stands. Because the new grids showed no difference in species composition and abundance, the old grids were used for analysis.

In 1984, snap trap grids (12 x 12) with 15-m spacing between grid locations also were used to sample the small-mammal fauna. Trapping took place in July and August, and each stand was trapped for 4 consecutive nights. Two Museum Special traps (Woodstream Corp., Lititz, PA) baited with a mixture of peanut butter and rolled oats were placed within a 1.5-m radius of each grid location.

Mammals caught in the pitfall traps usually had drowned or otherwise died by the time of collection. All animals were identified to species, sexed, measured, and preserved in the Conner Museum at Washington State University as skulls, skeletons, or skins and skulls. Identifications were verified by museum staff. Even with the examination by museum personnel, many Soricidae could not be identified to species.

Vegetative Measurements

The physical and vegetative characteristics of the trapping grids were sampled at 9 points within the pitfall grid and 16 points within the snap trap grids, with the center of each sampling point equidistant from four stations. Measurements were made using a nested-plot design, with 5.6-m and 15-m radius circles (appendix table 12). Percentage cover was visually estimated. The species capture rates (corrected for actual trap nights of operation) were compared to these environmental variables.

Statistical Analysis

Data analysis was based on two major statistical goals: testing the hypotheses that animal abundance did not differ among age-classes, moisture-classes, and locations, and number of species (species richness) did not differ among these classes; and using exploratory statistics to associate individual species with individual habitat components and with either age-classes or moisture-classes.

We used nonparametric analysis of variance (ANOVA) to test the hypothesis that abundance (number of captures per 1000 trap-nights) of animals and species richness did not differ among the age- and moisture-classes or locations. We used detrended correspondence analysis (DCA) (Hill 1979a) to explore the relations between animal abundances and habitat-classes or environmental variables. Detrended correspondence analysis is an ordination technique that arranges a matrix of species' abundances (communities) by samples (stands) in low-dimensional space so that the communities occurring in each stand are represented in space along several axes. Thus, many components are reduced to a few important ones and variability is reduced. Communities with similar species composition and relative abundances occupy positions near each other within the space described by the first and second DCA axes. In this way, it functions as a principal components analysis. To determine whether stands grouped themselves according to a physiographic gradient, a plot of the detrended correspondence analysis axes scores was examined to detect clustering.

To classify sites into community phases, two-way indicator species analysis (TWINSPAN) (Hill 1979b) was used. This method, based on a multi-level two-way partitioning of the correspondence analysis scores, was used to classify species into categories related to location or to age- or moisture-classes. Species found to be associated with old-growth forests, from TWINSPAN analysis or from Spearman rank correlations of animal abundances with stand age, were then correlated (Spearman rank correlations) with individual environmental and vegetative variables to examine the relation between animal species and individual habitat features.

Statistical significance was determined as $P \leq 0.05$. Means are given ± SE.

Results

Pitfall Trap Results

A total of 18 species of small mammals were caught in the pitfall traps in 1984. Species richness was greatest at Mt. Hood (16) and lower at Andrews (11) and Rogue-Umpqua

(13). Species' abundances (number of captures per 1000 trap-nights) varied by subprovince, with five species having significantly more captures at Mt. Hood and two more at Rogue-Umpqua (table 1). Trowbridge's shrew, by far the most common species at all three locations, accounted for 62.6 percent of all captures and ranged from 53.0 percent at Mt. Hood to 59.2 percent at Rogue-Umpqua and 75.8 percent at Andrews (table 2). The Soricidae represented 76.9 percent of the total captures. The western red-backed vole was the only nonshrew species to represent more than 10 percent of the captures (14.6 percent) mainly because of a relative abundance of 26.5 percent at Rogue-Umpqua.

Old-growth stands had 17 species, mature 15, and young 12. The average number of individuals captured by age-class was old-growth (49.5 ± 5.0), mature (46.5 ± 5.7), and young (49.1 ± 12.9). The deer mouse ($R = 0.35$, $P = 0.01$) and the red tree vole ($R = 0.37$, $P = 0.005$) were significantly positively associated with stand age. No species were significantly associated with any age category in the chronosequence (ANOVA, $P < 0.05$) (table 3). The average number of captures per stand was not different along the moisture gradient (wet 47.3 ± 5.7, mesic 50.8 ± 7.5, dry 53.0 ± 12.1), and no species were significantly associated with the moisture gradient (ANOVA, $P < 0.05$) (table 3). DECORANA analysis confirmed that age and moisture conditions did not influence the mammal distribution (figs. 1,2). A location effect was related to the pitfall captures (fig. 3), however. TWINSPAN analysis showed no indicator species for age or moisture conditions, but the Pacific jumping mouse, the montane shrew, the heather vole, Townsend's chipmunk, the northern flying squirrel, and the ermine separated out as Mt. Hood indicators; Townsend's vole and the northern pocket gopher were indicator species for Rogue-Umpqua.

No significant differences were found between the old and new grids in species abundances or richness ($P < 0.05$). Significantly more small mammals were caught in young stands (average 59.0 ± 4.6) than in old-growth stands (29.8 ± 4.2) in 1985. The mature-stand average (46.7 ± 6.8) was not different from the other two age-categories. Fourteen species were captured in 1985 compared to 10 in the same stands in 1984. The four additional species (red tree vole, Pacific shrew, Townsend's chipmunk, and the montane vole) were represented only by 1 to 3 specimens each.

None of the small mammals captured in 1985 were significantly related to old growth in the chronosequence, although five species showed an association with mature or young stands (table 4). The coast mole and red tree vole were only captured in mature and old-growth stands. The only significant difference in age- or moisture-classes for any species between 1984 and 1985 was the increased proportion of Trowbridge's shrew caught in young stands in 1985 ($x^2 = 56.6$, $P < 0.0001$).

Table 1-Signiflcant ANQVA values for small mammal abundance based on pitfall captures corrected for effort (number of captures per 1000 trap-nights) related to subprovince location, Oregon Cascades 1984

Species	Location[a]	F-Value	P
Western red-backed vole	RRU > HJA,MTH	25.59	<0.0001
Pacific shrew	RRU > HJA, MTH	11.33	<0.0001
Deer mouse	RRU > HJA	4.81	0.01
sorex spp.	HJA > MTH, RRU		<0.05
Pacific jumping mouse	MTH > HJA, RRU	45.37	<0.0001
Northern flying squirrel	MTH > HJA, RRU	35.64	<0.0001
Montane shrew	MTH > HJA, RRU	16.40	<0.0001
Ermine	MTH > HJA, RRU	8.10	<0.0009
Townsend's chipmunk	MTH > HJA, RRU	3.91	<0.03
Heather vole	captured only at MTH	2.91	0.06

[a] RRU = Rogue River-Umpqua; HJA = H.J. Andrews; MTH = Mt. Hood.

Table 2-Small mammal relative abundance (captures per 1000 trap-nights) from pitfall trapping by location, Oregon Cascades, 1984 (values in brackets are percentage of capture at that location)

Species	Rogue-Umpqua	Andrews	Mt. Hood
Trowbridge's shrew	331.1 (59.2)	316.9 (75.8)	244.2 (53.0)
Western red-backed vole	148.3 (26.5)	21.2 (5.1)	39.9 (8.7)
sorex spp.	8.3 (1.5)	42.2 (10.1)	2.7 (<1.0)
Montane shrew	0.6 (<1.0)	1.7 (<1.0)	76.0 (16.5)
Pacific shrew	39.0 (7.0)	12.8 (3.1)	0.0 (0.0)
Vagrant shrew	2.8 (<1.0)	2.2 (<1.0)	12.3 (<1.0)
Marsh shrew	2.7 (<1.0)	4.4 (1.1)	5.1 (1.1)
Water shrew	0.0 (0.0)	0.0 (0.0)	0.5 (0.0)
Pacific jumping mouse	1.2 (<1.0)	1.7 (<1.0)	35.1 (7.6)
Shrew-mole	6.1 (1.1)	8.8 (2.1)	11.2 (2.4)
Deer mouse	12.9 (2.3)	1.1 (<1.0)	7.3 (1.6)
Northern flying squirrel	0.0 (1.0)	0.0 (0.0)	11.9 (2.6)
Coast mole	3.8 (<1.0)	4.5 (1.1)	6.2 (1.3)
Townsend's chipmunk	0.0 (0.0)	0.0 (0.0)	3.4 (<0.0)
Creeping vole	1.7 (<1.0)	0.6 (<1.0)	0.5 (<1.0)
Townsend's vole	0.5 (<1.0)	0.0 (0.0)	0.0 (0.0)
Heather vole	0.0 (0.0)	0.0 (0.0)	0.6 (<1.0)
Northern pocket gopher	0.6 (<1.0)	0.0 (0.0)	0.0 (0.0)
Douglas' squirrel	0.0 (0.0)	0.0 (0.0)	1.1 (0.0)
Ermine	0.0 (0.0)	0.0 (0.0)	2.9 (<1.0)

Snap Trap Results

Eighteen species and 1493 individuals were captured in the snap traps (table 5). Trowbridge's shrew was the dominant species at all locations (44.8-55.4 percent of all captures). The Pacific shrew was the second most captured species (24.1 percent) at Andrews, the montane shrew (14.2 percent) at Mt. Hood, and the western red-backed vole (29.4 percent) at Rogue-Umpqua. Species richness was not significantly different between locations. The western red-backed vole, the deer mouse, and the marsh, montane, and Pacific shrews were significantly associated with location (table 6). This

Table 3—Captures of individual mammals in pitfall traps (mean number captured per stand, corrected for effort in parentheses) for age- and moisture-classes, Oregon Cascades 1984

	Age			Moisture		
	Young	Mature	Old	Dry	Mesic	Wet
Red tree vole	—	2 (0.1)	6 (0.3)	—	6 (0.7)	3 (0.3)
Western red-backed vole	58 (7.3)	100 (6.1)	189 (8.6)	95 (10.7)	86 (9.6)	55 (4.4)
Townsend's chipmunk	3 (0.3)	—	—	—	—	—
Northern flying squirrel	6 (0.7)	2 (0.1)	6 (0.3)	—	6 (0.7)	7 (0.6)
Creeping vole	—	4 (0.2)	2 (0.1)	—	1 (0.1)	1 (0.1)
Townsend's vole	—	—	2 (0.1)	—	1 (0.1)	2 (0.2)
Ermine	1 (0.1)	2 (0.2)	—	—	—	2 (0.2)
Shrew-mole	3 (0.3)	10 (0.7)	22 (1.1)	7 (1.0)	7 (0.8)	19 (1.7)
Deer mouse	7 (0.8)	6 (0.4)	19 (1.0)	4 (0.6)	12 (1.4)	8 (0.8)
Coast mole	3 (0.3)	10 (0.7)	9 (0.4)	2 (0.3)	4 (0.4)	7 (0.6)
Marsh shrew	1 (0.2)	8 (0.8)	9 (0.4)	1 (0.1)	4 (0.4)	7 (0.6)
Montane shrew	46 (5.1)	37 (2.4)	8 (0.4)	1 (0.1)	6 (0.8)	47 (3.8)
Sorex spp.	5 (0.6)	19 (1.1)	15 (0.7)	10 (1.6)	13 (1.4)	19 (1.7)
Heather vole	—	1 (0.1)	—	—	—	1 (0.1)
Pacific shrew	7 (0.8)	29 (1.7)	58 (2.8)	17 (2.9)	24 (2.8)	17 (1.4)
Trowbridge's shrew	241 (28.9)	482 (28.4)	695 (31.0)	254 (34.4)	264 (29.6)	334 (27.7)
Vagrant shrew	8 (1.0)	4 (0.5)	6 (0.5)	4 (1.3)	2 (0.2)	12 (1.1)
Douglas' squirrel	—	—	2 (0.1)	—	2 (0.1)	—
Northern pocket gopher	—	1 (0.1)	—	—	—	—
Pacific jumping mouse	12 (1.3)	19 (1.1)	15 (0.7)	—	13 (1.4)	24 (2.2)

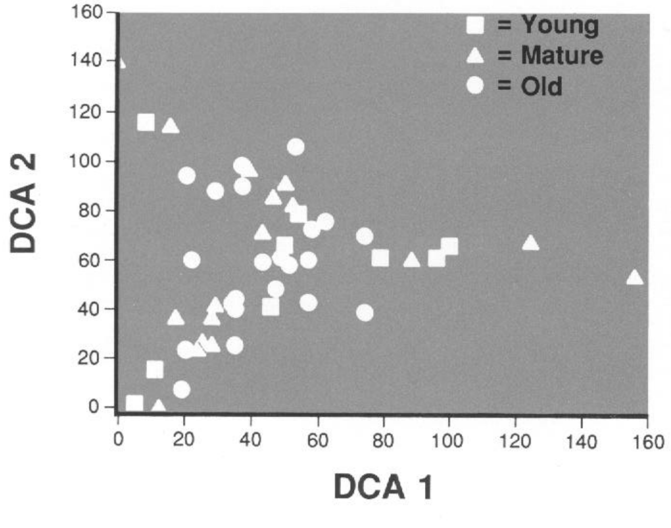

Figure 1—Detrended correspondence analysis of 1984 pitfall capture data for small mammals compared to age of stands, Oregon Cascade Range.

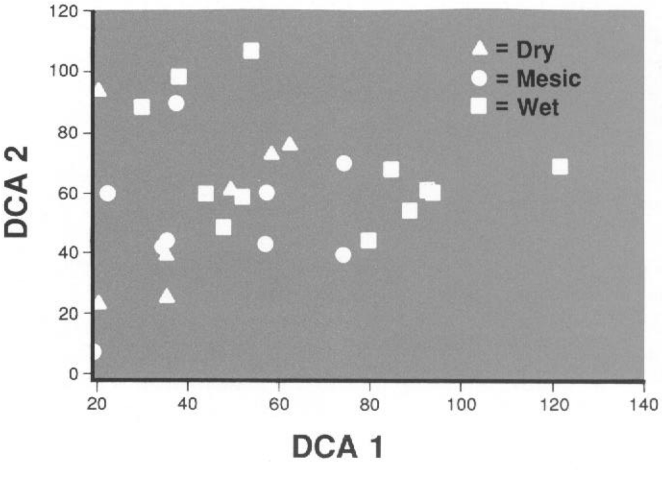

Figure 2—Detrended correspondence analysis of 1984 small mammal pitfall capture data compared to the moisture gradient, Oregon Cascade Range.

location effect was verified by the DCA scores, which showed definite clustering (fig. 4). No similar moisture or age effects were found (table 7; figs. 5, 6).

The mean captures per stand were highest in mature (29.2 ± 3.6) and lower in old-growth (26.3 ± 2.5) and young stands (15.5 ± 3.5) (ANOVA, $F = 3.24$, $P < 0.05$). The mature and young values were significantly different, but the values for old-growth did not differ significantly from the other two age-classes. Captures of the Pacific shrew were significantly associated with mature stands (ANOVA, $F = 3.62$, $P < 0.04$). Spearman rank correlations showed the shrew-mole and Trowbridge's shrew to have a positive association with stand age that neared significance ($P = 0.06$). The mean capture rates of all species did not differ along the moisture gradient (wet 26.4 ± 3.7, mesic 30.3 ± 3.9, dry 21.0 ± 3.5). Only the

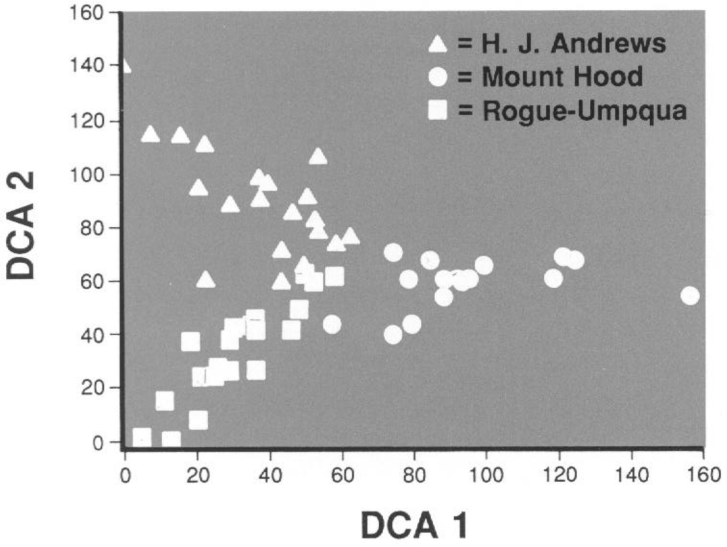

Figure 3—Detrended correspondence analysis of 1984 small mammal pitfall capture data by location within the Oregon Cascade Range.

Table 4—Small mammals significantly associated (ANOVA) with age of stand for pitfall captures, Oregon Cascades 1985

Species	Stand age association
Western red-backed vole	Mature > old-growth
Coast mole	Mature
Montane shrew	Young > old-growth
Trowbridge's shrew	Young > old-growth
Vagrant shrew	Mature > old-growth

western red-backed vole showed a relation to moisture conditions that was near significance, with average captures in mesic conditions (6.4) greater than dry (4.0) or wet (2.8) (ANOVA, $F = 3.14$, $P = 0.06$).

No differences were found in the average number of small mammals caught per stand by location (Rogue-Umpqua, 27.7 ± 2.8; Andrews, 24.9 ± 3.1; Mt. Hood, 24.0 ± 3.6). The western red-backed vole and the deer mouse were captured more frequently ($P < 0.05$) at Rogue-Umpqua, the marsh and the montane shrew at Mt. Hood, and the Pacific shrew at Andrews (table 5). The marsh, montane, vagrant, and Pacific shrews all had significant ($P < 0.05$) Spearman rank correlations for latitude.

Habitat Relations

Pitfall results—In 1984, the shrew-mole had a significant positive association with very large trees in the overstory, a feature of old-growth stands. It was found in stands dominated by very large western hemlock ($R = 0.31$, $P = 0.02$). The Douglas' squirrel was caught at sites with very large sugar pine ($R = 0.29$, $P = 0.03$), and incense-cedar ($R = 0.37$, $P = 0.005$).

Table 5—Small mammal captures on the snap-trap grids, Oregon Cascades 1984

	Location			
Species	Rogue-Umpqua	Andrews	Mt. Hood	Total
Trowbridge's shrew	247	262	217	726
Western red-backed vole	165	54	47	266
Pacific shrew	52	121	2	175
Deer mouse	46	15	11	72
Sorex spp.	8	60	3	71
Montane shrew	0	2	50	52
Shrew-mole	11	11	17	39
Townsend's chipmunk	14	13	3	30
Vagrant shrew	0	4	11	15
Marsh shrew	0	3	11	14
Coast mole	3	3	4	10
Creeping vole	7	1	1	9
Pacific jumping mouse	3	3	2	7
Townsend's mole	0	1	1	2
Montane vole	0	1	0	1
Microtus spp.	1	0	0	1
Dusky-footed woodrat	1	0	0	1
Scapanus spp.	1	0	0	1
Western pocket gopher	0	1	0	1
Totals	559	555	379	1493

Table 6—Small mammal species-abundance values corrected for effort (number of captures per 1000 trap-nights) snap-trapped in the Oregon Cascades, 1984, showing significant (ANOVA) associations with location

Species	Capture location[a] association	F-value	P
Western red-backed vole	RRU>HJA, RRU>MTH	9.67	0.0003
Deer mouse	RRU>HJA	4.35	<0.02
Marsh shrew	MTH>RRU	3.51	<0.04
Montane shrew	MTH>HJA, MTH>RRU	20.03	<0.0001
Pacific shrew	HJA>RRU, HJA>MTH	13.23	<0.0001

[a] RRU = Rogue River-Umpqua; HJA = H.J. Andrews; MTH = Mt. Hood.

The forest floor conditions at the capture sites differed. For example, the western red-backed vole, the red tree vole, and the deer mouse were all caught at sites with lichen (table 8). The Pacific jumping mouse's capture locations were significantly associated with ground cover of moss and logs of decay-classes 3 and 4. The understory components at Pacific jumping mouse capture sites included ferns, berry-producing, and deciduous shrubs (table 9) and tended to exclude broadleaf evergreen trees of all height-classes. The deer mouse

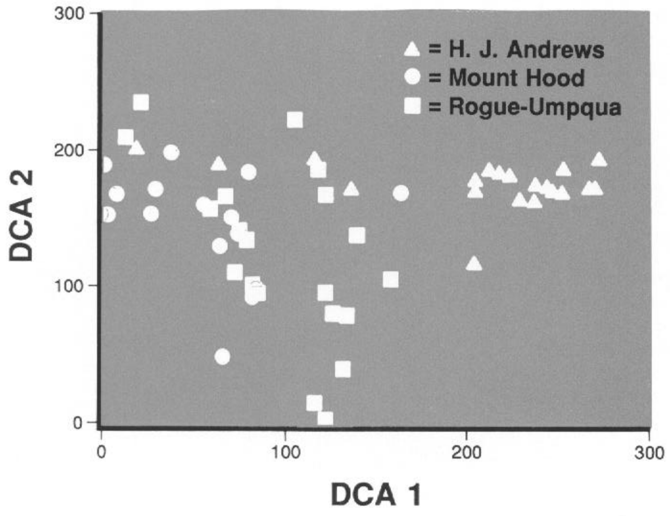

Figure 4—Detrended correspondence analysis of 1984 small mammal snap-trap capture data by location within the Oregon Cascade Range.

Table 7—**Captures of individual mammals in snap traps (mean number captured per stand corrected for effort in parentheses) for age- and moisture-classes, Oregon Cascades, 1984**

	Age			Moisture		
	Young	Mature	Old	Dry	Mesic	Wet
Western red-backed vole	32 (4.0)	104 (6.1)	101 (4.6)	28 (4.0)	58 (6.4)	34 (2.8)
Townsend's chipmunk	3 (0.4)	10 (0.6)	14 (0.6)	1 (0.1)	4 (0.4)	11 (0.9)
Montane vole	—	1 (0.1)	—	—	—	—
Creeping vole	3 (0.4)	2 (0.1)	4 (0.2)	—	4 (0.4)	—
Shrew-mole	2 (0.3)	10 (0.6)	13 (0.6)	4 (0.6)	2 (0.2)	19 (1.6)
Deer mouse	7 (0.9)	25 (1.5)	33 (1.5)	13 (1.9)	9 (1.0)	18 (1.5)
Coast mole	1 (0.1)	3 (0.2)	5 (0.2)	1 (0.1)	3 (0.3)	1 (0.1)
Townsend's mole	—	1 (0.1)	1 (0.1)	—	—	1 (0.1)
Marsh shrew	1 (0.1)	1 (0.1)	4 (0.2)	1 (0.1)	3 (0.3)	8 (0.7)
Montane shrew	8 (1.0)	15 (0.9)	7 (0.3)	1 (0.1)	6 (0.7)	21 (1.8)
Pacific shrew	9 (1.1)	92 (5.4)	63 (2.9)	18 (2.6)	21 (2.3)	24 (2.0)
Trowbridge's shrew	56 (7.0)	221 (13.0)	319 (14.5)	77 (11.0)	157 (17.4)	167 (13.9)
Vagrant shrew	2 (0.3)	3 (0.2)	3 (0.1)	—	3 (0.3)	6 (0.5)
Sorex spp.	—	5 (0.3)	6 (0.3)	2 (0.3)	1 (0.1)	4 (0.13)
Western pocket gopher	—	1 (0.1)	—	—	—	—
Pacific jumping mouse	—	1 (0.1)	4 (0.2)	1 (0.1)	1 (0.1)	3 (0.3)
Dusky-footed woodrat	—	—	1 (0.1)	—	1 (0.1)	

also was captured at sites with deciduous shrubs and trees (table 9). The western red-backed vole was positively associated with needleleaf evergreen trees in all height-classes.

The montane shrew was the most widely distributed shrew based on shrubs and understory trees. It was positively associated ($R = 0.51$-0.59; $P < 0.0001$) with berry-producing shrubs of all three height-classes and deciduous shrubs in the first two height-classes ($R = 0.42$-0.46; $P < 0.001$). The montane shrew was the only species associated with evergreen shrubs (0.5-2 m; $R = 0.36$; $P = 0.007$).

The northern flying squirrel was positively associated with large and medium sized (10-50 ± cm d.b.h.), tall (15-m) snags of decay-classes 3 and 4, as well as medium snags of decay class 5. The Douglas' squirrel was found in stands with various-sized snags of decay-class 5.

Pitfall results—In 1985, the red tree vole was captured at sites with small bigleaf maple, ($R = 0.53$, $P = 0.04$) large golden chinkapin, and very large grand fir. Also, it was highly correlated with sites with medium Pacific dogwood ($R = 0.995$; $P < 0.0001$). In 1984, it was associated only with

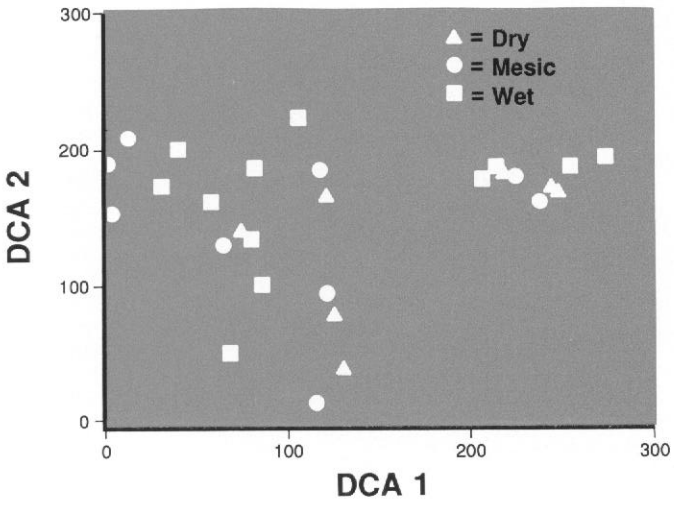

Figure 5—Detrended correspondence analysis of 1984 small mammal snap-trap capture data compared to moisture gradient of old-growth stands, Oregon Cascade Range.

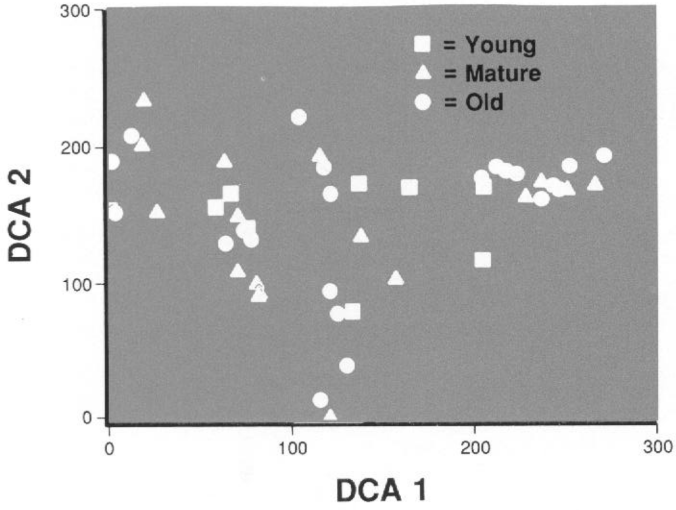

Figure 6—Detrended correspondence analysis of 1984 small mammal snap-trap capture data related to the age of stands, Oregon Cascade Range.

medium canyon live oak ($R = 0.29$; $P < 0.03$). Limited consistency was found in vegetative and physical characteristics with which the small mammal species were positively or negatively associated between years. The red-backed vole was negatively associated with moss ground cover ($R = -0.55$, $P = 0.04$) in 1985 as was Trowbridge's shrew ($R = -0.58$, $P = 0.02$). Both showed similar results in 1985.

Table 8—Significant Spearman rank correlations ($P \leq 0.05$) for forest floor characteristics at the pitfall grids and selected small mammals captured, Oregon Cascades, 1984

Species	Forest floor variable	R-value	P
Western red-backed vole	Bare rock	0.27	0.04
	Moss	–0.30	0.02
	Lichen	0.56	0.0001
	Down log, decay-class 5	0.31	0.02
Red tree vole	Lichen	0.38	0.004
	Down log, decay-class 2	0.27	0.04
Deer mouse	Lichen	0.46	0.0005
Pacific jumping mouse	Bare soil	–0.38	0.003
	Fine litter	–0.45	0.0006
	Moss	0.36	0.007
	Down log, decay-class 3	0.33	0.01
	Down log, decay-class 4	0.30	0.02

Table 9—Significant Spearman rank correlations ($P \leq 0.05$) for understory and ground-cover characteristics at the pitfall grids and selected small mammals captured, Oregon Cascades, 1984

Species	Vegetative variable	R-value	P
Western red-backed vole	Grasses (0-0.5 m)	0.45	0.0006
	Fern (0-0.5 m)	–0.47	0.0003
	Fern (0.5-2 m)	–0.44	0.0008
Red tree vole	Deciduous shrubs (0-0.5 m)	0.27	0.05
	Deciduous trees (0-0.5 m)	0.50	<0.0001
	Deciduous trees (0.5-2 m)	0.47	0.0003
	Needle-leaf evergreen (2 m-midstory)	0.34	0.01
Deer mouse	Berry-producing shrubs (0-0.5 m)	0.29	0.03
	Deciduous shrubs (0-0.5 m)	0.29	0.03
	Deciduous trees (0-0.5 m)	0.42	0.001
	Deciduous trees (0.5-2 m)	0.32	0.02
	Deciduous shrubs (2 m-midstory)	0.32	0.02
Pacific jumping mouse	Grass (0-0.5 m)	–0.43	0.001
	Fern (0-0.5 m)	0.31	0.02
	Berry-producing shrubs (0.0.5 m)	0.50	<0.0001
	Evergreen shrubs (0-0.5 m)	–0.42	0.0001
	Deciduous shrubs (0-0.5 m)	0.35	0.009
	Deciduous shrubs (0.5-2 m)	0.43	0.001
	Berry-producing shrubs (2 m-midstory)	0.54	<0.0001

Most species varied between years in the characteristics of the sites at which they were caught, but few significant changes (Spearman rank correlations) occurred from positive to negative or from negative to positive. The more common result was that some characteristics were significantly associated one year and not the other.

The montane shrew was positively associated with berry-producing shrubs up to the midstory level ($R = 0.26$-0.50; $P <$ 0.05) and all deciduous shrubs ($R = 0.34$; $P =$ 0.001) up to 2.0 m high (table 10). The montane shrew, the marsh shrew, and Trowbridge's shrew were caught at sites where ferns were a dominant ground cover. The Pacific shrew was associated with broadleaf evergreen trees in the 0.5- to 2.0-m zone (R = 0.50, P c 0.0001); it was negatively associated with berry-producing and deciduous shrubs ($R = 0.32$) and was caught at sites with evergreen shrubs ($R = 0.47$) up to 0.5 m tall (table 10). Forest floor characteristics associated with the marsh shrew were logs of decay-class 1 ($R = 0.26$) and 3 (R = 0.26), and with the montane shrew were lichen and aspect ($R = 0.30$; $P = 0.02$); the vagrant shrew was negatively associated ($R = -0.38$) with lichen (table 11). Townsend's mole was caught in traps with logs of decay-classes 2 to 5 ($R = 0.27$-0.32) nearby.

Discussion

The red tree vole, deer mouse, Trowbridge's shrew and the shrew-mole were the only small mammals positively associated with older stands in our study, and none seemed dependent on the availability of old growth. Corn and others (1988) generally concur with this and found that only the red tree vole was significantly associated with old-growth Douglas-fir stands in their study of the Oregon Cascades. Raphael (1984, 1988c) and Raphael and Barrett (1984) listed 10 small mammals significantly associated with old-growth Douglas-fir forests in northern California, an area not dissimilar to Rogue-Umpqua. Trowbridge's shrew can be discounted as an old-growth associate because it is a very common species that occurs in all ages of stands.

The mean species richness observed in this study was higher and more variable on the chronosequence than that observed by Corn and others (1988) or Raphael (1984). Species diversity studies are limited usually by the short temporal span of sampling the environment, and, because studies such as ours tend to rely on data gathered from many single sample surveys, erroneous correlations can be drawn (Wiens 1981b). Greater replication, especially between years, would have been useful. Temporal fluctuations in small mammal communities and their use of the environment are known to occur (Asher and Thomas 1985, McCloskey 1975, Nel 1978, Whitford 1976). The relations to habitat structure may be highly variable if temporal shifts are occurring. Yet many authors have shown or inferred that habitat factors are important in determining small mammal community structure (for example, Dueser and Shugart 1979, McCloskey 1975, Morris 1984, Rosenzweig and Winakur 1969). Generally, the animals we trapped were found associated with different vegetation conditions between years and between times of year.

Table M-Significant Spearman rank correlations for vegetative characteristics at snap-trap capture locations for small mammals, Oregon Cascades, 1984

Species	Vegetative characteristics	R-value	*P*
Western red-backed vole	Grass (0-0.5 m)	0.54	<0.00
	Fern (0-0.5 m)	-0.36	0.007
	Evergreen shrub (0-0.5 m)	0.26	0.05
	Fern (0-5.-2 m)	-0.28	0.04
	Berry-producing shrub (2 m-midstoty)	-0.28	0.04
	Deciduous shrubs (2 m-midstory)	0.29	0.03
	Needleleaf evergreen trees (super canopy)	0.39	0.003
Trowbridge's shrew	Fern (0-0.5 m)	0.40	0.002
	Fern (0.5-2 m)	0.40	0.002
Marsh shrew	Grass (0-0.5 m)	-0.31	0.02
	Fern (0-0.5 m)	0.35	0.007
	Fern (0.5-2 m)	0.28	0.04
	Berry-producing shrubs (0.5-2 m)	0.29	0.03
	Needleleaf evergreen tree (super canopy)	-0.37	0.005
Pacific shrew	Berry-producing shrubs (0-0.5 m)	-0.41	0.002
	Evergreen shrubs (0-0.5 m)	0.47	0.0003
	Deciduous shrubs (0-0.5 m)	-0.32	0.02
	Broadleaf evergreen trees (0-0.5 m)	0.50	<0.0001
	Broadleaf evergreen trees (0-0.5 m)	0.61	<0.000l
	Needle-leaf evergreen trees (0-0.5 m)	-0.28	0.04
	Needleleaf evergreen trees (2 m-midstory)	-0.28	0.03
Montane shrew	Grass (0-0.5 m)	-0.27	0.04
	Fern (0-0.5 m)	0.29	0.03
	Berry-producing shrubs (0-0.5 m)	0.49	<0.000l
	Evergreen shrubs (0-0.5 m)	-0.38	0.003
	Broadleaf evergreen trees (0-0.5 m)	-0.55	<0.0001
	Berry-producing shrubs (0.5-2 m)	0.50	<0.000l
	Deciduous shrubs (0.5-2 m)	0.34	0.001
	Broadleaf evergreen trees (0.5-2 m)	-0.40	0.002
	Berry-producing shrubs (2 m-midstory)	0.26	0.05
	Evergreen shrubs (2 m-midstory)	-0.27	0.05
	Broadleaf evergreen trees (2 m-midstory)	-0.41	0.002
	Broadleaf evergreen trees (main canopy)	-0.32	0.02
	Needleleaf evergreen trees (super canopy)	-0.45	0.0004

Table 11-Significant Spearman rank correlations for forest-floor characteristics at snap-trap capture sites for small mammals, Oregon Cascades, 1984

Species	Variable	R-value	*P*
Trowbridge's shrew	Logs, decayclass 2	*0.31*	*0.02*
Marsh shrew	Fine litter	**-0.30**	**0.03**
	Logs, decay-class 1	**0.26**	**0.05**
	Logs, decay-class 3	**0.26**	**0.05**
Pacific shrew	Lichen	-0.37	0.006
Montane shrew	Bare soil	*-0.33*	0.01
	Lichen	0.35	0.008
Townsend's mole	Bare rock	-0.29	0.03
	Coarse litter	0.28	0.04
	Logs, decay-class 2	0.39	0.02
	Logs. decay-class 3	0.30	0.03
	Logs, decay-class 4	0.27	0.04
	Logs, decay-class 5	0.32	0.02
Coast mole	Bare rock	**-0.26**	*-0.05*

This supports the speculation that temporal variation of habitat use occurred, which reduced the predictability of results based on physiognomy.

We captured too few red tree voles for meaningful statistical analysis or to conclude that they are related to older stands of Douglas-fir. Such a relation has been suggested for this species by other authors, and old-growth Douglas-fir is considered to be optimum habitat (Corn and Bury 1986, Franklin and others 1981, Meslow and others 1981). We, and the other authors, found the red tree vole primarily in mesic to wet old-growth stands but the strong associations with medium Pacific dogwood, berry-producing shrubs, and deciduous trees of smaller diameter may be a function of the small sample size. They may have been selecting such vegetation for food, however. Some of the animals we captured may have been dispersing; most of the males were juveniles, and the species is supposed to be arboreal and thus seldom found on the ground (Maser and others 1981). The females were mainly adult, and the sex ratio was almost equal. Although we cannot draw any conclusion as to the function of terrestrial activity in the species, it obviously occurs. Terrestrial nesting has been suggested for males (see Corn and Bury 1986). but we found equal numbers of females. Corn and Bury (1986) caught predominantly females in their pitfall traps.

The shrew-mole is an insectivore (Terry 1978, Whitaker and Maser 1976) and, in a study in King County, WA, it was found in forested areas with a high organic content to the soil (Terry 1981). We found no such clear delineation of habitat use, although the shrew-mole is a known shallow burrower (Dalquest and Orcutt 1942). What associations did exist in our study suggested an ubiquitous use of the environment, similar to the findings of Corn and others (1988).

Red-backed voles were negatively associated with sites with fern as a dominant ground cover. Ferns were often found with shrub or other understory cover, which suggests avoidance of such areas. As a mycophagist (Maser and others 1978, Ure and Maser 1982), the red-backed vole would be expected to occur in conifer-dominated locations, at least at the time of foraging for fungi. Negative associations with Pacific dogwood and golden chinkapin support this. Lichens are preferred food for red-backed voles in the Pacific Northwest (Vre and Maser 1982), and these voles were highly associated with areas of lichen ground cover in our study. Maser and others (198 1) say that the distribution of red-backed voles is influenced by the presence of rotting, punky logs. Hayes and Cross (1987) found capture of the species to be positively correlated with mean log diameter and size of the log overhang, suggesting they use this space as travel corridors. Our captures were positively associated with logs of decay-class 5, and many of our captures (Gilbert, pers. obs.) were in the space under log overhangs.

The Soricidae were segregated somewhat in the western Oregon Cascades. The vagrant shrew was found primarily in higher elevation stands in the northern Oregon Cascades. Although the montane shrew was also associated with Mt. Hood, it selected young stands and thus was significantly associated with shrubby areas. The Pacific shrew was restricted to the central and southern subprovince locations, and it was a generalist in its use of the habitat. A lot of the shrews from Andrews could not be identified to species (other than that they definitely were not Trowbridge's shrew) because of mixed characters. Hennings and Hoffman (1977) and Findley (1955) have discussed the taxonomic difficulties with the montane, Pacific, and vagrant shrews, and, until the taxonomic issue is resolved we decided to identify these individuals only to genus. Terry (1981) could not correlate the montane shrew with any vegetational factors and found the vagrant shrew may have been excluded competitively by Trowbridge's shrew. Dalquest (1941) considered the vagrant shrew to be dominant over Trowbridge's shrew. Our findings did not reject competitive exclusion by either species.

Although this study provided data on habitat usage by small mammals, it showed the difficulties that occur in time-restricted analyses of vertebrate communities. Three of the four species that had some old-growth association were either weakly linked (the shrew-mole), relatively abundant species in other age-classes (western red-backed vole and the deer mouse), or both (the deer mouse). The deer mouse is of interest because other authors (for example, Gashwiler 1970a, Hooven 1973, Hooven and Black 1976, Martell and Radvanyi 1977) consider the species to be most abundant in early successional forests. We trapped during a low in the population cycle of the deer mouse in the Oregon Cascades, and the species seemed to be related to older successional forests. Anthony and others (1987) had similar results trapping riparian zones at Andrews in 1983, as did Raphael (1984) in northern California. Scrivner and Smith (1984) found the species to be most associated with older successional stages (>80 yr) of spruce-fir forests in Idaho, and Monthey and Soutiere (1985) had similar results with a related subspecies in Maine conifer forests. Sullivan (1979) stated that clearcut areas may be population sinks for dispersing deer mice. Although the species is not restricted by any means to older successional stages, older forests may provide its best habitat.

Douglas' squirrels were not sampled adequately by trapping to provide any information on their dependence on old-growth. Data derived from avifauna surveys (Gilbert 1985) provided no evidence of dependence on old-growth, although Raphael (1984,1988) and Raphael and Barrett (1984) found a significant positive correlation with stand age for the Douglas' squirrel in Douglas-fir forests in northern California. Flying squirrel abundance was positively correlated with large-snag density (Volz 1986, this study), suggesting this habitat feature is necessary for suitable den trees and cavities and may be limiting for that species. Maser and others (1981), however, note that in locations in western Oregon where these more suitable nesting sites have been removed by logging, the species will build outside nests. We noticed some of these nests as well.

One cautionary note is that virtually all the stands we studied were natural and not the intensively managed stands that can be expected in the future. Even the young stands had large amounts of coarse woody debris and snag numbers almost equivalent to old-growth stands. Vegetational features and coarse woody debris in stands originating from logging rather than fire are considerably different. We did sample a few such stands with a previous history of logging, and these young and mature stands had fewer species and individuals in the small mammal communities than comparable natural stands (Gilbert 1985). Other evidence supports such impacts of logging on particular species; Corn and others (1988), state that we have probably already eliminated much of the red tree vole habitat by extensive logging of low elevation, old-growth forests. The habitat features supporting the abundance of small mammals we observed in the Oregon Cascades will be reduced or eliminated in managed forests, creating a risk that species richness will decline (compare to Weisbrod 1976) unless forest management practices provide opportunities for maintaining such elements as coarse woody debris and large trees in the managed Douglas-fir forests of the future. Some of the species we captured were definitely linked with these features of structural diversity (for example, the red tree vole, flying squirrel, and western red-backed vole). Therefore, although old-growth may not be itself limiting to very many species, the structural complexity of naturally regenerated forests may be required for maintaining small mammal diversity.

Acknowledgments

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Appendix

Table 12-Vegetation and site measurements for pitfall and snap trap grids, Oregon Cascades, 1984

I. Measurements on a 100 m^2 area (5.6-m radius)

Forest floor:

1. Cover of logs by decay-class (%) (>lO cm diameter).
2. Litter depth at three points (01, 02) (mm).
3. Coverage of forest floor by various substrates: exposed bare rock, exposed bare mineral soil, fine organic litter (<l0-cm diameter), coarse organic litter (>10-cm diameter), moss, lichen.
   (Total - 100%).

A. Vegetation characteristics
  4. Coverage of foliage by height interval and life form (%).
  a. Height intervals
    1. 0-0.5 m (100 m^2 area)
    2. *0.5-2.0* m (100 m^2 area)
    3. 2.0 m through midstory (shrubs and trees not entering main canopy) (707 m^2 area).
    4. Canopy trees forming main canopy layer (707 m^2 area).
    5. Super canopy trees (crowns extending well above main canopy layer) (707 m^2 area).

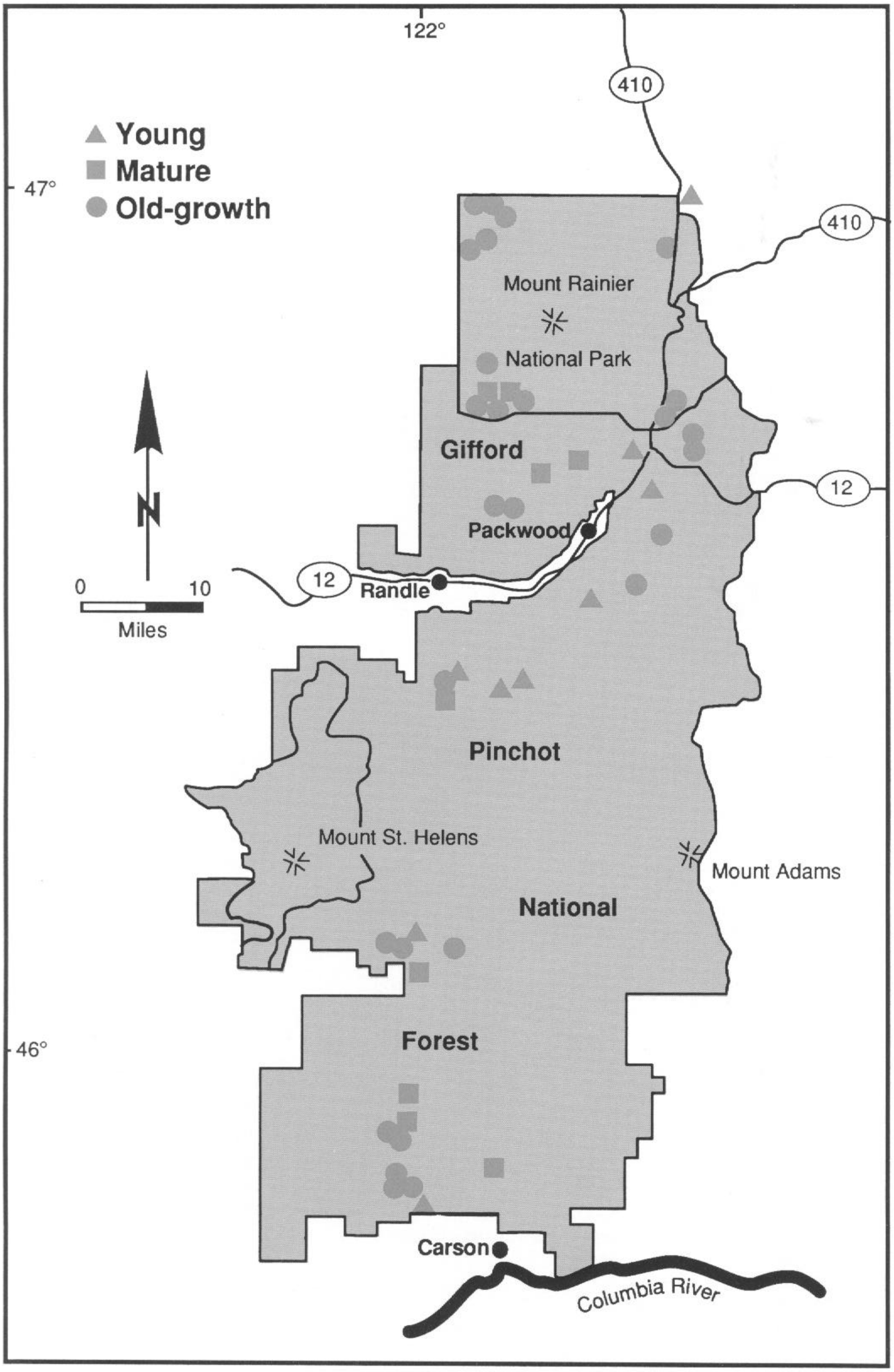
  b. Life forms
    1. Herbs
    2. Graminoids (grass & grasslike plants including sedges)
    3. Ferns
    4. Berry-producing ericaceous shrubs ***(Vaccinium** and **Gaultheria)***
    5. Evergreen shrubs (including shrubs of #4)
    6. Deciduous shrubs (including shrubs of #4)
    7. Deciduous trees
    8. Broadleaf evergreen trees
    9. Needleleaf evergreen trees

B Stand characteris tics
  5. Number and species of small diameter, live trees (l-10 cm d.b.h.).
  6. Number and species of medium diameter, live trees (l0-50 cm d.b.h.).
  7. Number by decay-class of large diameter, medium tall snags (>50 cm d.b.h. and 5-15 m tall).
  8. Number by decay-class of medium diameter, medium tall snags (l0-15 cm d.b.h. and 5-15 m tall).
  9. Number by decay-class of short snags (any d.b.h., 1.5-5 m tall).
  10. Number stumps (<l.5 m tall, natural or cut).

II. Measurements on a 707 m^2 area (15-m radius, the distance to next trap station).

A. Stand characteristics
  11. Number and species of large live trees (50-100 cm d.b.h.).
  12. Number and species of very large live trees (>l00 cm d.b.h.).
  13. Number by decay-class of large diameter, tall snags (>50 cm d.b.h. and 15 m tall).
  14. Number by decay-class medium diameter, tall snags (l0-50 cm d.b.h. and >15 m tall).

B. Site characteristics
  15. Surface water (presence/absence).
  16. Type of water: I (intermittent stream), P (perennial stream); S (seep); 0 (pool/pond).
  17. Rock outcrop (>l% of area) (presence/absence).
  18. Exposed talus (>l% of area) (presence/absence).
  19. Number of recent tree-fall mounds-pits with exposed roots and mineral soil.



Location of study sites.

Small Mammal Communities in the Southern Washington Cascade Range

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Abstract

Small mammal faunas on the western slope of the southern Washington Cascade Range were sampled to describe patterns of abundance along gradients of forest age and moisture and to identify structural, vegetative, and environmental features associated with these patterns. Forty-five primary sites were sampled by snap and pitfall trapping in 1984 and 1985, resulting in the capture of 6751 individuals of 20 species, of which 11 were regularly caught and statistically analyzed. Four of these 11 species had different abundances between years. The abundance of two species differed between forest age-classes. The deer mouse was caught more often in old-growth than young forest, and the forest deer mouse was caught more often in mature and old-growth than young forest. The abundance of three species differed between moisture-classes of old-growth forest. The marsh shrew was caught more often in wet than in moderate old-growth forest, and the southern red-backed vole was caught more often in dry than in moderate or wet old-growth forest. In 1985 only, the deer mouse was caught more often in moderate than in wet old-growth forest. Elevation (404 to 1218 m) was not a strong factor influencing small mammal abundance. Clustering sites by similarity coefficients (Jaccard's) based on mammalian presence-absence data or by the abundance of frequently captured species (K-means) did not indicate a mammalian community that was strongly organized with respect to gradients of forest age or moisture. Habitat variables were weakly correlated with the abundance of mammalian species. The forest-floor small mammal community in these naturally regenerated forests appears adapted to a broad range of conditions related to forest age and moisture.

Introduction

The small mammal communities of the western slopes of the southern Washington Cascade Range are composed of species from two mammalian faunas (Dalquest 1948). Before the last glacial period (Vashon-Wisconsin), species characteristic of the temperate forests of the Pacific coast, such as the shrew-mole, Townsend's mole, Trowbridge's shrew, the marsh shrew, Townsend's chipmunk, the deer mouse, Townsend's vole, and the creeping vole, probably were the most common species in the region. As glacial advance proceeded, species associated with boreal conditions to the north, such as the water shrew, the yellow-pine chipmunk, the heather vole, the southern red-backed vole, the water vole, and probably the forest deer mouse, moved southward through the Cascades. At glacial maximum, species of both faunas inhabited this unglaciated region. With retreat of glacial ice, these species expanded their distributions generally north and east, colonizing the Cascades as habitats became suitable (Dalquest 1948).

Small mammals, therefore, have inhabited the southern portion of the Washington Cascades longer than areas farther north. If consistent associations occur between small mammals and naturally occurring gradients of forest age and moisture, they might be expected to occur in the south. Do unique species combinations occur along these gradients, or are the constituent species capable of persisting in an array of forest conditions? These questions have gained importance in recent years, with increasing attention to the issue of preserving old-growth forests. This study addresses the relationships between small mammal communities and naturally regenerated forests. Extrapolation of conclusions from this work to potential relationships in managed forests will be difficult, as discussed below.

The central objective of this paper is to describe the patterns of small mammal species abundances over a gradient of forest age, and within old-growth forests, to describe patterns of abundance over a gradient of moisture. This paper also will investigate correlations between small mammal abundances and selected environmental and vegetational variables.

Methods

Study Sites

This work was conducted on 54 sites on the western slopes of the southern Washington Cascade Range. Sites were located predominantly within the Western Hemlock Zone (Franklin and Dymess 1973) at elevations ranging from 404 to 1218 m. Some of the higher elevation sites extended into the Pacific Silver Fir Zone. Most forested sites had Douglas-fir as the dominant tree species, although wet old-growth forests had a large proportions of western redcedar. The sites chosen for small mammal studies form a subset of a large number of sites investigated botanically. For an extensive treatment of the vegetational composition and structure of the study stands, see Spies (this volume) and Spies and Franklin (this volume).

Of the 54 sites, 8 were on areas recently clearcut (cut 6-21 years previously). These sites were sampled for small mammals in 1984, but could not be included in sampling during 1985. One forested site was sampled only in 1985, and the remaining 45 sites were sampled in both years. These 45 sites (see frontispiece), which ranged in size from 51 to 1690 ha (mean size = 488 ha), are the focus of this paper.

Sites were chosen based on several physical and vegetational characteristics (Carey and Spies, this volume), and subsequently placed into classes along gradients of age and moisture (Spies and Franklin, this volume). Of the 45 sites, 36 were judged sufficiently similar in site moisture conditions (moderate vs. very wet or dry) to be compared along an age gradient. Elimination of very wet or dry sites resulted in a chronosequence consisting of 9 sites in young forest (55-75 years old), 9 sites in mature forest (80-190 years old), and 18 sites in old-growth forest (210-730 years old). All 27 old-growth sites were classified into moisture-classes, yielding 9 wet sites, 11 moderate sites, and 7 dry sites.

Small Mammal Sampling

Sampling techniques varied, reflecting the different natural histories of the small mammal fauna. This study used four techniques: vocalization frequencies of tree squirrels, track records from smoked aluminum plates, snap-trapping, and pitfall trapping. Vocalization frequency data were collected as part of the spring avian surveys, using variable circular plots (Manuwal, this volume). These data were used in conjunction with the other techniques to assess the presence or absence of squirrels on the study sites. Data on track frequency (Carey and Witt 1991) were used in the same fashion. They were particularly useful in establishing the presence of squirrels and chipmunks, species not sampled efficiently by snap or pitfall trapping. By far the most important techniques, and the ones yielding information on relative abundance, were snap-trapping and pitfall trapping.

As noted by Briese and Smith (1974), Bury and Corn (1987), and Williams and Braun (1983), capture efficiency differs consistently between snap and pitfall traps. In general, pitfall traps sample nonjumping rodents and insectivores more effectively than do snap traps, which sample more agile rodents most effectively. Species lists exclusively derived from one technique will reflect this sampling bias. Estimates of relative abundance in this paper consequently combined information from both techniques. West (in press) describes the snap-trapping methods used in this study and a rationale for developing this particular protocol. Briefly, we used two Museum-Special traps at each of 144 trapping stations. Most of the traps were new-model Museum Specials with plastic treadles (West 1985). Stations were arrayed on a 12 by 12 grid with 15-m interstation distances. Traps were baited with peanut butter and whole oats, and operated for four consecutive days. We trapped each site once during July and August in both years. Trapping grids were relocated within sites between years to avoid sampling potentially depleted populations in 1985. Corn and Bury (1990) also describe methods of pitfall trapping that were developed primarily for sampling amphibians and reptiles. Mammals and herpetofauna were sampled simultaneously. Pitfall arrays consisted of 36 traps on a 6 by 6 grid with 15-m spacing between traps. Pitfall traps were operated continuously for 30 to 34 days each fall, beginning in October. Traps were checked once a week and were relocated within sites between years. All captured animals were given to the Burke Memorial Museum at the University of Washington.

Vegetation Sampling

Information on the physical features of the sites and their vegetational composition and structure was gathered on the snap and pitfall trapping grids in a similar manner. Variables appropriately measured at a small scale, such as coverage of the forest floor by different substrates, percentage cover of logs by decay-class, and percentage cover of herbs, ferns, most shrubs, and small trees, were recorded on 100-m^2 circular plots. Variables of larger scale, such as large trees, large standing snags, and site characteristics (presence and type of water, rock outcrops, or talus) were measured on 707-m^2 circular plots centered on the smaller plots. Centers of the concentric plots were equidistant from four pitfall traps or snap-trapping stations, resulting in 9 vegetation plots on the pitfall grids and 16 plots on the snap-trapping grids. Because these grids were relocated between years, we collected data from different grids each year.

Data Analyses

This paper is concerned with the responses of small mammal populations at the site or stand scale. Abundance patterns were characterized, and correlations with habitat features were sought, from summations of snap and pitfall captures in each year with site and vegetation variables averaged over all plots in both years. Such an approach was taken to provide a comprehensive data set. As discussed above, combining snap and pitfall data enlarges sample sizes and helps reduce the known biases of each method. By combining information from all vegetation plots (n = 50), a good average value could be obtained for most variables. All statistical work was done with SYSTAT microcomputer programs (Wilkinson 1988).

Counts of captured animals are reported as numbers per 100 trap-nights. For snap-trap data, these counts were corrected for empty, snapped traps, and for traps occupied by another species. Because pitfall traps were multiple-capture traps, such adjustments to the capture totals were unnecessary. Before statistical analyses, capture data were transformed logarithmically ($ln(x$+1)).

All variables measured on the vegetation plots were inspected for statistical normality and transformed using logarithmic ($ln(x$+1)), square root ((x+3/8)), and arcsine ($asn(x)$) functions as appropriate. Redundant variables were either eliminated from further analysis or combined with similar variables after inspecting the Pearson correlation matrix of the data. Of the field-recorded variables, a subset of 31 variables consisting of original and combined variables was used to examine correlations between small mammal abundance and habitat features (appendix table 7).

Small mammal responses to forest-age and moisture gradients, and to selected environmental variables were investigated in three general ways. Analyses of variance (repeated measures ANOVA) of small mammal abundance with forest age (young, mature, and old-growth forest) and moisture-classes (dry, moderate, and wet old-growth forest) assessed the variation in abundance for successive years across both gradients. When significant class-by-year interactions were present, I used separate one-way ANOVAs with Tukey's HSD test for multiple comparisons. I used Pearson correlation coefficients to test for associations with selected environmental parameters, and multiple regression to assess the consistency and strength of association between vegetative physiographic variables and the abundance of mammals. The ANOVAs and correlation coefficients were calculated for species for which at least 40 individuals were captured. The composition of mammalian communities, based on the presence or absence of species for each site, was obtained by combining capture totals in both years with information from the avian surveys and the track plates. The resulting matrix of presence-or-absence data by sites (species in table 1 plus the Douglas' squirrel) was clustered hierarchically by Jaccard's similarity coefficients (Jaccard 1912) to reveal community pattern along the forest-age and moisture gradients. In addition, K-means clustering (Hartigan 1975) on the abundance of the most frequently captured species (11 species) was used to investigate community pattern from a different perspective.

Table 1—Small mammals captured in snap (July and August) and pitfall traps (October and early November) on 45 forested sites in the southern Washington Cascade Range

Common name	1984	1985	Total
Insectivora			
Vagrant shrew[a]	20	48	68
Montane shrew[a]	452	859	1,311
Water shrew	6	3	9
Marsh shrew	21	25	46
Trowbridge's shrew[b]	1,105	841	1,946
Unidentified shrew	26	12	38
Shrew-mole	116	115	231
Coast mole	11	10	21
Lagomorpha			
Pika	1	1	2
Rodentia			
Yellow-pine chipmunk	1	11	12
Townsend's chipmunk	26	16	42
Unidentified chipmunk	0	1	1
Northern flying squirrel	2	27	29
Northern pocket gopher	0	1	1
Deer mouse	101	125	226

Footnotes on next page.

Continue

Table l-continued

Common name	1984	1985	Total
Rodentia			
Forest deer mouse[b]	539	375	914
Unidentified deer mouse	96	60	156
Southern red-backed vole	737	775	1512
Long-tailed vole	4	0	4
Creeping vole	29	30	59
Water vole	1	6	7
Unidentified vole	1	7	8
Pacific jumping mouse	39	51	90
Carnivora			
Ermine	5	13	18
All species totals	3339	3412	6751

[a] Captured more frequently in 1985 than in 1984.
[b] Captured more frequently in 1984 than in 1985.

Table 2Small mammals captured in snap traps during 1984 on 8 clearcut areas in the southern Washington Cascade Range

Common name	Total
Insectivora:	
Vagrant shrew	2
Montane shrew	34
Marsh shrew	1
Trowbridge's shrew	7
Unidentified shrew	3
Shrew-mole	2
Rodentia:	
Yellow-pine chipmunk	19
Townsend's chipmunk	15
Cascade golden-mantled ground squirrel	2
Northern pocket gopher	4
Deer mouse	61
Forest deer mouse	36
Unidentified deer mouse	64
Southern red-backed vole	6
Long-tailed vole	3
Heather vole	6
Creeping vole	12
Unidentified vole	1
Pacific jumping mouse	10
All species total	288

Results

A total of 7084 individuals of 23 species were caught over 2 years on the 54 sites. Of this total, 333 individuals of 17 species were caught on eight clearcut sites that were sampled only in 1984 (table 2), and on one old-growth moderate site sampled in 1985 (table 3). The remaining 6751 captures of 20 species, made on 45 sites sampled in both years, constitute the focus of this paper (table 1). A consistent feature of these trapping returns is that they are numerically dominated by four species (table 1). Trowbridge's shrew was the most common species (1946 captures), followed in abundance by the southern red-backed vole (1512 captures), the montane shrew (13 11 captures), and the forest deer mouse (9 14 captures). Insectivorous mammals (genera *Sorex*, *Neurotrichus*, and *Scapanus*) and rodents were roughly equal in the sample, with 3670 insectivores to 3061 rodents (table 1).

Table 3—Small mammals captured with snap and pitfall traps on an old-growth moderate site in 1985 in the southern Washington Cascade Range (this site was not sampled in 1984)

Common name	Snap traps	Pitfall traps
Montane shrew	6	10
Trowbridge's shrew	0	1
Vagrant shrew	1	2
Coast mole	0	1
Deer mouse	5	6
Forest deer mouse	6	7
Totals	18	27

Identification of all individuals to species is incomplete; 38 *Sorex*, one chipmunk, and eight microtine rodents, could not be reliably identified (table 1). The largest group of unidentified animals are deer mice (156 young individuals, table 1). Resolution of this problem awaits discovery of a reliable morphological means of distinguishing juvenile and subadult forest deer mice from deer mice (Bangs 1898). Recent work on this problem (Allard and others 1987, Gunn and Greenbaum 1986) was conducted on adult animals, and as the discriminating variables all depend on growth allometries, they do not help with young animals. Adult deer mice were assigned to species based on the tail-length criterion of Allard and others (1987).

If captures for 1984 and 1985 are combined, at least 40 individuals were caught for 11 of the 20 species (fig, 1 and table 1). The remaining nine species, although discussed below with respect to their general habitat preferences, are not considered further here. When compared over all 45 sites, 4 of the 11 species were caught with different frequency between years (t-test, $P < 0.05$). The vagrant shrew and the montane shrew were caught more frequently in 1985 than in 1984, but Trowbridge's shrew and the forest deer mouse were captured more frequently in 1984 than in 1985 (table 1).

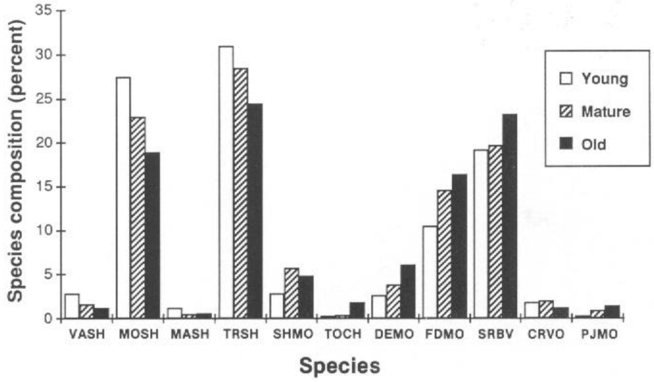

Figure 1—Patterns of abundance by forest age-class for the 11 most common small mammal species (minimum 40 captures) in the southern Washington Cascade Range. Captures for 1984 and 1985 are combined. Species codes are: VASH = vagrant shrew; MOSH = montane shrew; MASH = marsh shrew; TRSH = Trowbridge's shrew; SHMO = shrew-mole; TOCH = Townsend's chipmunk; DEMO = deer mouse; FDMO = forest deer mouse; SRBV = southern red-backed vole; CRVO = creeping vole; and PJMO = Pacific jumping mouse.

Species Response to Gradients of Forest Age and Moisture

Forest-age gradient—Only deer mice showed statistically significant differences between age-classes. The deer mouse was more abundant in old-growth than in young forest, and the forest deer mouse was more abundant in both mature and old-growth forest than in young forest (table 4). Two species, the Townsend's chipmunk and the Pacific jumping mouse, were caught in higher numbers in old forest than in young forest, although the differences were not statistically significant (table 4).

The frequency of capture differed between years for four species in the 36 sites comprising the chronosequence. The vagrant shrew, the montane shrew, and the deer mouse were caught more frequently in 1985 than in 1984. Trowbridge's shrew was captured more frequently in 1984 than in 1985. Change in capture frequency between years was apportioned similarly across age-classes for the montane shrew, Trowbridge's shrew, and the deer mouse, but the vagrant shrew was captured much more often in mature and old-growth sites in 1985 than in 1984 (table 4).

Table 4—Means, standard deviations, and frequency of occurrence (percent) of small mammal captures (number per 100 trap-nights) in snap (July and August) and pitfall traps (October and early November) on 36 forested sites representing an age gradient in the southern Washington Cascade Range. (where ANOVA is significant, differences between means are indicated with different letters (A, B); $\alpha = 0.05$)

	1984			1985		
Common name	Young (n=9)	Mature (n=9)	Old growth (n=18)	Young (n=9)	Mature (n-9)	Old growth (n=18)
Insectivores						
Vagrant shrew[a]						
Mean	0.161	0.041	0.031	0.175	0.104	0.069
S.D.	.151	.068	.081	.391	.182	.138
%	.22	.33	.17	.44	.44	.28
Montane shrew[a]						
Mean	1.190	1.198	.612	2.070	2.060	1.004
S.D.	.899	.427	.283	1.343	.863	.294
%	.89	1.00	1.00	1.00	1.00	1.00
Marsh shrew						
Mean	.051	.022	.019	.031	.021	.030
S.D.	.067	.043	.047	.046	.041	.054
%	.44	.22	.17	.33	.22	.28
Trowbridge's shrew[b]						
Mean	1.836	2.551	1.147	1.797	2.257	.946
S.D.	.858	1.058	.284	.977	1.365	.273
%	1.00	1.00	1.00	1.00	1.00	1.00

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Table 4—continued

	1984			1985		
Common name	Young (n=9)	Mature (n=9)	Old growth (n=18)	Young (n=9)	Mature (n-9)	Old growth (n=18)
Insectivores						
Shrew-mole						
Mean	0.135	0.266	0.223	0.082	0.341	0.187
S.D.	0.262	0.335	0.221	0.157	0.404	0.198
%	0.33	0.56	0.67	0.33	0.56	0.72
Rodents						
Townsend's chipmunk						
Mean	0.010	0.033	0.095	0.010	0.000	0.062
S.D.	0.030	0.071	0.160	0.031	0.000	0.084
%	0.11	0.22	0.44	0.11	0.00	0.44
Deer mouse[a]						
Mean	0.062 A	0.143 A, B	0.168 B	0.128 A	0.223 A, B	0.332 B
S.D.	0.104	0.174	0.112	0.213	0.261	0.226
%	0.33	0.67	0.89	0.44	0.67	0.94
Forest deer mouse						
Mean	0.565 A	0.822 B	0.730 B	0.334 A	0.900 B	0.687 B
S.D.	0.491	0.539	0.388	0.336	0.415	0.310
%	0.89	1.00	1.00	0.67	1.00	1.00
Southern red-backed vole						
Mean	0.890	1.405	0.993	1.030	1.445	1.009
S.D.	0.859	1.164	0.607	0.502	1.019	0.499
%	0.89	1.00	1.00	1.00	1.00	1.00
Rodents						
Creeping vole						
Mean	0.041	0.061	0.041	0.093	0.041	0.059
S.D.	0.094	0.080	0.114	0.212	0.123	0.164
%	0.22	0.44	0.17	0.33	0.11	0.28
Pacific jumping mouse						
Mean	0.000	0.021	0.050	0.020	0.063	0.067
S.D.	0.000	0.062	0.151	0.040	0.099	0.114
%	0.00	0.11	0.17	0.22	0.33	0.33
Total mammals						
Mean	5.074 A	6.884 A, B	7.583 B	5.881 A	7.725 A, B	7.990 B
S.D.	1.436	2.639	2.665	2.463	3.027	2.542
Species richness						
Mean	6.778	7.444	7.278	6.556	7.444	8.389
S.D.	1.481	1.424	1.487	1.740	1.590	1.852

[a] Captured more frequently in 1985 than in 1984.

[b] Captured more frequently in 1984 than in 1985.

More total mammals were caught in mature and old-growth forests than in young forests (table 4). Although not statistically significant, the trend was toward more species in older forest age-classes (table 4, $P = 0.07$).

Forest moisture gradient—Within the 27 old-growth forest sites, only the marsh shrew had an unambiguous response to the moisture gradient (table 5, fig. 2). The marsh shrew was caught in greater numbers on wet old-growth than on moderate sites, and showed a trend of higher captures on wet than dry sites ($P = 0.07$). The southern red-backed vole was caught more frequently in dry than moderate or wet old-growth forests (table 5), although this pattern is complicated by an interaction with the high elevation of dry sites as discussed below.

Table 5—Means, standard deviations, and frequency of occurrence (percent) of small mammal captures (number per 100 trap-nights) in snap (July and August) and pitfall traps (October and early November) on 27 forested sites representing a moisture gradient within old-growth forest in the southern Washington Cascade Range (where ANOVA is significant, differences between means are indicated with different letters; $\alpha = 0.05$)

	1984			1985		
Common name	Dry (n = 7)	Moderate (n = 11)	Wet (n = 9)	Dry (n = 7)	Moderate (n = 11)	Wet (n = 9)
Insectivores						
Vagrant shrew						
Mean	0.064	1.016	0.046	0.092	0.076	0.062
S.D.	0.134	0.054	0.080	0.244	0.120	0.131
%	0.29	0.09	0.33	0.14	0.36	0.22
Montane shrew[a]						
Mean	0.911	0.769	0.654	1.607	1.853	1.528
S.D.	0.473	0.594	0.505	1.064	0.837	0.853
%	1.00	1.00	1.00	1.00	1.00	1.00
Marsh shrew						
Mean	0.013 A, B	0.008 A	0.122 B	0.029 A, B	0.051 A	0.123 B
S.D.	0.035	0.027	0.158	0.078	0.065	0.131
%	0.14	0.36	0.56	0.14	0.45	0.56
Trowbridge's shrew[b]						
Mean	2.530	2.183	2.251	1.738	1.626	1.531
S.D.	0.771	1.888	0.796	0.460	0.813	1.119
%	1.00	1.00	1.00	1.00	1.00	0.89
Insectivores						
Shrew-mole						
Mean	0.315	0.272	0.233	0.320	0.190	0.369
S.D.	0.286	0.303	0.199	0.387	0.182	0.494
%	0.86	0.64	0.89	0.86	0.73	0.67
Rodents						
Townsend's chipmunk						
Mean	0.183	0.063	0.032	0.045	0.082	0.032
S.D.	0.322	0.111	0.048	0.081	0.104	0.096
%	0.57	0.27	0.33	0.29	0.55	0.11
Deer mouse						
Mean	0.132	0.249	0.445	0.409 A	0.449 A	0.095 B
S.D.	0.104	0.161	0.884	0.302	0.373	0.114
%	0.71	1.00	0.89	0.86	1.00	0.67

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Table 5—continued

Common name	1984 Dry (n = 7)	1984 Moderate (n = 11)	1984 Wet (n = 9)	1985 Dry (n = 7)	1985 Moderate (n = 11)	1985 Wet (n = 9)
Forest deer mouse[b]						
Mean	1.101	1.479	1.625	1.049	1.193	0.604
S.D.	1.005	1.038	0.991	0.662	0.694	0.363
%	1.00	1.00	1.00	1.00	1.00	1.00
Southern red-backed vole						
Mean	3.584 A	1.385 B	0.921 B	3.156 A	1.362 B	1.679 B
S.D.	2.594	1.131	1.032	1.977	0.934	1.944
%	1.00	1.00	0.89	1.00	1.00	0.89
Rodents						
Creeping vole						
Mean	0.083	0.027	0.109	0.158	0.017	0.052
S.D.	0.221	0.063	0.195	0.378	0.037	0.068
%	0.14	0.18	0.33	0.29	0.18	0.44
Pacific jumping mouse						
Mean	0.000	0.133	0.236	0.088	0.268	0.093
S.D.	0.000	0.285	0.393	0.146	0.646	0.186
%	0.00	0.27	0.44	0.43	0.36	0.22
Total mammals						
Mean	8.957	6.778	6.909	8.947	7.561	6.430
S.D.	3.277	1.850	1.273	3.263	2.096	4.177
Species richness						
Mean	7.429	7.091	8.333	8.000	9.182	8.333
S.D.	1.134	1.700	1.323	2.449	1.471	2.398

[a] Captured more frequently in 1985 than in 1984.
[b] Captured more frequently in 1984 than in 1985.

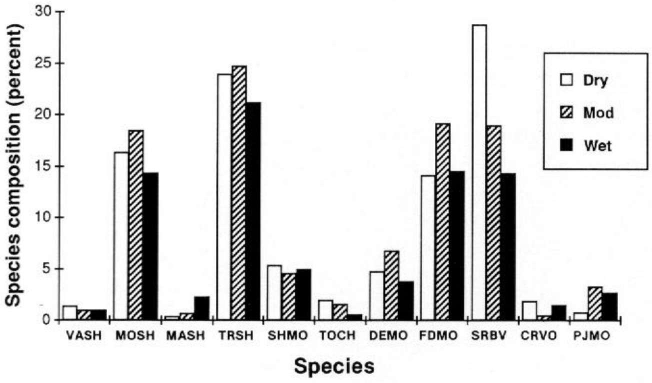

Figure 2—Patterns of abundance by forest moisture-class for the 11 most common small mammal species (minimum 40 captures) in the southern Washington Cascade Range. Captures for 1984 and 1985 combined. See figure 1 for definitions of species codes.

The pattern of capture across moisture-classes was different between years for both deer mice species. Because of the significant interaction of moisture-class by year, each year was analyzed separately. Captures of the deer mouse in 1984 were not significantly different across moisture-classes, but deer mice were infrequently captured in wet (relative to moderate), old-growth forest in 1985 (table 5, $P = 0.02$), and tended to be captured in dry rather than wet old-growth forest as well ($P = 0.08$). In parallel fashion, captures of the forest deer mouse were not significantly different in 1984, but forest deer mice tended to be caught in wet relative to moderate old-growth forest (table 5, $P = 0.06$).

The frequency of capture differed between years for three species in the 27 sites representing the moisture gradient (table 5). The montane shrew was caught more frequently in 1985 than in 1984, but Trowbridge's shrew and the forest deer mouse were captured more often in 1984 than in 1985. As was true across forest age-classes, changes in capture

Table 6—Multiple correlations between individual habitat variables and small mammal abundance and species richness for the southern Washington Cascade Range (statistically significant regression coefficients ($P < 0.05$) are given for each variable; adjusted multiple R^2 is listed at bottom of table)

	Deer mouse		Forest deer mouse		Southern red-backed vole		Total mammals		Species richness	
Variable	1984	1985	1984	1985	1984	1985	1984	1985	1984	1985
BSNGSMT	−0.05									
MCCTREE	−.06									
TREPIT		0.07								
MSHRUB		.12				0.27				
CSNGL		−.07								
LCONIF		.09	0.13	0.17		.09				0.82
LOGC			.16	.12		−.10				
ROCK					0.16					
FERN					−.23		−0.11			
LOGAB					−.16					
MCDTREE					−.16	−.48		−0.15		
WATER					.23	.12	.15			
SLOPE						.16				
ASTUMP							−.10			
BCSTUMP								−.16		
LICH									−0.81	
SOIL										−.70
BSNGL										.58
R^2	.30	.50	.26	.33	.65	.78	.31	.30	.29	.31

frequency between years was apportioned similarly across moisture-classes for montane and Trowbridge's shrews (table 5). The forest deer mouse, however, tended to be captured less frequently only in wet old growth.

Environmental Correlates With Mammalian Abundance

Elevation—Site elevation was not strongly correlated with the abundances of most species. Only three species showed a significant association with elevation, and of these, only the southern red-backed vole showed a consistent relationship between years [Trowbridge's shrew in 1984 only, $r = -0.417$ ($P < 0.01$); the shrew-mole in 1984 only, $r = 0.417$ ($P < 0.01$); the southern red-backed vole in 1984, $r = 0.533$ ($P < 0.001$) and in 1985, $r = 0.527$ ($P < 0.001$)].

Vegetative and physiographic variables—Three mammalian species and two community variables were significantly correlated with sets of vegetative and physiographic variables (table 6). Of the 18 vegetative and physiographic variables correlated with mammalian abundance, only six were correlated in more than one instance.

Although the abundance of the deer mouse was significantly correlated with vegetative and physiographic variables in each year, the variables were different between years (table 6). In 1984, the number of medium tall snags of intermediate decay class (BSNGSMT) and the percentage cover of mid-canopy by coniferous trees (MCCTREE) were negatively correlated with deer mouse abundance, but deer mouse abundance in 1985 was positively correlated with the number of treepits (TREPIT, or holes and root tangles associated with fallen trees), the percentage cover of mid-canopy shrubs (MSHRUB), and the number of large coniferous trees. Deer mouse abundance in 1985 was negatively correlated with the number of large, well-decayed snags (CSNGL). Correlations between the forest deer mouse and vegetative and physiographic variables were consistent between years, with positive associations for the number of large coniferous trees (LCONIF) and the percentage cover of well-decayed logs (LOGC). In general, the weak nature of the correlations underscores the fact that although more abundant in older forests, both species also were found in younger forests.

The pattern of correlation for the southern red-backed vole was different in that some associations held between years but others did not. Vole abundance in 1984 was positively correlated with the percentage cover of rock (ROCK) and the presence of water (WATER), but it was negatively correlated with the percentage cover of ferns (FERN), logs of early decay-classes (LOGAB), and mid-canopy deciduous trees (MCDTREE). In 1985, the correlations for WATER and MCDTREE remained, but new positive correlations were observed for the percentage cover of mid-canopy shrubs

(MSHRUB), the number of large coniferous trees (LCONIF), and slope of the site (SLOPE), and a new negative correlation was seen for the percentage cover of well-decayed logs (LOGC).

The total number of mammals captured (TMAM) and species richness (SPRICH) were not consistently correlated between years with individual vegetative and physiographic variables, although the multiple correlations were significant in each year (table 6).

Community Composition on Gradients of Forest Age and Moisture

The composition of mammalian communities based on presence or absence of species was not clearly related to the forest-age gradient. The hierarchical clustering of sites using Jaccard's coefficient of similarity on the age gradient (36 sites) produced clusters of sites with similar mammalian composition along the left side of the dendrogram in figure 3. Increasingly dissimilar sites (in terms of mammalian composition) were joined to the right side of the dendrogram. If forest age was a primary influence on mammalian composition, major clusters would be expected to reflect the age gradient. In other words, different clusters should be composed of sites in different age-classes, which was not observed. Each of the five major clusters (cluster 1 = sites 1-6; cluster 2 = sites 7-14; cluster 3 = sites 15-20; cluster 4 = sites 21-26; cluster 5 = sites 27-36) contain sites from all three age-classes. Inspection of the dendrogram at higher levels of similarity yields some smaller clusters of similar age-class (for example, sites 9-13 and sites 27-31), but few clusters of similar age were found. K-means clustering (specifying three clusters) by the abundance of the most frequently captured species (11 species) showed the same lack of association between clusters and site age. The first cluster consisted of eight young, four mature, and nine old-growth sites; the second cluster of four mature and six old-growth sites; and the third cluster of one young, one mature, and three old-growth sites.

Hierarchical clustering on the moisture gradient (27 sites) showed little correspondence between old-growth forest moisture-classes (dry, moderate, and wet) and the clusters of sites with similar mammalian species composition (fig. 4). No clusters consisted of just one moisture-class, although some clusters were composed of two classes, either moderate and wet (sites 15-21) or moderate and dry (sites 22-27). The K-means clustering procedure suggested that moisture status exerts somewhat more influence on community composition. Specifying three clusters, the first cluster was composed of two dry, eight moderate, and eight wet sites; the second cluster of five dry, two moderate, and one wet site; and the third cluster of just one moderate site. The grouping of five of the seven dry sites in the second cluster might indicate a tendency for similar mammalian communities on drier sites. Sites in the second cluster supported rather high populations of red-backed voles. This relationship is clouded by the fact that several dry sites were at high elevation, and as discussed below, whether the primary influence is due to moisture or conditions related to high elevation is not clear.

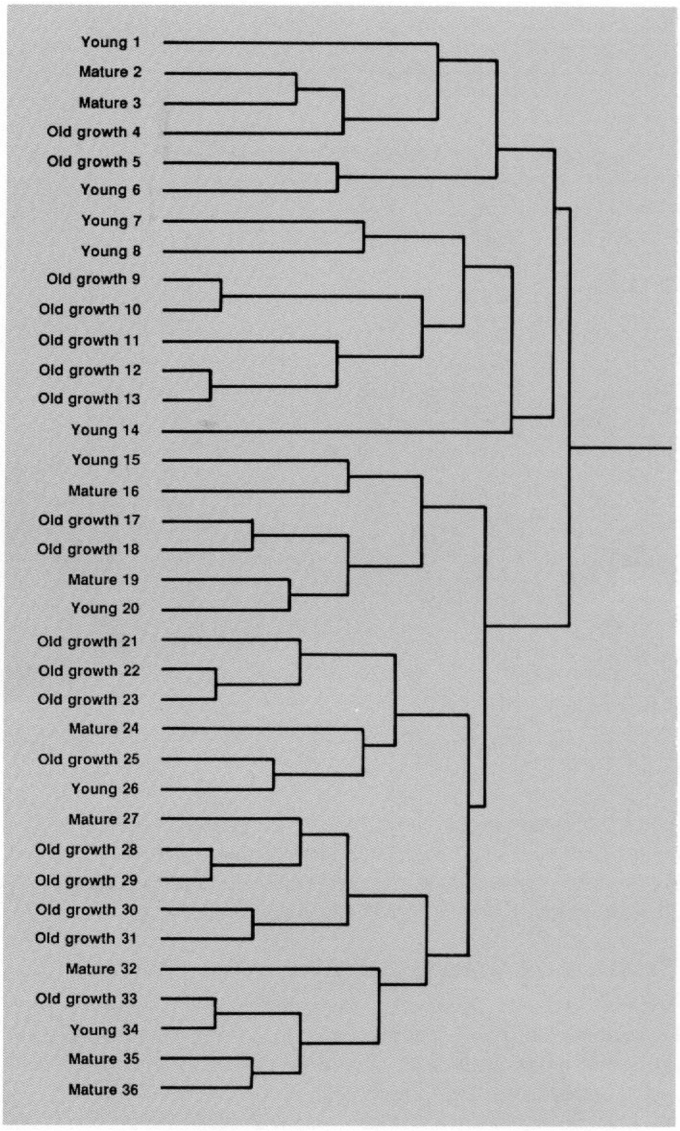

Figure 3—Small mammal community similarity dendrogram for the 36 sites of the forest chronosequence. Sites with similar small mammal composition (presence or absence of 21 species) join to the left of the figure; increasingly dissimilar sites join farther to the right.

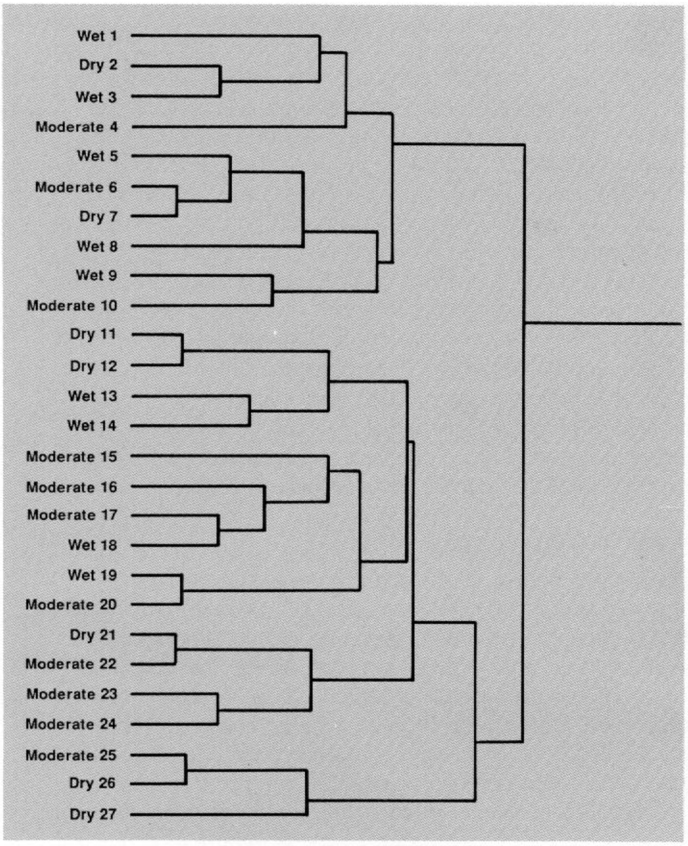

Figure 4—Small mammal community similarity dendrogram for the 27 old-growth sites of the forest moisture gradient. Sites with similar small mammal composition (presence or absence of 21 species) join to the left of the figure; increasingly dissimilar sites join farther to the right.

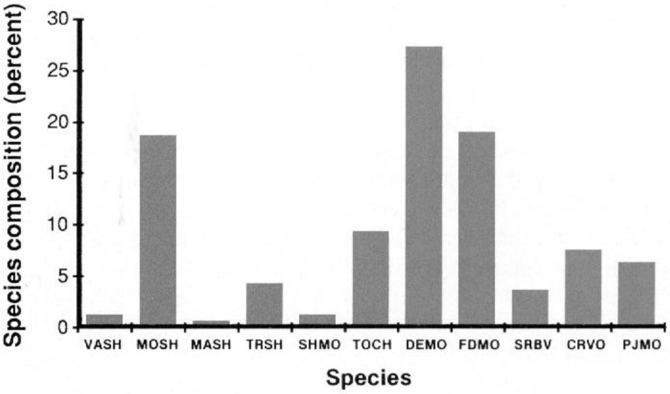

Figure 5—Patterns of abundance on eight clearcut areas for the 11 most common small mammal species (minimum 40 captures) in the southern Washington Cascade Range. Reported captures are from 1984 only. See figure 1 for definitions of species codes.

Discussion

Species Response to Gradients of Age and Moisture

Forest age gradient—The relationships of deer mice to patterns of forest succession in Washington are being reevaluated in light of the recent elevation of the forest deer mouse to species status (Gunn and Greenbaum 1986, Allard and others 1987). The forest deer mouse has mostly been considered a subspecies of the deer mouse (Osgood 1909, but see Liu 1954, Ingles 1965, and Sheppe 1961), and that view has enhanced the conception of the deer mouse as an extreme habitat generalist. A substantial part of the habitat thought to be occupied by the deer mouse was actually occupied by the forest deer mouse. As demonstrated in this study for the southern Washington Cascade Range, the forest deer mouse is the more abundant of the two species in forested habitat (tables 1, 4; figs. 1 and 5). Research has just begun to describe the distributions and patterns of abundance of these species, and work is underway on the taxonomic affinities of the forest deer mouse and other *Peromyscus* species in coastal British Columbia. The currently recognized range of the forest deer mouse may expand, a consequence of synonymizing some of the coastal forms with the forest deer mouse. Relative to the deer mouse, which has one of the widest geographic distributions of all species in North America and inhabits many different habitats, the forest deer mouse is a forest specialist. It is found in pre-canopy stages of forest succession (table 2, fig. 5), but is generally outnumbered by the deer mouse in such habitat.

A positive relationship between abundance and forest age was an expected pattern for the forest deer mouse. As a forest specialist, the forest deer mouse would be expected to reach high abundance in the well-developed forests that, historically, were the prevailing forest condition in the Pacific Northwest. Observing the same pattern for the deer mouse, however, was a little surprising. Deer mice were also more abundant in old-growth than in mature or young forest on the western slopes of the central Oregon Cascades (Anthony and others 1987), and more abundant in riparian zones of old-growth forest than in mature- and sawtimber-classes (sites 50-150 years) in northwestern California (Raphael 1988c). The deer mouse may be more abundant in old rather than young forest because of the diversification of ground vegetation with forest succession (Spies, this volume). Older forests may more closely resemble the diversity and abundance of herbaceous plants characteristic of pre-canopy successional stages than those of many closed-canopy young and mature forests. This resemblance is partially related to the uneven nature of old-forest canopies, which allow the growth of ground-layer plant species that depend on increased light. Deer mouse patterns of peak abundance in old forests, however, are only relevant to the stages of forest succession that follow canopy closure. As in other regions (Anthony and others 1987, Raphael 1988c), the deer mouse is much more abundant in habitats that occur before canopy closure (table 2, fig. 5).

Like the deer mouse, Townsend's chipmunk and the Pacific jumping mouse are rather common in habitats without closed forest canopies (table 2, fig. 5), and are known to inhabit meadows and edge environments (Dalquest 1948). Their tendency toward higher abundance in old-growth forest might well be a response to the complex and patchy forest floor environment of old forests, which may be more similar to their preferred habitats than ground conditions in young forests. Anthony and others (1987) found these species in greater numbers in riparian zones of young, rather than mature or old-growth forests. This difference may have been due to the younger ages (25-50 years) of sites in their "young-forest" age-class compared to those in this study (55-75 years). Given younger sites, the same pattern may hold in the Washington Cascades.

Forest moisture gradient-The marsh shrew frequents wet areas (Cowan and Guiguet 1965, Pattie 1973), but it is not as tied to standing water as the water shrew. I have taken marsh shrews at a considerable distance from water in quite dry, second-growth, Douglas-fir forests. Nonetheless, the species appears to be most abundant in wet forest, regardless of forest age. Anthony and others (1987) caught six shrews in riparian zones of the western Oregon Cascade Range, three individuals in old-growth, one in mature, and two in young forests.

At first inspection, the southern red-backed vole appears strongly associated with dry old-growth forest (table 5). Although these data indicate that the voles can do well in dry old-growth forests, dry conditions *per se* have not clearly been shown to be critical. Southern red-backed voles were caught more often at trap sites near water (table 6), and at high elevation sites, patterns that held in both years. Dry sites as a group tended to be at higher elevations (mean = 838 m) than wet (762 m) or moderate sites (754 m). More important, no dry sites were lower than 689 m in contrast to moderate and wet sites with two sites less than 500 m, four less than 600 m, and five less than 660 m. Captures of red-backed voles in these low elevation sites were few, averaging just 2.5 animals per site in 1984 and 0.5 animals in 1985. As a further demonstration of this interaction, the correlation of vole abundance for both years combined with the elevation of dry sites was quite high ($r = 0.83$; $P = 0.02$). The primary relationship may be with the environmental conditions related to high elevation, rather than to moisture. Six of the seven dry sites were located south and southeast of Mount Rainier, a region that yielded the highest capture totals for red-backed voles. In fact, nine of the ten sites with the highest capture totals for red-backed voles were from this region; these included four dry and three moderate old-growth sites, and two mature forest sites. Even though the relationship of red-backed vole abundance to dry forest appeared to be positive, it is clearly not simple; elevation and biogeographic factors must also be considered.

Both deer mice species shared the interaction between forest moisture-class and years, and followed the same patterns of capture in each moisture-class and year (table 5). For each species, the major difference in capture frequency across moisture-classes was the small number of captures in wet sites during 1985. With only 2 years of data, determining which, if either, of the 2 years represents the "usual" response to moisture condition is impossible. Both species may have responded to a rather widespread influence. Meteorological data from the southern (Wind River), central (Packwood), and northern (Longmire) portions of the study area indicate that 1984 was generally cooler and wetter than 1985 (Manuwal, pers. comm.). Given consistent meteorological differences between years, these may conceivably have influenced population growth differentially across moisture-classes; however, speculations on mechanisms must await clarification of the general response to moisture condition.

Trends in Other Species

Nine species poorly represented in the capture totals were not tested statistically for their numeric responses to forest age and moisture gradients. Because species that occur in low abundance are a special concern, noting that the small number of captures for these species (table 1: water shrew, coast mole, yellow-pine chipmunk, pika, northern flying squirrel, northern pocket gopher, water vole, long-tailed vole, and ermine) does not necessarily indicate regional scarcity is important. Most species either reach maximum abundance in adjacent habitats or were not effectively sampled by the techniques targeted for forest-floor mammals. The yellow-pine chipmunk, the northern pocket gopher, the water vole, and the pika are all found more commonly at higher elevations than were sampled in this study (Dalquest 1948). The coast mole is present in many habitats (Dalquest 1948; Hartman and Yates 1985, Maser and others 1981) and is probably most common in habitats without closed canopies at lower elevations. It was not readily caught by pitfall and snap traps and is no doubt more abundant in these forests than the capture returns would indicate. The coast mole can be sampled more effectively with traps designed to capture moles, or by indexing activity via mole-run counts (West, in press). The ermine, although typically not an abundant species, is found in a great variety of habitats (Cowan and Guiguet 1965, Maser and others 1981).

Other species that were poorly represented in the capture totals are of interest for different reasons. The northern flying squirrel has received attention because of its importance as prey for the spotted owl. As expected, pitfall or snap traps did not adequately sample this species. Track plates were used to index flying squirrel activity, and the resulting frequency-counts were not positively associated with forest age or moisture condition. Whether track frequencies are highly correlated with squirrel abundance is not clear, however (Carey, pers. comm.). Recent work on the flying squirrel by the Forestry Sciences Laboratory (USDA Forest Service, Olympia) in both Oregon and the Olympic Peninsula of Washington should help clarify patterns of squirrel abundance and their association with gradients of forest age or moisture.

The habitat affinities of the long-tailed vole are poorly understood in Washington. This species is captured sporadically, although it has been recorded from many different habitats (Cowan and Guiguet 1965, Dalquest 1948, Maser and others 1981, Randall and Johnson 1979). It has been found most commonly in forest-edge environments and brushy riparian zones where grass cover is usually present. I collected three individuals in clearcut areas (table 2), one in a young, one in an old-growth wet, and two in old-growth dry forests (table 1). Although it is not a species that is closely associated with old forests, it needs further ecological study.

The water shrew is a riparian specialist. The techniques used in this study probably would be effective in sampling the water shrew if they were concentrated along permanent watercourses, but because the sampling did not focus on riparian strips, captures of this species were few. The water shrew is also more common at elevations higher than most sites in this study (Dalquest 1948). Its requirements for water are understood, but whether it is more abundant in riparian zones in old rather than young forests is unclear. In this study, two shrews were caught in young forests, four in old-growth moderate, and three in old-growth wet forests. In a study focused on riparian habitat, Anthony and others (1987) caught two shrews in old-growth, one in mature, and none in young forest. All three individuals were caught at streamside (about 1 m from water), rather than in adjacent riparian habitat (15-25 m from water).

Community Patterns in the Southern Washington Cascade Range

The mid-elevation forests of the southern Washington Cascades are inhabited by a small mammal fauna that is broadly adapted to naturally regenerated forests. Unique small mammal communities were not seen in forests of different age or in old-growth forests of different moisture condition. With the exception of the deer mice, no species was significantly correlated with the forest-age gradient. Four common species (Trowbridge's shrew, southern red-backed vole, montane shrew, and forest deer mouse) and a few less common species typically were found at a given site (table 4 and fig. 1). This pattern resulted in a very similar ranking of species by abundance in each year. Clustering of similar sites by small mammal presence or absence and by abundance of common species yielded clusters that related poorly to the age gradient (fig. 3). Similarly, only the marsh shrew was unambiguously related to the moisture gradient,, and clustering of sites by abundance and by small mammal presence or absence produced clusters not clearly related to the moisture gradient (fig. 4). In concordance with these findings, correlations between small mammals and variable means describing the forest environment were generally weak. Statistically significant correlations, especially those similar in both years, were restricted to a few species which generally occurred widely across both gradients (table 6). These patterns are essentially ones found in all three provinces (Oregon Cascades, Oregon Coast Range, and southern Washington Cascades) in this study (Aubry and others, this volume; Corn and others 1988). Aside from differences in species composition related to geographic distribution, small mammal communities of Douglas-fir forests in this region are structured similarly.

Community composition did not vary appreciably with forest age, but total mammalian abundance was higher in old-growth than in young forests (table 4). The higher abundance partially resulted from the presence of more species in old forest (table 4). Higher abundance may be linked to age-related differences in the structure and productivity of the ground environment, which is more diverse in old forests. Whether the average number of species is typically greater in old-growth forests is uncertain, as is the associated question of whether variation in species number is related to the age gradient. In this study, coefficients of variation (C.V.) for species richness were similar between years on the age gradient (from table 4: C.V. 1984 = 21.9, 19.1, and 20.4 for young, mature, and old-growth forests; C.V. 1985 = 26.5,21.4, and 22.1). Variation in species number might be expected to be higher in young than in old-growth forest, as a reflection of the higher proportion of dispersal sinks in young forest, and perhaps as a function of the less-diverse and productive resource-base at ground level and the less physically buffered environment. Such a trend may exist, although slight, in the above coefficients, but a thorough answer to these questions requires long-term study. Of particular interest would be the variation in species number with season in young versus old forest. The initial design of this study, which was not fully implemented, included a spring and fall sampling-period for each site as a way of addressing this question. This study, therefore, cannot characterize the magnitude of seasonal changes. That snap-trapped animals were breeding is important to note; however, site occupancy was thus not simply due to the capture of individuals dispersing from favored or survival habitats (Anderson 1980). This spilling-over effect that resulted from the movement of individuals from high-density to low-density habitats (Fretwell 1972), or from saturation dispersal (Lidicker 1975), would be more evident later in the fall and early winter.

What does the apparent lack of strong community patterns on gradients of forest-age and moisture mean? Is it really true that the small mammals of this region are insensitive to variation in forest structure? Not at all; noting that this survey was done exclusively on naturally regenerated stands, clearly-from this study, from work in Oregon (Corn and Bury, this volume a; Gilbert and Allwine, this volume a), and from work on the successional changes in the compositional and structural features of these forests (Spies and Franklin, this volume; Spies and others 1988)—thresholds of critical habitat-variables are met for most forest-dwelling species soon after canopy closure.

In a naturally regenerating landscape, the major change in the species composition of small mammals occurs before and during canopy closure. At the transition from grass- and forb-dominated plant communities to later stages dominated by shrubs and young trees, small mammal communities characterized by the deer mouse, several species of meadow voles, Townsend's and yellow-pine chipmunks, the Pacific jumping mouse, and shrews of open habitats (the vagrant shrew and the montane shrew) begin to give way to communities of the closed-canopy forest described in this study. Rather minor changes in species composition and relative abundance among species takes place in subsequent successional stages. As a consequence of this pattern of mammalian species replacement, we would expect poor correlations between small mammal abundance and habitat elements in studies that use a data set based on naturally regenerated forests, as was observed.

If thresholds for limiting habitat-elements for small mammals are usually met or exceeded in naturally regenerated forests, this data set presents an interesting problem. In terms of information to guide management on forests regenerated after timber harvest, this data set is not usable for identifying critical habitat-elements, or to assess their threshold values-a straightforward consequence of the fact that the range of variation in these variables was insufficient to provide strong correlations or to indicate threshold values. For such a purpose, knowing under what conditions a species is absent is just as important as knowing the conditions under which it is present. On the one hand, this study shows that most species have a fair amount of adaptability in their use of forest habitats, but on the other, it tells us little about sufficient values for habitat elements. If forests managed for timber production are to retain most of their native small mammals, we need to begin the process of identifying critical habitat-elements and assessing their minimum threshold values. That second- and third-rotation forests would resemble naturally regenerated forests in a number of respects seems unlikely, and they certainly would exceed the range of variation in habitat variables sampled in this study. The required information, consequently, can only come from a data set based on stands that are intensively managed for timber production, or an array of experimental sites designed to mimic such conditions. To this end, manipulative field experiments conducted on spatial scales sufficiently large to avoid the problem of animal movement from adjacent edges probably hold the most promise. Because of the need for large scale, such studies might best be undertaken cooperatively between the scientific community and government agencies or private companies.

Acknowledgments

In the course of this study, over 60 people contributed to the field work and data analyses. Field work required long hours under hard conditions, and I am indebted to these people for completing it. Diane Converse deserves special thanks for her leadership and perseverence over the course of the study. Funding was provided by the USDA Forest Service, Pacific Northwest Research Station. I thank personnel of the Wind River, Mount Adams, Packwood, and Randle Ranger Districts of the Gifford Pinchot National Forest, the White River Ranger District of the Mount Baker-Snoqualmie National Forest, and Mount Rainier National Park for their advice and logistical help.

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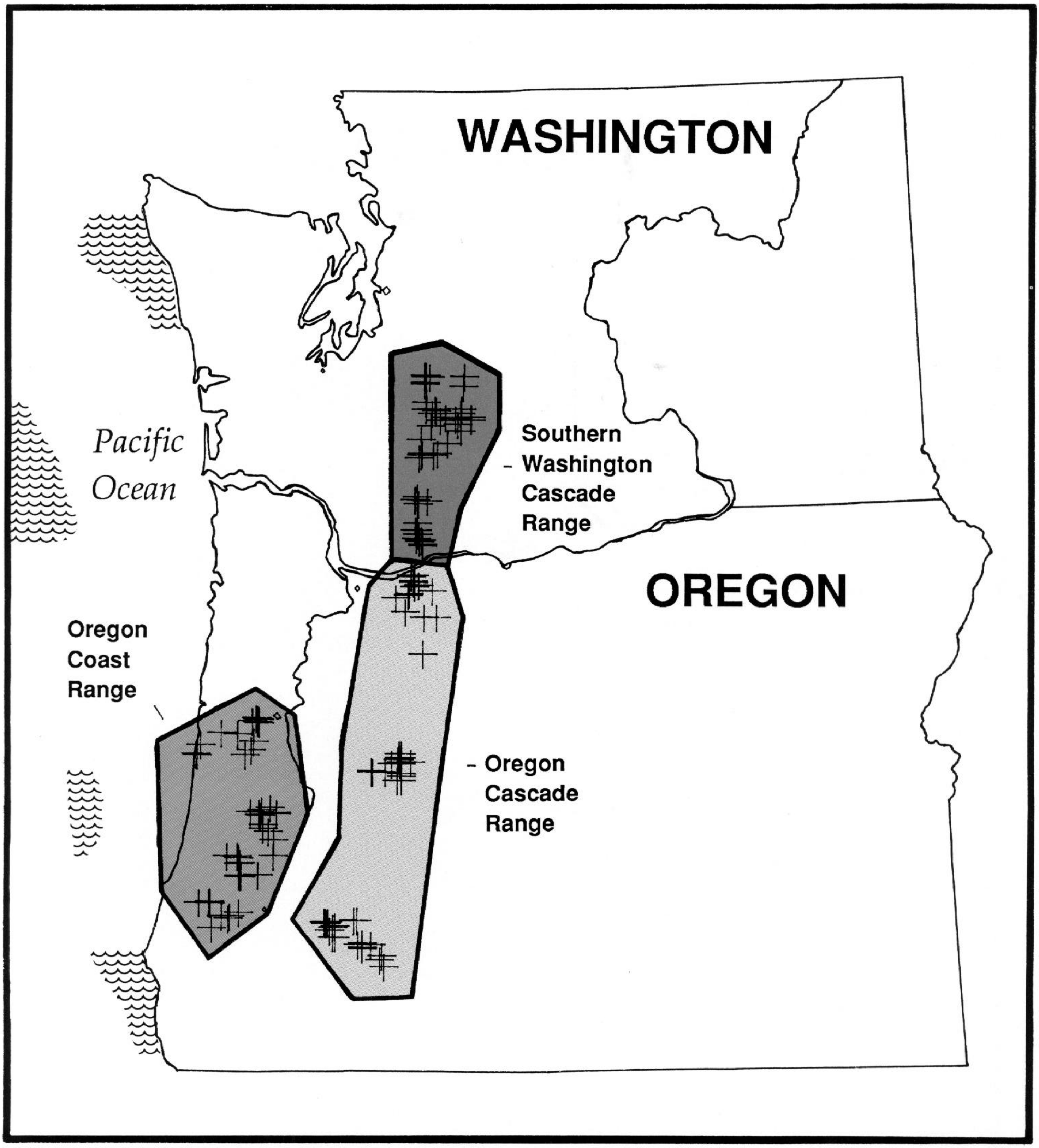
Appendix

Table 7-Physiographic and vegetative variables that describe habitats in the southern Washington Cascade Range

Variable	Description
SLOPE	Percentage slope
WATER	Presence of permanent water
ROCK	Percentage cover of rock
GRASS	Percentage cover of grasses
HERB	Percentage cover of herbs
SOIL	Percentage cover of mineral soil
MOSS	Percentage cover of moss
LICH	Percentage cover of lichens
LITT	Percentage cover of fine litter (<10-cm diameter)
LITDEP	Litter depth (cm)
FERN	Percentage cover of ferns
SHRUB	Percentage cover of ground-layer shrubs
MSHRUB	Percentage cover of mid-canopy shrubs
MCCTREE	Percentage cover of canopy and mid-canopy coniferous trees
MCDTREE	Percentage cover of canopy and mid-canopy deciduous trees
CONIFSM	Number of small and medium-diameter coniferous trees (l-50 cm)
DECIDSM	Number of small and medium-diameter deciduous trees (l-50 cm)
LCONIF	Number of large-diameter coniferous trees (>50 cm)
LDECID	Number of large-diameter deciduous trees (>50 cm)
SCAN	Presence of supercanopy trees
TREPIT	Number of tree-fall pits
ASTUMP	Number of slightly decayed stumps
BCSTUMP	Number of moderately to well-decayed stumps
LGGAB	Number of slightly to moderately decayed logs, d.b.h. > 10 cm
LOGC	Number of well-decayed logs, d.b.h > 10 cm
ASNGSMT	Number of slightly decayed small and medium-diameter (l-50 cm) short (<l.5 m), medium (5-15 m), and tall (>I5 m) snags
BSNGSMT	Number of moderately small and medium-diameter (l-50 cm) short (<l.5 m), medium (5-15 m), and tall (>15 m) snags
CSNGSM	Number of well-decayed small and medium-diameter (l-50 cm) short (<l.5 m) and medium (5-15 m) snags
ASNGL	Number of slightly decayed large-diameter (>50 cm), medium and tall snags
BSNGL	Number of moderately decayed large-diameter (>50 cm). medium and tall snags
CSNGL	Number of well-decayed large-diameter (>50 cm), medium and tall snags

Continue



Location of study sites within the three physiographic provinces.

Regional Patterns of Small Mammal Abundance and Community Composition in Oregon and Washington

Keith B. Aubry, Mark J. Crites, and Stephen D. West

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Abstract

Pitfall traps were used by a team of investigators to study forest-floor small mammal communities in 144 different-aged Douglas-fir forest stands in three physiographic provinces in the Pacific Northwest: the Oregon Coast Range, Oregon Cascade Range, and Southern Washington Cascade Range. All three small mammal assemblages were numerically dominated by a few species. The Trowbridge's shrew was the most abundant species in all three provinces and accounted for 47 percent of 8661 small mammals captured. Most remaining captures were of only one or two other species: in the Coast Range, the western red-backed vole and Pacific shrew; in the Oregon Cascades, the western red-backed vole; and in the southern Washington Cascades, the southern red-backed vole and montane shrew. Other species each accounted for less than 6 percent of total captures in all three provinces.

Ordination analysis of small mammal communities, both among and within provinces, revealed few ecologically interpretable patterns or differences among forest age-classes. Most variation was attributable to differences in species composition resulting from zoogeographic barriers. The shrew-mole and red tree vole were closely associated with old-growth forests in all provinces where they occurred. These species should be given high priority in the development of management strategies for small mammals in Pacific Northwest forests.

Introduction

The fate of old-growth Douglas-fir forests in the Pacific Northwest has become one of the most controversial resource management issues of this century (see Norse 1990, Norse and others 1986, Wilcove 1988). Research on the composition, structure, and function of these forests, however, has only recently been undertaken (see Franklin and others 1981, Gutierrez and Carey 1985, Meehan and others 1984, Raphael 1984, Raphael and Barrett 1984, Spies and others 1988).

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Before these studies, lists of small mammal species believed to be associated with old-growth forests were based primarily on natural history observations and speculation (for example, Franklin and others 1981, Lumen and Neitro 1980, Meslow and others 1981). The comprehensive program of research described in this volume was undertaken to provide quantitative information on wildlife habitat relationships in Douglas-fir forests, and to provide a scientific basis for the management of old-growth forests (Carey and Spies, this volume; Ruggiero and Carey 1984).

The primary objectives of the small mammal studies conducted in the Oregon Coast Range (Corn and Bury, this volume a), Oregon Cascade Range (Gilbert and Allwine, this volume a), and southern Washington Cascade Range (West, this volume) were to identify small mammal species that are associated with old-growth Douglas-fir forests within each province, and to investigate potential correlations between small mammal abundances and vegetative or structural features of unmanaged Douglas-fir forests. The purpose of this paper is to combine these three data sets and compare and contrast observed habitat association patterns among physiographic provinces to evaluate the extent to which observed patterns vary on a regional scale. Data from studies conducted in the Northern California province were not included because the ecological characteristics of stands occurring there were considered to be too different from those in Oregon and Washington for the data to be combined into a single data set (T. Spies and J. Franklin, pers. comm.).

By combining the data in a single analysis, results from each province can be compared quantitatively with those from other provinces. In addition, larger sample sizes resulting from the pooling of data increase the power of statistical analyses, especially for relatively rare species. Knowledge of regional variation in the habitat relationships of small mammal species associated with old-growth forests will enable wildlife managers to set priorities for management activities within different areas of the Pacific Northwest, and will provide additional insights into the habitat relationships of small mammals in unmanaged Douglas-fir forests. The specific objectives of this paper are to:

- Describe the forest-floor small mammal communities occurring in unmanaged Douglas-fir forests in three physiographic provinces in Oregon and Washington; and
- Compare patterns of community composition, species abundances, and habitat associations among provinces.

Methods

Study Areas

Forest-floor small mammals were studied in 144 stands in Oregon and Washington in 1984 and 1985 by a team of investigators. Study sites were located in three physiographic provinces (Franklin and Dymess 1973): 45 in the Oregon Coast Range, 54 in the Oregon Cascade Range, and 45 in the southern Washington Cascade Range. Data were collected in all stands in both years, with the exception of the Oregon Cascades province in which only 15 stands in the central Cascade Range were sampled in 1985.

Homogeneous forest stands of at least 20 ha with Douglas-fir as the dominant tree species were selected for study. None of the sites had been logged; all had resulted from natural regeneration after catastrophic wildfires. All stands are within the Western Hemlock Zone and lower elevations of the Pacific Silver Fir Zone (Franklin and Dyrness 1973).

Stands were classified into three broad age-classes: young (35-79 yrs), mature (80-195 yrs), and old-growth (200-730 yrs). Ages were based on growth-ring counts, either by increment coring or examination of cut stumps in nearby stands (Spies and others 1988). Old-growth stands typically contained high proportions of Douglas-fir and western hemlock and, in wet sites, western redcedar. Mature and young stands were dominated by Douglas-fir. In all age-classes, other species such as red alder, vine maple, bigleaf maple, Pacific silver fir, and western hemlock occurred in lesser amounts. See Spies and Franklin (this volume) and Spies (this volume) for more detailed descriptions of the vegetative and structural characteristics of the study stands.

Within each province, stands of comparable moisture condition were placed into an age gradient as a means of assessing variation in small mammal abundances resulting primarily from differences in stand age-class. The age gradient consisted of 127 stands, including 43 from the Coast Range, 48 from the Oregon Cascades, and 36 from the southern Washington Cascades. Although the range of ages sampled was similar among provinces, old-growth stands in the southern Washington Cascades contained nine stands that were 25 to 205 years older than the oldest stands sampled in either the Coast Range or the Oregon Cascades, Ranges for the age-classes in each province are: Oregon Coast Range, young, 40 to 75; mature, 80 to 120; and old-growth, 200 to 525 years old; Oregon Cascades, young, 35 to 79; mature, 84 to 180; and old-growth, 200 to 500 years old; and southern Washington Cascades, young, 55 to 75; mature, 80 to 195; and old-growth, 210 to 730 years old.

Small Mammal Sampling

Within each province, forest-floor small mammals were sampled with pitfall traps, snap-traps, and tracking stations (see Carey and Spies, this volume). Only pitfall trapping, however, was used in all three provinces in both years. Other techniques were used either in only one or two provinces, or were not equally applied in both years. To compare results among physiographic provinces, we therefore used only data derived from pitfall trapping.

Thirty-six pitfall traps were installed in each stand in a 6 x 6 square array with traps spaced 15 m apart. New pitfall grids were established in each stand in the southern Washington Cascades during the second year of the study; in the Coast Range and Oregon Cascades, grids were retrapped in the second year. Comparisons of results between new grids and a subset of grids retrapped the second year showed no differences in small mammal species composition or abundances (Gilbert and Allwine, this volume a). All stands were sampled for about 30 days each fall, and checked about once per week. All specimens were collected for identification and all salvageable specimens were preserved.

Pitfall traps were opened after the onset of fall rains in 1984 and again in 1985 in the southern Washington Cascades and in the Coast Range; traps were opened a month earlier in the Oregon Cascades. Trapping dates for each province were: Coast Range, 1 October-7 November 1984 and 30 September-1 November 1985; Oregon Cascades, 28 August-6 October 1984 and 29 August-5 October 1985; and southern Washington Cascades, 30 September-5 November 1984 and 27 September-3 November 1985.

Data Analyses

For all analyses, we included only data for species that had >20 total captures or that occurred in >10 percent of the stands sampled. Species not meeting these criteria were considered to be inadequately sampled with our techniques. Although we captured 77 Pacific jumping mice, 58 of these captures were from the Oregon Cascades where trapping probably occurred before the onset of hibernation for this species (Dalquest 1948). Because of potential bias resulting from regional differences in the influence of hibernation on our results, and the likelihood of jumping mice escaping from pitfall traps (Bury and Corn 1987), this species was excluded from all analyses. The extent to which differences in sampling dates may have influenced results for other species is unknown.

Three species, the red tree vole, Pacific shrew, and western red-backed vole, occur in both of the Oregon provinces, but not in Washington. Conversely, the southern red-backed vole and forest deer mouse occur only in the southern Washington Cascades. One species, the montane shrew, occurs throughout the southern Washington Cascades but is found only in the northernmost portion of the Oregon Cascades (Carey and Spies, this volume; Ingles 1965). Stand sample sizes were adjusted for these species.

Community analyses-Although yearly variations in population numbers may influence results in studies of wildlife habitat relationships, 2 years of data is not sufficient to adequately evaluate temporal variation in small mammal abundances. Furthermore, without corresponding demographic information, causative factors for observed variation cannot be determined (Van Home 1983). For these reasons, we pooled data from both years, and calculated abundance indices for each stand as mean captures for both years per 100 trap-nights. We examined community patterns of small mammal abundance with detrended correspondence analysis (DCA) using DECORANA (Hill 1979a). We interpreted ordination axes by correlating ordination scores for the small mammal communities with major physiographic and vegetative gradients by using Spearman rank correlations (Norusis 1988a). The vegetative gradients we included as variables represented multivariate gradients derived by Spies and Franklin (this volume) in their analyses of the vegetative characteristics of the study stands. These variables represented gradients of stand development (primarily stand age and abundance of western hemlocks), coarse woody debris, stand temperature, and stand moisture.

We conducted ordination analyses at two scales: region-wide analyses that included stands of all age- and moisture-classes from all three provinces (144 stands), and province-specific ordinations conducted separately for each province (Coast Range, 45; Oregon Cascades, 54; and southern Washington Cascades, 45 stands). We conducted region-wide ordinations both on the 15 species that were considered to be adequately sampled with our techniques, and on data from only the subset of nine species that occur in all areas studied. The first approach identifies regional community patterns that include variation resulting from differences in species composition, and the second approach examines differences in community composition and structure independent of the confounding effects of differences in species' distributions. We also conducted province-specific ordinations to examine community-scale variation among age-classes within each province. This approach enabled us to evaluate the effects of stand age on small mammal community patterns for each province, and provided a means of comparing these patterns among provinces that is not affected by differences in potential community composition or by deleting a substantial portion of the community.

Species analyses-To investigate the extent to which patterns of association due to differences in stand age vary regionally, we conducted all species analyses using data only from stands within each age gradient (127 stands). We used two-way ANOVA (Norusis 1988a) on abundance data for species with >100 captures, and log-linear analysis (Kennedy 1983) of presence-or-absence data for species with <100 captures.

Because of the limited number of sites that could be studied with available resources, study areas were preferentially selected to sample the full range of variation occurring in each stratum (Carey and Spies, this volume). Because study sites were not selected randomly, rigorous statistical inference based on hypothesis testing is not possible with our data sets. We used statistical tests only as a means of examining patterns of variation in the data. However, because we intentionally sampled the full range of variation within each stratum, the variances in our data would be expected to exceed those resulting from random sampling. Consequently, observed differences are less likely to result from chance than if our sites had been selected randomly (Ruggiero and others, this volume).

To identify regional patterns in the habitat relationships of small mammals occurring along environmental gradients, we examined the relationships between individual species' abundances and major physiographic and vegetative gradients using Spearman rank correlations (Norusis 1988a). We used only abundance data for species with >l00 captures in these analyses.

Results

Altogether, 8661 small mammals of 29 species were captured, including 6 shrews, 3 moles, 4 squirrels, 1 gopher, 14 mice and voles, and 1 weasel. Only 15 species had >20 total captures or occurred in >10 percent of stands studied: the marsh, montane, Pacific, Trowbridge's, and vagrant shrews; the shrew-mole and coast mole; the deer mouse and forest deer mouse; the red tree, southern and western red-backed, and creeping voles; the northern flying squirrel; and the ermine (table 1).

The structure and composition of the small mammal communities sampled varied somewhat among provinces (fig. 1). The Trowbridge's shrew was captured in every stand sampled, and it was the most abundant small mammal in all three provinces. This species accounted for 47 percent of total captures for all provinces combined. In all three provinces, the Trowbridge's shrew and one or two other species accounted for most captures. In the Coast Range, the Trowbridge‘s shrew represented 56 percent of total captures; the western red-backed vole, 21 percent; and the Pacific shrew, 11 percent. All other species contributed less than 4 percent each to total captures. In the Oregon Cascades, 69 percent of total captures were of the Trowbridge‘s shrew. The western red-backed vole accounted for 13 percent, and all other species each represented less than 5 percent of total captures. In the southern Washington Cascades, Trowbridge's shrews were relatively less important, representing only 36 percent of total captures. Two other species, the montane shrew and southern red-backed vole, were captured in relatively high numbers, with each representing about 23 percent of total captures. No other species accounted for more than 6 percent of captures.

Community relationships-Ordination analysis of the combined abundance data from all provinces for 15 small mammal species revealed community patterns that reflect differences in the species composition and diversity of small mammals occurring in each province (fig. 2). The Coast Range cluster forms a subset of the Oregon Cascades cluster, indicating less variability in the composition and structure of small mammal communities in the Coast Range stands compared to the Oregon Cascades stands. The Coast Range and the Oregon Cascades are most similar in small mammal species composition (fig. l), and their ordination clusters separated out almost completely from the southern Washington Cascades cluster.

The first ordination axis (X axis) was significantly correlated to gradients of increasing moisture ($P = 0.000$), elevation ($P = 0.000$), and stand age ($P = 0.010$), and decreasing temperature ($P = 0.000$). The second axis (Y axis) was more difficult to interpret, as would be expected based on the lack of separation of clusters in this direction. This axis was correlated primarily with decreasing moisture ($P = 0.009$) and increasing temperature ($P = 0.034$).

Ordination results using only the nine species that occur in all three provinces (table 1) revealed a high degree of overlap in the structure and composition of the communities occurring within each province (fig. 3). Community patterns observed in figure 2, however, are still evident. The Coast Range cluster is again much smaller than the Oregon Cascades cluster and constitutes a subset of that cluster, and the southern Washington Cascades cluster still contains points unique to that cluster. Environmental gradients represented by the ordination axes are virtually identical to those reported for figure 2.

Table 1—Mean, standard error, and percentage occurrence of small mammal species with >20 total captures in pitfall traps by province and age-class (number of stands sampled is in parentheses)

		Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range		
Species		Old growth (25)	Mature (10)	Young (8)	Old growth (22)	Mature (17)	Young (9)	Old Growth (18)	Mature (9)	Young (9)
Marsh shrew	$\bar{x}$[a]	0.016	0.022	0.006	0.012	0.020	0.006	0.018	0.016	0.041
	SE[b]	0.004	0.012	0.006	0.009	0.009	0.006	0.008	0.008	0.009
	%[c]	36	30	13	14	24	11	28	33	78
Montane shrew	$\bar{x}$	—[d]	—	—	0.093[e]	0.463	0.556	0.912	1.079	0.965
	SE	—	—	—	0.093	0.161	0.334	0.115	0.141	0.233
	%	—	—	—	33	100	100	100	100	100
Pacific shrew	$\bar{x}$	0.256	0.599	0.256	0.131[e]	0.094	0.077	—	—	—
	SE	0.033	0.158	0.070	0.046	0.027	0.043	—	—	—
	%	96	100	100	53	57	50	—	—	—
Trowbridge's shrew	$\bar{x}$	1.677	1.905	1.360	1.322	1.101	1.422	1.374	1.559	1.439
	SE	0.111	0.221	0.086	0.134	0.168	0.324	0.112	0.217	0.257
	%	100	100	100	100	100	100	100	100	100
Vagrant shrew	$\bar{x}$	0.009	0.052	0.005	0.010	0.020	0.030	0.046	0.061	0.082
	SE	0.004	0.029	0.005	0.006	0.009	0.015	0.026	0.035	0.065
	%	20	40	13	14	29	33	33	44	44
Shrew-mole	$\bar{x}$	0.101	0.080	0.051	0.068	0.013	0.025	0.151	0.112	0.072
	SE	0.025	0.030	0.019	0.020	0.007	0.013	0.038	0.045	0.035
	%	68	70	63	45	18	33	72	56	56
Coast mole	$\bar{x}$	0.061	0.039	0.044	0.022	0.056	0.019	0.013	0.020	0.021
	SE	0.013	0.012	0.022	0.008	0.015	0.013	0.006	0.011	0.016
	%	64	60	38	32	53	22	22	33	22
Northern flying squirrel	$\bar{x}$	0.032	0.018	0.017	0.017	0.011	0.021	0.036	0.026	0.015
	SE	0.013	0.010	0.012	0.010	0.011	0.014	0.013	0.014	0.011
	%	32	30	25	14	6	22	39	33	22
Deer mouse	$\bar{x}$	0.144	0.054	0.135	0.029	0.009	0.049	0.235	0.112	0.077
	SE	0.020	0.017	0.085	0.012	0.007	0.039	0.037	0.036	0.041
	%	96	60	75	27	12	22	83	78	33
Forest deer mouse	$\bar{x}$	—	—	—	—	—	—	0.308	0.251	0.082
	SE	—	—	—	—	—	—	0.056	0.059	0.040
	%	—	—	—	—	—	—	94	100	56
Red tree vole	$\bar{x}$	0.020	0.000	0.006	0.014	0.003	0.000	—	—	—
	SE	0.007	0.000	0.006	0.007	0.003	0.000	—	—	—
	%	32	0	13	18	6	0	—	—	—
Western red-backed vole	$\bar{x}$	0.607	0.830	0.562	0.313	0.221	0.285	—	—	—
	SE	0.072	0.150	0.118	0.069	0.055	0.123	—	—	—
	%	100	100	88	82	71	78	—	—	—
Southern red-backed vole	$\bar{x}$	—	—	—	—	—	—	1.166	0.845	0.529
	SE	—	—	—	—	—	—	0.205	0.162	0.114
	%	—	—	—	—	—	—	100	100	100
Creeping vole	$\bar{x}$	0.005	0.018	0.000	0.004	0.008	0.000	0.015	0.031	0.062
	SE	0.003	0.010	0.000	0.004	0.006	0.000	0.005	0.022	0.051
	%	12	30	0	5	12	0	33	22	33
Ermine	$\bar{x}$	0.007	0.000	0.011	0.000	0.012	0.000	0.020	0.021	0.005
	SE	0.003	0.000	0.011	0.000	0.008	0.000	0.008	0.011	0.005
	%	16	0	13	0	12	0	33	33	11

[a] Mean number per 100 trap-nights.

[b] Standard error of mean.

[c] Percentage of stands sampled in which species was found.

[d] Does not occur in this geographic area.

[e] Does not occur in all subprovinces in the Oregon Cascades. Number of stands sampled within the geographic range of montane shrews is 3 in old-growth, 3 in mature, and 3 in young stands; and for Pacific shrews is 19 in old-growth, 14 in mature, and 6 in young stands.

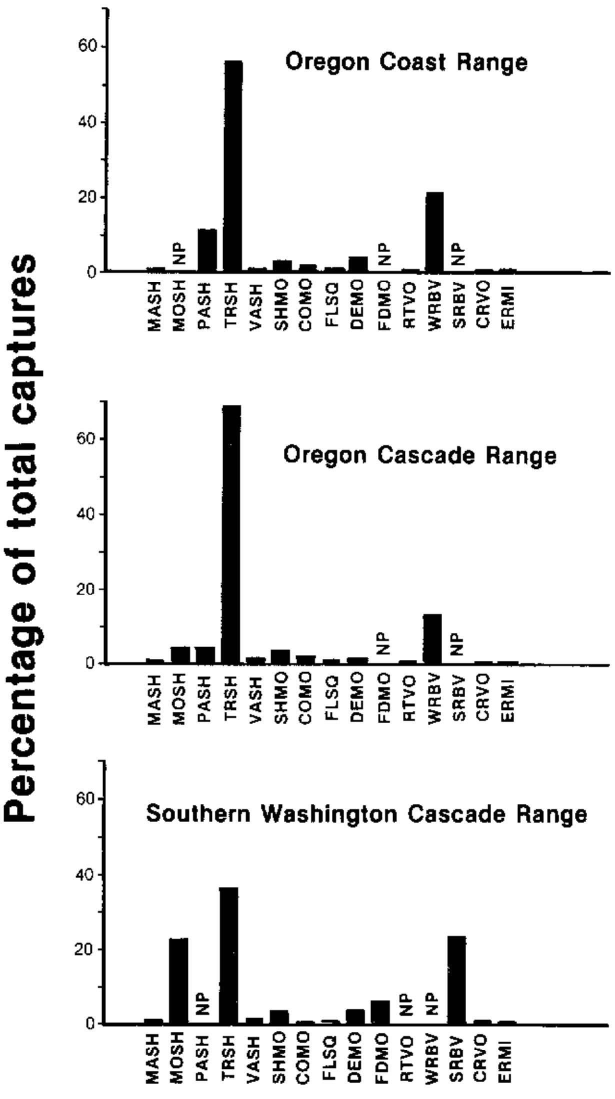

Figure 1—Histograms showing the percentage contribution of each species to total captures within each province. MASH, marsh shrew; MOSH, montane shrew; PASH, Pacific shrew; TRSH, Trowbridge's shrew; VASH, vagrant shrew; SHMO, shrew-mole; COMO, coast mole; FLSQ, northern flying squirrel; DEMO, deer mouse; FDMO, forest deer mouse; RTVO, red tree vole; WRBV, western red-backed vole; SRBV, southern red-backed vole; CRVO, creeping vole; ERMI, ermine; and NP, the species is not present in that province.

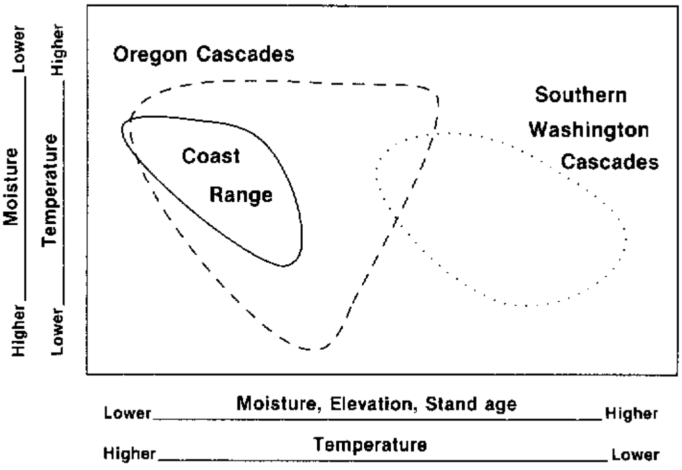

Figure 2—Ordination analysis of mean abundances of small mammals among provinces using data from all 15 species. All ordination points for each province are contained within the lines drawn; for clarity, individual points were omitted.

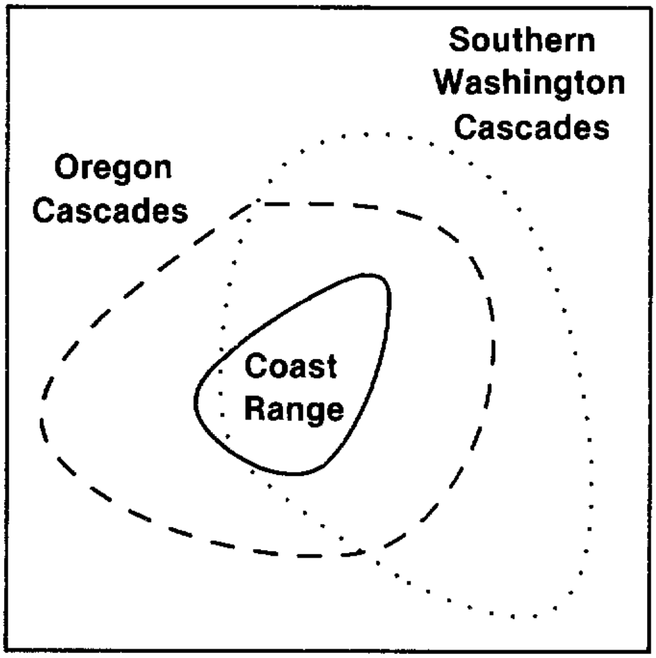

Figure 3—Ordination analysis of mean abundances of small mammals among provinces using only data from the nine species that occur in all three provinces. All ordination points for each province are contained within the lines drawn; for clarity, individual points were omitted. Environmental gradients associated with the X and Y axes are the same as for figure 2.

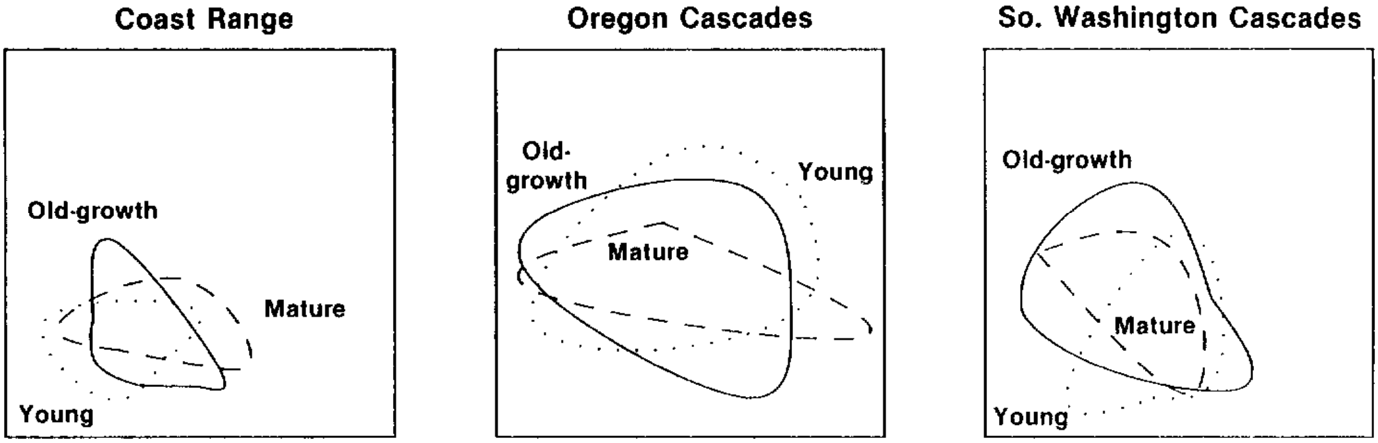

Figure 4—Ordination analysis of mean abundances for each province clustered by age-class. Scales used for both ordination axes are the same for each province. The number of species included in each analysis is as follows: Oregon Coast Range, 12; Oregon Cascades, 13; and southern Washington Cascades, 12. All ordination points for each age-class are contained within the lines drawn; for clarity, individual points were omitted.

Results of province-specific ordinations showed little variation among age-classes for any province (fig. 4). No distinct clusters resulted from these analyses, which indicates that the structure and composition of the forest-floor small mammal communities we studied is largely independent of stand age. As would be expected from these results, none of the ordination axes were correlated with stand age. Attempts to correlate ordination axes with major environmental gradients revealed no interpretable patterns in community structure or composition within provinces.

Species relationships—Two-way ANOVA (table 2) and log-linear analysis (table 3) revealed strong stand age-effects for only two species: the shrew-mole ($P = 0.070$) and red tree vole ($P = 0.067$). Both species reached highest abundances or occurred most frequently in old-growth stands (table 1). The shrew-mole showed a strong province-effect ($P = 0.005$), but the effect appeared to be largely due to varying abundance values for young and mature stands (table 1). For the red tree vole, no province-effect was found ($P = 0.191$), indicating that patterns of occurrence were consistent between provinces. Although a very strong age-effect was also found for the deer mouse ($P = 0.001$), a strong interaction-effect between stand age and province ($P = 0.058$) complicates the interpretation of these results. Furthermore, the deer mouse occupies virtually all available habitats in the Pacific Northwest (Dalquest 1948; Ingles 1965; West, this volume; and others); it is not primarily a forest-dwelling species. As such, it should not be considered a species of concern to forest managers. The strong province-effects found for most species indicate that patterns of abundance are extremely variable among the provinces studied.

Table 2—Results of two-way ANOVA on abundance data for stand age vs. province (analyses were conducted only on data from stands within the age gradient for species that occurred in more than one province and had >100 total captures)

	Source of variation		
Species	Stand age	Province	Interaction
Montane shrew	0.268[a]	0.001	0.468
Trowbridge's shrew	0.835	0.022	0.301
Pacific shrew	0.143	0.000	0.130
Shrew-mole	0.070	0.005	0.830
Deer mouse	0.001	0.000	0.058
Western red-backed vole	0.756	0.000	0.288

[a] P value.

Table 3—Results of log-linear analysis on presence-or-absence data for stand age vs. province (analyses were conducted only on data from stands within the age gradient for species that occurred in more than one province and had <100 total captures)

	Source of variation		
Species	Stand age[a]	Province	Interaction
Marsh shrew	0.691	0.047	0.117
Vagrant shrew	0.238	0.230	0.811
Coast mole	0.213	0.013	0.798
Northern flying squirrel	0.849	0.052	0.777
Red tree vole	0.067	0.191	0.652
Creeping vole	0.595	0.018	0.575
Ermine	0.691	0.015	0.367

[a] P values for stand age-effect are component chi-squares after province-effects have been removed from the analysis.

Table 4-Significant Spearman rank correlations *(P ≤* 0.1) between small mammal abundances and major physiographic and vegetative gradients (only species that occurred in more than one province and had >100 captures were included)

					Vegetative gradients’			
Species	Stand age	Elevation	Aspect	Slope	STDV	CWDB	TEMP	MOE
Montane shrew				+ 0.094[b]			- 0.000	
Trowbridge’s shrew		- 0.017						
Pacific shrew		- 0.000					+ 0.000	
Shrew-mole	+ 0.002			***- 0.067***	***+ 0.007***	+ 0.015		+ 0.001
Deer mouse	***+ 0.030***	- 0.001			+ 0.000			
Western red-backed vole		- 0.021						- 0.002

[a] STDV represents a stand-development gradient; CWDB, a coarse woody debris gradient; TEMP, a temperature gradient; and MOIS, a moisture gradient.
[b] ***P*** value.

Correlation analyses for the six most abundant species are shown in table 4. These analyses support the results of ANOVA for the shrew-mole and deer mouse; abundances for both species were significantly correlated with increasing stand age. The shrew-mole was also associated with old, moist, relatively flat stands with large amounts of coarse woody debris.

Discussion

The small mammal assemblages described here represent only subsets of the total small mammal communities in each stand. **As with any one technique for sampling an entire** vertebrate community, pitfall trapping is more effective at sampling certain species than others (Bury and Corn 1987, Williams and Braun 1983). Consequently, our results apply only to **the** subset of species that are well-sampled with pitfall traps; extrapolation of our results for species not included here is unwarranted.

Community relationships-Variation in the structure and composition of small mammal communities in unmanaged, closed-canopy, Douglas-fir forests is influenced more by geography and climate than by stand age. Ecologically interpretable patterns were detected only in the region-wide analyses (see figs. 2-4). Although differences between the Southern Washington Cascades province and the Oregon provinces largely disappeared when only the nine species common to all three provinces were included (figs. 2,3), several important patterns remain. In both analyses, small mammal communities were more variable in the Oregon Cascades than in the Coast Range; the Coast Range communities represent a subset of those occurring in the Oregon Cascades. Also, a subset of the stands in the Southern Washington Cascades province separate out ‘from both of the Oregon provinces along the first ordination axis.

The first ordination axis is correlated to many of the environmental and physiographic features that distinguish the Southern Washington Cascades province from the Oregon provinces: older stands, higher elevations, and cooler, wetter forest environments (Franklin and Dymess 1973; Spies and Franklin, this volume). The second axis, which separates the Coast Range stands from a portion of the Oregon Cascades stands, represents a gradient of increasingly warmer and drier conditions. Thus, although the Oregon Cascades and Coast Range provinces have very similar small mammal species composition (fig. l), only the warmest and driest stands in the Oregon Cascades contain mammal communities comparable to those occurring in the Coast Range. In terms of both environmental conditions (T. Spies, unpubl. data; Spies and Franklin, this volume) and the composition of small mammal communities, the Coast Range stands are most similar to the southernmost stands in the Oregon Cascades. Additionally, the oldest and wettest stands in the southern Washington Cascades contain small mammal communities **unlike any in the Oregon provinces.**

In contrast, we could detect little interpretable variation in community composition and structure among age-classes within each province (fig. 4). This finding agrees with the province-specific ordinations of understory floristics conducted by Spies and Franklin (this volume) and with the province-specific small mammal studies reported elsewhere in this volume by Corn and Bury, Gilbert and Allwine, and West. Within these physiographic provinces, unmanaged, closed-canopy Douglas-fir forests apparently support small mammal communities of similar composition and structure, regardless of stand age. Our results agree with the conclusion of Corn and Bury (this volume a) that different age-classes of unmanaged, closed-canopy forest appear to represent a single habitat type for most species. Although the communities as a whole are very similar among age-classes, several individual mammal species do exhibit a significant association with stand age in unmanaged Douglas-fir forests.

Species relationships-Only two forest-dwelling species, the shrew-mole and the red tree vole, were closely associated with older forests (tables 3,4). Abundance values for the shrew-mole and frequencies of occurrence for the red tree vole were highest in old growth in each of the provinces in which they occur (table 1).

The results of several other studies using similar sampling designs provide support for these results. Raphael (1984) reported a significant positive association with stand age for the shrew-mole in Douglas-fir forests in northern California, although results were based on only 1 year of data. A later report, based on 3 years of data (Raphael 1988c), showed that shrew-moles reached highest abundances in stands older than 50 years and were very low in abundance in clearcuts or in brush/sapling stands (0-20 yrs). In the Oregon Coast Range, Corn and Bury (this volume a) found shrew-moles to be 2.0 and 1.3 times more abundant in old-growth than in young and mature stands, respectively.

Other studies in Oregon and Washington reported here and elsewhere, however, have revealed no clear pattern of association between shrew-mole abundances and stand age. The shrew-mole was reported to be weakly associated with old-growth forests in the Oregon Cascades (Gilbert and Allwine, this volume a), or to show no age-effect at all (Corn and others 1988). Several studies in the southern Washington Cascades have found little evidence that shrew-moles are associated with stand age (Corn and others 1988; West, this volume). Results reported by Corn and others (1988), however, are based on only 1 year of data collected in 12 stands, and West (this volume) reported the combined results of pitfall trapping and snap-trapping as a means of evaluating responses of the broadest possible assemblage of small mammals. As mentioned previously, however, these techniques are not equally effective at sampling insectivores. Meaningful patterns in the data for this species may have been obscured by the addition of snap-trap results. Based only on pitfall data, results from the southern Washington Cascades also showed a trend of increasing abundance of shrew-moles with stand age (table 1). Consequently, increased sample sizes resulting from the pooling of data revealed a strong pattern of association that was not clearly evident at the province scale.

Shrew-mole abundances were also highly correlated with increasing stand age, stand development, stand moisture, amounts of coarse woody debris, and flatter slopes (table 4). As with any series of statistical tests, these results should be viewed with some caution. With 48 separate correlation analyses, we would expect five (10 percent) to be significant by chance alone at $P \leq 0.1$. Fifteen (31 percent) of the tests were significant, however, and all but two were significant at $P \leq 0.05$, indicating that most of these correlations reflect actual patterns of association.

Terry (1974, 1981) described preferred shrew-mole habitat in west-central Washington to consist of closed forests containing few herbs or shrubs to interfere with its burrowing activities, and a high organic matter content in the soil. She also reported that shrew-moles were significantly correlated with the cover of dead wood.

Tevis (1956) described shrew-moles as primarily inhabitants of unmanaged forests; he rarely found them in cutover areas. Results from other studies provide support for this assertion. In west-central Oregon, Hooven and Black (1976) found shrew-moles to be most abundant in unmanaged forest. Shrew-moles were less abundant in an area that had been cut and not burned, leaving coarse slash on the site, and were not present at all in an area that had been cut and broadcast-burned, leaving only fine litter. Dalquest and Orcutt (1942) reported shrew-moles to be very scarce in logged areas in western Washington. Corn and Bury (this volume a) sampled three clearcuts and adjacent old-growth stands in the Coast Range, but captured shrew-moles only in the old-growth stands. West (this volume) captured only two shrew-moles in eight clearcuts sampled in southern Washington.

These results indicate that shrew-moles are closely associated with moist old-growth forests containing relatively deep soils and many logs. However, shrew-moles appear to be responding primarily to microhabitats that occur most frequently in old-growth forests, since they are found in relatively high numbers in younger forests with appropriate forest-floor conditions (table 1). Catastrophic wildfires or clearcut logging practices that include removing most of the small and large woody debris, however, would be expected to eliminate shrew-moles from that site until canopy closure is reestablished and forest-floor conditions again become suitable.

Corn and Bury (this volume a) reported the red tree vole to be present significantly more often in old-growth forests than in either mature or young forests. Although they collected relatively few data, Gilbert and Allwine (this volume a) reported capturing red tree voles only in mature and old-growth forests in the Oregon Cascades. Similar studies conducted by other workers in the Oregon Cascades (Corn and Bury 1986, Corn and others 1988) indicated that red tree voles were associated with old-growth forests, but their data were insufficient to generate statistically significant results.

Our results (table 3) indicate that red tree voles are closely associated with old-growth forests in both the Coast and Cascade Ranges in Oregon. This species showed a significant age-effect, with nonsignificant province- or interaction-effects, indicating that patterns of variation were the same in both provinces. Although this species has been reported to nest in second-growth stands in the Coast Range (Maser 1966), recent work based on nest surveys in the Coast Range (Gillesberg and Carey, this volume) and in northern California (Meiselman and Doyle, in press) provide support for a close association with old-growth forests. Both studies also indicated a strong preference for very large (>l00 cm in d.b.h.) Douglas-fir trees for nesting and foraging. Bailey (1936) speculated that because red tree voles move about the forest largely within the canopy, they would be expected to occur only in areas of extensive, or recently isolated, forest.

Although the data are minimal, existing information indicates that red tree voles are largely restricted to old-growth forests; younger forests apparently do not provide suitable habitat for this species.

Management Implications

The similarity of species composition and structure of the small mammal communities in the Coast Range and Oregon Cascades provinces (figs. l-3) suggest that management strategies intended to provide for the habitat needs of small mammals in these provinces need not be designed specifically for either province. If management activities are conducted on a province, rather than a regional scale, stands in the southern Oregon Cascades should be considered to be more closely allied with stands in the Coast Range, rather than those in the central and northern Oregon Cascades. Very old (>500 yr) and wet stands in the southern Washington Cascades contain distinct small mammal communities that may require unique management approaches.

Shrew-moles are closely associated with moist, relatively flat, old-growth stands, Silvicultural prescriptions that remove the forest canopy, disturb the upper soil layers, and remove large amounts of coarse woody debris would be expected to eliminate this species from the site. Extensive clearcutting that creates large expanses of unsuitable habitat could result in local population extinctions. Shrew-moles could probably be maintained in managed landscapes, however, if old-growth areas are preserved as survival refugia to enable the species to recolonize younger forests when suitable microhabitats are reestablished.

Although relatively little is known about their specific habitat requirements, red tree voles apparently require old-growth stands containing large Douglas-fir trees for nesting and foraging. For this reason, and because they use the forest canopy as travel routes (but see Corn and Bury 1986), extensive loss or fragmentation of old-growth forests could eliminate this species from forested landscapes.

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Forest Age Associations of Bats in the Southern Washington Cascade and Oregon Coast Ranges[1]

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Abstract

We studied the use by bats of old-growth, mature, and young Douglas-fir stands in the southern Washington Cascade and Oregon Coast Ranges. Bat activity was measured with ultrasonic detectors. In Washington, the *Myotis* species were detected 2.7 to 5.7 times more frequently in old-growth than in younger stands. In Oregon, the *Myotis* species and the silver-haired bat were detected 2.5 to 9.8 times more frequently in old growth. Feeding rates were extremely low in the forest stands, and most bat activity was confined to a brief peak during the first 15 minutes of the evening, which suggests that bats used old-growth stands for roosting. Vegetation features, such as the abundance of damaged or diseased trees and snags, appeared to be important to bat populations, but correlations of bat activity with these features were weak. No reproductive females were captured at sites >300 m in elevation on the western slope of the Washington Cascades, but they were common to the east and south. Old-growth forests appear to be important habitats for bats in the Cascade and Coast Ranges, but management priority should be given to the latter region.

Introduction

The area west of the crest of the Cascade Range and extending from mid-Washington to southern Oregon supports 12 species of insectivorous bats (Barbour and Davis 1969, Thomas 1988). If biological importance is measured by taxonomic diversity, then the Chiroptera rank second only to the Rodentia in this region. Yet little is known about how bat species use the range of age and composition of forest patches in the Pacific Northwest. Because timber harvest and stand-management practices are rapidly restructuring the landscape, such knowledge is of increasing importance. Without it, no predictions can be made of the effect of vegetation changes on bat populations, and no management decisions can be reached to alleviate any negative effects.

In this paper, we describe how bat activity varied across a range of age- and moisture-classes of Douglas-fir forests in the southern Washington Cascade Range and Oregon Coast Range, bat use of forest stands in relation to the availability of food or roost resources, and specific vegetation characteristics that may influence the use of stands by bats.

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[1] Portions of this paper were drawn directly from "The distribution of bats in different ages of Douglas-fir forests" (Journal of Wildlife Management. 52: 619-624. 1988) with permission of The Wildlife Society.

Methods

Study Sites

In summer 1984, our field work was concentrated on the western slope of the southern Washington Cascades; in summer 1985, the study area was expanded to the Oregon Coast Range. In each region, 45 stands were selected; nine Douglas-fir stands in each of five stand types represented important age and soil-moisture conditions [old-growth (OG) wet, OG mesic, OG dry, mature mesic, and young mesic]. Descriptions of stand characteristics and selection criteria are presented elsewhere in this volume.

Capture and Sampling Methods

To provide an index of what bat species were common at the Washington and Oregon study sites, as well as to record their echolocation calls, we captured bats in 10-m mist nets set over streams and ponds during June, July, and August. No capture sites were inside any of the study plots, but most were within 20-km distance and 100-m elevation of the stands. We identified bats to sex, age, and species and recorded females as parous (pregnant, lactating, or postlactating) or nonparous (no evidence of reproduction in the current year). Bats were then released and their echolocation calls were recorded with a "divide-by-lo" ultrasonic detector (Miller and Andersen 1984) coupled with a Panasonic RQ-355 tape recorder to store the calls. See Fenton (1988) and Thomas and West (1989) for further details on the recording and analysis of bat echolocation calls. We also netted bats on the eastern slope of the Washington Cascades (near Goldendale) on 5 and 6 August 1985 to provide a contrast with captures on the western slope.

In 1984 and 1985, we used ultrasonic bat detectors to detect and identify bats flying in the study stands. The methods used to sample bat activity in the forest stands differed somewhat between the two years, however. In 1984, we sampled bat activity in 41 of the 45 stands by using hand-held, divide-by-10 detectors coupled with sound-activated Panasonic RQ-355 tape recorders to store echolocation calls. Each stand was visited three times between mid-July and early September. In each stand, we sampled bat activity by recording echolocation calls for 15 minutes at each of five stations spaced at 100-m intervals along a transect through the stand. We began sampling when the green of the vegetation could no longer be discerned (about 30 minutes after sunset, depending on canopy coverage). This light intensity corresponds roughly with the onset of bat activity.

In 1985, we used automated detector systems (Thomas and West 1989) to detect and record bat echolocation calls in Washington and Oregon. In each study stand, we set out two detector systems, one to sample the subcanopy (ground) stratum and the other to sample the mid- to upper-canopy stratum about 30 m above the ground. Both detectors were left in place to sample bat activity continuously over two consecutive nights. The automated detectors began sampling about 30 minutes after sunset and continued for 9 hours each night. The detectors entered time markers at intervals of 32 ± 1 minute after start-up. We sampled all 45 stands in each of the two regions in June and again in July and about half the stands in August. Many samples, however, were either lost because of equipment malfunctions or cut short when insect or other noise interference caused the tapes to run out.

We analyzed the tapes containing the echolocation calls in the laboratory by using a period meter to display the echolocation frequency and time characteristics on a calibrated Telequipment D32 oscilloscope (Fenton 1988, Simmons and others 1979, Thomas and West 1989). Recordings from known species, together with previously published information (Thomas and others 1987), provided the reference data base on frequency, time, and shape characteristics of echolocation calls. These call characteristics were used to identify the bats detected and recorded in the stands. For each stand, bat activity was measured as the number of bat passes recorded in a given sample period; a bat pass is defined as a sequence of two or more echolocation calls recorded as a bat flies by the detector microphone. For the 1985 data, we standardized bat activity as passes per 100 minutes of sampling. We recognized feeding efforts by the high repetition rate (about 100 pulses per second) "feeding buzz" associated with each prey capture attempt. We measured feeding rates as the percentage of passes that contained a feeding buzz. To provide a comparison with feeding activity within the stands, we also measured the feeding activity over three stream or pond sites in Washington (5 sample-hours) and over two pond sites in Oregon (3 hours).

Species Recognition and Groupings

Ultrasonic bat detectors permit species to be assigned to categories according to their echolocation characteristics. Some categories contain single species, but others contain assemblages of species with similar call structures (see Thomas and West 1989). In the Pacific Northwest, we were able to identify the following seven groups: Myotis A (the little brown and Yuma myotis, or both); Myotis B (the California, Keen's, long-eared, and western small-footed myotis, or combinations): the long-legged myotis; the silver-haired bat; the hoary bat; Townsend's big-eared bat; and the big brown bat or fringed myotis. Because the fringed myotis appeared to be uncommon in our study area, we will refer to the last group as the big brown bat only.

Prey Abundance

In August 1984, we used Bioquip ultraviolet light traps to provide an index of the relative abundance of nocturnal, phototactic, flying insects in the stands and over water. At each site, we set one trap 1.5 m above the ground and activated it for 90 minutes, starting at dusk. Any insects on or inside the trap at the end of this period were killed with a spray insecticide and sorted into three size-classes based on total body length (small: <5 mm, medium: 5-10 mm, large: >l0 mm). The sorted samples were dried to constant mass at 60 °C. We obtained samples from 44 stands (9 OG dry, 8 OG wet, 9 OG mesic, 9 mature, and 10 young) and three stream sites.

Vegetation Sampling

Vegetation in the study stands was sampled in a parallel study (see Spies and Franklin, this volume) that characterized the stands by age- and moisture-class and provided data on 35 variables (appendix table 5) that might affect bat abundance.

Statistical Analyses

Bat detection rates did not meet the assumptions required for parametric statistical tests. For all species, detection rates were highly leptokurtic (Kolmogorov-Smirnov test for normality; P < O.OOl), and the variances were unequal (F_{max} test; $P < 0.001$). Because no simple transformation rectified these problems, only Mann-Whitney and Kruskal-Wallis tests (Seigel 1956) were used to compare detection rates among stand types. Significance levels in all tests were a = 0.05.

To test for significant correlations between bat detection rates and vegetation characteristics, we replaced the classical discriminant function analysis, which is highly sensitive to departures from normality (Press and Wilson 1978), with the nonparametric stepwise logistic regression (SAS computer package; LOGIST, Frank E. Harrell, Jr., Duke University Medical Center, Durham, NC). The logistic regression model requires that the dependent variable (here, bat detection rates for each species) be categorical. Depending on the species, we regrouped detection rates into two or three equal categories. The number of independent variables that the logistic regression can test is approximated by n/10, where n is the sample size of the smallest category. In our data sets, categories contained 50 to 70 entries, which limited the number of variables that could be tested to five to seven. To circumvent this limitation, we ran logistic regressions seven times for each species, using five or six new variables each time (total of 35 variables) to identify potentially significant effects. We then combined the significant variables from the preliminary runs and reran the tests. Those variables that had significant correlation coefficients $(r_{ij.k})$ in the final grouping were considered to have a significant influence on bat detection rates.

Results

Sex and Age of Netted Bats

Important differences in the sex and age structure of the three bat communities were shown by netting over streams and ponds in the western and eastern Washington Cascades and in the Oregon Coast Range (table 1). In the western Washington Cascades, the netting effort yielded 191 individuals of 12 species; males constituted 88.8 percent of the 161 adults. None of the 18 adult females showed any signs of reproduction in the current year. Juveniles constituted 16 percent of the captures, but they were never captured before 21 August. In the Oregon Coast Range, males comprised 72 percent of the adults (N = 49). Unlike the western Washington Cascades, 91 percent of the adult females were pregnant, lactating, or postlactating-indicating that they would produce or had produced young in the current year. Juveniles constituted 20 percent of the catch and made their first appearance in late July. In the eastern Washington Cascades, only 56 percent of the adults caught were male (N = 61). The majority of adult females (82 percent) were either lactating or postlactating. Juveniles comprised 34 percent of the catch on 5 and 6 August. These data suggest that the females present in the western Washington Cascades were not reproductively active, but those present in the Oregon Coast Range and the eastern Washington Cascades were.

Bat Activity in 1984

In 1984, 153.8 hours of sampling yielded only 277 detections, of which only 151 were sufficiently clear to be identified to species group. The low number of identified detections rendered a rigorous analysis of stand use by the different bat groups impossible. We thus regrouped the bats into two categories based on their probable roosting locations: cavity-roosting bats (*Myotis* A, *Myotis* B, the long-legged myotis, and the big brown bat) and foliage-roosting bats (the silver-haired and hoary bats). We also grouped the three moisture-classes of old-growth stands. Detections of both cavity- and foliage-roosting bats were significantly different across the three stand age-classes (cavity: $X^2 = 7.9$, 2 df, $P < 0.05$; foliage: $X^2 = 6.1$, 2 df, $P < 0.05$). Young and mature stands did not differ significantly (cavity: X = 0.4, 1 df, $P > 0.05$; foliage: $X^2 = 1.2$, 1 df, $P > 0.05$), indicating a disproportionately high use of old-growth stands by both cavity- and foliage-roosting bats.

Table 1—Sex and age composition of bats netted in the Washington Cascades and the Oregon Coast Range in 1984 and 1985

	Males		Females		
Bat species	Adult	Juvenile	Nonparous	Parous	Juveniles
Western Washington Cascades:					
Big brown bat	3	0	0	0	0
California myotis	26	1	10	0	1
Western small-footed myotis	4	0	0	0	0
Long-eared myotis	5	0	0	0	0
Little brown myotis	92	27	7	0	1
Keen's myotis	2	0	0	0	0
Fringed myotis	1	0	0	0	0
Long-legged myotis	6	0	0	0	0
Yuma myotis	2	0	0	0	0
Silver-haired bat	0	0	1	0	0
Hoary bat	1	0	0	0	0
Townsend's big-eared bat	1	0	0	0	0
Eastern Washington Cascades:					
Big brown bat	2	3	0	2	3
Western small-footed myotis	5	4	1	7	1
Long-eared myotis	0	1	0	0	0
Little brown myotis	10	5	2	7	3
Hoary bat	5	0	0	0	0
Oregon Coast Range:					
Big brown bat	8	0	0	2	0
California myotis	4	0	1	6	2
Western small-footed myotis	1	0	0	0	0
Long-eared myotis	0	0	0	2	0
Fringed myotis	1	0	0	0	0
Long-legged myotis	3	0	0	0	0
Yuma myotis	8	5	0	0	3
Silver-haired bat	3	0	0	0	0

Bat Activity in 1985

In Washington, the total sample effort of 1599 hours yielded 3029 detections of all recognizable species (table 2). The genus *Myotis* (*Myotis* A, *Myotis* B, the long-legged myotis, and unidentified *Myotis* species) accounted for 94 percent of these detections and the silver-haired bat for 5 percent. Detections of the big brown, hoary, and Townsend's big-eared bats were too rare to be subjected to statistical analysis. In Oregon, the total sample effort of 1500 hours yielded 6211 bat passes for all species (table 2). The genus *Myotis* accounted for 79 percent of all detections, and the silver-haired and big brown bat accounted for 6 and 4 percent of all detections, respectively. Detections of the hoary bat and Townsend's big-eared bat (2 and 1 percent of detections, respectively) were too rare for statistical analysis.

The detection rates for the first and second nights of each 2-night sample in a given stand were significantly correlated in both Washington and Oregon (Spearman rank correlation, $P < 0.05$ for all species). These two consecutive nights clearly did not represent independent samples of bat activity, so the two nights were pooled and the mean detection rate (passes per 100 sample-minute) was calculated for each stand visit.

Sampling height (ground vs. canopy) had no clear effect on detection rates for either Washington or Oregon. In Washington, detections of only the silver-haired bat differed significantly between ground and canopy layers (Mann-Whitney U test; $P < 0.001$, canopy>ground). All other species were

Table 3—Detection of bats in old-growth, young, and mature stands in the southern Washington Cascades and the Oregon Coast Range

Species or group[a]	Old growth	Younger	Old growth/ younger[b]	P[c]
Washington				
Myotis A	1.23±0.27[d]	0.33±0.09	3.73	<0.005
Myotis B	2.41±1.75	0.91±0.25	2.65	<0.001
Long-legged myotis	0.34±0.08	0.06±0.02	5.67	<0.01
Silver-haired bat	0.27±0.11	0.15±0.64	—	Ns
Oregon				
Myotis A	6.29±1.98	2.48±1.13	2.54	<0.001
Myotis B	6.54±1.81	1.48±0.50	4.42	<0.001
Long-legged myotis	1.46±0.50	0.53±0.30	2.75	<0.01
Silver-haired bat	2.73±1.15	0.28±0.22	9.75	<0.005
Big brown bat	0.53±0.26	0.16±0.08	3.31	<0.05

[a] *Myotis* A includes the little brown and Yuma moytis. *Myotis* B includes the California, Keen's, long-eared, and western small-footed moytis.

[b] Detection rates are expressed as a ratio of old-growth to younger stands.

[c] Differences between detection rates in old-growth and younger stands were tested by a Mann-Whitney test and P is the resulting probability.

[d] Detection rate as bats per 100 sample minutes ($\bar{x}$ ± SE).

both Washington and Oregon. Feeding rates ranged from 1 percent for the silver-haired bat to 4 percent for *Myotis* A in Washington. In the Oregon Coast Range, feeding rates ranged from 1 percent (silver-haired bat) to 4 percent (*Myotis* A). Feeding rates were dramatically higher over water in the same areas, ranging from 27 percent (long-legged myotis) to 39 percent (*Myotis* A) in the Cascades and from 20 percent (long-legged myotis) to 38.5 percent (*Myotis* B) in the Coast Range. For all *Myotis* species, feeding rates averaged 10.3 (Cascades) and 10.1 times (Coast Range) higher over water than in the forest stands. Forest stands do not appear to be primary feeding sites for the *Myotis* species.

Some evidence was found of higher feeding activity in old-growth stands than young and mature stands. *Myotis* B in the southern Washington Cascades and *Myotis* A and *Myotis* B in the Oregon Coast Range all had higher feeding rates in old-growth stands (2 × 2 contingency tests, $P < 0.05$). Sample sizes were too small to permit testing for other species.

Detection Rates in Washington and Oregon

Detection rates in old-growth stands were significantly higher in Oregon than in Washington for all species except the long-legged myotis (table 3). The Oregon Coast Range had detection rates 2.2 times higher than the Washington Cascades when all detections were pooled. *Myotis* A, *Myotis* B, and the silver-haired bat were detected at rates 5.1, 2.7, and 10.1 times higher, respectively, in Oregon old-growth stands than in comparable stands in Washington.

Patterns of Prey Abundance

Insect biomass did not differ significantly among stand types for any insect size-class. Stream samples had significantly more small and medium-sized insects than did forest samples (small: $F = 1539.8$, $P < 0.001$; medium: $F = 108.7$, $P < 0.001$), but the mass of large insects did not differ between the two ($F = 3.1$, $P > 0.05$). The approximately 166-fold increase in small and 10-fold increase in medium-sized insects over water as compared with forest stands resulted in a major shift in the biomass and size distribution of insects. In forests, large insects accounted for 65 percent of the total insect biomass, and small insects represented only 5 percent. The pattern was reversed over water: large-bodied insects accounted for only 11 percent of the insect mass, and small-bodied insects accounted for 64 percent.

Vegetative Variables

The logistic regression models showed a confusing pattern of significant relations (table 4). In both Washington and Oregon, seven variables were significantly correlated with the detection rates for one or more bat species; however, they explained only a small proportion of the total variance in bat activity among stands. In Washington, only 6 to 8 percent and in Oregon only 4 to 17 percent of the variance was explained by variables used in the regression models. Also, these variables did not explain the significant association of various bat species with the old-growth age-class. Detection rates for the long-legged myotis were significantly higher in old-growth stands in Washington, but they were not correlated with any variables in the regression models. Stand age was not a significant variable for any bat species in Washington and was only significant for *Myotis* B in Oregon. Clearly, the significant regression variables do not adequately explain the old-growth associations observed for bats, nor do they have a strong predictive value for use in further studies.

Discussion

Detection rates cannot be directly converted into density estimates because individual bats may be detected more than once as they fly near the microphone and because resident and transient individuals cannot be differentiated. Both factors negate any simple one-to-one correlation between detection rates and quantitative measures of bat population density (Thomas and LaVal 1988). Because any biases are likely to be constant across sample sites, however, detection rates can provide a relative index of bat abundance in different habitats or stand types. With the exception of the silver-haired bat in Washington, all the common bat species in the southern Washington Cascades and the Oregon Coast

Table 4—Vegetative variables that were significantly associated with bat activity in the southern Washington Cascades and the Oregon Coast Range

Variable	*Myotis* A[a]	*Myotis* B[a]	Long-legged myotis	Silver-haired bat
Washington				
Broken tops	0.15**[b]	Ns	Ns	Ns
Frost scars	−0.16**	Ns	Ns	Ns
Conks	0.13*	Ns	Ns	Ns
Snag 3	Ns	−0.26***	Ns	Ns
Snag 4	Ns	0.10**	Ns	Ns
Snag DC1	Ns	0.14**	Ns	Ns
Snag Vol1	0.09*	Ns	Ns	Ns
Overall R^2	0.06	Ns	0.08	Ns
Oregon				
Snag D.B.H.	0.20***	Ns	0.15*	Ns
Snag DC3	Ns	0.15*	Ns	Ns
Snag Vol	Ns	0.20***	Ns	Ns
Snag Vol4	Ns	−0.09*	Ns	Ns
Age	Ns	0.24***	Ns	Ns
Elevation	0.27***	Ns	0.20**	Ns
Dens 50	Ns	Ns	Ns	−0.21**
Overall R^2	0.12	0.09	0.17	0.04

[a] *Myotis* A includes the little brown and Yuma myotis. *Myotis* B includes the California, Keen's, long-eared, and western small-footed myotis.

[b] Values are the partial regression coefficients ($r_{ij.k}$) and *, **, and *** indicate significance levels of 0.05, 0.01, and 0.001, respectively. Ns indicates not significant.

Ranges have dramatically higher detection rates in old-growth than in mature or young stands. Thus, this study indicates that bats are 2.5 to 9.8 times more abundant in old-growth than in young or mature stands in both study regions. Clearly, old-growth stands provide important habitats for bats in the Pacific Northwest.

Forest stands can provide bats two critical resources: food and day roosts. The short duration of activity in early evening and the low feeding rates during this time suggest that forest stands are not important feeding sites for bats. Early evening peaks in activity over ponds and streams and in adjacent riparian habitat have been described for several species, including the California, long-eared, little brown, Keen's, long-legged, and Yuma myotis and big brown and silver-haired bats (Anthony and Kunz 1977, Bell 1980, Cross 1976, Kunz 1973, O'Farrell and Bradley 1970). These early activity peaks over water generally last 45 to 180 minutes, much longer than the peaks observed in the forest stands (about 15 minutes). The length of activity peaks over water appears to be determined by the insect capture rate that bats achieve and the amount of food they require. Pregnant and lactating little brown myotis foraging over water capture only 19 percent and 28 percent of their first meal in 20 minutes despite capture rates as high as five to eight insects per minute (Anthony and Kunz 1977; Gould 1955, 1959). Similarly, wild European pipistrelles and captive western small-footed myotis achieve high capture rates when feeding on insect swarms (10 insects per minute), but have feeding periods lasting ≥45 minutes (Griffin and others 1960, Racey and Swift 1985). Because feeding rates decline with decreasing insect abundance (Racey and Swift 1985), habitats with lower insect abundance than aquatic sites have should show prolonged activity peaks, which was clearly not true in forest stands. Although insects in the size range taken by *Myotis* species (<10 mm; Anthony and Kunz 1977, Belwood and Fenton 1976) were only 1 to 10 percent as abundant as over water, the activity peak in forests was brief, lasting only about 15 minutes. Thus, this peak is unlikely to correspond with any significant feeding activity, but rather originated from bats commuting from day roosts to feeding sites located outside the stands and over water. That feeding rates of the *Myotis* species were more than 10 times higher over ponds and streams in Washington and Oregon lends further support to this conclusion.

Our data suggested that the activity of the *Myotis* species and the big brown and silver-haired bats (Oregon) was skewed towards old-growth forests because they offer an increased variety or abundance of day roosts. Although the highest densities of snags occur in young and mature forests, these snags are typically dominated by small-diameter Douglas-fir with low longevity (Cline and others 1980). The greatest species diversity, largest diameters, the most advanced decay-classes, and the greatest snag longevity all occur in old-growth compared with younger forests. These features likely provide a greater abundance and diversity of bat roosts in old growth than in younger forests.

Although bat activity was greater in old-growth stands in both Washington and Oregon, important differences were found between the two regions. Detection rates were significantly lower in the southern Washington Cascades for all species except the long-legged myotis, and no evidence of reproduction was found in this region. In the western Washington Cascades, few bats were female (11 percent), none showed any evidence of reproductive activity, and juveniles were only captured after the dissolution of maternity colonies in late August (Humphrey and Cope 1976). This contrasted sharply with the Oregon Coast Range and the eastern Washington Cascades, where pregnant and lactating females were abundant and juveniles constituted a higher proportion of the captures during the late maternity period. These data suggest that reproductive females were absent from the 300- to 600-m elevation zone on the western slope of the Cascades, but that they were present at similar elevations to the east and south. Similar skews towards nonreproductive females and males at high elevations and towards reproductive females at lower elevations have been reported in the Cascades and the Rocky Mountains (Fenton and others 1980, Perkins 1983).

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Variable	*Myotis* A”	**Myotis** B[a]	Long-legged myotis	Silver-haired bat
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Frost scars	-0.16**	**Ns**	Ns	Ns
conks	0.13*	**Ns**	Ns	Ns
Snag 3	Ns	-0.26***	Ns	Ns
Snag 4	Ns	0.10**	Ns	Ns
Snag DC1	Ns	0.14**	Ns	Ns
Snag Voll	0.09*	**Ns**	Ns	Ns
Overall R^2	0.06	**Ns**	0.08	Ns
Oregon				
Snag D.B.H.	0.20***	Ns	0.15*	Ns
Snag DC3	Ns	0.15*	Ns	Ns
Snag Vol	Ns	0.20***	Ns	Ns
Snag Vo14	Ns	-0.09*	Ns	Ns
Age	Ns	0.24***	Ns	Ns
Elevation	0.27***	Ns	0.20**	Ns
Dens 50	Ns	Ns	Ns	-0.21**
overall R^2	0.12	0.09	0.17	0.04

[a] Myotis A includes the little brown and Yuma myotis. Myotis B includes the California, Keen’s, long-eared, and western small-footed myotis.

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Differences in the incidence of reproductive females may be related to climate. Forests in the western Washington Cascades receive higher rainfall, more days of rain, and are more frequently shrouded by low clouds during the pregnancy and lactation periods (April to July) than sites to the east, to the south, and at lower elevations (NOAA 1960-85). These factors may cause more frequent interruptions in foraging activities and make timing of food availability less predictable. Racey (1973) and Racey and Swift (1981) showed that pregnant females that could not forage daily were incapable of sustaining the energy demands of homeothermy. Torpor in females delayed parturition both in the laboratory and under natural conditions (Racey 1973, Racey and Swift 1981). Low clouds and frequent rain in the western Washington Cascades may make timing of insect availability too patchy for pregnant or lactating females to remain homeothermic. Females may not be able to complete the reproductive season and prehibernation fattening in the limited time available during summer. If nonreproductive females and males are able to resort to torpor without a reproductive penalty, they would be less sensitive to temporal patchiness in prey availability and so could make use of the more adverse, high-rainfall sites (Kurta and Kunz 1988).

Vegetative Relationships

The correlations of bat activity to vegetative features indicate that the abundance of damaged or diseased trees or snag size and decay states were associated with higher bat activity. These variables explained such a small proportion of the total variance in bat activity that they did not identify specific vegetation features that affect bat abundance. These weak correlations are probably a result of the study design; vegetative characteristics were measured to describe differences in stand types rather than to quantify roosting sites for bats. Until more precise data on the roosting requirements of bats in the Pacific Northwest become available, the only way to manage for bat populations will be to retain undisturbed stands of old-growth forest. The minimum size of these stands can only be determined by the size in which the full range of snag sizes and decay-classes are represented. If the abundance and diversity of snags and diseased or damaged trees influences bat abundance in stands, then several avenues for future research are apparent. Managed and thinned stands where damaged trees and snags have been removed should be essentially devoid of bats and can provide a valuable contrast with fire-generated young and mature stands. Young stands produced from old-growth stands damaged by canopy fires should retain the snag characteristics of the original stand for about 41 years (Cline and others 1980), and they may have an increased diversity of roost sites because these stands have more standing dead trees. These stands should have bat activity equivalent to or higher than intact old-growth stands. In contrast, young stands produced by logging operations that remove the large snags should have low bat activity. Because most of the young stands studied here were not a product of logging, this contrast was not tested. Coupled with these possible contrasts based on ultrasonic detection, locating and characterizing suitable roosts would seem imperative.

This study shows that old-growth forests provide important habitats to bats in both the Cascade and Coast Ranges. We predict that forestry practices that remove old growth and thus reduce the overall age structure of forests without retaining snags and damaged trees will significantly affect bat populations. The evidence that reproductive females are less abundant on or absent from the western Washington Cascades suggests that protection of old growth in the Coast Ranges and mountains to the south should receive highest priority.

Acknowledgments

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This paper is contribution 117 of the Wildlife Habitat Relationships in Western Washington and Oregon Research Project, Pacific Northwest Research Station, USDA Forest Service. n

Appendix

Table 5-Vegetation, elevation, and topography variables used in logistic regressions

Variable	Description
Broken tops	Live trees with broken tops
Dead tops	Live trees with dead tops
AnScar	Trees with animal-induced scars
LiScar	Trees with lightning scars
Frost Scar	Trees with frost scars
ExCav	Trees or snags with excavated cavities
NatCav	Trees or snags with natural cavities
conks	Trees with conks of primary pathogens
Snag3[a]	Snags: height = 1.5-5.0 m; d.b.h. = l0-50 cm
Snag4	Snags: height >15 m; d.b.h. = l0-50 cm
Snag5	Snags: height = 5-15 m; d.b.h. >50 cm
Snag6	Snags: height >15 m; d.b.h. >50 cm
SnagDCl-5[b]	Snags: decay classes 1 to 5
SnagD.B.H.	Snags: mean d.b.h.
SnagMass	Snags: total biomass
SnagVol	Snags: total volume
SnagVol1-5	Snags: volumes in decay classes 1 to 5
Age	Chronological age in years
Topo	Topography: crest; upper, middle, lower slope, depression
Elevation	Mean stand elevation
Species	Total number of tree species
TotDens	Total tree density
D.B.H.	Mean tree d.b.h.
D.B.H.75	D.b.h. of the 75 percent quantile
Dens50	Density of trees with d.b.h. = 50-99 cm
Dens100	Density of trees with d.b.h. = 100-149 cm
Dens150	Density of trees with d.b.h. >149 cm

[a] Snag number designators conform with those used in vegetation studies (this volume).

[b] Snag decay-classes follow those in Clime and others (1980).

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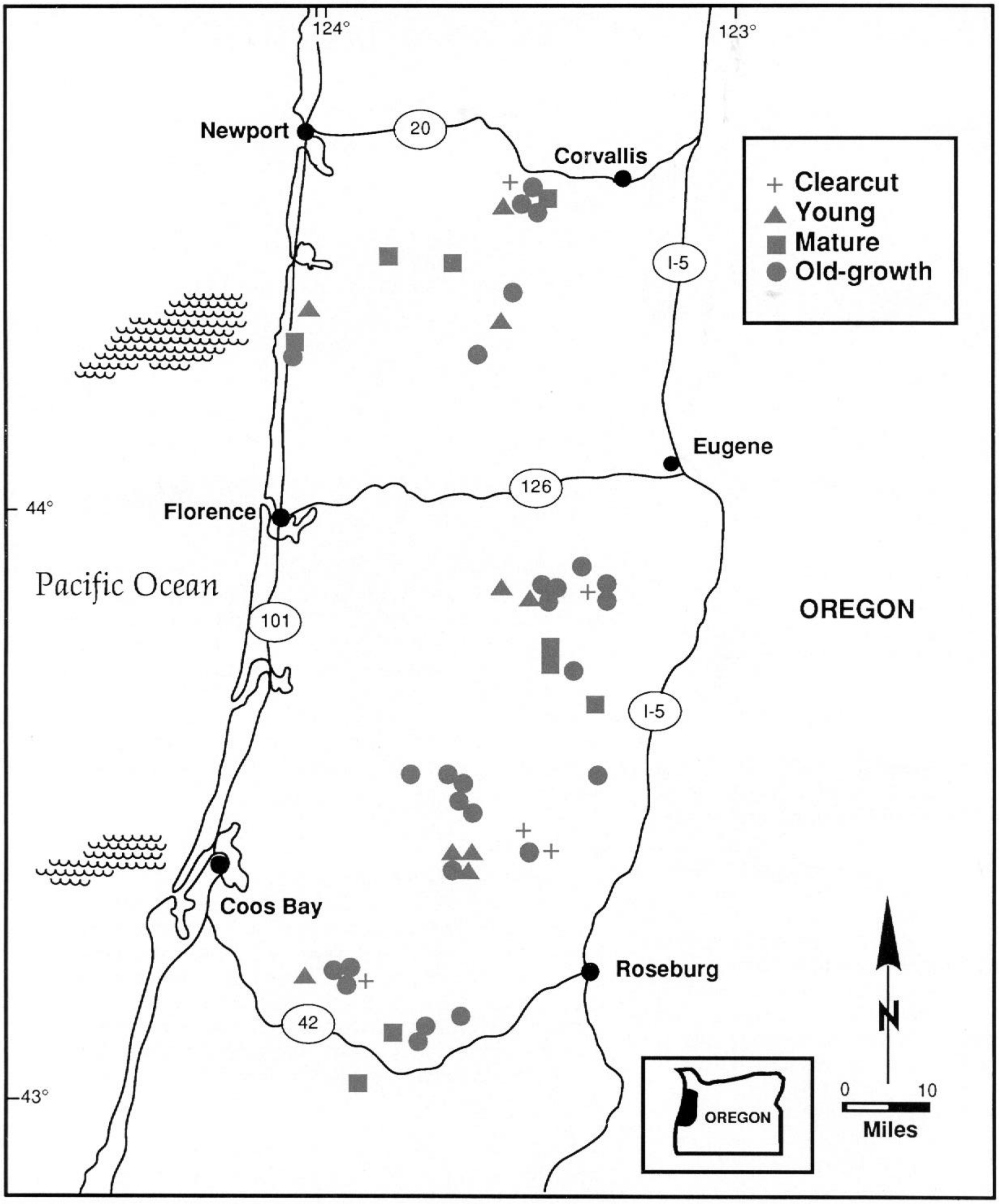
Continue

Part 6

Amphibians of Oregon and Washington



Location of study sites.

Terrestrial Amphibian Communities in the Oregon Coast Range

Paul Stephen Corn and R. Bruce Bury

Authors

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Abstract

We used pitfall trapping and surveys of down wood to sample amphibian populations on clearcuts, young, mature, and old-growth forests on Forest Service or Bureau of Land Management land in the Coast Range of Oregon in 1984 and 1985. We attempted to identify species or unique groups of species associated with old-growth forests and structural components of the habitat associated with abundance of amphibians. Pitfall traps captured 10 species and 1878 individual amphibians in 45 forested stands and three clearcuts in 80 nights in 1984 and 1985. Western redback salamanders, ensatinas, and roughskin newts were the species most commonly captured by pitfall traps in both forested stands and clearcuts. Significantly more Olympic salamanders were captured in old-growth compared to mature and young forest stands. On a moisture gradient in old growth, tailed frogs were more abundant in wet stands. Western redback salamanders were most abundant on steep, rocky slopes, but few strong correlations were found between amphibian abundance and habitat features characteristic of old-growth forests. We also sampled 536 logs in 18 stands and captured 328 amphibians (seven species). Clouded salamanders (166 individuals, compared to only 13 caught in pitfalls), and ensatinas (111 captures) were the most common salamanders found associated with down wood. Habitat preferences differed markedly. Clouded salamanders preferred large Douglas-fir logs with bark still attached, but ensatinas were found more often in well-decayed logs. Based on amounts of down wood available in Douglas-fir forests, we predict densities of clouded salamanders to be highly correlated with stand age, and we expect this species to be rare in intensively managed forests where down wood is reduced.

Introduction

Amphibians and reptiles are the subjects of less than 10 percent of recent studies in ecology and wildlife ecology (Gibbons 1988), yet they are numerically dominant in many habitats and supply an important component of the energy present in terrestrial and aquatic ecosystems. Hairston (1987) estimated that energy present in salamanders in southern Appalachian forests exceeds that of all other vertebrate predators combined. Terrestrial salamanders typically have stable populations that are suitable for assessing impacts of disturbance (Hairston 1987).

Although the number of species of amphibians and reptiles in Douglas-fir forests of the Pacific Northwest is low relative to mammals and birds (Harris and Maser 1984), the herpetofauna are a distinctive and important component of the vertebrate fauna (Bury 1988). Several species of amphibians that occur in the Coast Range in Oregon, including the tailed frog, Olympic salamander, Pacific giant salamander, clouded salamander, Dunn's salamander, western redback salamander, and roughskin newt, are endemic to the Pacific Northwest (Nussbaum and others 1983). Species adapted to a specific habitat (Douglas-fir forests) might be expected to be sensitive to major disturbance of that habitat (logging). Studies in northern California found differences among seral stages of Douglas-fir and redwood forests in composition and abundance of the herpetofauna (Bury 1983; Raphael 1984, 1988c; Raphael and Barrett 1984).

The Old-Growth Program was designed, in part, to gather information on abundance of forest. amphibians and their habitat preferences in Oregon, Washington, and California (Ruggiero and Carey 1984). Pilot studies were conducted in the Cascade Range in 1983 (Bury and Corn 1988a), and in 1984, vertebrate community studies were extended to the Coast Range in Oregon. We used pitfall traps and hand collecting (Bury and Corn 1987, Bury and Raphael 1983, Campbell and Christman 1982) to sample the terrestrial herpetofauna.

Pitfall trapping provides good estimates of relative abundance of many amphibian species, but it severely undersamples salamanders that are closely associated with down wood (Bury and Corn 1988a). Time-constrained collecting is effective for capturing individuals of these species, but the technique produces potentially biased estimates of relative abundance (Bury and Corn 1988a; Corn and Bury 1990). To estimate the relative abundance of salamanders associated with down wood, we searched uniform numbers of down logs.

In this paper, we report the results of sampling amphibians over a large area of the Coast Range in 1984 and 1985. Our objectives were to:

- Identify amphibians associated with old growth by determining the relative abundance of amphibians in young, mature, and old-growth forests and across a moisture gradient in old growth;
- Compare the abundance of amphibians to major physiographic and vegetation gradients, and to identify important habitat features that could be incorporated into managed forests to maintain the diversity of amphibians;
- Contrast changes in abundance of amphibians between old-growth forests and clearcuts as a first step in comparing managed and natural forests; and
- Estimate abundance of salamanders associated with down wood, and describe differences among species in the use of this microhabitat.

Methods

Study Areas

We studied 45 closed-canopy forest stands and 5 recently clearcut stands in the Coast Range of Oregon (see frontispiece). Most stands were in the interior or on the eastern flank (valley margin) of the Coast Range. Most of the stands south of Eugene were on land managed by the Bureau of Land Management (BLM) Eugene, Roseburg, and Coos Bay Districts. Stands north of Eugene were on BLM (Salem District) land, the Siuslaw National Forest (including Cape Perpetua and Drift Creek Wilderness Areas), or land managed by the city of Corvallis (Marys Peak).

Stand Selection and Classification

Stands initially were selected to conform to a chronosequence of four categories beginning with five clearcuts (<10 years old), eight closed-canopy young stands (40 to 75 years), 10 mature stands (80 to 120 years), and 27 old-growth stands (150 to 525 years). Most forest stands were composed of naturally regenerated forests. Ages of stands were estimated a *posteriori* by increment coring or by examining stumps in adjacent clearcuts and roadsides (Spies and others 1988).

A moisture gradient (wet, moderate, and dry) was examined for old-growth stands. The moisture classification was based on a multivariate ordination of understory vegetation (Spies and Franklin, this volume).

Pitfall Trapping

We installed 36 pitfall traps (6.41 volume, 15 m apart in a 6 x 6 grid) in each forest stand and three clearcuts in summer 1984. Details of trap construction and installation are in Bury and Corn (1987) and Corn and Bury (1990, this volume a). Before and after each trapping season, traps were closed with a tight-fitting plastic lid. Each grid was placed at least 100 m from the edge of the stand. This distance was a compromise between the need to avoid edge effects and the need for a field crew to be able to check the grids in five to seven stands in one day.

We opened traps during the first week in October and trapped continuously for 50 days in 1984 and for 30 days in 1985. The same grids were used in both years. No water was put in the traps because amphibians that drowned did not preserve well. In practice, most traps accumulated some water and some amphibians drowned. Traps were checked about once a week; nine times in 1984 and five times in 1985. Any water that had accumulated was bailed out.

Amphibians taken from traps were killed in dilute chloretone (a saturated solution of hydrous chlorobutanol in 95-percent ethanol, diluted to about a 5-percent solution in water). After identifications were verified, we determined the sex and measured snout-vent length (SVL), total length, and mass. Amphibians were fixed at least 24 hours in 10 percent formalin and then rinsed in water and preserved permanently in 50 percent isopropyl alcohol. Amphibians that had drowned were identified. sexed, and measured, and stomachs and eggs (if any) were dissected and preserved. Specimens were deposited in the National Museum of Natural History, Washington, DC.

Vegetation Sampling

We sampled vegetation at nine points within the pitfall grid, with the center of each sampling plot equidistant from four pitfall traps (Corn and Bury, this volume a). We estimated physiographic, coarse woody debris, live tree, and ground cover variables (see appendix in Corn and Bury this volume a) in two nested circles of 5.6-m radius (100 m) and 15-m radius (707 m^2). Percentage cover was estimated by eye. Count variables were converted to density (number per hectare).

Surveys of Down Wood

We conducted surveys of down wood in 18 stands (nine old-growth, three mature, three young, and three clearcuts) between 19 March and 10 April 1985. We searched 30 logs in each stand (26 in one stand) with minimum diameter of 10 cm and minimum length of 1 m. Down wood was classified on a five-point scale (Franklin and others 1981, Maser and others 1979): (1) intact, recently downed trees; (2) intact wood with loose bark; (3) bark beginning to slough off and decayed sapwood; (4) loss of most bark and decayed heartwood; and (5) hummocks of wood chunks and organic material. In each stand, we sampled equal numbers of logs in three broader categories: 10 class 1 and 2 logs, 10 class 3 logs, and 10 class 4 and 5 logs. We recorded the slope, aspect (to the nearest 459, tree species, length, diameter, and decay-class of each log sampled. We then searched for amphibians under the bark, in the wood, under the log, and under bark on the ground adjacent to the log for a maximum of 20 staff minutes (a staff minute is one person searching for 1 minute). We recorded the length and diameter of the portion of the log that was searched. For every amphibian encountered, we determined the sex, measured SVL, and recorded where found (such as under bark or in log) and the depth inside the log. A series of voucher specimens was preserved from each stand, but most amphibians were released at the site of capture.

Logs were sampled as the crew traced an irregular path through a portion of the stand away from the pitfall grid. Logs were generally sampled as encountered, except that we attempted to maintain about equal numbers in each decay category as the survey progressed. Therefore, logs in abundant decay categories were occasionally passed in the search for the next log in a less abundant category.

Statistical Analyses

Captures in pitfall traps-All statistical analyses were done on a microcomputer using SYSTAT (Wilkinson 1988). Analysis of the chronosequence was originally intended to compare young, mature, and old-growth stands with similar moisture conditions, and so was to exclude wet and dry old-growth stands (Carey and Spies, this volume). Because mature and young stands had much greater variation on the moisture gradient than expected (Spies and Franklin, this volume), however, only those old-growth stands that were outliers on the moisture gradient were excluded. In the Coast Range, all but two old-growth stands were retained in the chronosequence analyses. Analysis of the moisture gradient was restricted to old-growth stands.

We measured abundance as the number captured per 100 trap-nights. Pitfall traps may capture large numbers of young-of-the-year amphibians that are dispersing from breeding ponds or streams (Bury and Corn 1987). To reduce the bias introduced by the proximity of breeding habitats to grids, the analyses of abundance used only adult tailed frogs ($\geq$ 35 mm SVL), red-legged frogs (235 mm SVL), northwestern salamanders (270 mm SVL), and roughskin newts ($\geq$ 40 mm SVL). Analysis of the abundance of individual species depended on numbers captured. “Common” species were species with more than 50 total captures, and differences on the age and moisture gradients were analyzed by analysis of variance (ANOVA) of ($\log_e$ abundance + 1). “Rare” species had fewer than 50 and greater than 10 total captures. Because of the low sample sizes, we used all captures of these species in both years. We put “common” and “rare” in quotes, because captures in pitfalls may not reflect the actual abundance of these species. For example, clouded salamanders are rarely captured by pitfalls but commonly are taken in time-constrained surveys (Bury and Corn 1988a). Differences in numbers captured among age- and moisture-classes were tested using the G-test (log likelihood ratio) for goodness of fit (Sokal and Rohlf 1981).

Physiographic and vegetation variables-variables measuring percentage cover were arcsin-transformed (Sokal and Rohlf 1981) before analysis. Count variables had large variances which were log-transformed. **We** computed Pearson product-moment correlation coefficients between continuous physiographic and vegetation variables and abundance of common species. Associations between abundance and categorical physiographic variables were tested with ANOVA. For **rare** species, we compared mean values of physiographic and vegetation variables between stands where each species was present or absent, or we computed log likelihood ratios based on the presence or absence of amphibians and categorical physiographic variables.

We performed a principal components analysis using a subset of eight vegetation variables (Corn and Bury, this volume a) representing habitat features that have been used in ecological definitions of old-growth Douglas-fir forests (Franklin and Spies 1984, Morrison 1988, Spies and Franklin 1988). Three factors accounted **for** 67.6 percent of the variance. Factor 1 (33.1 percent of variance) describes an age gradient, factor 2 (19.3 percent) was associated with down wood, and factor 3 (15.2 percent) was associated with shrub cover (Corn and Bury, this volume a). We tested the abundance of common species against these three factors using multiple regression, and we tested the three factors against the presence or absence of rare species using multivariate analysis of variance.

Salamanders in down wood-The density in down wood of each species of salamander (number per cubic meter) was calculated as the number caught in each log divided by the volume of wood sampled in each log. Mean densities in down wood in each stand were calculated for each of the three decay-categories (decay-classes 1 and 2, class 3, classes 4 and 5). We used a nested ANOVA (stands within forest age-classes) to test whether density (log transformed) in down wood of any species varied among decay-categories or age-classes (old-growth, mature, and young).

We **compared** slope and log dimensions for sites where each species was captured versus sites where each species was absent with one-way ANOVA. For the categorical variables aspect (four categories; N and NE, E and SE, S and SW, W and NW), tree species (Douglas-fir versus other), decay-category, and position (under bark, in log, or on ground; either under log or under bark), we compared total captures of each species among categories using log likelihood ratios.

We calculated predicted densities of plethodontid salamanders in 45 forest stands from the following formula:

$$D = \sum_{i=1}^{3} (d_i * V_i)$$

where D = number of salamanders per hectare, d_i = density in down wood in decay-category i, and V_i = m^3 of down wood per hectare in category i (data provided by T. Spies). If d varied among age-classes, then D was calculated using the mean density in down wood for each age-class. Predicted densities are minimum estimates, because we did not investigate salamander populations in other microhabitats.

Results

Pitfall Trapping

Abundance of amphibians--In 1984 and 1985 combined, we captured 1797 individuals and 10 species of amphibians in 45 forest stands (table 1), and an additional 81 individuals in three clearcuts. Only a few young-of-the-year northwestern salamanders, roughskin newts, and red-legged frogs were captured, but 28 juvenile tailed frogs (30 percent of captures) were excluded from further analyses. Combined abundance of amphibians was higher in 1985 (1.767 per 100 trap-nights) than in 1984 (1.158 per 100 trap-nights; Wilcoxon signed-ranks test, $P < 0.001$), but among individual species, only ensatina was captured significantly more often in 1985 (0.728 per 100 trap-nights) than in 1984 (0.348 per 100 trap-nights; $P < 0.001$). The patterns of combined abundance and abundance of ensatina across the age and moisture gradients were similar in both years, and because abundance did not differ between years for any other species, all further analyses used the combined abundance (captures in 1984 + 1985 with 80 nights of trapping [2880 trap-nights] per grid).

Five species (Pacific giant salamanders, ensatinas, western redback salamanders, roughskin newts, and tailed frogs) were considered common, with 61 to 737 captures. Four other species, including northwestern salamanders, Olympic salamanders, clouded salamanders, and Dunn's salamanders had 13 to 45 captures and were considered rare. Fewer than 10 adult red-legged frogs were captured, and the abundance of this species was not analyzed.

Table 1-Total numbers of amphibians captured by pitfall grids in 45 forest stands in the Oregon Coast Range in 1984 and 1985 (grids were open for 50 days in 1984 and 30 days in 1985)

Species	1984	1985	Total
Salamanders”			
Northwestern salamander	12 (15)	6 (7)	18 (22)
Pacific giant salamander	42	19	
Olympic salamander	22	8	30
Clouded salamander	6	7	13
Ensatina	282	354	636
Dunn's salamander	21	24	45
Western redback salamander	412	325	737
Unidentified			
Roughskin newt	93 (97)	52 (61)	14: (158)
Frogs			
Tailed frog	25 (44)	40 (49)	65 (93)
Red-legged frog	3 (4)	5 (6)	8 (10)
Total	911 (938)	839 (859)	1750 (1797)

[a] Only adults of northwestern salamanders (snout-vent length 270 mm), roughskin newts (snout-vent length 540 mm), tailed frogs (snout-vent length ≥ 35 mm), and red-legged frogs (snout-vent length 235 mm) were used in analyses of abundance. Total captures of these species am in parentheses.

Table 2—Mean abundance, mean relative abundance,[a] and percentage occurrence of common amphibians (>50 total captures) in different forest types in the Oregon Coast Range

		Stand type (N)		
Species	Measure	Old-growth (25)	Mature (10)	Young (8)
All amphibians	Number/100 TN[b]	1.303	1.330	1.636
Pacific giant salamander	Number/100 TN	0.050	0.042	0.043
	Relative abundance	4.6	6.2	3.0
	Percentage of stands	64.0	70.0	62.5
Ensatina	Number/100 TN	0.454	0.542	0.569
	Relative abundance	38.6	40.3	52.7
	Percentage of stands	100	90.0	100
Western redback salamander	Number/100 TN	0.532	0.490	0.812
	Relative abundance	39.1	26.6	29.1
	Percentage of stands	88.0	80.0	50.0
Roughskin newt	Number/100 TN	0.111	0.076	0.026
	Relative abundance	7.7	5.2	3.3
	Percentage of stands	68.0	60.0	62.5
Tailed frog	Number/100 TN	0.033	0.101	0.035
	Relative abundance	2.1	16.8	2.1
	Percentage of stands	28.0	60.0	12.5

[a] Relative abundance = the percent of total captures contributed by each species.
[b] TN = trap-nights.

One northern alligator lizard not listed in table 1 was captured in a clearcut in 1984. This contrasts with 120 reptiles captured by pitfall arrays (pitfall traps with drift fences) at 30 sites in the Cascade Mountains of Oregon and Washington in 1983 (Bury and Corn 1988a). The lack of reptiles in 1984 and 1985 reflects both the absence of drift fences (Corn and Bury 1990) and the trapping season (reptiles are less active in the fall after the rains begin).

Variation on the chronosequence—Neither combined abundance nor abundance of any of the five common amphibian species were significantly different among age-classes of forest stands (table 2), but the patterns of relative abundance appeared to differ somewhat. The ensatina was the most common species captured in young and mature stands, while the western redback salamander was the most common species in old growth. Roughskin newts were a higher proportion of captures in old-growth stands than in mature and young stands. Abundance of western redback salamanders was highly variable and not well correlated to frequency of occurrence. Mean abundance of this species was 0.812 per 100 trap-nights in young stands and 0.532 per 100 trap-nights in old-growth stands, but western redback salamanders occurred in only 50 percent (4 of 8) of young stands compared to 88 percent (22 of 25) of old-growth stands. The high mean abundance in young stands was due to two stands with extraordinarily high abundance (3.056 and 2.014 per 100 trap-nights).

Captures of two rare species varied among age-classes. Olympic salamanders (fig. 1) were captured more often in old-growth stands than in mature or young stands ($G = 9.30$, 2 df, $P = 0.01$). Pitfall traps captured 11 clouded salamanders in old-growth stands versus two clouded salamanders in young and mature stands combined ($G = 4.25$, 1 df, $P = 0.039$). Numbers of northwestern salamanders ($P = 0.97$) and Dunn's salamanders ($P = 0.43$) did not differ among old-growth, mature, and young stands (fig. 1).

Variation on the moisture gradient—Tailed frogs (table 3) were absent from dry stands in old growth and much more abundant in wet stands than moderate stands ($F = 10.5$; 2, 24 df; $P = 0.001$). Ensatinas composed a higher proportion of captures in dry stands compared to wet stands, but this was probably a result of the lower number of species captured in dry stands because abundance did not vary significantly across the moisture gradient. Too few clouded salamanders were captured by pitfall traps for analysis, but none were captured in dry stands. Captures of the other rare species did not vary significantly across moisture-classes (fig. 2).

Table 3—Mean abundance, mean relative abundance,[a] and percentage occurrence of common amphibians (>50 total captures) on the moisture gradient in old-growth stands in the Oregon Coast Range

		Stand type (N)		
Species	Measure	Wet (5)	Moderate (14)	Dry (8)
All amphibians	Number/100 TN[b]	1.604	1.270	1.276
Pacific giant salamander	Number/100 TN	0.049	0.062	0.031
	Relative abundance	3.3	5.9	2.7
	Percentage of stands	80.0	71.4	50.0
Ensatina	Number/100 TN	0.451	0.419	0.500
	Relative abundance	31.1	34.9	46.2
	Percentage of stands	100	100	100
Western redback salamander	Number/100 TN	0.563	0.556	0.452
	Relative abundance	35.0	42.7	32.4
	Percentage of stands	100	92.8	75.0
Roughskin newt	Number/100 TN	0.215	0.079	0.192
	Relative abundance	10.8	5.4	13.4
	Percentage of stands	60.0	50.0	100
Tailed frog	Number/100 TN	0.153	0.032	0
	Relative abundance	10.1	2.2	0
	Percentage of stands	80.0	35.7	0

[a] Relative abundance = the percentage of total captures contributed by each species.

[b] TN = trap-nights.

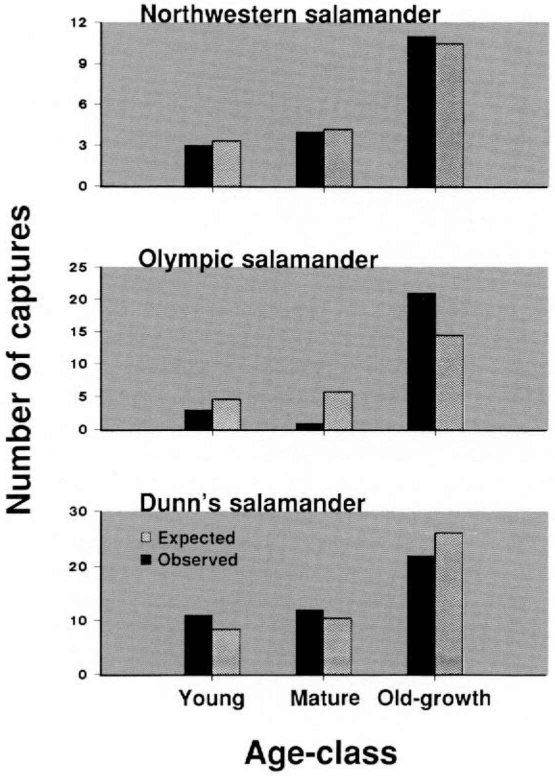

Figure 1—Observed and expected numbers of rare salamanders captured in young, mature, and old-growth stands in the Oregon Coast Range. Rare species had fewer than 50 and greater then 10 total captures.

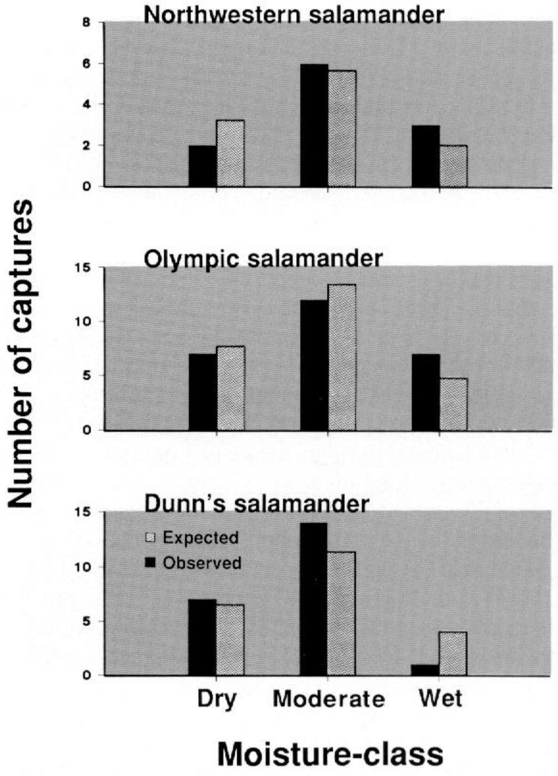

Figure 2—Observed and expected numbers of rare salamanders captured in dry, moderate, and wet old-growth stands in the Oregon Coast Range. Rare species had fewer than 50 and greater then 10 total captures.

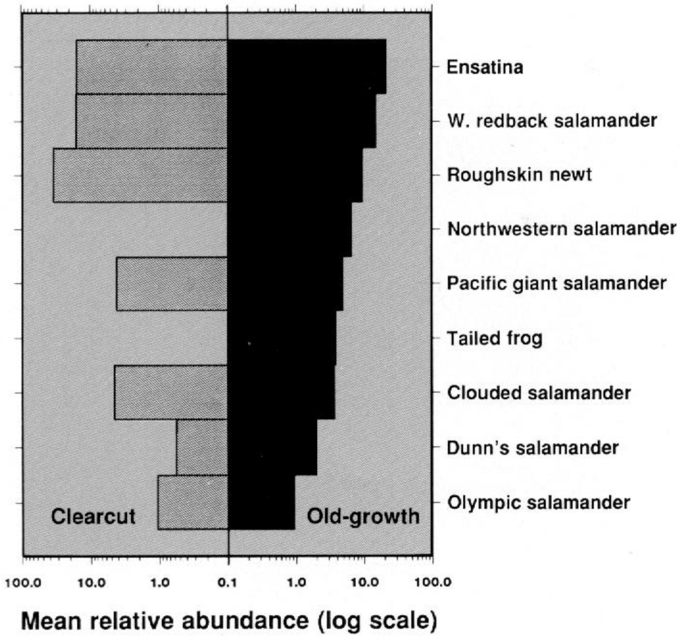

Figure 3—Mean relative abundance of amphibians in three paired clearcuts and old-growth stands.

Old growth versus clearcuts—We captured seven species in three clearcuts ($\bar{x} = 4.3$ per stand) and nine species in three adjacent old-growth stands ($\bar{x} = 4.7$ per stand). Two species, northwestern salamanders and tailed frogs, were captured in old growth and not in clearcuts. No species captured in the clearcuts were absent from old-growth stands. Total abundance in old growth (1.25 per 100 trap-nights) was not significantly greater than total abundance in clearcuts (0.76 per 100 trap-nights, $P = 0.40$). Aside from the two missing species, the pattern of relative abundance was not very different in clearcuts compared to old growth (fig. 3). The ensatina, western redback salamander, and roughskin newt were the most abundant species in both old-growth stands and clearcuts. Newts had the highest mean relative abundance in clearcuts because they were the only amphibians captured in one clearcut (relative abundance = 100 percent).

Microhabitat associations—We compared abundance or occurrence of amphibians with physiographic variables measured at the pitfall grids plus stand age, latitude, and longitude. The strongest associations were with plethodontid salamanders. Dunn's salamander occurred more often on steep slopes ($F = 16.7$; 1, 43 df; $P < 0.001$), where exposed talus was present ($G = 10.5$, 1 df; $P = 0.001$), and in stands at higher latitudes ($F = 8.23$; 1, 43 df; $P = 0.006$). Western redback salamanders were more abundant on steep slopes ($r = 0.603$, $P < 0.01$) and in stands with talus present ($F = 18.0$; 1, 43 df; $P < 0.001$). Stands where Olympic salamanders were present were older than stands where they were absent ($F = 4.23$; 1, 43 df; $P = 0.046$). Roughskin newts were more abundant in stands at higher latitudes ($r = 0.463$, $P < 0.01$), but they were less abundant in stands with surface water present in the pitfall grid ($F = 4.69$; 1, 43 df; $P = 0.036$). Tailed frogs were more abundant in western stands ($r = 0.505$, $P < 0.01$), and northwestern salamanders occurred more often in eastern stands ($F= 4.56$; 1, 43 df; $P = 0.038$). Ensatinas were less abundant on warmer (south-facing) slopes ($r = -0.376$, $P < 0.05$).

Twenty of 32 vegetation variables were significantly associated with abundance or occurrence of one or more amphibian species (table 4). Few of the significant correlations were very large; most were between 0.3 and 0.5. One exception was the positive correlation between abundance of western redback salamanders and amount of ground cover by rocks ($r = 0.566$, $P < 0.01$), but this reflected the presence of talus. Mean rock cover was 1.12 percent where talus was present and 0.11 percent where talus was absent ($F= 14.2$; 1, 43 df; $P < 0.001$). Abundance of tailed frogs was correlated to nine vegetation variables, most of which were negative correlations to understory hardwood trees and shrub cover (table 4). This pattern probably reflects the absence of tailed frogs from dry old-growth stands, where the understory was more dense than in moderate or wet stands (Spies and Franklin, this volume).

The tailed frog was the only species significantly associated with the three habitat variables generated from the principal components analysis (multiple $r^2 = 0.323$; $F = 6.53$; 3, 41 df; $P = 0.001$). Abundance was negatively associated with factor 3 (shrub cover, $P = 0.001$) and positively associated with factor 2 (down wood, $P = 0.016$), but abundance was unrelated to factor 1 (age, $P = 0.365$).

Salamanders in Down Wood

We searched 536 logs ($\bar{x} = 18$ staff minutes per log), and the amphibians comprised seven species dominated by clouded salamanders (166 captures), ensatinas (111), and western redback salamanders (40). We also captured six Dunn's salamanders, three roughskin newts, one Pacific giant salamander, and one Olympic salamander. Reptiles were encountered in the three clearcuts. We captured six northern alligator lizards, two western fence lizards, one western skink, and one northwestern garter snake. All analyses involve the three commonly captured salamanders.

Clouded salamanders were found in 110 logs, and the density was 1.48 per cubic meter of down wood (table 5). Significant differences in density were found among decay-categories (table 6); density was highest in class 1 and 2 logs and lowest in class 4 and 5 logs. Density of clouded salamanders in down wood did not vary significantly among age-classes. We found ensatinas in 82 logs, and the mean density was 1.30 per cubic meter of down wood. Density varied significantly

Table 4—Significant associations between abundance[a] of common amphibians or occurrence of rare amphibians and vegetation variables measured at pitfall grids (table 1) in the Oregon Coast Range

Variable	Northwestern salamander	Pacific giant salamander	Olympic salamander	Ensatina	Dunn's salamander	Western redback salamander	Roughskin newt	Tailed frog
DLOGSC (Percentage cover)				(-)				
STUMP (Number/ha)				(-)				
MSNAG (Number/ha)			(- -)					
CTREEM (Number/ha)							(- -)	
BTREES (Number/ha)	+							(- -)
BTREEM (Number/ha)						++		(-)
MDTREE (Percentage cover)						++	++	(-)
MCTREE (Percentage cover)		+						
CDTREE (Percentage cover)					+		+	
CBTREE (Percentage cover)								(-)
CCTREE (Percentage cover)								+
LITDEPTH (cm)				++				
SOIL (Percentage cover)				+		+		
ROCK (Percentage cover)					++	++		
FORB (Percentage cover)								++
GRASS (Percentage cover)				+				
FERN (Percentage cover)			+					
ESHRUB (Percentage cover)								(- -)
DSHRUB (Percentage cover)							+	(-)
MSHRUB (Percentage cover)							+	(-)

[a] Abundance and count variables were log transformed, percent variables were arcsin transformed. Negative associations are in parentheses. + (or –) = $P < 0.05$, and ++ (or - -) = $P < 0.01$.

Table 5—Density (number/m^3 of down wood) of clouded salamanders, ensatinas, and western redback salamanders by age- and decay-class

Species	Decay-class	Old-growth[a] (266)	Mature (90)	Young (90)	Clearcut (90)	All (536)
Clouded salamander	1 & 2	2.14	1.07	1.80	0.83	1.69
	3	1.03	3.90	3.48	1.34	1.98
	4 & 5	0.76	0.57	0.45	1.52	0.80
	All	1.31	1.80	1.91	1.23	1.48
Ensatina	1 & 2	0.61	1.98	1.43	0	0.87
	3	0.77	2.40	2.17	0.09	1.16
	4 & 5	1.26	3.19	2.40	1.60	1.84
	All	0.88	2.55	2.00	0.56	1.30
Western redback salamander	1 & 2	0.16	0	0.32	0.41	0.20
	3	0.19	3.22	0.06	0	0.64
	4 & 5	0.51	0.81	0.13	0	0.41
	All	0.29	1.33	1.09	0.14	0.42

[a] The number of logs searched in each age-class are in parentheses.

Table 6-Nested analysis of variance (stands within age-classes) of mean density (number/m^3 of down wood, log-transformed) of clouded salamanders, ensatinas, and western redback salamanders acre old-growth, mature, and young forest age-classes and 3 decay-classes of down wood (1 & 2; 3; 4 & 5)

Species	Factor	df	MSS	*F*	*P*
Clouded salamander	Stands	12	1.110	1.85	0.039
	Age-class	2	0.059	0.10	0.908
	Decay-class	2	3.081	5.13	0.006
	Error	429	0.600		
Ensatina	Stands	12	1.530	2.64	0.002
	Age-class	2	2.318	4.11	0.017
	Decay-class	2	1.844	3.19	0.042
	Error	429	0.579		
Western redback salamander	Stands	12	0.6%	3.43	<0.001
	Age-class	2	0.434	2.14	0.119
	Decay-class	2	0.475	2.35	0.097
	Error	429	0.203		

Table 7--Characteristics of logs where salamanders were captured (differences between capture sites with and without each species were tested with one-way ANOVA[a]

Category		Slope (percentage)	Log diameter (cm)	Log length (m)
All logs (n = 536)	x	20.6	45.1	9.8
	SE	0.50	0.86	0.42
Logs with clouded salamanders (n = 110)	x	21.3	52.4**	11.2**
	SE	1.10	2.12	1.07
Logs with ensatinas (n = 82)	$\bar{x}$	17.7*	44.7	9.1
	SE	1.17	0.94	0.45
Logs with redback salamanders (n = 34)	x	26.1**	51.2	10.2
	SE	1.70	4.00	1.74

[a] * $P < 0.05$, *+ $P < 0.01$.

Table Number of captures of clouded salamanders, ensatinas, and western redback salamanders by aspect and tree species

Variable	Category	All logs	cloded salamander	Ensatina	Western redback salamander
Aspect	N and NE	120	29	19	9
	W and NW	131	53	22	18
	E and SE	132	36	34	4
	S and SW	144	45	32	9
	G		6.02	4.16	10.31
	P		0.11	0.24	0.02
Trees	Douglas-fir	454	148	95	35
	Other[a]	78	15	16	5
	G		4.38	0.01	0.16
	P		0.04	0.92	0.69

[a] Western hemlock (30). western redcedar (21), grand fir (10). hardwoods (17).

both across age-classes and decay-categories (table 6). Density was highest in mature and young stands and class 4 and 5 logs, and it was lowest in clearcuts and old growth and class 1 and 2 logs (table 5). Western redback salamanders were found in 34 logs, and density did not vary significantly among either age-classes or decay-categories (table 6). Mean density of this species was 0.42 per cubic meter of down Wood.

Habitat characteristics-logs where we found clouded salamanders were larger (both diameter and length) than logs where we did not find this species (table 7). Clouded salamanders were found in Douglas-fir logs more often than in logs of other tree species (table 8). Logs with ensatinas present were on flatter slopes than logs without ensatinas, but the size of logs with and without this species did not differ (table 7). Logs with western redback salamanders were on steeper slopes than logs without redback salamanders (table 7), but redback salamanders were also captured more often where the aspect was to the west or northwest (table 8) and logs were on flatter slopes (19 percent) compared to the other three aspect categories (21-23 percent).

The strongest variation among species in use of microhabitats involved the decay-class of down wood and the locations occupied by salamanders in logs. Clouded salamanders were captured most often in class 1 and 2 logs and least often in class 4 and 5 logs (fig. 4, G = 33.6,2 df, P < 0.01). Captures of ensatinas were opposite; they were most common in class 4 and 5 logs and least often in class 1 and 2 logs (fig. 4, G = 13.8,2 df, P < 0.01). Western redback salamanders appeared to occur less frequently in class 1 and 2 logs (fig. 4), but the differences among decay-categories were not statistically significant (G = 5.16, 2 df, P = 0.08). Sites at each log where salamanders were captured were characterized as inside the log, under bark on the surface of the log, or in contact with the ground. All three species showed distinct preferences for specific sites in down wood (fig. 5, G = 71.2,4 df, P < 0.001). Clouded salamanders were found inside the log or under bark, but rarely in contact with the ground. Ensatinas were captured most often inside the log, and they were captured in contact with the ground more often than were clouded salamanders. Western redback salamanders were captured most often in contact with the ground. The mean depth inside the wood of 88 clouded salamanders found inside logs was 6.5 cm, and the mean depth of 64 ensatinas was 7.9 cm, but the difference was not significant (Student's t = 1.30, P = 0.19).

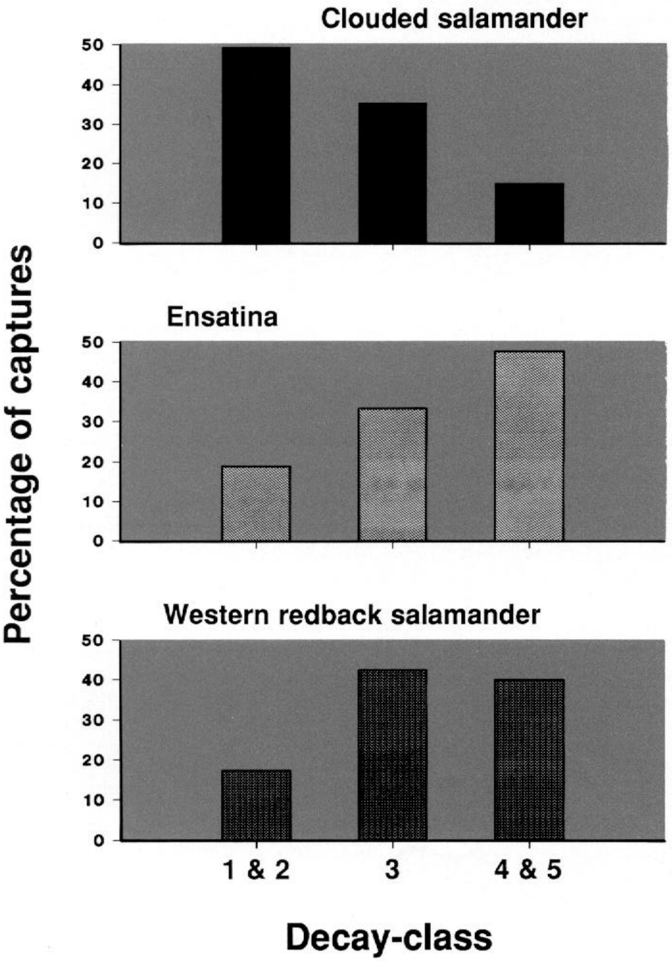

Figure 4—Captures of clouded salamanders, ensatinas, and western redback salamanders by decay-category of down wood.

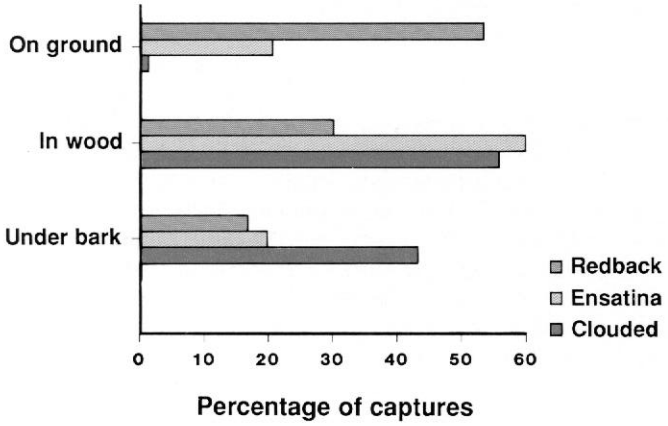

Figure 5—Locations of clouded salamanders, ensatinas, and western redback salamanders captured during surveys of down wood.

Discussion

Species Associated With Old-Growth Forests

Olympic salamanders were captured by pitfall traps more often in old-growth stands, and stands where this species was present were older than in stands where it was absent. Welsh and Lind (1988, this volume) obtained similar results in Douglas-fir forests in northern California. Olympic salamanders are closely tied to headwater streams and seeps (Bury 1988, Nussbaum and Tait 1977), however, and they are not often captured by pitfall traps in upland settings (Aubry and Hall, this volume; Bury and Corn 1987, 1988a; Gilbert and Allwine, this volume c; Raphael 1988c). The best evidence that Olympic salamanders are associated with old-growth forests comes from the stream surveys of aquatic amphibians (Bury and others, this volume b). Density was four times greater in streams in old-growth forests than in streams in young stands. Abundance of Olympic salamanders was greatly reduced in streams in the Coast Range that flowed through logged stands (Corn and Bury 1989), possibly resulting from increased siltation. Olympic salamanders may be very slow to recolonize areas from which they have been extirpated (Bury and Corn 1988b).

Other Coast Range amphibians that were sampled more effectively by pitfall traps showed little preference for old growth. This is in general agreement with data from the Cascades in Oregon and Washington (Aubry and Hall, this volume; Bury and Corn 1988a; Gilbert and Allwine, this volume c), although Aubry and Hall (this volume) found a greater abundance of northwestern salamanders in old-growth stands in the Southern Washington Cascades. Ensatinas (Raphael and Barrett 1984, Welsh and Lind 1988), Del Norte salamanders (Raphael 1988c, Welsh and Lind 1988) and black salamanders (Raphael 1988c) were more abundant in older Douglas-fir forests in northern California.

One major factor may be interfering with our ability to determine the habitat preferences of amphibians: terrestrial pitfall trapping largely ignores breeding habitats. A majority of the amphibian species we captured breed in water, either in cascading headwater streams (tailed frogs, Pacific giant salamanders, Olympic salamanders), or in ponds or backwaters of streams (red-legged frogs, northwestern salamanders, Pacific giant salamanders, roughskin newts). Most amphibians have poor dispersal abilities (relative to birds and mammals), so upland habitat use by aquatic-breeding species may be influenced heavily by proximity to water. Most pitfall grids were within a few hundred meters of a perennial stream, but we have little information about the distribution of ponds relative to our grids. Plethodontid salamanders lay their eggs on land where the embryos hatch into small replicas of the adults. These species do not require surface water but may be tied to other habitat features such as talus slopes (Dumas 1956, Herrington 1988, Herrington and

Continue

Larson 1985, Stebbins 1951) or large chunks of down wood (Aubry and others 1988, Bury and Corn 1988a, Whitaker and others 1986).

Plethodontid salamanders—One goal of our surveys of down wood was to provide estimates of the density of salamanders strongly associated with down wood. Estimated numbers of clouded salamanders and western redback salamanders per hectare were strongly correlated to stand age (fig. 6) because of the strong correlation between volume of down wood and stand age (Spies and others 1988). Because numbers of these two species (per cubic meter of down wood) did not vary among forest age-classes, changes in numbers per hectare apparently were solely due to changes in the volume of down wood. Predicted abundance of ensatinas did not increase with the age of the forest (fig. 6) because the number (per cubic meter of down wood) was significantly lower in old-growth stands. The increased volume in down wood in old-growth stands compensated for this, so the estimated numbers of ensatinas did not vary significantly among age-classes.

The estimated abundance of plethodontid salamanders (combined) was also positively correlated with stand age (fig. 6). The mean density (D) was 364 salamanders per ha in young stands, 387 per ha in mature stands, and 744 per ha in old-growth stands. These figures are considerably less than the 2367 redback salamanders per ha that Burton and Likens (1975) estimated for the Hubbard Brook Experimental Forest in New Hampshire, or the 7000 *Plethodon* per ha that Hairston (1987) estimated for forests in the southern Appalachian Mountains. The abundance we estimated, however, includes only salamanders closely associated with down wood. We may be somewhat close to estimating the actual abundance of clouded salamanders, but ensatinas and western redback salamanders use a broader range of habitats. These species were 49 and 56 times more abundant in pitfall traps than clouded salamanders, suggesting that neither species is closely associated with down wood. A recent 3-year study of western redback salamanders on two small plots on Vancouver Island found only about 15 percent of captures associated with down wood (Ovaska and Gregory 1989). Stebbins (1954) estimated 1708 ensatinas per ha at a site in the San Francisco Bay area, and Gnaedinger and Reed (1948) estimated 2833 ensatinas per ha in a ravine on the campus of Reed College in Portland. Ovaska and Gregory (1989) recorded surface activity of up to 1.16 western redback salamanders per square meter. Relative abundances of ensatinas and western redback salamanders were equivalent in our pitfall traps, so the true density of plethodontid salamanders in Douglas-fir forests in western Oregon may be several thousand per ha, similar to salamander densities in eastern forests.

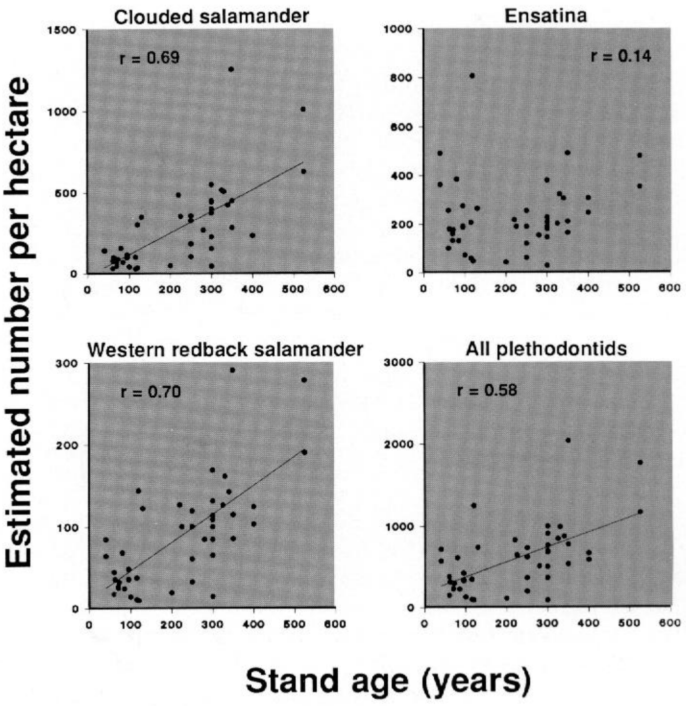

Figure 6—Predicted abundance in the Oregon Coast Range of plethodontid salamanders associated with down wood.

Microhabitat Features

We found few strong associations between amphibians and habitat features unique to old-growth forests. Upland habitats used by tailed frogs tended to be dense, moist forests, which is not unexpected for a species with low tolerance to high temperature and desiccation (Claussen 1973a, 1973b). These conditions may be supplied by young forests as well as old growth, however.

Three general microhabitats are available to terrestrial salamanders: rocky substrates, down wood, and leaf litter. The four plethodontid salamanders in the Coast Range segregate among these habitat types with various degrees of overlap. Dunn's salamander is most abundant in rock rubble in seeps and along small streams (Bury 1988, Bury and Corn 1988b, Corn and Bury 1989, Dumas 1956, Nussbaum and others 1983). Western redback salamanders are most abundant on rocky slopes (Dumas 1956, Nussbaum and others 1983, Ovaska and Gregory 1989), as are most western *Plethodon* (Herrington 1988, Herrington and Larson 1985, Nussbaum and others 1983, Ramotnik and Scott 1988, Stebbins 1951). Western redback salamanders apparently select drier habitats than Dunn's salamanders and are more tolerant of desiccation (Dumas 1956). Clouded salamanders are the dominant species associated with down wood, and prefer large, intact logs with loose bark (Bury and Corn 1988a; Bury and Martin 1973;

Welsh and Lind 1988, this volume: Whitaker and others 1986). Ensatina is the most primitive western plethodontid (Wake 1966) and has the most general habitat use (Gnaedinger and Reed 1948, Stebbins 1954). Ensatinas were common on rocky slopes and in older decay-classes of down wood; their abundance was positively correlated with litter depth.

Considerable evidence has been found that differences in habitat use by terrestrial amphibians are driven by competition (see Hairston 1987), and western plethodontids with similar adult body size have large overlap in diets (Altig and Brodie 1971, Lynch 1985). Our study was unable to determine whether competition is occurring in terrestrial salamanders in the Coast Range or whether current habitat preferences reflect past selective pressures.

The abundance of ensatinas in pitfalls was negatively correlated with percentage cover by decay-class 4 and 5 down wood, which initially seems paradoxical in view of the data from the log surveys, where ensatina preferred well-decayed wood. Salamanders that are closely tied to down wood, however, such as clouded salamanders or Oregon slender salamanders in the Cascades (Bury and Corn 1988a; Gilbert and Allwine, this volume c), are rarely captured in pitfalls. Surface activity of ensatinas should decline in stands with large amounts of well-decayed wood.

Managed Forests

Clearcutting may significantly affect terrestrial herpetofauna. Several studies have documented declining abundance, changes in the species composition of amphibians, or both (Buhlman and others 1988, Bury 1983, Bury and Corn 1988a, Pough and others 1987, Raphael 1988c). Meanwhile, populations of reptiles, particularly lizards, increase and exploit new openings in the forest canopy (Bury and Corn 1988a, Raphael 1988c). The three clearcuts we studied in the Coast Range did not display significant changes in amphibian populations. Abundance was slightly lower, and two species found in adjacent old-growth stands were absent, but the pattern of amphibian abundance was similar in old growth and clearcuts.

Three stands are inadequate to assess the effects of clearcutting in the Coast Range, but even in an intensively managed forest, a minority of the landscape will be in the open canopy stage (Bury and Corn 1988b, Harris 1984). The problem for most amphibian species will be how to exist in short-rotation second-growth forest that is structurally dissimilar from naturally regenerated forest. Harris and others (1982) predict a loss of about 25 percent of vertebrate species in managed forests, primarily because snags and down wood are eliminated. Raphael (1988c) predicted that the abundance of three plethodontid salamanders in northern California could decrease by 29 to 75 percent if logging of old-growth forest continues. Few actual studies have been made of the long-term effects of logging on amphibian populations, however. Terrestrial amphibians were reduced in some second-growth forests in the Eastern United States (Bennett and others 1980, Pough and others 1987), and density and biomass of stream amphibians in the Coast Range were greatly reduced in streams flowing through stands logged 14 to 40 years before (Corn and Bury 1989). Stream amphibians are particularly vulnerable in a managed landscape, because headwater streams are not protected and they are less than 0.4 percent of the landscape in Coast Range forests (Bury 1988).

Logging may have negative impacts on amphibians associated with talus (Herrington 1988, Herrington and Larson 1985), which is an important consideration for species with limited distributions (Bury and others, this volume a). Assuming that the talus slope is not destroyed by such activities as rock removal for road building (Herrington 1988, Scharpf and Dobler 1985), however, the habitat should persist. The main talus-dwelling salamander in the Coast Range is the western redback salamander, which is widely distributed, abundant, and unlikely to be seriously threatened by logging.

Managed forests have reduced amounts of coarse woody debris (Bartels and others 1985, Harmon and others 1986), which is exacerbated in each rotation as residual down wood decays and little new down wood enters the system (Spies and Franklin 1988, Spies and others 1988). Species associated with down wood, such as clouded salamanders and Oregon slender salamanders (Bury and Corn 1988a; Gilbert and Allwine, this volume c), are likely to decline in managed landscapes. Previous studies have found clouded salamanders to be common in clearcuts but always in association with large woody debris (Bury 1983, Bury and Corn 1988a, Whitaker and others 1986). Although we have said that this species does not appear to be associated with old-growth conditions (Bury and Corn 1988b), we believe that survival of clouded salamanders in managed forests over a few rotations is open to question.

Generalist species such as ensatinas are likely to persist in managed forests, although populations may be reduced. Female ensatinas use large, well-decayed down wood for nest sites (Aubry and others 1988), but considering the high abundance of this species in nearly all stands sampled in Washington, Oregon, and California (Bury and others, this volume a), down wood seems unlikely to be an absolute requirement.

Recommendations

Forests in the Coast Range of Oregon are among the most heavily impacted by logging in the Pacific Northwest (Harris 1984, Monthey 1984). Much of the second growth, however, results from past logging practices that left considerably more woody debris than current practices, and harvesting of second growth on Federal lands is just beginning. For this reason, we believe that none of the terrestrial amphibians in the Coast Range of Oregon are in immediate danger of extinction or severe reduction from logging, but we make the following suggestions for further research:

- Investigate amphibian populations in managed forests. Research to date has focused on naturally regenerated forests, and only a few clearcuts have been sampled:
- Determine ways to increase amounts of down wood in managed forests. Logging plans could be modified to increase the amount of cull timber left after cutting, but a more difficult problem is how to increase recruitment of new down wood before the next rotation;
- Determine the effects of forest fragmentation on amphibians. Amphibians may not be particularly sensitive to fragmentation (Rosenburg and Raphael 1986), but this needs more attention in the Coast Range;
- Increase our knowledge of the basic natural history of amphibian species. Much basic information, including population sizes and reproductive characteristics, is lacking; and
- Initiate long-term monitoring of amphibian populations in natural and managed forests immediately. Long-term studies of communities are critical for understanding the processes that are shaping them, but are rarely done (Scott and Campbell 1982).

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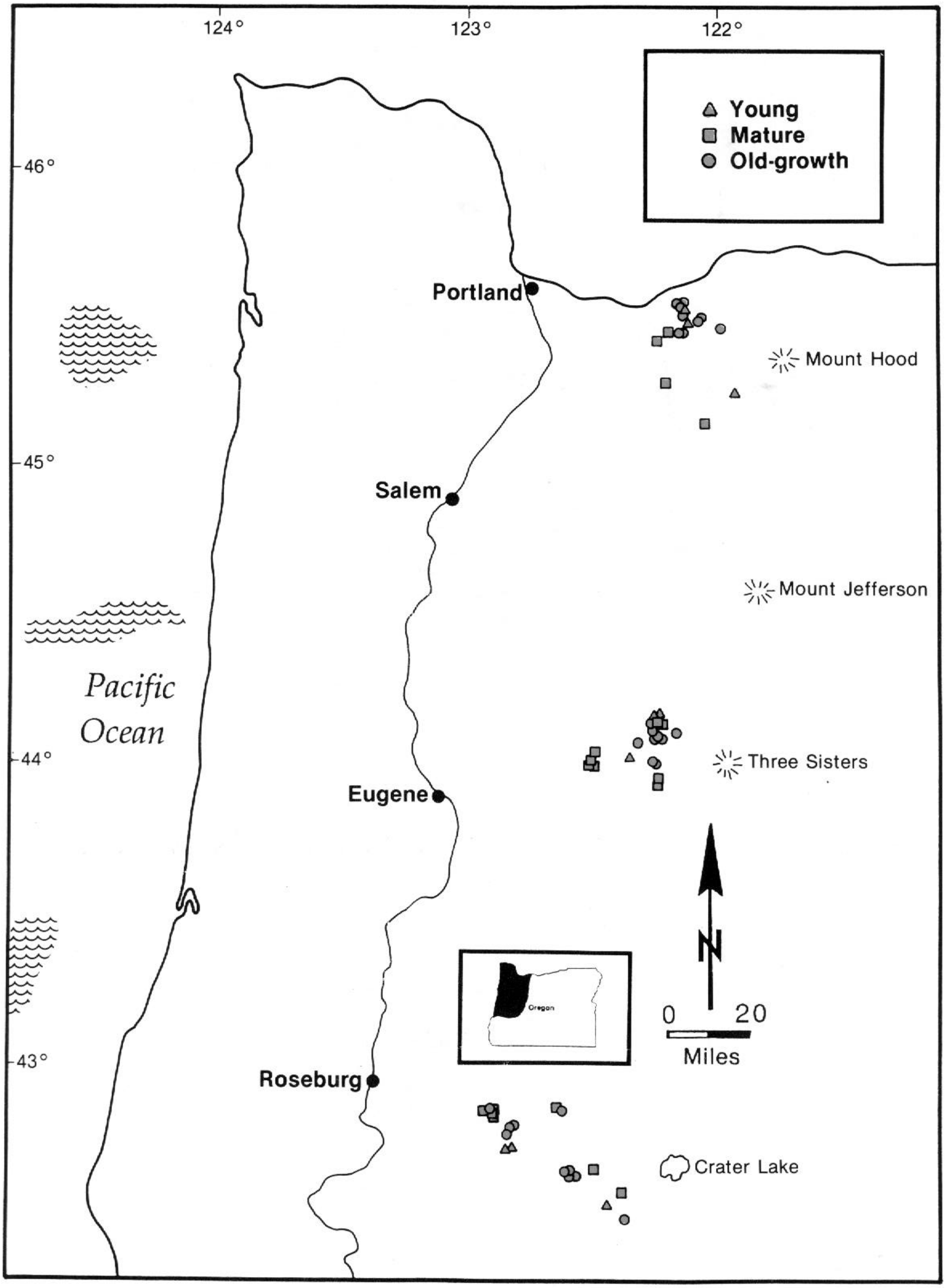

Location of study sites.

Terrestrial Amphibian Communities in the Oregon Cascade Range

Frederick F. Gilbert and Rochelle Allwine

Authors

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Abstract

Ensatina was the most common terrestrial amphibian in the Oregon Cascade Range, representing over 50 percent of all captures. The tailed frog was the second most abundant species but was the dominant species of the northernmost study location (Mount Hood). The roughskin newt was the only other species captured in the pitfall traps with 25 percent of the total captures. Species richness did not differ between locations or between years.

No species was significantly associated with old-growth stands, although time-constrained searches indicated the clouded salamander and the Oregon slender salamander were found primarily in logs of the older decay classes. The northwestern salamander was associated with old growth at Mount Hood. Most amphibians seemed to select the mesic to wet portion of the moisture gradient, but the Pacific giant salamander was the only species with captures significantly associated with wet sites. Ensatina was overrepresented in dry stands and was captured at sites with a high percentage of exposed rock and bare soil. Relation to ground cover was generally consistent between years, but the vegetative associations had little predictive value between years. The Oregon Cascades amphibians apparently can be retained as viable populations wherever crown closure has occurred and breeding streams remain cool and unsilted. Forest management practices for these species should include protecting riparian zones, maintaining topography favoring ephemeral ponds as breeding sites, and considering cutting practices that would provide stand structure and coarse woody debris like those in naturally regenerated stands.

Introduction

Amphibians are an often-neglected component of the vertebrate fauna, despite their relative abundance and contribution to the faunal biomass in most locations. Studies at the Hubbard Brook Experimental Forest, New Hampshire, indicate that amphibians contribute about twice the biomass of breeding birds and about the same biomass as small mammals (Burton and Likens 1975). Many forest amphibian species are aquatic in part or all of their life cycle, and much of the amphibian literature is devoted to them (for example, Bury and Corn 1988b, Hawkins and others 1983, Murphy and Hall 1981, Murphy and others 1981).

Aubry and Hall (this volume), Corn and Bury (this volume b) and Raphael (1988c) have used pitfall traps (with and without drift fences) and time-constrained sampling to identify amphibian communities in Douglas-fir forests from California to Washington. Our study was intended to provide information on these vertebrates in the Oregon Cascade Range and, where possible, to relate their presence and abundance to the age, moisture conditions, and vegetative structure of the Douglas-fin- stands where they were found.

Materials and Methods

Amphibian populations were sampled at three sites on the west side of the Oregon Cascades during 1984 (Mount Hood, Hood; H.J. Andrews, the Andrews; and Rogue River-Umpqua, Rogue-Umpqua). Only the Andrews was studied in 1985. Pitfall trapping was done in September and October both years. Grids (6 x 6) with stations 15 m apart were used in each of 56 stands in 1984 and 15 stands in 1985. An additional eight pitfall grids were placed in the Andrews stands in 1985 to determine effects on amphibian populations of the previous year's trapping (Gilbert and Allwine, this volume b: see appendix table 15). Time-constrained searches were conducted in the spring of 1984. Each stand was searched intensively for 4 person-hours. Ephemeral (melt-water) ponds, located in all the study stands when time-constrained searches were conducted, were examined at least twice during the spring of 1984 for amphibians and egg masses. Egg masses found were collected and allowed to hatch so species could be identifed. Water temperature, surface area, and water depth were measured at each visit.

The abundance and diversity of species related to the chronosequence (young, 30-80 years; mature, 80-200 years; and old-growth, >200 years), the moisture gradient (wet, mesic, and dry old-growth stands), and vegetational structure were analyzed. Vegetation was described by measurements within a 5.6-m radius (100 m^2) and a 15-m radius (707 m^2) centered on nine pitfall traps (Gilbert and Allwine, this volume a: see appendix table 12). Individual amphibian species were compared between the 1985 old and new grids in eight stands to determine if differences in abundance were significant.

Animals were weighed, measured (snout-vent length, total length), and either released at the capture location or preserved for food habits studies or as specimens for the Conner Museum at Washington State University.

Data analysis was based on two major statistical goals: testing the hypotheses that animal abundance and the number of species (species richness) did not differ among age-classes, moisture-classes, or locations; and using exploratory statistics to associate individual species with individual habitat components and with either age-classes or moisture-classes. We used nonparametric analysis of variance (ANOVA) to test the hypotheses that neither abundance of animals nor species richness differed among the age- or moisture-classes in each location. We used detrended correspondence analysis (DCA) (Hill 1979a) to explore the relation between animal abundance and habitat-classes as environmental variables. Detrended correspondence analysis is an ordination technique that arranges a matrix of species' abundances (communities) by samples (stands) in low-dimensional space so that the communities occurring in each stand are represented in space along several axes. Thus, many components are reduced to a few important ones and variability is reduced. Communities with similar species composition and relative abundances occupy positions near each other within the space described by the first and second DCA axes. The axes that explain (by the ranking of their eigenvalues) the largest variability with the original matrix are determined as being important in exploring distribution with the data set. To determine whether stands were grouped according to a physiographic gradient, a plot of the DCA axes scores was examined to detect clustering.

To classify sites into community phases, two-way indicator species analysis (TWINSPAN) (Hill 1979b) was used. This method, based on a multilevel, two-way partitioning of the correspondence analysis scores, was used to classify species into categories related to location and age- or moisture-classes.

Species found to be associated with old-growth forests from TWINSPAN analysis or from Spearman rank correlations of animal. abundance with stand age were then correlated with individual environmental and vegetative variables to examine the relation between animal species and individual habitat features.

The log-likelihood ratio was used to test for significance in the use of logs by salamanders collected during time-constrained searches. Three decay-class categories (see Fogel and others 1973) were used: category 1 includes decay-classes 1 and 2; category 2 includes decay-class 3; and category 3 includes decay-classes 4 and 5. A G test (likelihood ratio chi-square) was performed after comparison of use to availability.

Statistical significance was at the $P \leq 0.05$ level (Zar 1974). Means are presented with standard errors.

Results

1984

A total of 951 amphibians were collected in pitfall traps in 1984. With the exception of ensatina, the amphibian species were most abundant at the Hood location (table 1). Hood produced significantly more specimens than either of the

Table 1—Amphibians captured in pitfall traps by subprovince in the Oregon Cascades, 1984

Species	Rogue-Umpqua (N=20)	Andrews (N=20)	Mt. Hood (N=16)	Totals
Northwestern salamander	6	1	31*	38
Clouded salamander	0	2	4	6
+Tailed frog	4	38	196*	238
Oregon slender salamander	0	4	2	6
Western toad	0	2	0	2
+Pacific giant salamander	4	8	31*	43
+Ensatina	185*	101	52	338
Pacific treefrog	1	1	0	2
+Dunn's salamander	0	29	46	75
+Roughskin newt	8	35	110*	153
Red-legged frog	12	0	11	23
+Frog[a]	12*	0	0	12
Olympic salamander	0	0	3	3
+Western redback salamander	12*	0	0	12
Totals:	244	221	486	951

* Significant ANOVA value for location.

\+ Significant Spearman rank correlation with latitude.

[a] Twelve frogs could not be identified because of their condition; they may have been foothill yellow-legged or Cascade frogs, as well as red-legged frogs.

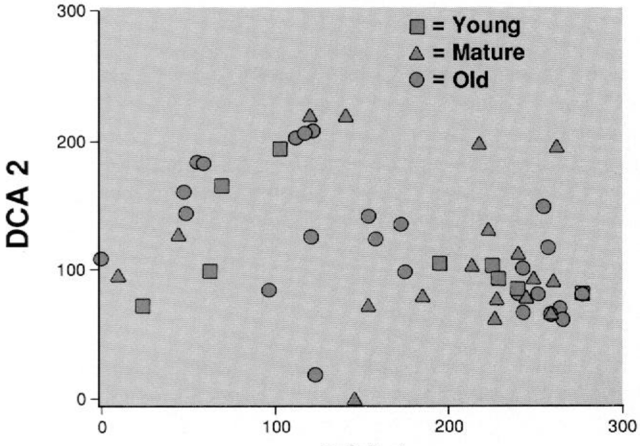

Figure 1—Plot of detrended correspondence analysis axes scores for amphibians caught in pitfall traps related to age of stand, Oregon Cascades, 1984.

others (31.3 ± 6.8 vs. 12.4 ± 1.4 at Rogue-Umpqua and 11.2 ± 2.0 at Andrews). Ensatina was the most common amphibian at Andrews (45 percent of captures) and at Rogue-Umpqua (78 percent of captures). At Hood, the tailed frog (40 percent of captures) was the most common amphibian. The average number of amphibians caught compared to the age of the stand was not significantly different (old-growth 14.0 ± 2.7, mature 15.8 ± 2.1, young 29.7 ± 10.7 (ANOVA F value 2.87, $P < 0.07$).

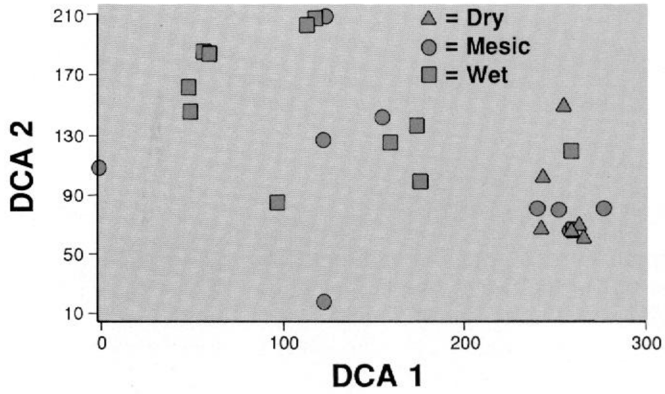

Figure 2—Plot of detrended correspondence analysis axes scores for amphibians caught in pitfall traps related to moisture condition of old-growth stands, Oregon Cascades, 1984.

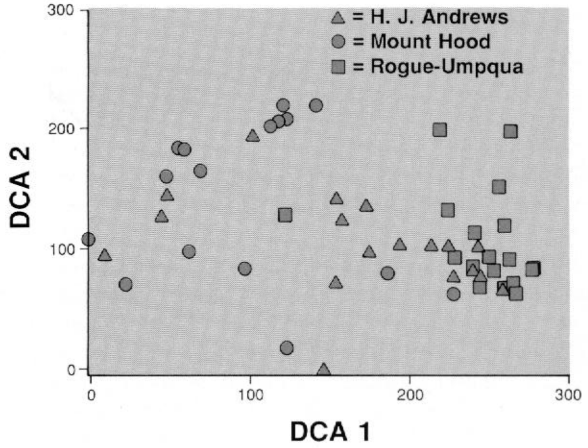

Figure 3—Plot of detrended correspondence analysis axes scores for amphibians caught in pitfall traps related to location, Oregon Cascades, 1984.

DECORANA analysis showed no influence of stand age on the amphibians captured (fig. 1). Some separation appeared between wet and dry stands, indicating some selection was occurring (fig. 2), and a definite location effect was found as Rogue-Umpqua separated from Hood with the Andrews interfacing with both (fig. 3).

No species were significantly associated with old-growth stands, although the frogs were found only in mature and old-growth stands and the Olympic salamander was found only in old-growth stands. The tailed frog (ANOVA *F* value 2.71, $P < 0.08$) and the roughskin newt (ANOVA *F* value 4.99, $P < 0.01$) captures were associated with young stands.

Although the most amphibians were collected in mesic stands (average 19.6 ± 5.8; wet 12.0 ± 3.3; dry 11.1 ± 3.5), no significant differences were found along the moisture gradient. Ensatina was the only species significantly associated with

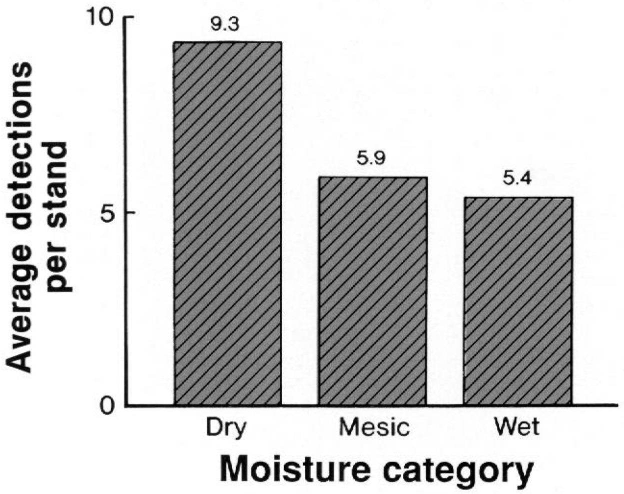

Figure 4—Relative pitfall capture rates for ensatina across the moisture gradient, Oregon Cascades, 1984.

dry sites (ANOVA *F* value 4.81, $P = 0.02$) and the Pacific giant salamander, the only species significantly associated with wet stands (ANOVA *F* value 3.88, $P = 0.03$) (figs. 4-5).

Fifteen different species were captured, and species richness was identical (10) at all three sites. The northwestern salamander was significantly associated with old-growth at Hood. Although Dunn's salamander generally was found in younger stands in the Oregon Cascades, it was found primarily in mature stands at the Andrews. The tailed frog was associated with young stands at Hood, mature stands at the Andrews, and found only in old-growth stands at Rogue-Umpqua.

The presence of water near the pitfall site was not related to capture for any species, with the possible exception of the unidentified frogs (ANOVA $P = 0.06$).

Ensatina was found where forest-floor conditions had a high percentage of bare soil (Spearman rank correlation $R = 0.32$, $P = 0.02$), and this species was negatively associated with moss ground cover (Spearman rank correlation $R = -0.44$, $P = 0.0001$). The tailed frog and the Pacific giant salamander by contrast, were captured at locations with moss cover ($R = 0.40, 0.30$; $P = 0.002, 0.02$, respectively). The tailed frog was negatively associated with areas of bare soil and fine litter, another characteristic selected by ensatina. Areas with high coverage by grass were negatively correlated with the roughskin newt ($R = -0.39$, $P < 0.003$), Dunn's salamander ($R = -0.31$, $P < 0.02$), and the Oregon slender salamander ($R = -0.31$, $P < 0.02$). The Pacific giant salamander was captured at sites with fern cover (0-0.5 m high $R = 0.42$, $P = 0.001$; 0.5-2.0 m high $R = 0.37$, $P = 0.005$), as were the clouded salamander (0-0.5 m $R = 0.36$, $P = 0.006$; 0.5-2.0 m $R = 0.37$, $P < 0.005$) and Dunn's salamander (0-0.5 m $R = 0.30$, $P = 0.02$; 0.5-2.0 m $R = 0.40$, $P = 0.002$).

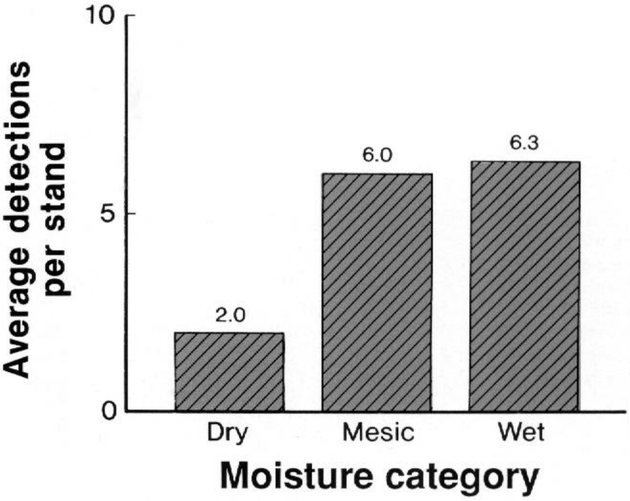

Figure 5—Relative pitfall capture rates for the Pacific giant salamander across the moisture gradient, Oregon Cascades, 1984.

Time-constrained searches produced 375 amphibians representing nine species (table 2). Eight species were captured at Hood and six each at the Andrews and Hood ($P > 0.05$). Ensatina was the most abundant amphibian (50.7 percent of captures), followed by the Oregon slender salamander (25.3 percent of captures) and clouded salamander (13.3 percent of captures). The tailed frog, the Pacific treefrog, the Olympic salamander, Dunn's salamander, the western redback salamander, and the roughskin newt were the only other species represented.

The Oregon slender salamander and the western redback salamander were associated with the wet portion of the moisture gradient and ensatina with the dry. No species was significantly associated with the chronosequence, although the only specimens of the tailed frog (2) and the Olympic salamander (1) were taken in old-growth stands. Use of logs by decay-classes (1+2, 3, 4+5) by ensatina, the clouded salamander, and the Oregon slender salamander was tested to see if it varied by species. The *G* test was highly significant ($P = 0.001$). Of these common species, the Oregon slender salamander ($G = 2.25$, $P < 0.001$) and ensatina ($G = 6.32$, $P = 0.04$) deviated from availability for decay-class 4 and 5 logs, but the clouded salamander showed no significant differences from expected values ($P = 0.88$).

Surveys showed that at least four species—the red-legged frog, the Pacific treefrog, the northwestern salamander, and the roughskin newt—used meltwater ponds as breeding sites.

Table 2-Amphibians collected during time-constrained searches in the Oregon Cascades, spring 1984, related to stand age (values in brackets are mean captures/stand)

Species	Old-growth	Mature	Young	Total
Ensatina	92 (3.41)	69 (3.45)	29 (3.22)	190 (3.39)
Oregon slender salamander	34 (1.26)	42 (2.10)	19 (2.11)	95 (1.70)
Clouded salamander	26 (0.96)	20 (1.00)	4 (0.44)	50 (0.89)
Western redback salamander	8 (0.30)	5 (0.25)	1 (0.11)	14 (0.25)
Dunn's salamander	9 (0.33)	3 (0.15)	0 (0.00)	12 (0.21)
Roughskin newt	4 (0.15)	1 (0.05)	3 (0.33)	8 (0.14)
Pacific treefrog	0 (0.00)	1 (0.05)	2 (0.22)	3 (0.05)
Tailed frog		0 (0.00)	0 (0.00)	2 (0.04)
Olympic salamander	1 (0.04)	0 (0.00)	0 (0.00)	1 (0.02)
	-	-	-	-
Totals	176 (6.52)	141 (7.05)	58 (6.44)	375 (6.69)

Red-legged frog adults and egg masses were found in all but one of the 35 ponds surveyed. Pond depth, temperature, and surface area were all unrelated to presence or absence of amphibians. Ponds were only studied in old-growth or mature stands because none of the young stands studied had melt-water ponds.

Studies in 1985

Of the 462 amphibians captured in pitfall traps in 1985, ensatina contributed 267 and the roughskin newt 98 specimens (79.1 percent of all captures). The tailed frog was the only one of the other seven species to have more than 3 percent of the captures (table 3). The roughskin newt was significantly associated with young stands (ANOVA F value 4.86, $P < 0.03$). Young stands had more amphibians caught (average 52.7 ± 15.8) than either mature (34.0 ± 10.1) or old-growth stands (22.7 ± 3.8) (F value 3.92, $P < 0.05$). Wet stands produced more amphibians (average 27.5 ± 6.3) than did mesic (25.5 ± 10.5) or dry stands (14.3 ± 2.4), but the differences were not significant.

Although some forest-floor characteristics differed significantly between 1984 and 1985, general patterns were similar. For example, Dunn's salamander continued to be captured at sites with high percentages of bare rock and bare soil (1984 values $R = 0.44$, $P = 0.10$; $R = 0.43$, $P < 0.11$ and 1985 values $R = 0.62$, $P = 0.01$; $R = 0.75$, $P = 0.001$), and the Pacific giant salamander was caught at sites with a high percentage of moss (1984 $R = 0.55$, $P = 0.03$; 1985 $R = 0.43$, $P < 0.11$) based on Spearman rank correlations. Ensatina was found associated with logs of decay-class 1+2 (1984 $R = 0.52, P < 0.05$; 1985 $R = 0.47, P < 0.08$).

Table 3-Herpetofauna captured in pitfall traps at the H.J. Andrews, fall 1985 (values in brackets represent percentages)

Species	original grids (15)	New grids (8)	Total
Ensatina	174 (66.4)	93 (46.5)	267 (57.9)
Roughskin newt	38 (14.5)	60 (30.0)	98 (21.2)
Tailed frog	29 (11.1)	25 (12.5)	54 (11.7)
Dunn's salamander	8 (3.1)	4 (2.0)	12 (2.6)
Pacific treefrog	2 (0.8)	7 (3.5)	9 (1.9)
Pacific giant salamander	6 (2.3)	2 (1.0)	8 (1.7)
Oregon slender salamander	2 (0.8)	4 (2.0)	6 (1.3)
Red-legged frog	3 (1.1)	2 (1.0)	5 (1.1)
Northwestern salamander	0 (0.0)	3 (1.5)	3 (0.6)
	-	-	-
Total	262	200	462

Comparison between years showed that only the tailed frog had a difference in its relation to the chronosequence, moisture gradient, or both. More captures were made in the dry portion of the moisture gradient in 1985 (chi-square = 5.669, 2 df, $P = 0.06$).

Although no significant difference was found in the amphibian species captured in the old and new grids of the same stands, the number of amphibians captured was different (chi-square = 20.164, 8 df, $P < 0.01$). The roughskin newt, the Pacific treefrog and the tailed frog were more abundant in the new grids.

Discussion

Porter (1972) suggested that amphibians tend to be restricted by dry conditions. Our findings support this generalization because Rogue-Umpqua, the subprovince with the least average annual precipitation, had the lowest number of amphibians, and many species selected mesic-wet stands over dry stands. Some species though, such as ensatina, may prefer drier sites. In general, we found similar relations between the amphibians and habitat conditions to those described in Nussbaum and others (1983) and Stebbins (1985).

Clouded salamanders and Oregon slender salamanders were seldom taken in pitfall traps. Both species live under the bark on logs, or within the logs, so time-constrained searches were the only effective way of sampling their presence and abundance (Bury and Corn 1988a). They were the second and third most abundant amphibians taken in me searches, and the Oregon slender salamander used more-decayed logs than did the clouded salamander. The decay-class use by these two species was similar to Bury and Corn's (1988a) observation that the clouded salamander used logs of decay-class 2 and 3 and the Oregon slender salamander used the older decay classes. Raphael (1988c) considered the clouded salamander to be associated with old growth because of its dependence on logs.

Tailed frogs seemed dependent on ambient temperature. They used stands of different ages at the three sites. At the warmest location (Rogue-Umpqua), old growth seemed to be selected; at the intermediate location (Andrews), mature stands had the most captures; and at the coolest location (Hood), the species was most abundant in young stands. This species breeds and the larvae develop in cool flowing streams, so the temperature in the streams may be what restricts distribution (Bury and Corn 1988b, Gilbert 1985). At Rogue-Umpqua, most of the streams were in old-growth stands; streams in the younger stands may be mostly intermittent and thus incapable of supporting tailed frogs. The Olympic salamander is more restricted to the vicinity of cool streams and seeps. It, too, is likely to be temperature dependent, but the major threat to these aquatic forms may be stream siltation, which destroys their prey base (Corn and Bury 1989).

The roughskin newt and northwestern salamander, like the red-legged frog, used meltwater ponds as breeding sites. Unlike the frog, the other two species were more ubiquitously distributed along the chronosequence and perhaps not as restricted in their movements. In partial contradiction, however, the roughskin newt may have been partially trapped out in 1984 because the old pitfall grids produced fewer of this species than the new grids in the same stands.

None of the amphibians we found was restricted to old growth, although some, such as the Olympic salamander, selected habitat conditions that may be most abundant in old growth, which may also be true for the Oregon slender salamander. This species used logs of the older decay-classes, a feature usually associated with old-growth forests (Franklin and others 1981). Logs in all age-classes were abundant in the natural stands we studied, however.

Because all the common (>6 observations) species were found in young as well as older stands, closed canopy conditions are apparently sufficient to sustain these species in the Oregon Cascades. Nonetheless, Bury (1983) and Bury and Corn (1988b) may well be correct that logging, especially clearcutting, can be disruptive to amphibian populations.

Clearcuts are unlikely to have the coarse woody debris or stand structure characteristic of the natural conditions in our study stands. If these characteristics could be maintained in managed forests, all the amphibian species we found in the Oregon Cascades should also be present in such forests.

Vegetative structure was not predictably related to species captures between years, probably because of the time of year of the pitfall trapping and the high percentage of juveniles in the populations. "Pulses" of high capture rates corresponded with periods of precipitation, a finding similar to other studies (Bury and Corn 1987, Bury and Corn 1988b). These pulses consisted of dispersing juveniles, so the capture sites may not represent actual habitat requirements.

When amphibian communities are studied, recognizing that shifts occur in resource use is important, as exemplified by differences between breeding and nonbreeding communities. Such factors as spatial or temporal partitioning of available breeding sites like meltwater ponds or of male calling sites generally organize the community (Bogert 1960, Collins 1975, Dixon and Heyer 1968, Wiest 1982). In essence, the community structure shifts; our studies in the Oregon Cascades have not fully analyzed any single structural entity. As Crump (1982) stated, "There has been little integration of reproductive ecology and community dynamics." We have some tantalizing hints of these relations but often little beyond life histories. Scott and Campbell (1982) stress the need for long-term studies of herpetological communities if we are to understand the roles of competition and intra-population social behavior. Our understanding is sketchy and our findings, particularly from this study, hardly predictive-except for the obvious need for adequate breeding conditions, whether that means clear, cool streams or sufficient ephemeral ponds, and for adequate substrate, such as logs for certain salamanders. None ,of these factors requires old-growth forests if forest planning and management succeed in ensuring uneven-aged structure, maintaining coarse woody debris, and protecting riparian zones.

Acknowledgments

The Oregon Cascades study was made possible by the contributions of many people, including U.S. Forest Service personnel. Effective field supervision was given by Wynn Cudmore, and crew leaders Jim Reichel and Troy Cline at Rogue River-Umpqua, Kathleen Fulmer at H.J. Andrews, and Jeff Picton at Mount Hood in 1984. The 1985 crew leader was Tony Fuchs. John Teburg, Dick Gilbert, Rich Alldredge, and Betsy Piersone all assisted in data entry and analysis. The hard-working field crews, primarily made up of Washington State University wildlife students, were essential to successful completion of the work.

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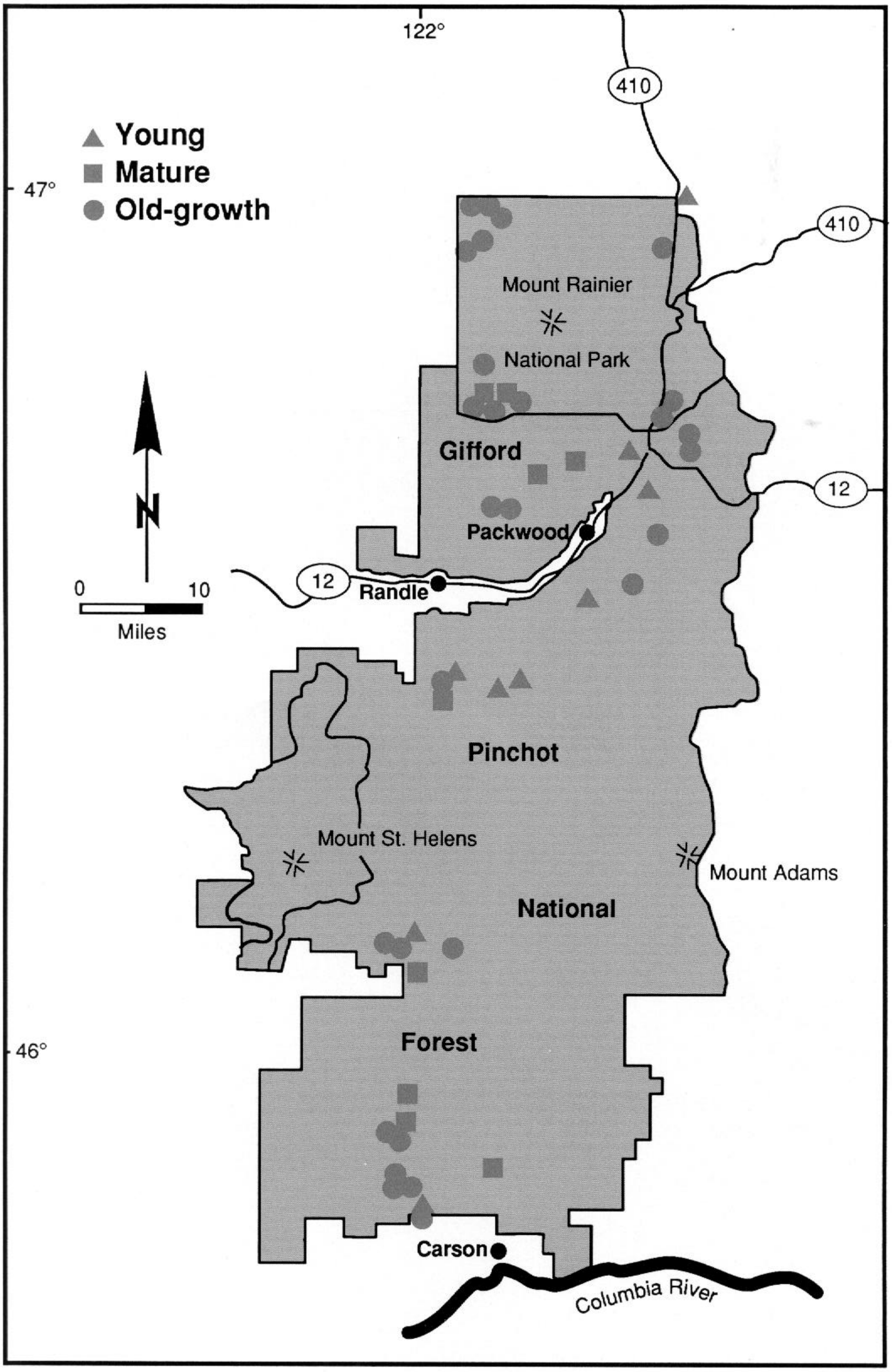

Location of study sites.

Terrestrial Amphibian Communities in the Southern Washington Cascade Range

Keith B. Aubry and Patricia A. Hall

Authors

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Abstract

We surveyed terrestrial amphibian communities with pitfall traps in 46 forest stands of various ages and moisture conditions in the southern Washington Cascade Range in 1984 and 1985. We captured a total of 1516 individuals of 13 species. Data were sufficient to examine community- and species-habitat relationships for seven species: ensatina, western redback salamander, northwestern salamander, roughskin newt, tailed frog, red-legged frog, and Cascades frog. We found no significant differences among stand age-classes for either species richness or diversity. Species richness, however, decreased significantly with both increasing elevation and increasing stand moisture. Detrended correspondence analysis (DCA) of amphibian communities revealed non-overlapping clusters of stands with distinct community composition; DCA axes were associated with gradients of slope, stand age, temperature, elevation, and moisture. In general, older stands with cooler temperatures and relatively flat slopes had the highest amphibian species richness.

The tailed frog was significantly more abundant in mature stands than in young stands. Although differences across the age gradient for other species were not significant, patterns of abundance for these species were evident. The ensatina and western redback salamander were most abundant in young stands, the red-legged frog in mature stands, and the north-western salamander, roughskin newt, and Cascades frog in old growth. Only abundances for the roughskin newt varied significantly among old-growth moisture-classes; abundance of this species was low in wet old-growth stands compared to either moderate or dry stands. The ensatina and north-western salamander also were least abundant in wet stands. The northwestern salamander and roughskin newt are associated with old-growth Douglas-fir forests in the southern Washington Cascades during the fall, whereas the ensatina, western redback salamander, and possibly the red-legged frog are associated with coarse woody debris that is characteristic of old-growth forests and unmanaged young forests.

Introduction

In recent years, harvest of old-growth Douglas-fir forests in the Pacific Northwest and its potentially detrimental effects on biological diversity have become a political and economic issue of national significance (see Lumen and Neitro 1980,

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Meslow and others 1981, Norse 1990, Norse and others 1986, Wilcove 1988). Most research on the habitat relationships of species associated with old-growth forests has been directed primarily at larger birds and mammals (for example, Meehan and others 1984), especially the spotted owl (GmZrrez and Carey 1985), which has become the social and political focus of concern over the loss of old-growth Douglas-fir forests.

Little work had been done on the habitat relationships of other birds, small mammals, amphibians, or reptiles in old-growth Douglas-fir forests, with the exception of vertebrate community studies conducted in the early 1980s in northern California (Raphael 1984, Raphael and Barrett 1984). In 1983, a comprehensive program of research was initiated throughout the Pacific Northwest to identify wildlife species that are associated with old-growth Douglas-fir forests and to investigate the ecological basis of observed patterns of association (this volume; Ruggiero and Carey 1984).

As part of this program of research, amphibian communities in different-aged Douglas-fir forests in the southern Washington Cascade Range were sampled with time-constrained searches, stream surveys, and pitfall trapping. Results of time-constrained searches were reported previously (Aubry and others 1988), and results of stream surveys are reported here by Bury and others (this volume b). In this paper, we report the results of pitfall trapping conducted in the fall of 1984 and 1985. Our objectives are to:

- Characterize the structure and composition of terrestrial amphibian communities in Douglas-fir forests of southern Washington and relate community patterns to features of the environment;
- Describe the habitat relationships of terrestrial amphibians in these forests;
- Identify terrestrial amphibian species that are associated with old-growth Douglas-fir forests; and,
- Make recommendations for further research.

Methods

Study Areas

We studied terrestrial amphibian communities in 46 closed-canopy forest stands on the western slope of the Cascade Range in southern Washington from Mount Rainier south to the Columbia River Gorge (see frontispiece). Stands were 55 to 730 years old, at least 20 ha in extent, and at elevations ranging from 404 to 1218 m. All had resulted from natural regeneration after catastrophic wildfires; none had undergone silvicultural manipulations.

All stands were in the Western Hemlock Zone and lower elevations of the Pacific Silver Fir Zone (Franklin and Dyrness 1973), which are characterized by a wet and mild maritime climate. Old-growth stands typically contained high proportions of both Douglas-fir and western hemlock. Old growth stands in wet sites also contained a high proportion of western redcedar. Mature and young stands consisted predominantly of Douglas-fir. In all age-classes, other species such as red alder, vine maple, bigleaf maple, Pacific silver fir, and western hemlock occurred in lesser amounts . See Spies and Franklin (this volume) and Spies (this volume) for more detailed descriptions of the vegetative and structural characteristics of the study stands.

Stands were selected for study in accordance with a "T-matrix" design consisting of an age gradient of stands of comparable moisture condition ranging from young to old growth, and an old-growth moisture gradient that consisted of old-growth stands ranging from wet to dry. See Carey and Spies (this volume) for a detailed description of the experimental design.

At least nine stands were selected in each of five age- and moisture-classes: wet old growth (210-730 years old), moderate old growth, and dry old growth; moderate mature (80-190 years old); and moderate young (55-75 years old). The average age of each stand was determined by growth-ring counts from increment coring or examination of cut stumps in nearby stands (Spies and others 1988). Stands were selected and tentatively classified into moisture-classes during initial field reconnaissance based on vegetation, physiography, and soils. Subsequent analyses of vegetation data collected in each stand resulted in refinements to the original classifications (Spies and Franklin, this volume). These analyses indicate that the young and mature stands we sampled encompass a broader range of environmental conditions than originally intended. Some of the wet and dry old-growth stands, for example, were comparable in moisture condition to the 'moderate' mature and young stands. Several old-growth stands were therefore reclassified as moderate for inclusion in age-gradient analyses. As a result, the age gradient of stands of comparable moisture condition for the southern Washington Cascade Range consisted of 37 stands: 19 old growth, 9 mature, and 9 young.

To compare moisture-classes of old-growth stands, Spies and Franklin (this volume) used ordination analyses of the species composition of old-growth stands to reevaluate the relative moisture condition of each stand. The resulting classification consisted of 9 wet, 12 moderate, and 7 dry old-growth stands. Because this classification is independent of the age-gradient classification, data from these two gradients were analyzed separately. Variation related to age was

Continue

assessed with data from stands in the age gradient, whereas variation from relative differences in moisture condition among old-growth stands was assessed with data from stands in the moisture gradient.

These analyses, and others conducted by Spies and Franklin (this volume), resulted in the construction of complex environmental gradients along which each stand could be assigned a quantitative value. We included these scores in our analyses to provide a means of identifying amphibian habitat relationships occurring along broad environmental gradients.

Amphibian Sampling

We sampled amphibians with pitfall traps in each stand after the onset of fall rains in 1984 and 1985. We installed 36 pitfall traps in each stand in a 6 x 6 square array with traps spaced 15 m apart. To prevent bias from the depletion of individuals in the immediate area of sampling, we moved each grid at least 50 m within the stand in 1985. We sampled all stands for 30 to 34 days each fall (with the exception of one stand that we sampled for only 24 days in 1984), and we checked the traps about once a week. All salvageable specimens were collected, preserved, and deposited in the University of Washington Burke Museum in Seattle.

Vegetation Sampling

We sampled vegetation at nine points within each grid, such that each vegetation point was uniquely associated with four traps. We sampled live vegetation and dead woody debris in two concentric circles around each vegetation point. We visually estimated the cover of vegetation and woody debris in the herb and shrub layers within a 5.6-m radius (100 m^2), and estimated physiographic midstory, and canopy variables within a 15-m radius (707 m^2). A list and description of the variables collected on each pitfall grid, the combined variables we constructed, and additional physiographic variables and environmental gradients that were used are included in appendix table 4.

Data Analyses

Because samples from 1984 and 1985 are not independent, we used the mean value for vertebrate and vegetation data from both years in all analyses. We calculated abundance indices for amphibian species as captures per 100 trap-nights for each stand. Data from time-constrained searches conducted in these stands in the spring of 1984 (Aubry and others 1988) were included only in species richness and presence/absence data sets.

Community-habitat relationships-Several species did not occur throughout the geographic range encompassed in our study; we therefore calculated species richness as the number of species captured in a stand divided by the number of species known to occur in the geographic area of the stand. The Shannon diversity index (H') was used to characterize species diversity for each stand. Note that, although our knowledge about the geographic distributions of birds and mammals in the Pacific Northwest is virtually complete, this is not true for amphibians. New distribution records have recently been reported for the Larch Mountain salamander (Aubry and others 1987), Van Dyke's salamander (Aubry and others 1987), Cope's giant salamander (Jones and Aubry 1984), tailed frog (Welsh 1985), and clouded salamander (Jones and Raphael 1989), among others.

We examined community patterns of amphibian abundances with detrended correspondence analysis (DCA) using the computer program DECORANA (Hill 1979a), and we identified stand clusters with TWINSPAN (Hill 1979b). We identified environmental gradients associated with each DCA axis with Spearman rank correlations and used direct gradient analysis (Gauch 1982) to further elucidate community-habitat relationships.

Species-habitat relationships-We used nonparametric analysis of variance (Kruskal-Wallis test) on log-transformed abundance values to examine differences in amphibian abundances among age-classes within the age gradient, and among moisture-classes within the old-growth moisture gradient. Because the study sites were preferentially selected to sample the full range of variation occurring within each age- and moisture-class (Carey and Spies, this volume), the variances in our data would be expected to exceed those resulting from random sampling. We therefore used an alpha level of $P \leq 0.1$ for all tests of significance. Because sampled stands were not selected randomly, we used these analyses to evaluate ecologically meaningful patterns in the data, rather than to conduct rigorous hypothesis testing. We identified significant pairwise differences using the Tukey Studentized Range test ($P \leq 0.05$).

We converted count variables in the vegetation data-set to densities, and transformed each vegetation variable with log, square-root, square, reciprocal, and arcsine transformations. We examined the resulting distributions for normality and performed all subsequent analyses on the transformed variables that best approximated univariate normality. We examined the relationships between abundances of individual species and physiographic and vegetative variables with Spearman rank correlations of transformed variables.

We used presence/absence data to further examine species-habitat relationships. We conducted stepwise and canonical discriminant function analyses (DFA) of stands in which a species was present versus those in which it was absent to identify habitat variables that may determine whether a species occurs in a stand. Because stands were not selected randomly, we used DFA only as an exploratory tool, and not as a method for deriving a predictive model. We used a subset of 33 uncorrelated habitat variables in all discriminant analyses (appendix table 4).

Results

We captured 1516 amphibians of 13 species (table 1). We selected seven species for inclusion in community- and species scale analyses of habitat relationships: ensatina, western redback salamander, northwestern salamander, roughskin newt, tailed frog, red-legged frog, and Cascades frog. The last five species have aquatic larval stages. Because juveniles of these species disperse seasonally from ponds and creeks, we do not know if such individuals captured in our pitfall traps were resident or simply moving through the stand to preferred habitats. For this reason, we only used data from adult captures of these species for our analyses (see table 1).

Other species were excluded because their abundances or percentage occurrence in sampled stands were too low (long-toed salamander and Pacific giant salamander), because they did not occur in all of the geographic areas sampled (Larch Mountain salamander and Olympic salamander),, or because they are not effectively sampled with pitfall traps (western toad and Pacific treefrog). Data on Pacific giant salamanders and Olympic salamanders were only used in calculations of species richness.

Table l-Amphibians captured in pitfall traps in the southern Washington Cascade Range in 1984 and 1985

Species	Total captures[a]	Percentage of stands
Salamanders:		
Woodland salamanders-		
Ensatina	800	85
Western redback salamander	162	28
Larch Mountain salamander		2
Mole salamanders-		
Northwestern salamander	135	52
Long-toed salamander	5	2
Newts-		
Roughskin newt	87	46
Giant and Olympic Salamanders		
Pacific giant salamander	12	11
Olympic salamander	14	9
Frogs and toads:		
True frogs-		
Red-legged frog	69	48
Cascades frog	11	17
Tailed frogs-		
Tailed frog	203	67
Treefrogs-		
Pacific treefrog	5	4
True toads-		
Western toad	12	13
Total captures	1516	100

[a] Only adults are reported for the long-toed salamander (snout-vent length (SVL) >45 mm); northwestern salamander (SVL >70 mm); roughskin newt (SVL >40 mm); red-legged, Cascades, and tailed frogs (SVL >35 mm).

Community-Habitat Relationships

We found no significant differences in species richness or species diversity among stand classes within either the age gradient or the old-growth moisture-gradient. Our data, however, do suggest trends of increasing species richness and diversity with stand age, and with drier conditions in old-growth stands (fig. 1). Species richness and diversity were also less variable in old growth than in younger stands, suggesting that old-growth stands may be more stable in community composition. Species richness appears to be influenced more by elevation than by stand age. We found significant negative correlations ($P \leq 0.05$) between species richness and elevation for both the age gradient (fig. 2) and the old-growth moisture gradient (fig. 3).

Age gradient-Ordination of abundance data for amphibian communities occurring in stands within the age gradient resulted in two non-overlapping clusters of stands with distinct community composition (fig. 4). The first DCA axis (X axis) represents a gradient of increasing moisture and elevation; the second DCA axis (Y axis) is negatively associated with slope and temperature and positively associated with stand age. Most of the separation of clusters occurs along DCA 2. Stands in cluster 1 are located near the origin of DCA 1, whereas stands in cluster 2 occur along the entire length of this axis.

Ensatinas were abundant in most stands, but all other species occurred in high numbers in only one of the two clusters. Cluster 1 consists of stands with abundant pond-breeding frogs and salamanders (red-legged and Cascades frogs, northwestern salamanders, and roughskin newts) and few tailed frogs (a stream-breeding species) and western redback salamanders (a woodland salamander that breeds on land).

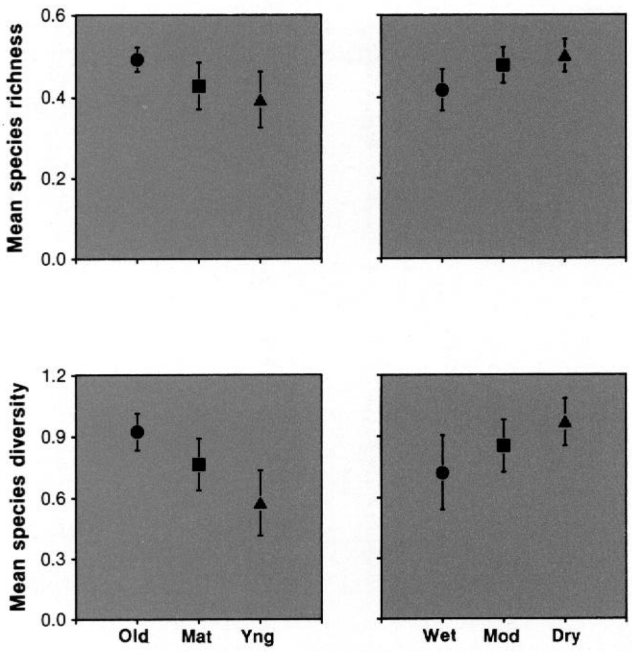

Figure 1—Mean species richness (upper graphs) and diversity (lower graphs) for the age gradient and old-growth moisture gradient. Vertical bars represent standard errors of the mean. Stand age-class: Old = old growth, Mat = mature, Yng = young. Old-growth moisture condition: Wet = wet old growth, Mod = moderate old growth, Dry = dry old growth.

Cluster 1 primarily consists of mature and old-growth stands that are relatively flat and cool; only one young stand occurred in this cluster.

The wettest and highest elevation stands occur in cluster 2, which is characterized by low numbers of the pond-breeding species and abundant tailed frogs, western redback salamanders, and ensatinas. The stands in this cluster are generally younger than those in cluster 1 and characterized by steeper slopes and warmer temperatures. They encompass the full range of variation in moisture and elevation that occurs in stands within the age gradient.

Old-growth moisture gradient—Ordination of the abundance data for only old-growth stands also resulted in two clusters of stands with distinct community composition (fig. 5). DCA 1 (X axis) represents a gradient of increasing elevation and moisture, whereas DCA 2 (Y axis) is weakly associated with a stand-development gradient that is primarily related to increasing basal area of western hemlock and other shade-tolerant species (Spies and Franklin, this volume).

Most of the stands occur in cluster 1 and all seven species are relatively abundant. Stands in cluster 2 were depauperate, by comparison, with low abundances of all species except tailed frogs and northwestern salamanders. Complete overlap of clusters 1 and 2 occurred along the stand-development gradient, but the clusters were fully distinguishable along the gradient of increasing elevation and moisture. Stands in cluster 2 consist of the wetter, higher elevation, old-growth stands.

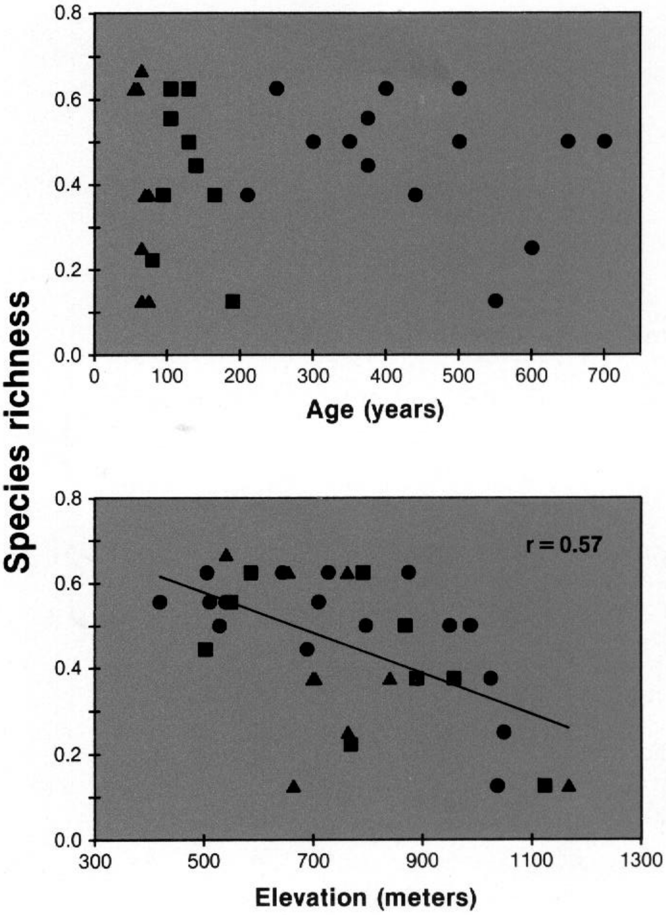

Figure 2—Gradient analyses of species richness vs. stand age (upper graph) and elevation (lower graph) for stands included in the age gradient. Age-class symbols: circle = old growth, square = mature, triangle = young.

Species-Habitat Relationships

Age gradient—Mean abundance values for the seven selected species and for all seven species combined within each age-class of the age gradient are shown in figure 6. Significant differences among age-classes were found only for the tailed frog, which was more abundant in mature stands than in young stands.

Although differences among age-classes for other species were not significant, patterns of association with age were evident. The ensatina and western redback salamander were most abundant in young stands. Western redback salamanders, in particular, occurred in very low numbers in mature

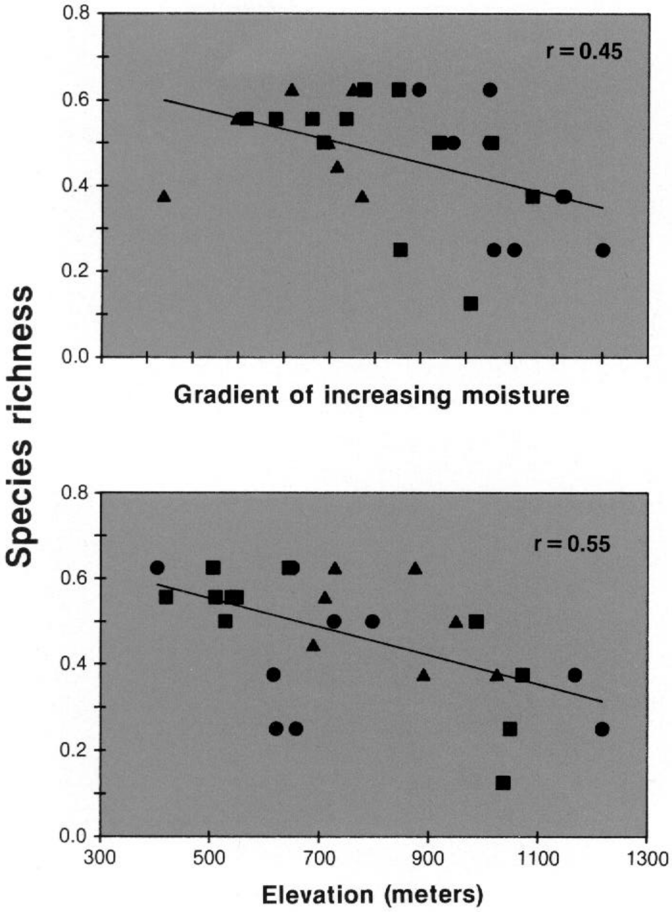

Figure 3—Gradient analyses of species richness vs. moisture condition (upper graph) and elevation (lower graph) for stands included in the old-growth moisture gradient. Moisture-condition symbols: circle = wet, square = moderate, triangle = dry.

and old-growth stands. The northwestern salamander, roughskin newt, and Cascades frog all reached their highest abundances in old growth. Tailed frogs and red-legged frogs were most abundant in mature stands and least abundant in young stands. Total combined abundances of all seven species was highest in young stands, although variation among stands in this age-class was high. Variation in total abundance among mature and old-growth stands, by contrast, was relatively low, which again suggests that older forests may provide more consistently suitable habitat for amphibians than do young forests.

Old-growth moisture gradient—Mean abundance values for amphibians among old-growth moisture-classes are depicted in figure 7. Abundances for the roughskin newt alone varied significantly among moisture-classes, but multiple-range tests failed to identify which moisture-classes differed significantly.

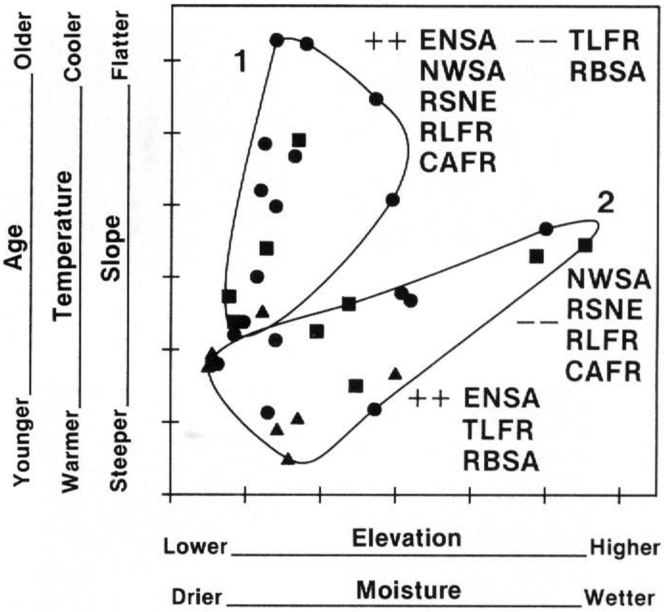

Figure 4—Ordination of species abundances for stands included in the age gradient. Axes represent associated environmental and physiographic gradients. Age-class symbols: circle = old growth, square = mature, triangle = young. Species abbreviations: ENSA = ensatina, RBSA = western redback salamander, NWSA = northwestern salamander, RSNE = roughskin newt, RLFR = red-legged frog, CAFR = Cascades frog, TLFR = tailed frog.

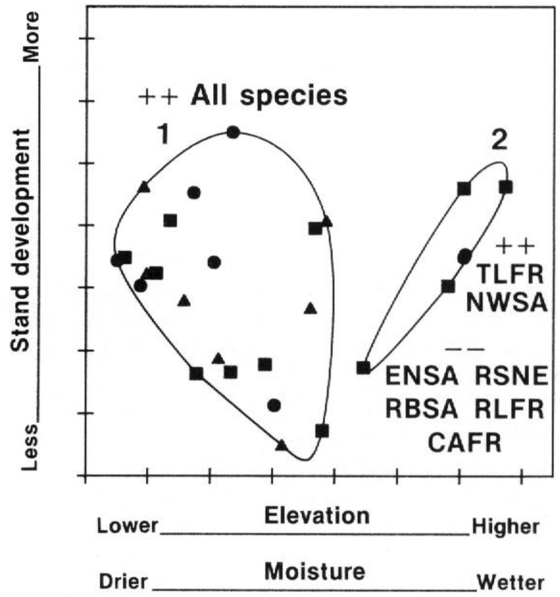

Figure 5—Ordination of species abundances for stands included in the old-growth moisture gradient. Axes represent associated environmental and physiographic gradients. Moisture-class symbols: circle = wet, square = moderate, triangle = dry. Species abbreviations: ENSA = ensatina, RBSA = western redback salamander, NWSA = northwestern salamander, RSNE = roughskin newt, RLFR = red-legged frog, CAFR = Cascades frog, TLFR = tailed frog.

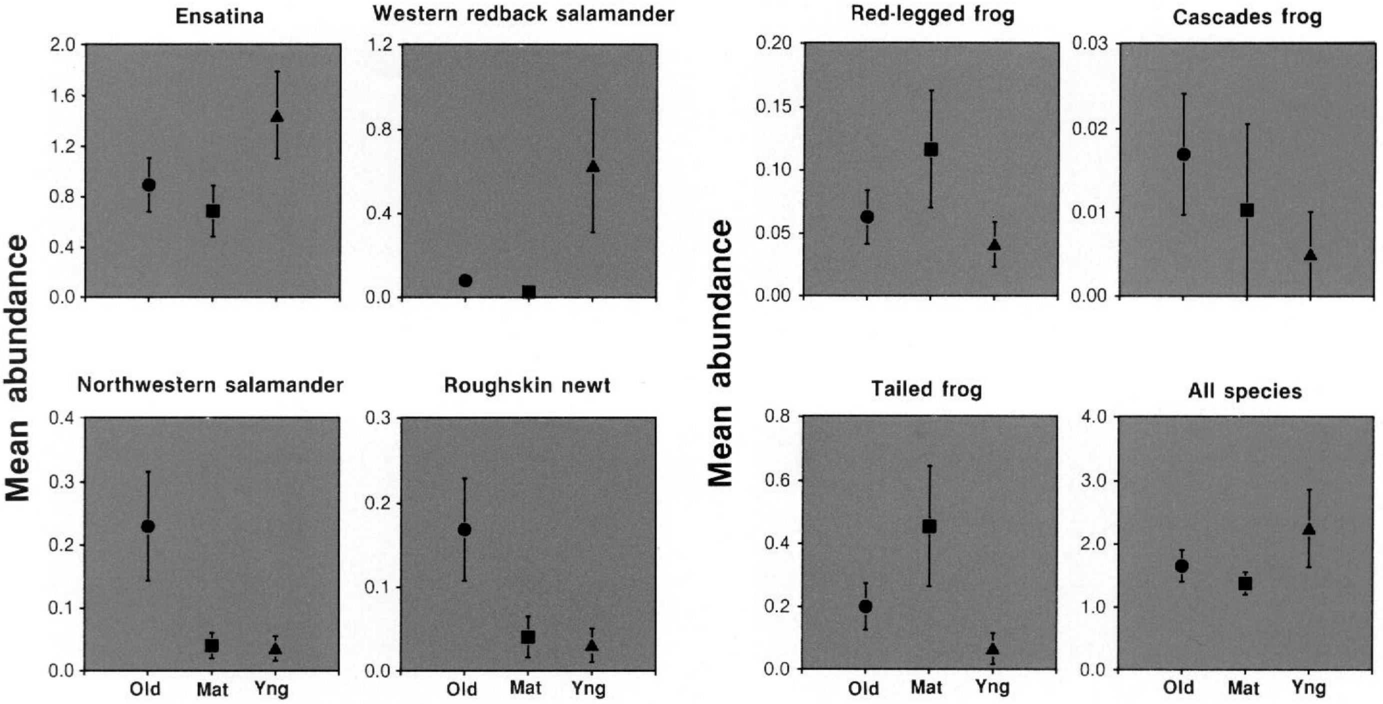

Figure 6—Mean abundance and standard error for seven selected amphibian species by age-class for stands included in the age gradient. Age-classes: Old = old growth, Mat = mature, Yng = young.

Wet old-growth stands appear to provide low-quality habitat for several species. The ensatina and roughskin newt were rarely found in wet stands, and mean abundance values for northwestern salamanders, and for all seven species combined, increased with drier conditions. Red-legged and Cascades frogs reached their highest abundances in stands with moderate moisture, whereas western redback salamanders and tailed frogs showed little association with moisture condition.

All stands—Significant correlations between species abundances and physiographic, vegetative, and structural habitat variables are listed in table 2. Several of the environmental variables associated with community organization (figs. 4, 5) and with abundance patterns across the age and moisture gradients (figs. 6-9) showed meaningful correlations. These included negative correlations with increasing elevation and moisture for the ensatina, roughskin newt, and red-legged frog; positive correlation with increasing elevation for the tailed frog; positive correlation with increasing temperature for the western redback salamander; negative correlation with increasing age for the ensatina; and negative correlation with increasing slope for the red-legged frog (table 2).

Table 2—Significant correlations ($P \leq 0.05$) between physiographic and vegetative variables and abundances of amphibian species in the southern Washington Cascade Range (variables are listed in order of decreasing importance, by column)

Species	Significant correlations		
Ensatina	MDTREE (+)	STUMPC (-)	CONIFL (-)
	WPDCA1 (-)	LMSNAGA (-)	LITTERD (-)
	ESHRUB (+)	WATER (-)	AGE (-)
	ELEV (-)	LMSNAGC (+)	CONIFVL (-)
	BRODLEAF (+)	LTSNAGC (+)	
	MTSNAGB (-)	MSHRUB (+)	
Western redback salamander	SNAGSB (-)	STUMPB (-)	WPDCA2 (+)
	CBTREE (-)	CDTREE (-)	
Northwestern salamander	LTSNAGA (+)	SSNAGA (-)	LMSNAGA (+)
Roughskin newt	ELEV (-)	WPDCA1 (-)	SHRUB (+)
	BRODLEAF (+)	SNAGSC (-)	MSNAGS (-)
	MDTREE (+)	STUMPC (-)	
Red-legged frog	ELEV (-)	TALUS (-)	SLOPE (-)
	OUTCROP (-)	BRODLEAF (+)	
	MDTREE (+)	WPDCA1 (-)	
Cascades frog	SSNAGC (+)		
Tailed frog	ESHRUB (-)	TALUS (+)	SNAGSB (-)
	ELEV (+)	FERN (-)	MSHRUB (-)
	MOSS (-)	BROADM (-)	DLOGSB (-)

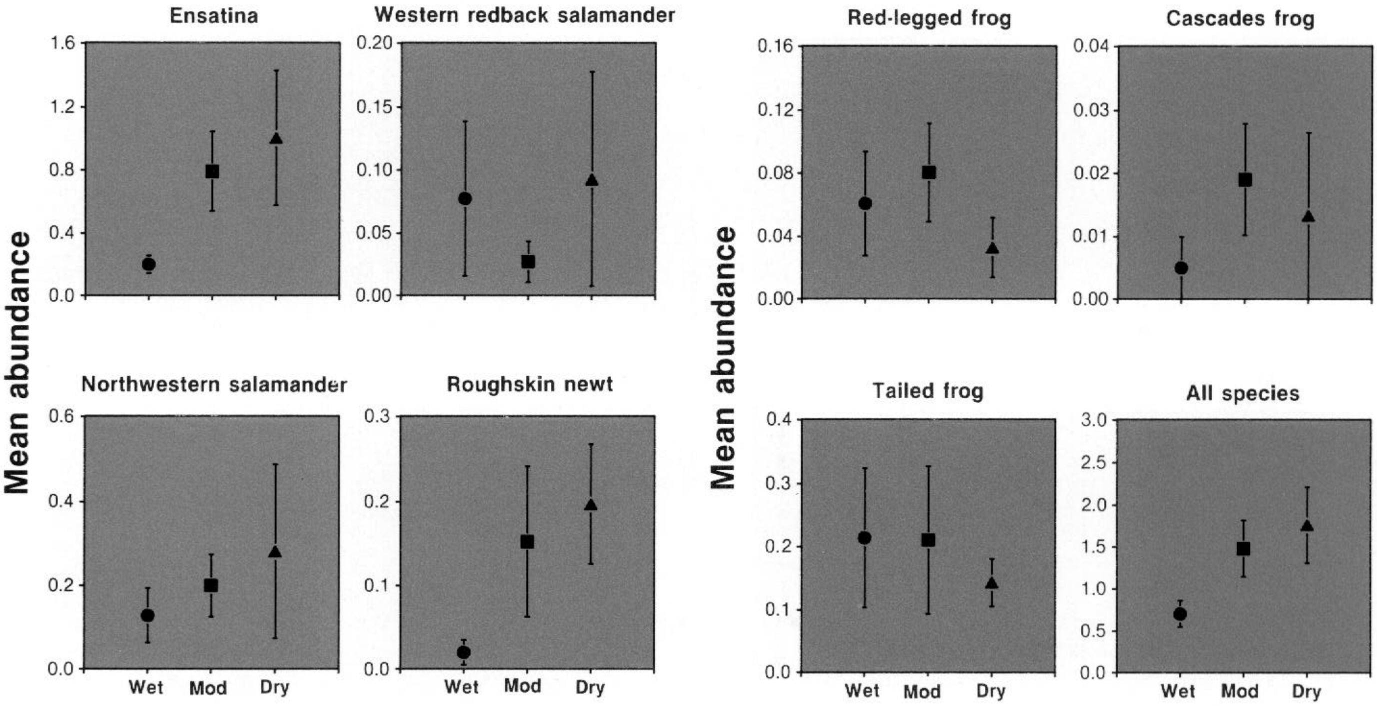

Figure 7—Mean abundance and standard error for seven selected amphibian species by moisture-class for stands included in the old-growth moisture gradient. Moisture classes: Wet = wet old growth, Mod = moderate old growth, Dry = dry old growth.

Correlations with vegetative and structural variables were difficult to interpret, especially for those variables that were positively correlated with abundance. Except for the northwestern salamander, which was positively correlated with only three different height- and diameter-classes of intact snags, most species were positively correlated with vegetative features of the shrub and canopy layers. Speculating about the habitat value of such features for amphibians occupying the forest floor is difficult.

Discriminant function analyses of presence/absence data revealed sets of variables for each species that differed somewhat from those generated with correlation analysis (table 3). Variables in the DFA models also generally supported the findings of detrended correspondence analysis of the composition of amphibian communities (figs. 4, 5). Ensatinas and red-legged frogs were typically absent from relatively wet stands. Ensatinas did not occur in stands containing surface water, however, whereas red-legged frogs were found in relatively flat stands where surface water was present. Tailed frogs occurred in relatively steep stands containing surface water. Both ensatinas and roughskin newts were absent from high-elevation stands. Northwestern salamanders occurred in stands containing surface water and a relatively deep litter layer. The red-legged frog was the only species of amphibian associated with high amounts of woody debris.

Discussion

Community-Habitat Relationships

A suite of environmental variables—of which stand age is but one minor factor—apparently determines the structure and composition of terrestrial amphibian communities in unmanaged Douglas-fir forests in the southern Washington Cascade Range. Young stands contained a relatively depauperate amphibian community compared to older stands, but young stands were also generally steeper and warmer. These conditions generally result in a lack of ponds and correspondingly poor habitat for the pond-breeding salamanders and frogs that represent the majority of species studied. Older stands with flatter slopes and cooler temperatures, which presumably favor formation of ponds, generally contained the most species (fig. 5). Species richness and diversity generally increased with stand age (fig. 1), but age appeared to have less influence on community composition than either elevation or moisture condition.

In our study sites, elevation and moisture condition were highly correlated; the highest elevation stands were also the wettest (see figs. 4, 5). Harsher climatic conditions at higher elevations in the Cascade Range (Franklin and Dyrness 1973) may account for lower species richness there, but very wet stands also appear to provide low-quality habitat for most amphibians. Ensatinas, which prefer moist habitats and are not tied to streams or ponds for reproduction, are rarely found

Table 3-Results of discriminant function analysis between stands in which a species was present versus those in which it was absent

Item	Ensatina (39:7)[a]	Western redback salamander (14:32)	North-western salamander (24:22)	roughskin newt (21:25)	Red-legged frog (22:24)	Cascades frog (9:37)	Tailed frog (31:15)
Variables[b]	WPDCAl MCTREE (+) CDTREE SSNAGS ELEV WATER CCTREE (+) DLOGS	CDTREE MCTREE (+) CBTREE CONIFERS LSNAGS SSNAGS	WATER (+) CANOPY CBTREE LITTERD (+) CONIFL BROADVL	ELEV SNAGSC ASPECT	WPDCAl CCTREE SLOPE WATER (+) DLOGS (+) TALUS	**DLOGSA** DLOGS CDTREE (+) FLITTER CCTREE (+) BRODLEAF (+: CBTREE (+)	ESHRUB SLOPE (+) CANOPY MCTREE (+) WATER (+)
R^2	0.63	0.45	0.36	0.47	0.51	0.42	0.57
Percentage correct[c]	90	69	51	60	72	68	75

[a] Numbers in parentheses indicate the number of stands in which a species was present in proportion to the number of stands in which a species was absent.

[b] Variables are listed in order of decreasing importance in the model. Variables that are associated with the Occurrence of a species are indicated with a plus (+).

[c] The percentage correct classification was established through cross-validation.

in wet old-growth stands where soils may be saturated with water (see also Aubry and others 1988). Northwestern salamanders and roughskin newts also rarely occurred in wet old-growth stands (fig. 7), even though these species were most abundant in old-growth stands in the age gradient (fig. 6). Among stands in the old-growth moisture gradient, species richness was lowest in wet stands (figs. 1,5), and combined abundances for all species were substantially lower in wet old-growth stands than in either moderate or dry stands (fig. 7).

The structural and functional complexity that is characteristic of old-growth Douglas-fir forests has resulted from hundreds of years of stand development. This ecological complexity would not be expected to occur in younger forests (Franklin and others 1981). We consequently expected to find significantly lower amphibian species richness and abundances in young stands. The reason we did not is probably related to the pattern of input and loss of coarse woody debris in stands that have regenerated after catastrophic wildfires. Naturally regenerated young stands have a large carryover component of snags and logs (Spies and others 1988). Younger-aged unmanaged stands therefore have many of the ecological characteristics of old-growth forests. In unmanaged closed-canopy forests, these features provide habitat for amphibians that would not be expected to occur in forest stands that result from current timber-harvesting practices (Aubry and others 1988; Bury and Corn 1988a, b; Spies and Cline 1988). Unmanaged closed-canopy forests of similar physiography apparently support similar terrestrial amphibian communities, regardless of age. Whether these communities would also occur in managed forests is not a question that can be adequately addressed with our data.

Species-Habitat Relationships

Ensatina-Ensatinas were most often found in young stands in the age gradient (fig. 6), and in moderate and dry stands in the old-growth moisture gradient (fig. 7). Relatively dry to mesic conditions at low to mid-elevations appear to be the major environmental influences on abundance for this species (tables 2,3).

Previous studies of microhabitat use in the Cascade Range indicate a positive association between ensatina abundances and amounts of coarse woody debris, especially with moderately and well-decayed logs and snags (Aubry and others 1988, Bury and Corn 1988a). Our pitfall results also support this hypothesis. Ensatinas were least abundant in mature stands (fig. 6), which typically contain less coarse woody debris than do either old-growth or young stands (Spies and others 1988). This pattern was primarily because of high inheritance of coarse woody debris in young stands resulting from catastrophic fires. Lower amounts accumulate in mature stands as existing debris decays, but inputs remain low. By comparison, old-growth stands accumulate high amounts of debris as the large Douglas-firs die and inputs are high. Ensatina abundances were also positively correlated to the density of well-decayed stumps and snags >50 cm d.b.h. and at least 1.5-m tall (table 2). Such features provide favorable habitat for ensatinas as the bark sloughs to the ground in piles around the snag and forms multilayered, structurally complex cover (Aubry and others 1988). Well-decayed stumps and snags may also provide below-ground habitat within the decomposing root system.

The ensatina is not associated with old-growth stands, but some evidence indicates that this species is associated with the large amounts of coarse woody debris characteristic of old-growth forests (Franklin and others 1981). Our results suggest that ensatinas may be adversely affected by timber harvesting because intensive forest management results in substantially less coarse woody debris than that encountered in unmanaged forests (Spies and Cline 1988). Provision for increased amounts of coarse woody debris in managed forests would be expected to benefit this species.

Western redback salamander-Western redback salamanders were most abundant in young stands. Young stands, however, were also relatively steep, warm, and dry (fig. 4), and analyses of habitat variables suggest that these factors are more important environmental influences for this species than is stand age. Abundance of western redback salamanders was positively correlated with a gradient of increasing temperature (table 2), yet neither analysis indicated a negative association with age.

Previous authors have reported that western redback salamanders are commonly found in talus slopes (Herrington 1988, Nussbaum and others 1983). Although this species favored steeper slopes, we found no evidence of an association with talus in the southern Washington Cascade Range. Our observations indicate that talus slopes are relatively rare in these forests. The drier conditions of steep slopes apparently are more important for this species than the presence of talus. Studies of cover-object use showed that western redback salamanders are most frequently found under moderately decayed logs >l0 cm in diameter (Aubry and others 1988). The western redback salamander is also not strongly associated with old-growth stands, but the retention of coarse woody debris in managed forests would probably also create conditions favorable for this species.

Northwestern salamander-Northwestern salamanders were five times more abundant in old-growth than in younger stands (fig. 6). The northwestern salamander was also the only species of salamander present in relatively high numbers in both clusters of the old-growth ordination (fig. 5). Mean abundance increased with drier conditions in old growth, but variation in abundances in dry stands was extremely high (fig. 7). The age-gradient ordination indicated that this species and all other pond-breeding salamanders and frogs reached their highest abundances in relatively old, cool, flat stands that were not extremely wet or high in elevation (fig. 4). We found a strong correlation with all sizes of relatively intact snags (table 2), but how these structural features might provide habitat for northwestern salamanders is not clear.

Our results showed the northwestern salamander to be closely associated with old-growth Douglas-fir forests in the southern Washington Cascade Range during the late fall. Bury and Corn (1988a) previously found little evidence that northwestern salamanders were associated with old-growth forests in the southern Washington Cascade Range, but differences in the timing of sampling probably explain our divergent results. Bury and Corn (1988a) ran their pitfall traps from May to November, and our traps were open from late September to November. Northwestern salamanders migrate seasonally to and from breeding ponds, and captures during the reproductive season may therefore simply reflect individual movement through the stand to and from breeding ponds rather than selection of the habitat in which they were captured. Suitable breeding ponds are essential habitat features for this species, but high-quality overwintering habitat may also be critical for population persistence. Our results indicate that old-growth forests are important habitats for northwestern salamanders during the nonbreeding season in southern Washington.

Regional comparisons by Bury and others (this volume a) showed that northwestern salamanders were associated with old-growth forests only in southern Washington, and that late-fall abundances in both the Oregon Cascade Range and the Oregon Coast Range were similar across the age gradient. Pitfall captures for northwestern salamanders were much lower in the Coast Range (38; Corn and Bury, this volume b) and the Oregon Cascade Range (38; Gilbert and Allwine, this volume c), than in the southern Washington Cascade Range (135; this study). Data on this species from the Oregon provinces, therefore, should be interpreted with caution. These results may, however, indicate a latitude effect whereby harsher climatic conditions in more northerly forests (Franklin and Dymess 1973) force north-western salamanders to seek overwintering sites in old-growth forests where climatic conditions are less extreme (Spies and Franklin 1988). Results from the Oregon Cascade Range provide additional support for this hypothesis. The northernmost 16 stands in the Oregon Cascades (in the vicinity of Mount Hood) accounted for 31 of 38 captures for this species in the Oregon Cascade Range. For these stands, northwestern salamanders occurred at significantly higher abundances in old-growth forests than in either mature or young forests (Gilbert and Allwine, this volume c).

Roughskin newt-Roughskin newts were four to five times more abundant in old growth than in younger stands (fig. 6). Unlike northwestern salamanders, however, this species was much less abundant in wet old-growth than in either moderate or dry stands (fig. 7). This difference was also evident in the old-growth ordination, where roughskin newts were found at lower abundances than northwestern salamanders in wetter stands at higher elevations (fig. 5). Ordination of stands in the age gradient showed that roughskin newts exhibited the same community associations as northwestern salamanders in stands where environmental conditions were relatively moderate (fig. 4). Unlike northwestern salamanders, however, roughskin newts were generally absent from high-elevation stands (table 3). Consequently, although the roughskin newt is closely associated with old-growth forests during the nonbreeding season in southern Washington, it does not occupy wet sites at high elevations.

Just as for northwestern salamanders, marked variation was found in regional abundance patterns for roughskin newts (see Bury and others, this volume a). In the Oregon Cascade Range, roughskin newts were associated with young forests (Gilbert and Allwine, this volume c). In the Oregon Coast Range, by contrast, no strong patterns were found in the data although roughskin newts reached highest abundances in old-growth stands (Corn and Bury, this volume b). These results may also reflect a latitude effect where old-growth forests provide critical overwintering habitat only at northern latitudes.

Red-legged frog-Red-legged frogs were most abundant in mature stands within the age gradient (fig. 6) and in moderate old-growth stands within the old-growth moisture gradient (fig. 7). In terms of community association, red-legged frogs exhibited the same patterns as the other pond breeders, with the exception of the northwestern salamander, which alone occupies the higher, wetter old-growth stands (figs. 4, 7). This species was negatively associated with elevation, stand moisture condition, talus, and steep slopes, and was positively associated with cover by woody debris and the presence of water (tables 2, 3). The presence and abundance of this species apparently was largely determined by conditions favoring the formation of ponds in relatively moderate stand conditions. This species showed little association with stand age, but its presence was correlated with high levels of woody debris, which suggests that red-legged frogs may require this habitat feature for hiding cover.

Cascades frog-Captures for Cascades frogs were low, but their abundance increased with stand age (fig. 6). Of 13 Cascades frogs captured (11 in pitfalls and 2 in time-constrained searches), 10 (77 percent) were found in old-growth stands. Community-association patterns for Cascades frogs were the same as for red-legged frogs (figs. 4,5), as were their apparent preferences for old-growth stands of moderate moisture condition (fig. 7). Patterns of association with individual habitat variables revealed little interpretable information, probably because of low abundance values. Further work is needed on this species to evaluate its potential preference for old-growth forests.

Tailed frog-The tailed frog was significantly more abundant in mature stands than in young stands (fig. 6). Its patterns of community association were the same as those for western redback salamanders within the age gradient (fig. 4) and for northwestern salamanders within the old-growth moisture gradient (fig. 5). Habitat analyses indicated that tailed frogs were associated with steep slopes, high elevations, talus, and the presence of water (tables 2,3).

Western redback salamanders appear to be correlated with the drier environmental conditions found on steep slopes, but tailed frogs are more likely associated with the cool, clear creeks that also occur on steep slopes (Nussbaum and others 1983). Our results do not show the tailed frog to be associated with old-growth forests; however, young stands apparently provide relatively unsuitable habitat for this species in the southern Washington Cascades.

Recommendations for Further Research

- Intensive research is needed on the northwestern salamander and roughskin newt to elucidate the ecological basis of their association with old-growth forests in southern Washington. These studies should be conducted during both the breeding and nonbreeding seasons to evaluate the potential seasonality of habitat association patterns.
- Research should also be directed at evaluating the importance of coarse woody debris as habitat features for the ensatina, western redback salamander, and possibly the red-legged frog, to determine if amounts of coarse woody debris in managed forests will be sufficient to maintain viable populations of these species in Douglas-fir forests.
- Studies of the tailed frog should be undertaken in both unmanaged and managed young forests to investigate the low habitat quality of young stands.
- Extensive studies of amphibian communities in managed forests should be initiated immediately.
- Long-term research on terrestrial amphibians in unmanaged and managed Douglas-fir forests should be initiated to determine if patterns of association and habitat relationships vary over time, and to evaluate the extent to which amphibian populations may be affected by forest management over the long term.

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Appendix

Table 4-Physiographic and vegetative variables examined in the southern Washington Cascade Range (variables used in discriminant function analyses are indicated with a solid circle)

Variable	Description
Physiographic:	
. ELEV	Elevation
• AGE	Age
. ASPECT	Aspect
• SLOPE	Percentage slope
. WPDCA1	Moisture gradient
. WPDCA2	Temperature gradient
CDACHRN1	Age gradient
CDACHRN2	Coarse woody debris gradient
CDAOLDG1	Stand-development gradient
CDAOLDG2	Stand-development gradient
. TALUS	Percentage of stations with talus present
OUTCROP	Percentage of stations with outcrops present
INTSTREM	Percentage of stations with intermittent streams present
PERSTREM	Percentage of stations with perennial streams present
POOLS	Percentage of stations with pools or ponds present
. WATER	Percentage of stations with a source of water present
Percentage cover:	
GRASS	Grass
HERB	Herbaceous vegetation
• ROCK	Rocks
• SOIL	soil
MOSS	Moss
• LICHEN	Lichen
. FLITTER	Fine litter
FERN	Fern
• ESHRUB	Evergreen shrubs
DSHRUB	Deciduous shrubs
• BSHRUB	Berry-bearing shrubs
SHRUB	All shrubs
TALLCOVR	All shrubs and ferns
MSHRUB	Shrubs in the midcanopy
. MCTREE	Conifer trees in the midcanopy
MDTREE	Deciduous trees in the midcanopy
. MBTREE	Broadleaved evergreen trees in the midcanopy
MCANOPY	Midcanopy
. CDTREE	Deciduous trees in the canopy
• CBTREE	Broadleaved evergreen trees in the canopy
• CCTREE	Conifer trees in the canopy
• CANOPY	Canopy
• DLOGSA	Intact woody debris
DLOGSB	Moderately decayed woody debris
DLOGSC	Well-decayed woody debris
• DLOGS	Woody debris
Live-tree density:	
CONIFS	Conifer trees, d.b.h. 1-10 cm
CONIFM	Conifer trees, d.b.h. 10-50 cm
. CONIFL	Conifer trees, d.b.h. 50-100 cm
• CONIFVL	Conifer trees d.b.h. >100 cm
. CONIFERS	All conifer trees
BROADS	Deciduous and broadleaved evergreen trees, d.b.h. 1-10 cm
BROADM	Deciduous and broadleaved evergreen trees, d.b.h. 10-50 cm
• BROADL	Deciduous and broadleaved evergreen trees, d.b.h. 50-100 cm
• BROADVL	Deciduous and broadleaved evergreen trees d.b.h. >100 cm
• BRODLEAF	All deciduous and broadleaved evergreen trees
Stump and snag density:	
STUMPA	Intact to slightly decayed stumps
STUMPB	Moderately decayed stumps
STUMPC	Well-decayed stumps
STUMPS	stumps
SSNAGA	Intact to slightly decayed snags, d.b.h. <10 cm, ht <1.5 m
SSNAGB	Moderately decayed snags, d.b.h. <10 cm, ht <1.5 m
SSNAGC	Well-decayed snags, d.b.h. <10 cm, ht <1.5 m
. SSNAGS	All snags, d.b.h. <10 cm, ht <1.5 m
MMSNAGA	Intact to slightly decayed snags, d.b.h. 10-50 cm, ht 1.5-15 m
MMSNAGB	Moderately decayed snags, d.b.h. 10-50 cm, 1.5-15 m
MMSNAGC	Well-decayed snags, d.b.h. 10-50 cm, ht 1.5-15 m
MTSNAGA	Intact to slightly decayed snags, d.b.h. 10-50 cm, ht >15 m
MTSNAGB	Moderately decayed snags, d.b.h. 10-50 cm, ht >15 m
MTSNAGC	Well-decayed snags, d.b.h. 10-50 cm, ht >15 m
• MSNAGS	All snags, d.b.h. 10-50 cm, ht >1.5 m
LMSNAGA	Intact to slightly decayed snags, d.b.h. 250 cm, ht 1.5-15 m
LMSNAGB	Moderately decayed snags, d.b.h. >50 cm, ht 1.5-15 m
LMSNAGC	Well-decayed snags, d.b.h. >50 cm, ht 1.5-15 m
LTSNAGA	Intact to slightly decayed snags, d.b.h. >50 cm, ht >15 m
LTSNAGB	Moderately decayed snags, d.b.h. >50 cm, ht >15 m
LTSNAGC	Well-decayed snags, d.b.h. >50 cm, ht >15 m
. LSNAGS	All snags, d.b.h. >50 cm, ht >1.5 m
SNAGSA	All intact to slightly decayed snags
SNAGSB	All moderately decayed snags
• SNAGSC	All well-decayed snags
Other:	
SCAN	Presence of super-canopy trees
● ☹✋❄❄☜☼👎	Depth of litter layer
TREPIT	Density of tree pits

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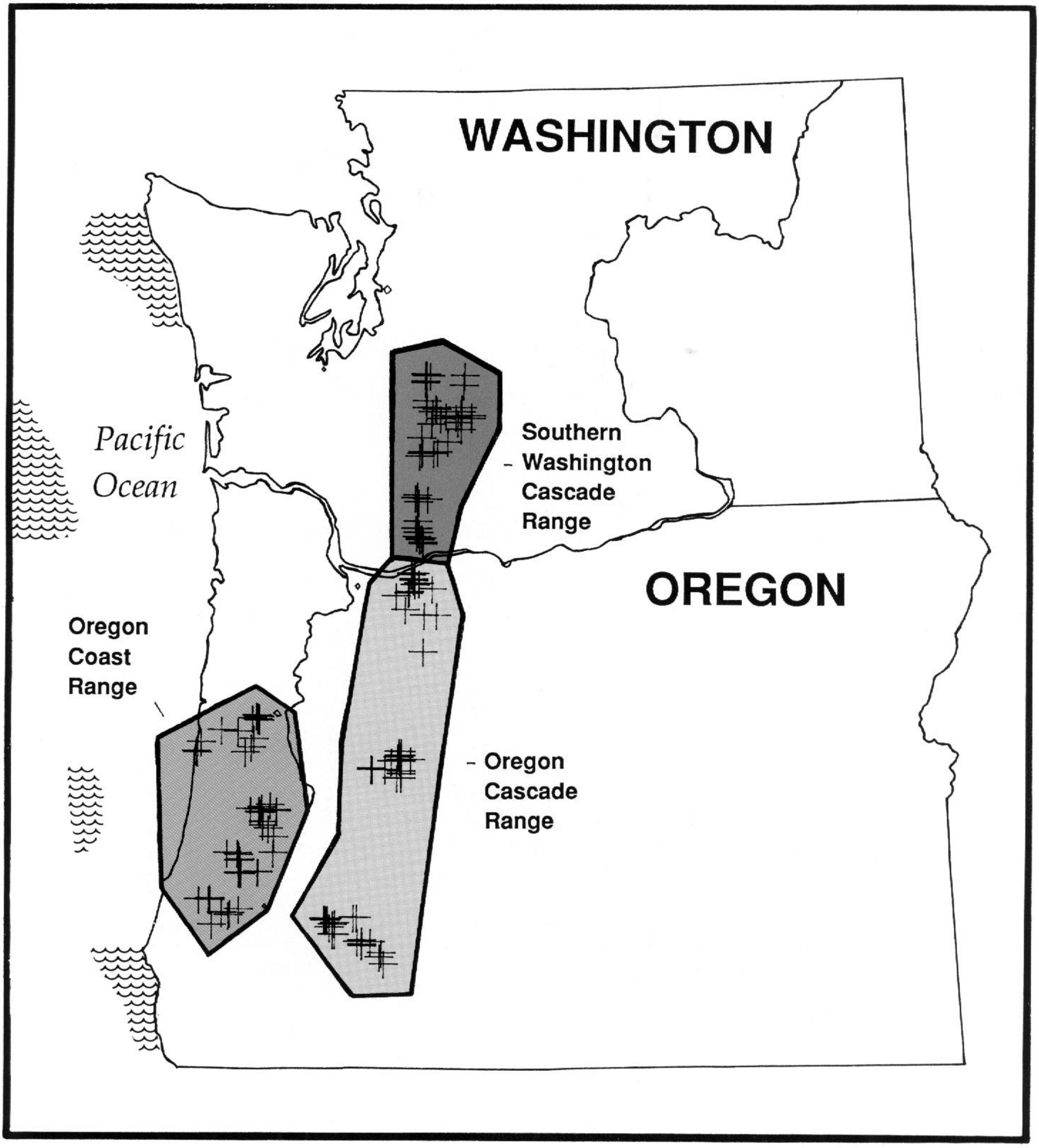

Location of study sites within the three physiographic provinces.

Regional Patterns of Terrestrial Amphibian Communities in Oregon and Washington

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Abstract

We examined the occurrence and abundance patterns of terrestrial amphibians in the Pacific Northwest, mostly based on captures in pitfall traps at 130 study sites. Seven of eight widespread species showed a marked variation in abundance between the Oregon Coast Range and the Cascade Range in Oregon and Washington. Only two species were associated with an age gradient (young, mature, and old-growth forests): the northwestern salamander was usually most abundant in old growth, whereas the western redback salamander occurred in highest numbers in young stands. Ensatina was most abundant in dry old growth in the Cascade Range and was the only species with a marked response across a moisture gradient (wet, moderate, and dry forests). Abundance of species was more often associated with physiographic variables than with vegetation features. On the basis of multidimensional scaling of species richness, the amphibian community in the Coast Range appears distinct from that in the Cascade Range. The highest species richness was in the Oregon Coast Range, whereas the lowest species richness was in the Cascade Range in Washington. The same analysis was unable to discriminate differences in the species richness of amphibians among young, mature, and old-growth stands. Special habitat features influenced the abundance of amphibians. Ponds and streams are required for several aquatic-breeding amphibians, but these waters were unevenly distributed in the stands we studied. Large, well-decayed down wood was essential for several terrestrial salamanders, and these species may eventually be reduced in numbers or extirpated in managed forests where down wood is scarce. Rocky substrate also appeared to influence the occurrence and abundance of several salamanders. The Pacific Northwest has several endemic species with restricted distributions and specialized habitat requirements. Unless management strategies are tailored to these unique species, they may decline locally or be extirpated.

Introduction

The value of old-growth forests for wildlife habitat and the effect of timber harvest on this resource is the subject of current debate (see Fosburg 1986, Harris 1984, Kerrick and others 1984, Meslow and others 1981, Norse 1990, Salwasser 1987, Wilcove 1987). Old-growth forests dominated by

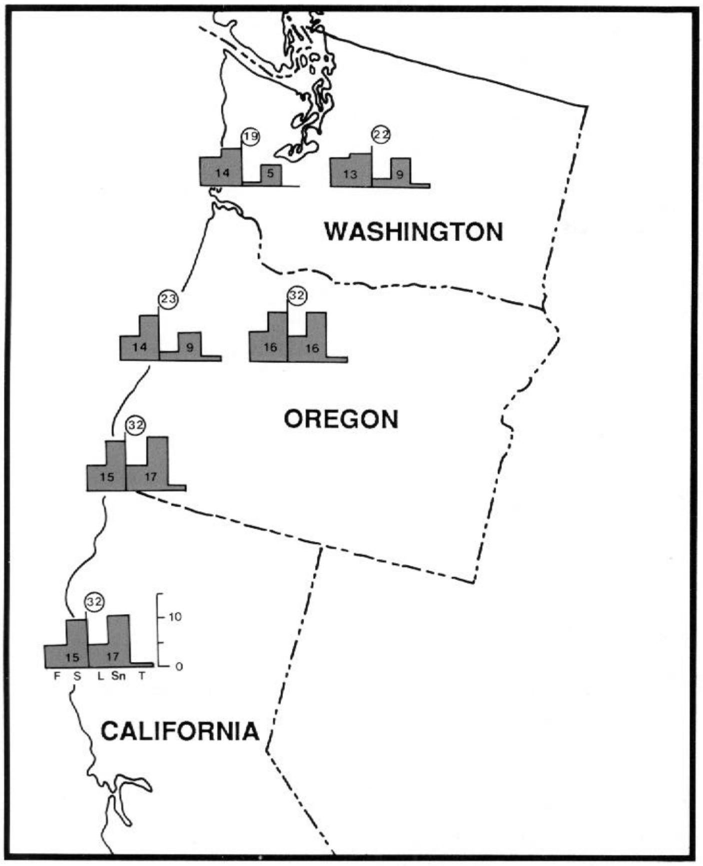

Figure 1—Numbers of species of amphibians and reptiles occurring in the Pacific Northwest (F = frogs, S = salamanders, L = lizards, Sn = snakes, T = turtles). Note the marked decrease in reptile species from south to north.

Douglas-fir have a wide range of tree sizes and ages, a deep multilayered canopy, large individual trees, and accumulations of large pieces of coarse woody debris (Franklin and Spies 1984). These distinctive attributes of old-growth forests may be important habitat elements for several species of the Pacific Northwest herpetofauna.

Most areas in the Pacific Northwest support as many as 19 to 23 species of amphibians and reptiles, based on published distribution maps (Nussbaum and others 1983, Stebbins 1985) and our field studies (fig. 1). Further, these herpetological communities may be ecologically important because of the high numbers and biomass of resident amphibians and reptiles (see Bury 1988).

Recently, the Old-Growth Forest Wildlife Habitat Program (see Ruggiero and Carey 1984) conducted several studies on amphibians and reptiles in forested habitats. Few reptiles were captured, and they are not discussed in this paper.

Reptiles are prevalent in open habitats such as oak woodland or grassland (Raphael 1987, Welsh 1987), where different techniques are needed to sample them adequately.

Results of sampling terrestrial amphibians have been reported for four provinces: Southern Washington Cascade Range, from Mount Rainier National Park south to the Columbia River (Aubry and others 1988; Aubry and Hall, this volume), Oregon Cascade Range (Bury and Corn 1988a; Gilbert and Allwine, this volume c), Oregon Coast Range (Corn and Bury, this volume b), and the Klamath Mountains province in southern Oregon and northern California (Raphael 1987b; Raphael 1988c; Welsh and Lind 1988, this volume). Aquatic amphibians were analyzed separately (Bury and others, this volume b; Bury and Corn 1988b; Corn and Bury 1989).

Here, we attempt to identify which species of the herpetofauna are associated with gradients of forest age and moisture condition in naturally regenerated forests for the three provinces north of the Klamath Mountains. Our specific objectives are:

- To compare the species richness and relative abundance of terrestrial amphibians among different forest stands;
- To elucidate regional differences in the structure and composition of terrestrial amphibian communities relative to their biogeographical patterns; and
- To provide guidelines for managing and protecting these species.

Methods

Methods of sampling amphibians included time-constrained collecting, which is useful for capturing certain terrestrial species, and pitfall trapping, which is effective for sampling most terrestrial species, especially migratory forms. These techniques are based on general herpetological sampling (see Bury and Raphael 1983, Campbell and Christman 1982, Jones 1986, Raphael and Barrett 1981), and specific methods developed for Pacific Northwest forests (Bury and Corn 1987; Corn and Bury 1990; Raphael 1988c).

We compared patterns of abundance among the three provinces by using several statistical approaches. We used two-way analysis of variance (ANOVA) to test for significant differences among provinces in the abundance of species that occur in all three provinces. Study sites were not selected at random because of logistical problems (for example, inaccessible wilderness) and land-use patterns (for example, private ownership or active logging nearby). Thus, we used statistical tests to identify major patterns in the data rather than to test specific hypotheses (see Carey and Spies, this volume).

Species included in the ANOVA analyses were the northwestern salamander, Pacificgiant salamander, Olympic salamander, ensatina, western redback salamander, roughskin newt, tailed frog, and red-legged frog. Only data derived from pitfall captures were used in these tests because abundance data from time-constrained collecting may be biased (Corn and Bury 1990, this volume b). Abundance was expressed as number captured per 100 trap-nights. We excluded juveniles of the northwestern salamander (<70 mm snout-vent length [SVL]), roughskin newt (<40 mm SVL), tailed frog (<35 mm SVL), and red-legged frog (<35 mm SVL) from the analyses so as to minimize the effects that seasonal pulses of aquatic breeders moving through the study sites would have on estimates of abundance (see Bury and Corn 1987,1988a).

Separate two-way ANOVAs were performed for amphibians across gradients of age and moisture. Most stands were naturally regenerated after catastrophic fire, and three age-classes were represented: young (35-79 years old), mature (80-195 years), and old-growth (200-730 years). A moisture gradient (wet, moderate, and dry) was established for the old-growth stands (see Spies and Franklin, this volume).

Pitfall trapping was conducted in 147 stands. We compared pitfall data among 130 stands across the chronosequence and 83 old-growth stands on the moisture gradient. We used a 6 by 6 grid of traps (15 m apart) in each stand, which is described in detail elsewhere (Corn and Bury 1990).

Some differences in techniques were used for each province. In the Oregon Cascade Range, trapping was conducted in 56 stands; all stands were sampled in 1984, and the same grids in the central stands (on or near the H.J. Andrews Experimental Forest) in 1985 (Gilbert and Allwine, this volume c). Stands in the southern Washington Cascade Range (n = 45) and the Oregon Coast Range (n = 46) were trapped in both 1984 and 1985, and trap grids were moved between years in Washington (Aubry and Hall, this volume) but not in the Coast Range (Corn and Bury, this volume b). Values are expressed as mean captures to facilitate comparisons between provinces that have different numbers of stands. We used 1985 data from the Oregon Coast Range and the Cascade Range in Washington because the analyses of these data within each province combined the captures from both years (Aubry and Hall, this volume; Corn and Bury, this volume b).

We used gradient analyses to investigate relations between the abundance of species and habitat variables (physiographic and vegetative). Physiographic variables were measured on each pitfall grid (see Corn and Bury, this volume b) and included stand age, elevation, aspect (cosine-transformed), percentage slope (arcsine-transformed), and the presence or absence of surface water or exposed talus. Individual vegetative variables were combined into broad stand-scale gradients using canonical discriminant analysis. Separate analyses resulted in four variables (Spies and Franklin, this volume): DF1A and DF2A from an analysis of stands in the chronosequence, and DF1M and DF2M from an analysis of stands in the moisture gradient. DF1A is positively correlated with stand development (for example, number of large trees, stand age, and variation in tree diameter), and DF2A is positively correlated with coarse woody debris (primarily volume of snags and down wood). DF1M was negatively correlated with the basal area of shade-tolerant trees and apparently represents a temperature gradient (stands from the Coast Range have high scores, Washington stands have low scores). DF2M was negatively correlated with the density of subcanopy trees and cover of evergreen shrubs, and it represents a moisture gradient (wet stands have high scores).

Because the abundances of most amphibian species varied among provinces, we tested for associations between abundance and continuously distributed habitat variables. We compared abundance among provinces by using the habitat variables as covariates. The presence or absence of variables (water and talus) were tested in a two-way ANOVA with province.

We compared the structure and composition of amphibian communities among provinces by determining the presence or absence of 12 species. Eight species occurred in all provinces, and four others were present in one or two provinces (the clouded salamander, Oregon slender salamander, Dunn's salamander, and the Cascades frog). We combined the results of time-constrained collecting and pitfall trapping to generate lists of species in each stand. Such an approach precludes the use of abundance data, but it provides a more complete list of species than pitfall data alone (Corn and Bury 1990).

Species richness was based on one time-constrained collection (or survey of down wood) and 2 years of pitfall trapping in each of 55 stands. Surveys of down wood (equivalent to time-constrained collection) were done in only 15 of the study sites in the Oregon Coast Range (Corn and Bury, this volume b), so we selected subsamples (the central stands) from both provinces in the Cascade Range. In Oregon, we used data from 19 stands in or near the H.J. Andrews Experimental Forest (Gilbert and Allwine, this volume c), and in Washington, we used data from 21 stands in the Packwood-Randle area (Aubry and Hall, this volume).

We used multidimensional scaling (MDS) to represent the pattern of presence or absence of the 12 species; MDS computes two-dimensional coordinates for a set of stands so that the distances between pairs of stands fit as closely as possible to their measured similarities (Wilkinson 1988). Similarity between pairs of stands was computed with Jaccard's index (Pielou 1984), which is the number of species present in one stand in proportion to the total number of species present in the pair of stands.

Table 1—Mean captures (number per 100 trap-nights) of amphibians across the chronosequence of forest stands (standard deviations are in parentheses)

	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range		
Species	Old growth $n = 25$	Mature $n = 10$	Young $n = 8$	Old growth $n = 22$	Mature $n = 19$	Young $n = 9$	Old Growth $n = 19$	Mature $n = 9$	Young $n = 9$
Northwestern salamander	0.015 (0.032)	0.014 (0.029)	0.013 (0.026)	0.022 (0.073)	0.010 (0.042)	0.013 (0.026)	0.227 (0.379)	0.041 (0.062)	0.036 (0.060)
Pacific giant salamander	.050 (.053)	.042 (.043)	.043 (.058)	.030 (.071)	.041 (.078)	.045 (.136)	.002 (.010)	0	.021 (.062)
Olympic salamander[a]	.029 (.048)	.003 (.011)	.013 (.026)	.011 (.039)	0	0	.007 (.017)	.020 (.052)	.052 (.147)
Ensatina	.454 (.227)	.542 (.525)	.569 (.242)	.453 (.296)	.491 (.360)	.439 (.327)	.825 (.954)	.686 (.612)	1.443 (1.036)
Western redback salamander	.532 (.359)	.490 (.739)	.812 (1.126)	.025 (.061)	.006 (.018)	.006 (.019)	.075 (.183)	.025 (.060)	.628 (.954)
Roughskin newt	.111 (.168)	.076 (.102)	.026 (.025)	.107 (.173)	.065 (.096)	.550 (.777)	.164 (.269)	.041 (.075)	.031 (.061)
Tailed frog	.033 (.061)	.101 (.122)	.035 (.098)	.144 (.591)	.016 (.032)	.172 (.274)	.127 (.101)	.455 (.573)	.067 (.152)
Red-legged frog	.003 (.010)	0	.026 (.031)	.026 (.084)	.025 (.054)	0	.063 (.093)	.116 (.140)	.041 (.054)

[a] Olympic salamanders do not occur at the north end of the Cascade Range in Washington or the south end of the Cascade Range in Oregon. Correct sample sizes are: Oregon old growth (12), mature (12), young (6); Washington old growth (13), mature (7), young (8).

Table 2—Separate two-way analysis of variance of abundance versus province and age-class, and abundance versus province and moisture-class

	Factor				
				Interactions	
Species	Province[a]	Age[b]	Moisture[c]	PxA[d]	PxM[e]
Northwestern salamander	XXXX[f]	XXXX		XXXX	
Pacific giant salamander	XXXX				
Olympic salamander					
Ensatina	XXXX		XXXX		
Western redback salamander	XXXX	XXXX			
Roughskin newt	XXXX			XXXX	
Tailed frog	XXXX				
Red-legged frog	XXXX				

[a] Southern Washington Cascade Range, Oregon Cascade Range, Oregon Coast Range.
[b] Old-growth, mature, young.
[c] Old-growth stands only: dry, moderate, wet.
[d] Province x age.
[e] Moisture x age.
[f] $P < 0.05$.

Using the same set of data on species richness, we performed a nonhierarchical clustering of stands using the K-means procedure of SYSTAT (Wilkinson 1988). The K-means procedure produces a specified number of nonoverlapping pools (clusters) of stands. We chose three pools because three provinces and three forest age-classes were analyzed.

Results

Variation Within the Chronosequence

Marked variation was found in the abundance of amphibians across the chronosequence of selected stands (table 1). Ensatina was usually the most common species captured in all stand ages for each province, followed by roughskin newts. Western redback salamanders were an exception, being more abundant in young and old-growth stands in the Oregon Coast Range than either of the other two species.

We found that seven of eight species showed marked variation in abundance among provinces (table 2). Only the northwestern salamander and the western redback salamander were significantly associated with the age gradient when variation among provinces was taken into account. The northwestern salamander was more abundant in old growth (this pattern was not apparent in the Coast Range) than in mature or young stands. They were most abundant in Washington. The western redback salamander was most abundant in young stands and in samples from the Coast Range; the species was rare in the Cascade Range in Oregon. A strong interaction was found between province and stand age for roughskin newts. This species was most abundant in old-growth forests in Washington and in the Coast Range, and in young stands in the Oregon Cascade Range.

Variation Within the Moisture Gradient

Ensatina was the only species with a significant response to the moisture gradient (tables 2 and 3). In both Cascade Range provinces, ensatina was most abundant in dry old-growth stands.

Continue

Table 3—Mean captures (number per 100 trap-nights) of amphibians across the moisture gradient in old-growth stands (standard deviations are in parentheses)

Species	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range		
	Dry $n = 8$	Moderate $n = 14$	Wet $n = 5$	Dry $n = 7$	Moderate $n = 9$	Wet $n = 12$	Dry $n = 7$	Moderate $n = 11$	Wet $n = 9$
Northwestern salamander	0.009 (.016)	0.015 (.033)	0.021 (.047)	0.013 (.023)	0.045 (.112)	0.097 (.202)	0.280 (.549)	0.209 (.268)	0.134 (.210)
Pacific giant salamander	.031 (.039)	.062 (.061)	.049 (.031)	0	.028 (.062)	.100 (.119)	0	.004 (.013)	.034 (.061)
Olympic salamander[a]	.030 (.051)	.030 (.051)	.049 (.047)	0	.027 (.061)	.006 (.019)	0	.015 (.024)	0
Ensatina	.500 (.209)	.419 (.258)	.451 (.107)	.587 (.381)	.370 (.224)	.211 (.287)	1.001 (1.132)	.746 (.909)	.199 (.174)
Western redback salamander	.452 (.383)	.556 (.342)	.563 (.352)	.008 (.021)	.029 (.058)	.019 (.067)	.092 (.225)	.021 (.056)	.077 (.185)
Roughskin newt	.192 (.235)	.079 (.127)	.215 (.406)	.008 (.022)	.161 (.171)	.166 (.238)	.197 (.188)	.158 (.325)	.020 (.046)
Tailed frog	0	.032 (.046)	.153 (.122)	.008 (.022)	.316 (.924)	.119 (.247)	.143 (.101)	.095 (.071)	.214 (.332)
Red-legged frog	.004 (.012)	.002 (.009)	0	.025 (.067)	.040 (.121)	.002 (.008)	.033 (.051)	.088 (.111)	.061 (.099)

[a] Olympic salamanders do not occur at the north end of the Cascade Range in Washington or the south end of the Cascade Range in Oregon. Correct sample sizes are: Oregon dry (3), moderate (5), wet (10); Washington dry (6), moderate (6), wet (3).

Table 4—Significant associations between amphibian abundances and major physiographic and vegetative gradients (negative associations in parentheses)

Variable	Northwestern salamander	Pacific giant salamander	Olympic salamander	Ensatina	Western redback salamander	Roughskin newt	Tailed frog	Red-legged frog
Stand age				(XXXX)[a]				
Elevation				(XXXX)		(XXXX)	XXXX	(XXXX)
Aspect		XXXX					XXXX	
Slope				XXXX	XXXX			(XXXX)
Water				(XXXX)				
Talus					XXXX			
DF1A[b]	XXXX							
DF2A[c]								
DF1M[d]	(XXXX)	XXXX						
DF2M[e]		XXXX		(XXXX)				

[a] $P < 0.05$.

[b] Correlated with stand development (Spies and Franklin, this volume).

[c] Correlated with amount of coarse woody debris (Spies and Franklin, this volume),

[d] Correlated with increasing temperature (Spies and Franklin, this volume).

[e] Correlated with increasing moisture (Spies and Franklin, this volume).

Habitat Associations

More significant associations of amphibian abundance with physiographic variables were found than with vegetation variables (table 4). Analysis of covariance controls for differences among provinces (for example, elevations were generally lower in the Coast Range), but gradients within provinces may complicate interpretation of these results. For example, elevation was highest in Washington in the north, but in the Cascade Range in Oregon the southern stands were highest.

Responses of individual species varied widely with habitat variables. Northwestern salamanders were more abundant in cool old-growth forest than in other combinations. Pacific giant salamanders were more abundant in warmer, wetter stands than in other conditions. The abundance of Olympic salamanders was low in all provinces, and this species was not related to any of the gradients examined.

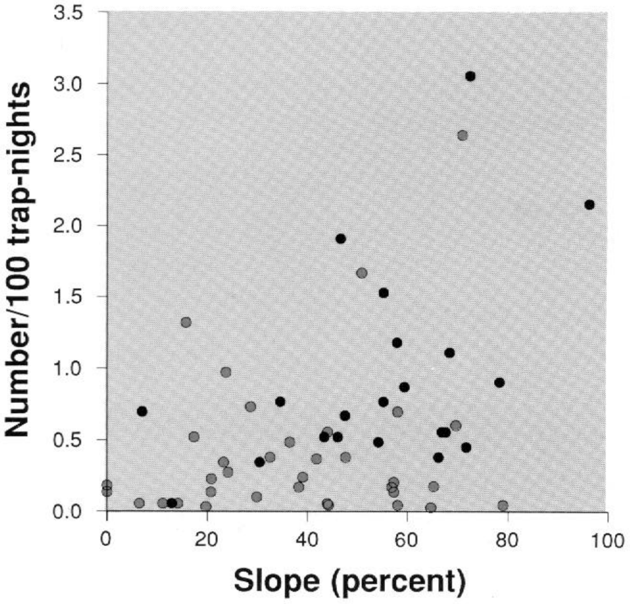

Figure 2—Abundance of western redback salamanders related to slope. Shown here are stands in Washington and the Oregon Coast Range where this species was present. Filled circles are stands with talus, open circles are stands without talus present on the pitfall grid.

Ensatina was more abundant in younger, drier stands, and steeper stands at lower elevations, than in other combinations of conditions. Western redback salamanders were more abundant on steep slopes (fig. 2). Roughskin newts were most abundant at lower elevations, and tailed frogs were more abundant at higher elevations with southern exposures than in other situations. Red-legged frogs were most abundant at lower elevations with flatter slopes.

Regional Patterns

Based on the multidimensional scaling of species richness, the Oregon Coast Range appears to be distinct from the Cascade Range, whereas the Cascade Range in Oregon and Washington shows a degree of overlap (fig. 3a). This observation is supported by a separate analysis: the nonheirarchical clustering of three pools of stands (table 5). Two of these pools identify stands in the Oregon Coast Range and Washington Cascade Range; the largest pool (pool 1) contains most of the stands in the Oregon Cascade Range and half of the Washington stands. The Coast Range pool had the highest species richness, with six species present in more than 50 percent of the stands, and the Washington pool had the lowest richness, with only three species present in more than 50 percent of the stands.

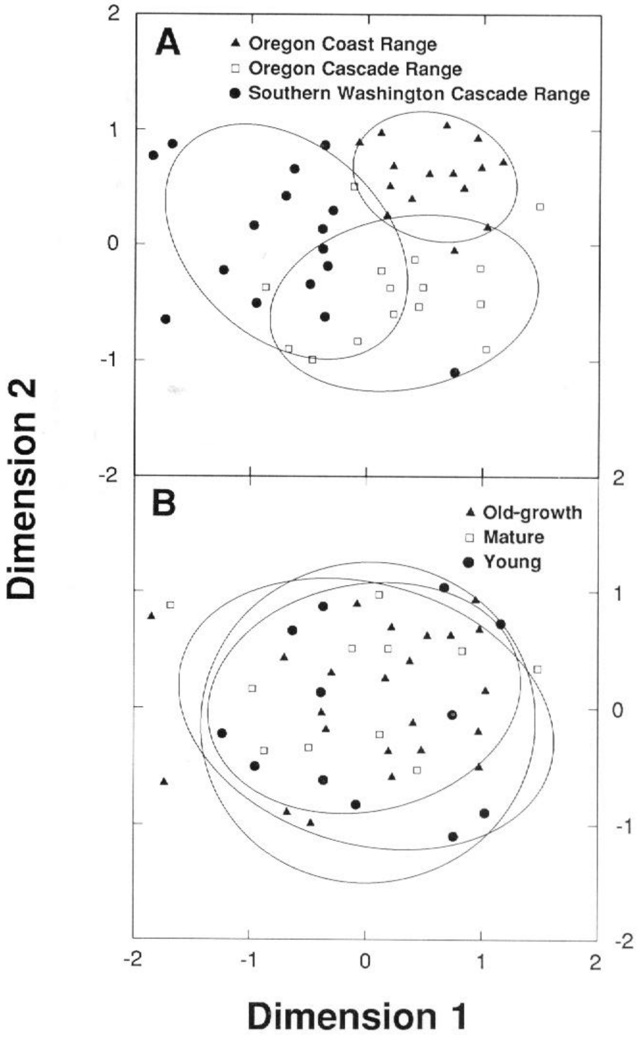

Figure 3—Multidimensional scaling of the presence or absence of 12 amphibians in 55 forest stands in Oregon and Washington: (a) stands identified by province (ellipses enclosing about 75 percent of the stands are drawn about the centroids of each province) and (b) stands identified by habitat type.

Plotting the MDS by age-class shows no discernible differences among old-growth, mature, and young stands (fig. 3b). Ellipses that enclose about 75 percent of the stands in each age-class essentially overlap completely.

Table 5—Nonhierarchical clustering of 12 amphibian species (presence-absence) in 55 forest stands in Oregon and Washington

Pool[a]	Province	Number of stands	Species present in at least 50 percent of stands in each pool (percentage)	Species absent from all stands in pool
1	Oregon Cascade Range Washington Cascade Range Oregon Coast Range	15 11 3	Ensatina (100) Roughskin newt (75) Tailed frog (71) Western redback salamander (50)	Cascades frog
2	Washington Cascade Range Oregon Cascade Range	10 3	Tailed frog (100) Ensatina (77) Red-legged frog (69)	Clouded salamander Pacific giant salamander Olympic salamander
3	Oregon Coast Range Oregon Cascade Range Washington Cascade Range	12 1 1	Ensatina (100) Clouded salamander (93) Pacific giant salamander (93) Western redback salamander (93) Roughskin newt (57) Northwestern salamander (57)	Cascades frog Oregon slender salamander

[a] Three nonoverlapping pools of stands were generated using K-means clustering.

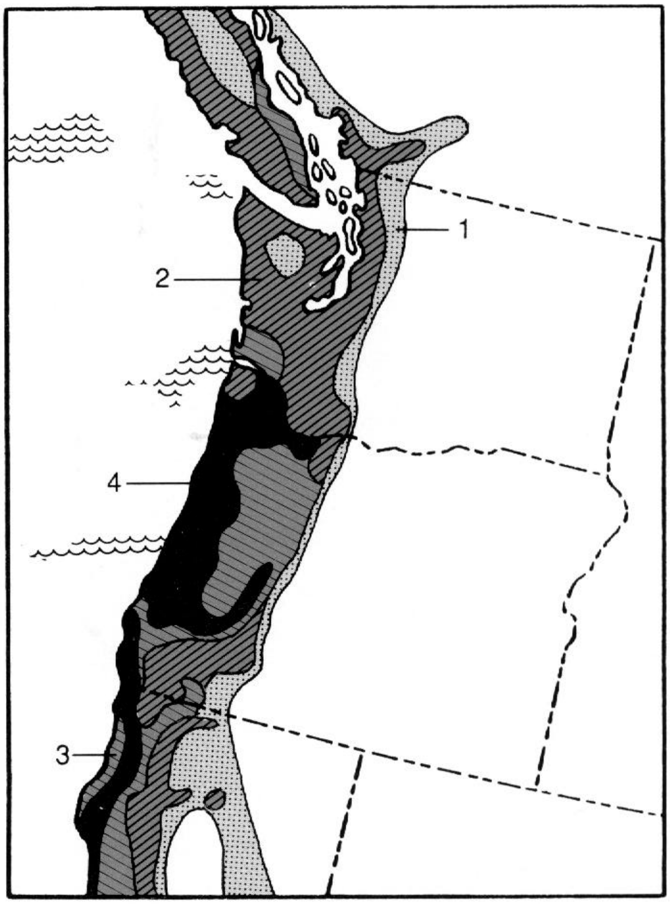

Figure 4—Overlap in the ranges of six widespread terrestrial salamanders (black, California slender, clouded, Dunn's, ensatina, and western redback) in the Pacific Northwest. Numbers (1-4) indicate number of co-occurring species.

Biogeography

The occurrence of amphibians among and within provinces varied greatly. Six species of terrestrial salamanders were widely distributed in the Pacific Northwest (fig. 4), and species richness was concentrated in western Oregon and north coastal California. Among these six species of widespread occurrence, the number present in any locality varied from zero to four and changed over relatively short distances.

Five salamanders were endemic in Oregon and Washington (fig. 5), and most had non-overlapping ranges. Three other endemic species in Idaho and northern California are not examined here.

Discussion

Variation Across Provinces, Chronosequences, and Moisture Gradients

The lack of response by terrestrial amphibians to the moisture gradient in the Coast Range might be due to several factors. The moisture gradient was not strong, and most stands tended to be relatively dry. Old-growth stands in the Coast Range tended to be similar to the drier old-growth forest in the Cascade Range (Spies and Franklin, this volume).

Mean abundance of species differed more among provinces than across either the chronosequence or moisture gradients (table 2). Most species were more common in one province than in the other two. Large numbers of both the roughskin newt and northwestern salamander were captured in only a few stands, resulting in high variance that clouds interpretation of trends. The observed geographic variation in

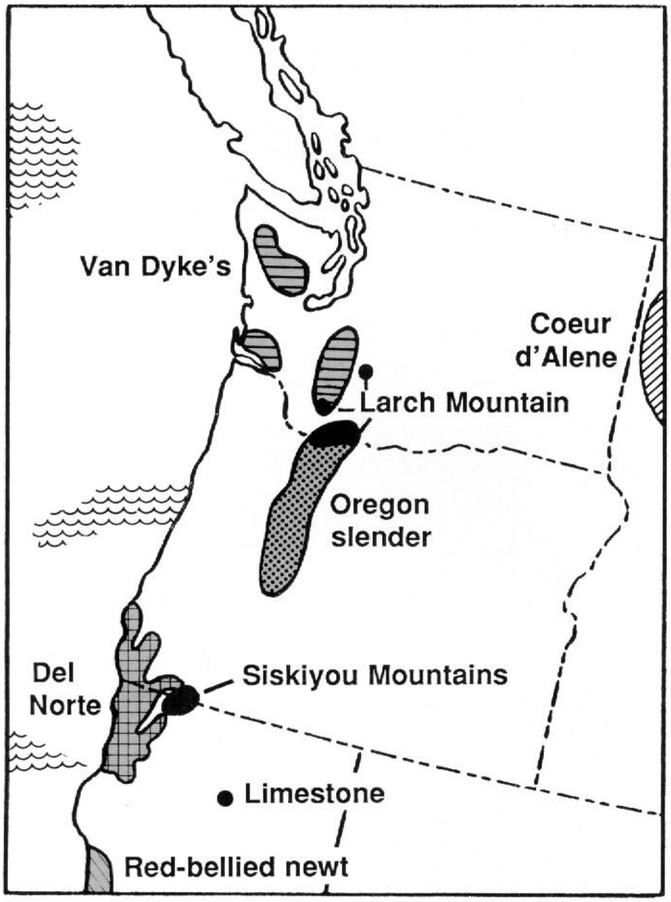

Figure 5—Distributions of eight salamanders endemic to the Pacific Northwest.

captures may reflect the location of special habitat features in certain stands more than any environmental differences among provinces.

The resident amphibians apparently are somewhat similar in naturally regenerated Douglas-fir forests. All stands sampled had established canopies and generally contained large amounts of coarse woody debris, which are characteristics that may reduce differences among stand types (young to old growth, wet to dry).

Habitat Associations

Some of the observed patterns of abundance may be due to special habitat features required by certain species. These may include aquatic habitats, down wood, and rocky slopes.

Proximity to water for aquatic breeders—The strong interaction between province and stand age for roughskin newts might be better explained by the proximity of breeding habitats than by dependence on unknown forest characteristics. Newts migrate to ponds, slow-moving streams, or other standing bodies of water to breed. Migration may extend over considerable distances. Twitty (1966), for example, reported that newts may move hundreds of meters to and from breeding sites, and that individuals displaced several kilometers away (some over 10 km) returned to home waters. Thus, a favorable site for breeding is a focal point for migration. Capture of newts in pitfall traps may represent no more than movement by the animal through the forest. The newt may only temporarily depend on that place of capture. Capture of migratory species in one type of habitat, however, may also suggest that they prefer or require these upland conditions after the breeding season.

Similarly, adult northwestern salamanders migrate to ponds for breeding, and then both adults and juveniles return to land. The proximity of ponds or slow-moving creeks may also determine the occurrence and abundance of this species in forested stands. Frogs and toads also breed and live most of their lives in or near water. In particular, ranid frogs are aquatic or mostly aquatic throughout their lives, and the tailed frog breeds in small streams. The location of these ponds or flowing waters will strongly influence the occurrence of these species in surrounding forest stands. During rains, however, frogs may move out onto the forest floor to forage, and they may occasionally disperse overland. Additional studies are needed to better address the importance of dual habitats (aquatic breeding and upland nonbreeding sites) in the life histories of forest amphibians.

Searches were conducted in vernal ponds in the Oregon Cascades (Gilbert and Allwine, this volume c). Most of the ponds were in mature and old-growth stands. These habitats proved to be important breeding areas for northwestern salamanders and ranid frogs. The relation between the stability (predictable occurrence) of vernal ponds and forest developmental stage needs further investigation.

Coarse woody debris—Time-constrained collecting and surveys of down wood suggest that coarse woody debris is important habitat for several species of plethodontid salamanders, including ensatina, clouded salamanders and Oregon slender salamanders (Aubry and others 1988; Aubry and Hall, this volume; Bury and Corn 1988a; Corn and Bury, this volume b; Gilbert and Allwine, this volume c). Natural disturbances (for example, fire) add appreciable debris to young stands, but these features do not persist as the stand matures. Forest stands do not accumulate new, large pieces of down wood until the forest reaches old-growth conditions and debris inputs increase as a result of natural tree mortality (Franklin and others 1981, Harmon and others 1986, Spies and others 1988).

Although ensatina was the only one of eight species suspected of having a strong association with down wood, none of the amphibians collected in pitfall traps were related to the habitat variable (DF2A) for coarse woody debris (table 4). Clouded salamanders and Oregon slender salamanders were not well-sampled by pitfall trapping, but time-constrained collection indicate that they are most abundant in stands with high amounts of coarse woody debris.

Ensatina is a generalist and may be competitively displaced by the clouded salamander where they are sympatric (Corn and Bury, this volume b). In Oregon, clouded salamanders were most abundant in less-decayed classes of down wood, mostly in decay-classes 1 and 2 (Bury and Corn 1988a; Corn and Bury, this volume b). Clouded salamanders and Oregon slender salamanders, however, do not occur in the Cascade Range in Washington, and in that region ensatina uses a broader range of microhabitats (Aubry and others 1988) than ensatina in the Cascade Range in Oregon, where all three species occur (Bury and Corn 1988a), or in the Oregon Coast Range where ensatina and clouded salamanders are sympatric (Corn and Bury, this volume b). The density of ensatina also may not be strongly related to the amounts of coarse woody debris in stands because that species is a generalist. Ensatina may, however, require coarse woody debris as breeding habitat (Aubry and others 1988).

Raphael and Barrett (1984) found that the abundance of ensatina in northern California was correlated to the density of large Douglas-fir trees. They found few ensatina in the youngest stands (less than 150 years old) they studied, however, and they included ensatina with species associated with old-growth stands. We cannot explain why ensatinas were ubiquitous in Oregon and Washington and had no apparent correlation with old growth.

Rocky habitats-We think the most underestimated environmental factor affecting salamanders is underlying soils, and particularly the occurrence of talus (rock rubble) in the Pacific Northwest. Western redback salamanders are associated with steep slopes and talus (fig. 2). Steepness of slope and the presence of talus are related factors because talus is more often exposed on hillsides than on valley floors where rocky soils are often covered with alluvium or deeper soils. Most western plethodontid salamanders frequent talus slopes (Dumas 1956, Herrington 1988, Nussbaum and others 1983, Ramotnik and Scott 1988), including the Larch Mountain, Siskiyou Mountain, and Del Norte salamanders. Also, Dunn's and Van Dyke's salamanders occur in talus habitat or along rocky streamsides (Dumas 1956, Corn and Bury 1989).

The strong association of the woodland salamanders with talus or rocky soils may override other habitat relations. For example, both Raphael (1988c) and Welsh and Lind (this volume) indicate that the Del Norte salamander is most numerous in the oldest seral stages of Douglas-fir/hardwood forest in northern California. Soil types were not indicated, however, so these relations may be incidental to an uneven distribution of rocky habitats. We suggest that the occurrence and abundance of most species of woodland salamanders are more likely to be related to the presence of rocky outcrops or underlying talus than to forest development (stand age) or amounts of coarse woody debris. Determining this relation is essential to future studies of western salamanders and their habitats.

Herrington and Larsen (1985) and Herrington (1988) suggest that forested talus slopes were required by the Larch Mountain salamander and some other salamanders. The response of salamanders to the removal of forested stands on talus slopes, however, has not been examined critically. Individuals may simply move underground (Ovaska and Gregory 1989; N. Scott, unpubl. manuscript). Insufficient evidence is available to resolve this question, but it is a major issue because many forested areas of the Cascade and Coast Ranges in the Pacific Northwest have soils dominated by talus or rock rubble. These areas may be open slopes, partly forested, or totally overgrown with trees. Thus, considering both the substrate (for example, soil versus talus) and forest conditions (for example, clearcut versus closed canopy) is increasingly important in evaluating the occurrence and abundance of terrestrial salamanders.

Managed Stands

Bury and Corn (1988a) used pitfall traps in five clearcut sites (all less than 10 years old) in the Cascade Range in Oregon and Washington to describe the occurrence and abundance of the herpetofauna in managed stands. The relative abundance of the herpetofauna in these clearcuts differed markedly from six comparable young stands that were naturally regenerated. Reptiles predominated in clearcuts, which most likely was a response to increased solar radiation and higher ambient temperatures. The Pacific treefrog also was most abundant in clearcuts, which reflects its propensity for invading openings (Bury 1983). Interestingly, clearcut stands that we sampled in the Oregon Coast Range in 1984-85 did not show such marked differences in terrestrial species (Corn and Bury, this volume b).

Although tailed frogs were captured in pitfall traps in closed-canopy forests, they were absent or rare in clearcuts (only 1 percent of the total catch). Both the Olympic salamander and the tailed frog seem to be sensitive to timber harvest, and the survival of these species may depend on the availability of cool streams for breeding and larval development as well as the presence of adjacent forested habitats for shade and retention of stream substrate quality (Bury and Corn 1988a; Bury and others, this volume b, Corn and Bury 1989). Assessing the effects of logging in streamside and upland forests is urgently needed.

Biogeography

Regional patterns-Both multidimensional scaling and nonhierarchical clustering generated clear patterns separating the three provinces (fig. 3a, table 5) but not the forest age-classes (fig. 3b). This result is underscored by the strong differences among provinces in the abundance of species that occurred in all provinces, and by the general lack of abundance differences among habitat types.

Analyses of the amphibian communities were somewhat surprising because distribution differences among the provinces for several species had little apparent influence on the results. Considerably more overlap was found between the Cascade Range in Oregon and Washington than between either Cascade Range group and the Oregon Coast Range despite the absence of clouded salamanders and Oregon slender salamanders in Washington. Biogeography, however, appears to play a much more important role in the organization of amphibian communities than do forest habitat gradients. Thus, a mandate exists to better document species' occurrence, and their centers of diversity, biogeographic relations, and distributional limits.

Importance of endemic amphibians-Eight species of terrestrial salamanders in the Pacific Northwest have restricted distributions (fig. 5), five in Oregon and Washington. Even widespread species, however, are not distributed over the entire region (fig. 4). The superimposing of the ranges of endemic and widespread species of salamanders would further complicate which species might be expected to occur in a given province or area. The specialized habitats and disjunct distributions of many species also confounds generalizations about herpetofaunas. Marked differences in the herpetofauna depend on the geographic location sampled.

We suspect that the distribution patterns of individual species may influence the organization of herpetological communities more than factors such as forest age, once canopy is reestablished. In most areas of the Pacific Northwest, however, herpetological studies have been insufficient to compile reliable community profiles (accurate lists of resident species and relative numbers of species).

Still, herpetological communities can be understood; relatively few species of amphibians and even fewer reptiles live in the Pacific Northwest. An intensive study in a project area usually can reveal almost all of the common species and many of the rarer ones, if the searcher knows what to look for and if sites are sampled during appropriate weather (Corn and Bury 1990).

Management Suggestions

Localized distributions and special habitat requirements of amphibians may make managing of selected species easier than might be anticipated. The presence of small permanent streams or headwaters is an indicator that Olympic salamanders or tailed frogs may occur in the area. Another key factor is to recognize the importance of distinct microhabitats. Presence of talus or rocky substrate, for example, is a clue that one or more species of plethodontid salamanders likely inhabit the site.

Management strategies need to be individually tailored. Most of the "common" amphibians, such as ensatina and clouded salamanders, are apparently not irreversibly affected by current timber harvest activities. Thus, we would recommend that most attention be directed at endemic species with small geographic ranges (fig. 5). All five of the endemic species in Oregon and Washington are already proposed for Federal listing as threatened or are protected by individual States.

A long-term perspective needs to be developed. Species that require large, well-decayed down wood may be continually reduced in numbers in managed forests because tree removal reduces or eliminates the input of fallen woody debris. Coarse woody debris, therefore, is not carried over from sequential harvests, and terrestrial amphibian populations may suffer as a result.

Acknowledgments

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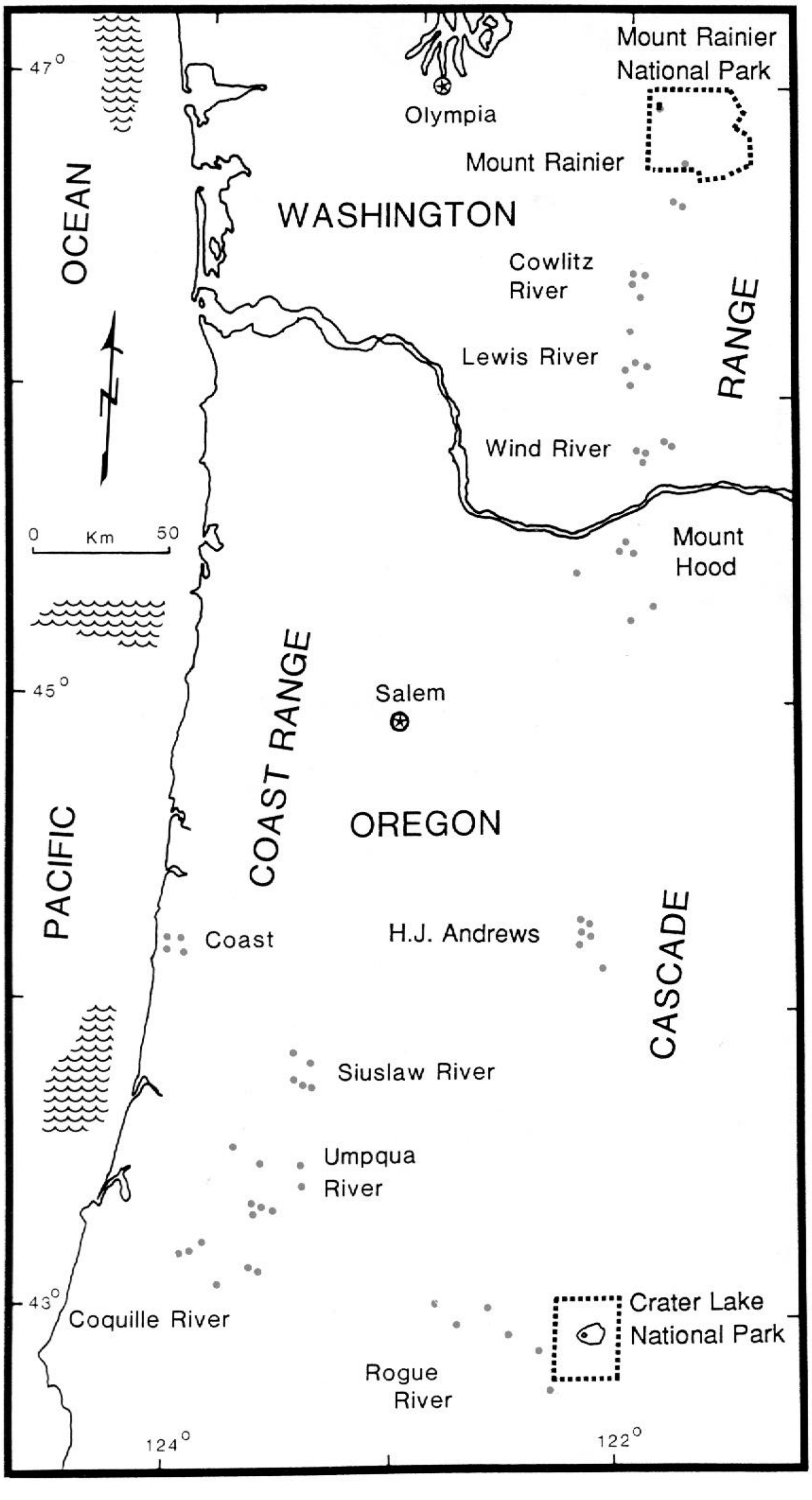

Locations of streams sampled.

Aquatic Amphibian Communities in Oregon and Washington

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Lawrence L.C. Jones

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Abstract

We sampled first- and second-order streams in naturally regenerated forests (young, mature, and old-growth stands) in three provinces: the Southern Cascade Range of Washington, the Oregon Cascade Range, and the Oregon Coast Range. We found no significant differences in physical habitat variables (except stream gradient in one of the three provinces) nor in densities of amphibians among the provinces. Giant salamanders were the most abundant amphibians, followed by tailed frogs. Dunn's salamander and Olympic salamander were less common, partly because they did not occur in all the watersheds we examined. These four species differed markedly in their microhabitat use: tailed frogs were most often found in riffles; Olympic salamanders frequented riffles and banks or shallow seeps; giant salamanders were about equally abundant in pools and riffles; and Dunn's salamanders mostly occurred on stream banks. Three species have aquatic larvae, and they appeared to occupy different ecological niches. Amphibian densities and biomass were 10 and 4 times greater, respectively, than those reported for salmonid fishes in small streams. Thus, amphibians can be the predominant vertebrates in headwaters in Pacific Northwest forests. In the Oregon Coast Range, we found that the number of species, the densities, and the biomass of resident amphibians were 2 to 7 times greater in streams flowing through uncut forests than in logged areas. Responses of amphibian populations to timber harvest may differ regionally, and more comparative studies are needed on amphibian communities in managed stands.

Introduction

Concerns have been expressed about how timber harvest affects salmonid fishes in Pacific Northwest streams (see Brown 1985, Meehan and others 1984, Salo and Cundy 1987). Recent studies in western Oregon indicate that both salmonids and the Pacific giant salamander are common in streams in uncut and logged habitats (Hawkins and others 1983, Murphy and Hall 1981, Murphy and others 1981). Other studies suggest, however, that logging has negative impacts on aquatic amphibians, particularly those with narrow environmental tolerances (Bury 1968, Bury and Corn

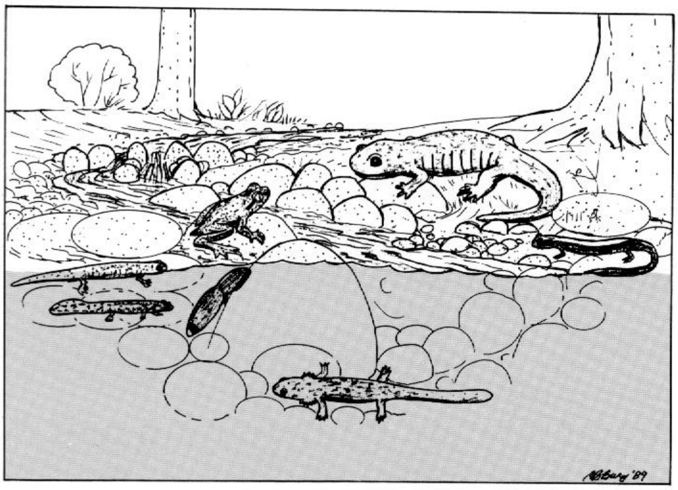

Figure 1—Aquatic and semi-aquatic amphibians of headwaters and small streams in Oregon and Washington (from left to right): Olympic salamander, tailed frog (adult above, tadpole below), Pacific giant salamander (adult above, larva below), Dunn's salamander (no aquatic larvae).

1988b, Metter 1964, Nussbaum and others 1983). Negative effects from logging also may be intensified in headwater streams (Corn and Bury 1989).

Integrated management of forests requires an understanding of the complex ecosystems of headwater streams, and how they function. Headwaters and other small channels provide nursery habitat for salmonids (Hartman and others 1987, Sedell and Swanson 1984) and are important in maintaining downstream fish habitat and water quality (Rice and others 1979). Everest and others (1985), furthermore, reported that upslope activities (for example, road development or timber harvest) and manipulation of canopy or streambank vegetation create immediate changes in the equilibrium of small streams.

Hairston (1987) estimated that the biomass of both terrestrial and aquatic salamanders was greater than that of any other vertebrate predators in the southern Applachian mountains. To date, we lack comparable estimates of the biomass of different vertebrate groups in Pacific Northwest forests. Although amphibians are the dominant vertebrates in some Northwestern headwater streams (Bury 1988, Murphy and Hall 1981, Nussbaum and others 1983), large gaps exist in our understanding of how these species function in aquatic or riparian communities. We know little about the effects of habitat alteration on their survival.

The structure of Douglas-fir forests varies considerably (Spies and Franklin, this volume) and, for that reason, we need to investigate how amphibian populations vary across successional gradients. In this paper, our objectives are to determine the occurrence and abundance of amphibians in streams flowing through three successional stages (young, mature, and old-growth) of naturally regenerated Douglas-fir forests in western Washington and western Oregon, compare amphibian communities in streams in uncut forests to streams in logged areas, discuss the major physical characteristics of streams and the microhabitat associations of aquatic amphibians, and identify regional patterns in the density and biomass of amphibians in headwater streams.

Geographic Distributions and Life Histories

Four species (or groups of sibling species) of aquatic amphibians (fig. 1) occur in the temperate forests of the Pacific Northwest: Olympic salamanders, giant salamanders (genus *Dicamptodon*), Dunn's salamanders, and tailed frogs. Distribution maps are based mostly on locality records in Nussbaum and others (1983), with additional information from Bury (1968), Good and others (1987), Green and Campbell (1984), and our recent field work. Range maps presented here are new interpretations; they were designed to denote areas lacking records as well as areas with known faunas.

Good and others (1987) indicate that the Olympic salamander comprises at least three genetically distinct groups in the following areas: the Olympic Peninsula to northwestern Oregon, the Coast Range from central Oregon to northern California, and the Cascade Range of Oregon and Washington (fig. 2). This species requires cool waters, and individuals are usually found only in the splash zone or shallows of seeps and streams (Nussbaum and Tait 1977, Nussbaum and others 1983).

Giant salamanders are widespread in the Pacific Northwest (fig. 2). Pacific giant salamanders are large (up to 350 mm long) and inhabit streams and standing water over a relatively wide range of temperatures. Their eggs and larvae occur in water, but transformed juveniles and adults may live on land. Cope's giant salamander is a smaller species that is mostly aquatic and neotenic (Nussbaum 1970). The Rocky Mountain giant salamander, which occurs in interior areas (Daugherty and others 1983), is not discussed here.

The tailed frog is distributed similarly to the giant salamander (fig. 3). Eggs and tadpoles of this frog require cool, flowing waters (Bury 1968, 1988; de Vlaming and Bury 1970; Metter 1964; Nussbaum and others 1983). Their larval stage reportedly lasts for 2 to 3 years (Metter 1967) and, in the Rocky Mountains, adults may not breed until 7 to 8 years of age (Daugherty and Sheldon 1982). Tailed frogs occur in disjunct populations, especially in interior or drier areas (Daugherty and Sheldon 1982, Metter 1967).

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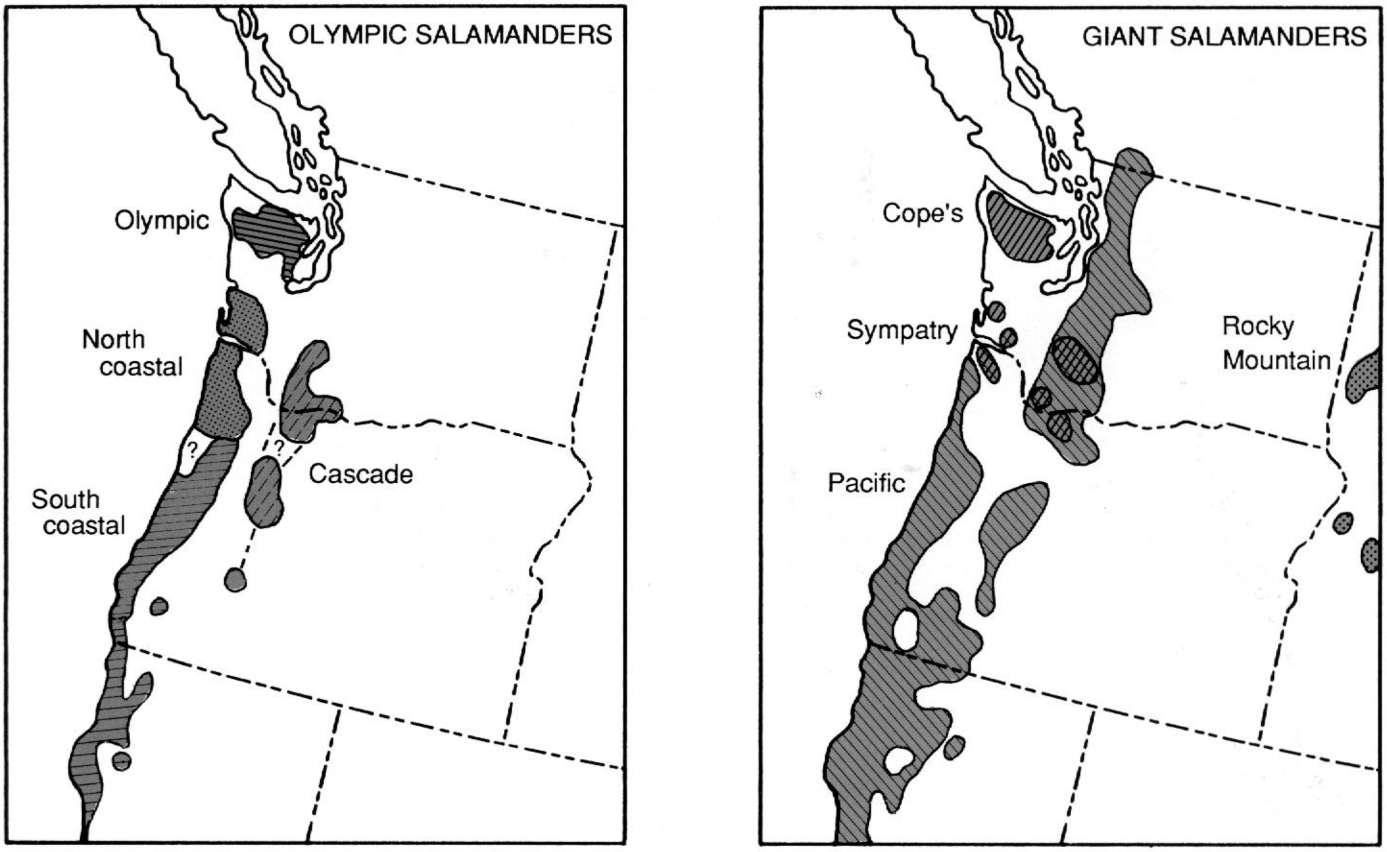

Figure 2—Distributions of the Olympic salamander and giant salamanders in the Pacific Northwest. Note the disjunct range of the Olympic salamander and that three species of giant salamander are now recognized.

Dunn's salamander often occurs along creeks and streams. In seeps and headwater habitats, the species may be found in the same microhabitat with the Olympic salamander (Nussbaum and others 1983). Dunn's salamander does not occur in the Cascade Range of Washington (fig. 3). This species lacks larvae; individuals develop directly from egg to adult.

Material and Methods

We sampled 59 streams (see frontispiece) in three physiographic provinces: the Southern Washington Cascade Range, the Oregon Cascade Range, and the Oregon Coast Range (Franklin and Dyrness 1973). A similar study was conducted in northwestern California and southwestern Oregon (Welsh and Lind, this volume). We sampled six streams in each forest age-class (young, mature, old growth) in the Oregon and Washington Cascades. In the Oregon Coast Range, we sampled streams in 3 young, 10 mature, and 10 old-growth stands. We sampled an additional 20 streams flowing through managed second-growth forests to study the long-term effects of logging (Corn and Bury 1989).

Proximity of streams to established terrestrial study-areas varied. In the Oregon Cascades, all of the streams flowed through stands used in the terrestrial community studies (see Gilbert and Allwine, this volume c). Few of the streams selected in the Oregon Coast Range or Washington Cascades were in the terrestrial study areas. Ages of these stands were based on visual inspection of dominant trees and available timber maps (USDA Forest Service and U.S. Department of the Interior, Bureau of Land Management). We selected permanent, 1- to 2-m wide, first- or second-order streams.

We adapted the habitat variables sampled from standard stream-survey techniques of Platts and others (1983). Bury and Corn (in press) and Corn and Bury (1989) describe these techniques in detail. Briefly, sampling consisted of an intensive search of 10 m of water and bank along a representative stretch of each stream. We used standarized techniques for measuring water depth, stream width, percentage gradient, pool-to-riffle ratio (100 percent pool = 1.0; 100 percent riffle = 0), percentage slope of the channel on each side of the stream, and water temperature.

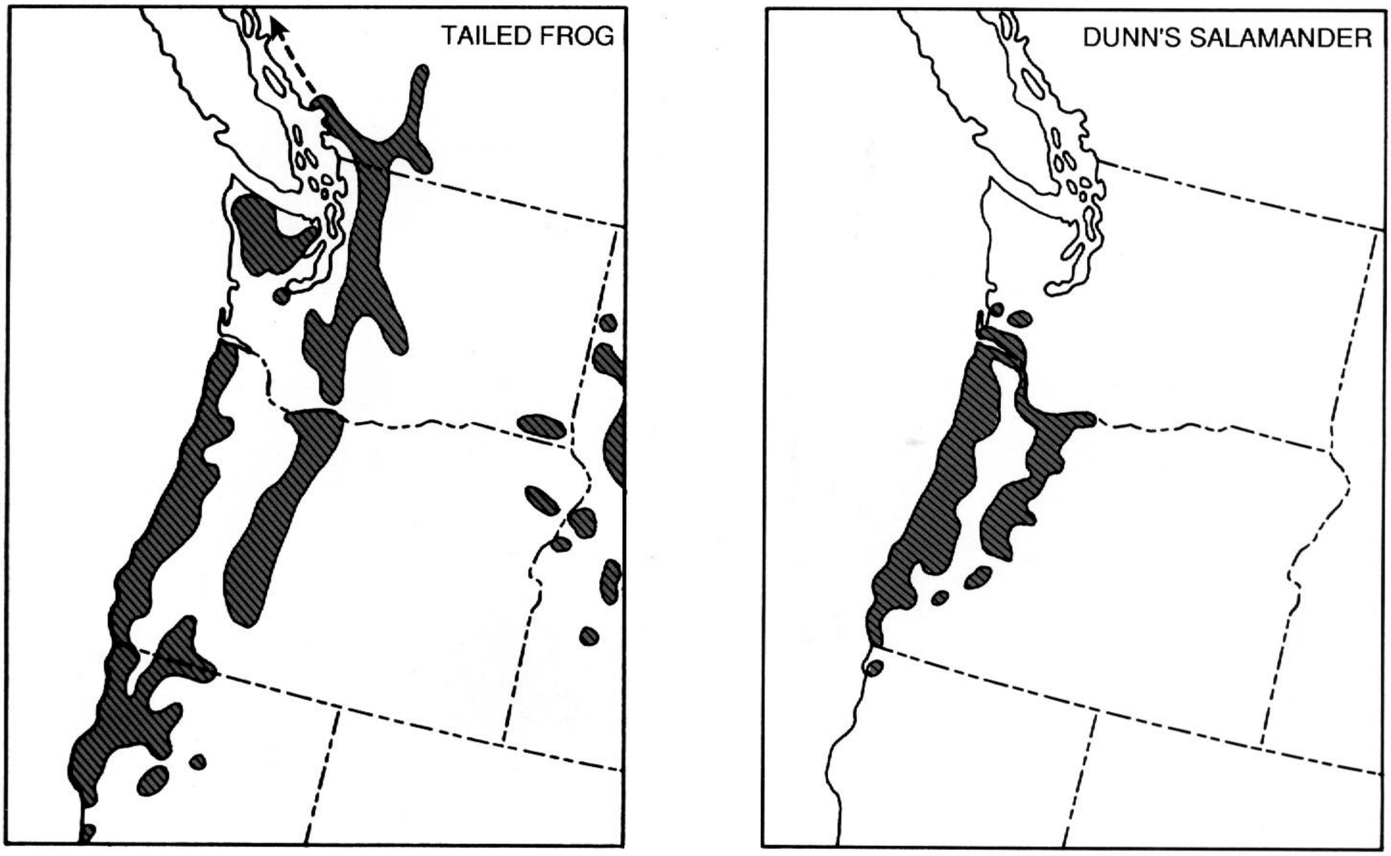

Figure 3—Distributions of the tailed frog and Dunn's salamander in the Pacific Northwest.

We estimated by eye the particle size of the substratum that was most abundant across the stream at ten 1-m intervals. We categorized substrata as silt or sand (<2 mm diameter), gravel (2-32 mm), pebble (32-64 mm), cobble (64-256 mm), and boulder (>256 mm). When possible, we recorded where each animal was first seen (pool, riffle or bank-seep) and measured the depth of water and size of the cover object over individual animals. All animals were collected by hand. Representative vouchers of each species were retained from many sites and deposited at the National Museum of Natural History in Washington, DC, the Burke Museum at the University of Washington, or the Conner Museum at Washington State University.

We identified significant differences in stream characteristics among forest age-classes and among provinces with a one-way analysis of variance, which we also used to test for differences in amphibian densities among age-classes. Densities were transformed as the natural log of (density + 1), and percentage variables (stream gradient, pool-to-riffle ratio) were arcsine-transformed.

Results and Discussion

Scope of Comparisons

Considerable variation was found in the biotic communities both within and among streams in each province we studied, yet we sampled a relatively small number of streams (minimum N = 18 in each province). Thus, our results should be viewed as a first attempt to compare aquatic amphibian communities in the Pacific Northwest.

Naturally Regenerated Stands

Stream characteristics—The streams we sampled in young, mature, and old-growth forests had similar gradients, widths, depths, side-slope gradients, and water temperatures (table 1). This finding was somewhat surprising considering the large geographic area and different mountain ranges where streams were examined (see frontispiece). We purposely selected headwaters and small streams that were about 1 to 2 m wide, however, and some variables (such as water depth) may simply reflect or be correlated to stream size (width). Sizes of substrata were evenly distributed ($P = 0.27$) in streams of young, mature, and old-growth forests (fig. 4).

Table 1—Mean values of physical characteristics of streams sampled during stream surveys

Variable	Old growth	Mature	Young	*P*
Number of streams	22	22	15	
Gradient (%)	11.4	14.4	8.3	0.23
Width (m)	1.23	1.16	1.17	0.85
Depth (cm)	4.8	4.6	4.5	0.81
Pool ratio	0.38	0.40	0.40	0.83
Side slope (%)	43.4	44.1	46.9	0.82
Water temperature (°C)	10.9	10.9	11.4	0.73

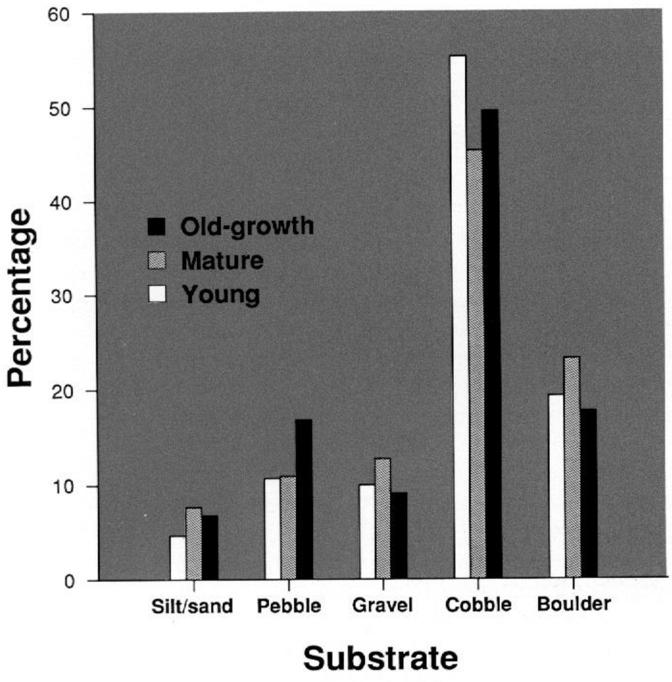

Figure 4—Distribution of sizes of substrates in streams in old-growth, mature, and young forests in Oregon and Washington.

Amphibian abundance and forest age—Abundance (individuals/m^2) of each amphibian species was highly varied, but no significant differences in abundance were found among any of the forest types (table 2).

Giant salamanders were the most common amphibians. Pacific giant salamanders were present in 50 of the 59 (85 percent) streams we sampled, and Cope's giant salamander occurred in 11 of 24 (46 percent) streams within their limited geographic range. Together, these species were present in 53 of the 59 (90 percent) streams sampled. Tailed frogs were the next most frequent species, occurring in 45 of 59 (76 percent) streams. Olympic salamanders do not occur in the Mount

Table 2—Mean density (individuals/m^2) of amphibians in streams for different forest age-classes

Species		Old-growth	Mature	Young	*P*
Tailed frog	Streams	22	22	15	
	Mean	0.86	0.98	0.84	0.98
	SD	1.14	1.71	1.03	
Olympic salamander	Streams	22	22	15	
	Mean	0.61	0.37	0.15	0.23
	SD	1.09	0.73	0.25	
Pacific giant salamander	Streams	22	22	15	
	Mean	1.21	1.39	1.26	0.93
	SD	1.48	1.70	1.48	
Cope's giant salamander	Streams	8	8	8	
	Mean	0.13	0.50	0.37	0.28
	SD	0.38	0.61	0.49	
Dunn's salamander	Streams	16	16	9	
	Mean	0.21	0.36	0.10	0.30
	SD	0.26	0.60	0.27	
Total amphibians	Streams	22	22	15	
	Mean	2.89	3.19	2.50	0.62
	SD	2.74	2.50	1.92	

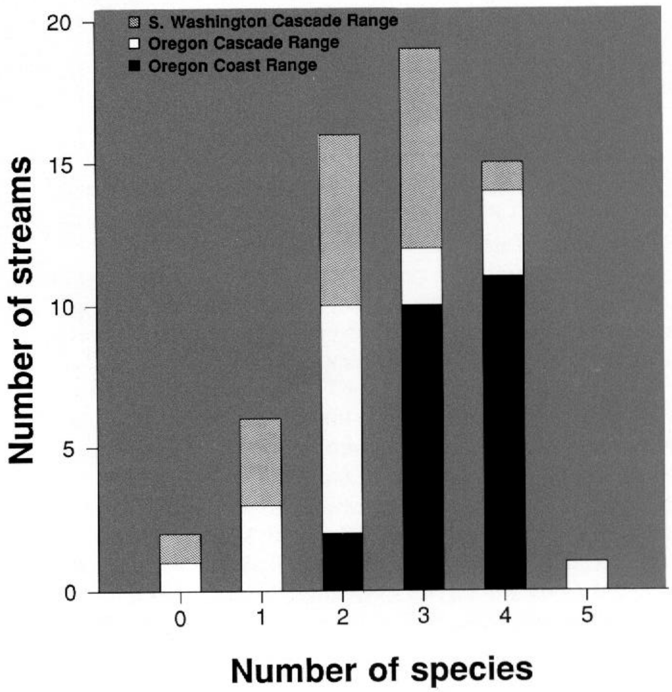

Figure 5—Number of species of aquatic amphibians captured in streams in the southern Washington Cascades, the Oregon Cascades, and the Oregon Coast Range.

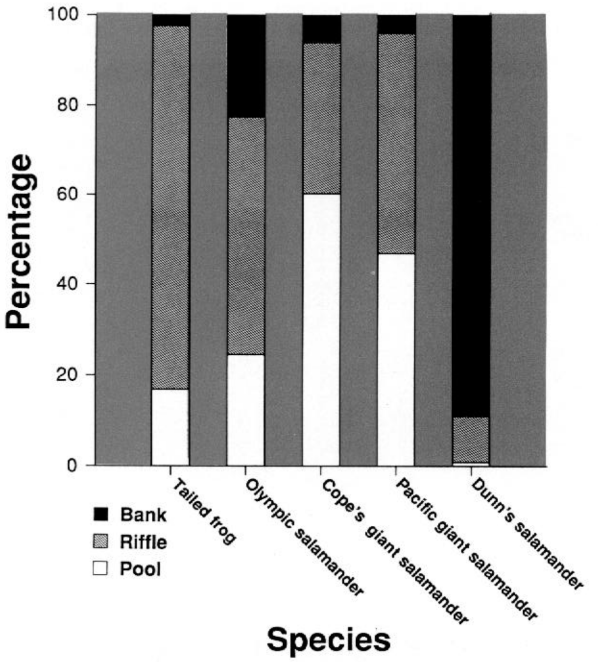

Figure 6—Percentage of amphibian captures in three different stream habitats.

Table 3—Depth of water and size of rocks used for cover for each species of stream amphibian (adult includes all transformed juveniles and sexually mature adults)

		Depth (cm)			Cover size (cm^2)		
Species	Age	N	Mean	SD	N	Mean	SD
Tailed frog	Adult	93	4.1	2.9	60	1,011	3,579
	Larva	491	4.9	4.1	302	415	668
Olympic salamander	Adult	36	3.9	8.3	27	629	637
	Larva	170	3.6	4.1	92	467	717
Pacific giant salamander	Adult	31	5.4	5.9	24	2,410	6,072
	Larva	728	6.8	6.2	347	712	2,032
Cope's giant salamander	Larva	76	8.0	7.5	37	807	699
Dunn's salamander	Adult	—	—	—	85	1,003	1,399

Rainier area, but we found this species in 31 of 55 (56 percent) streams within its geographic range. Dunn's salamander occurred in 23 of 41 (56 percent) possible streams in the Oregon Cascades and Coast Range. Two streams lacked amphibians, but most (88 percent) had 2 to 4 species present (fig. 5). Thus, almost all permanent streams flowing through the natural forests of the Pacific Northwest have multispecies communities of aquatic amphibians.

Microhabitat association—We found no significant relations between the abundance of any amphibian species and the physical habitat variables we measured (stream gradient, pool ratio, mean depth or median substrate values). Significant differences ($P < 0.05$) were found among species in their use of microhabitats within streams we studied (fig. 6), however. Both tailed frogs and Olympic salamanders were found most often in riffles, and about 25 percent of the Olympic salamanders were taken on stream banks or in shallow seeps at stream margins. Cope's giant salamander mostly frequented pools, but Pacific giant salamanders were taken about equally in riffles and pools. Dunn's salamander is often semi-aquatic, and our captures of this species were almost entirely on stream-bank or seep habitats.

The majority of amphibians were found under rock or log cover (we were unable to determine the exact undisturbed position of all animals). Of those captures that provided data on the position of animals, 471 of 722 (65 percent) Pacific giant salamanders, 418 of 564 (74 percent) tailed frogs, 184 of 239 (77 percent) Olympic salamanders, 65 of 78 (83 percent) Cope's giant salamanders, and 94 of 101 (93 percent) Dunn's salamanders were collected from under a cover object. Larval giant salamanders were often found in open water in pools, and tailed frog tadpoles were observed attached to rocks in riffles by means of their suctorial mouth.

Differences were found between amphibian age-classes (larvae versus all transformed individuals) and among species in the depth of water and the size of rock cover under which they were found (table 3). The larvae and neotenes of the Pacific giant salamander ($P = 0.056$) and tadpoles of the tailed frog ($P = 0.015$) were in deeper water than adults of each species. No difference was observed between the depth of occurrence for larval and adult Olympic salamanders ($P = 0.44$). We found that the larvae of both the Pacific giant salamander ($P < 0.001$) and tailed frog ($P = 0.001$) were under smaller rocks than were adults, but no significant differences were found between the use of rocks by larval and adult Olympic salamanders ($P = 0.11$).

Both adults ($P = 0.035$) and larvae ($P = 0.001$) of four species (excluding Dunn's salamander; table 3) were observed at different water depths. Differences in the size of rocks used for cover among five species (table 3) were also significant for both adults ($P = 0.029$) and larvae ($P < 0.001$). Many of these differences in the selection of cover objects likely reflect the marked variation in species size. Large adults of the Pacific giant salamander and adult tailed frogs were mostly found under larger rocks or boulders, whereas the smaller larvae of Olympic salamanders and tailed frogs often occurred under small rocks or in beds of gravel, pebble, and cobble.

Table 4—Physical characteristics of streams in each province

Variable	Oregon Coast Range	Oregon Cascades	Southern Washington Cascades	*P*
Number of streams	23	18	18	
Gradient (%)	8.2	19.1	8.8	0.001
Width (m)	1.25	1.10	1.20	0.45
Depth (cm)	5.0	4.2	4.6	0.42
Pool ratio	0.38	0.38	0.42	0.63
Side slope (%)	46.1	48.5	38.8	0.31
Water temperature (OC)	12.1	10.9	9.7	0.002

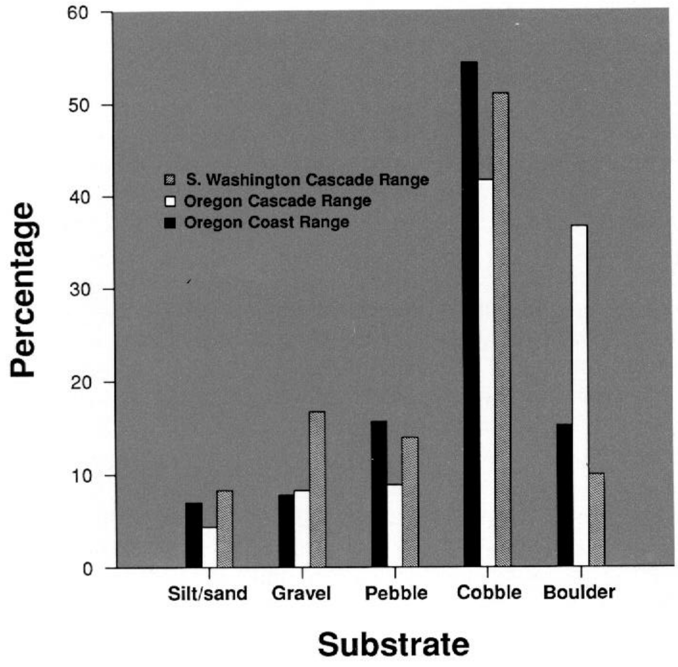

Figure 7—Distribution of sizes of substrates in streams in the southern Washington Cascades (SW), the Oregon Cascades (OC), and the Oregon Coast Range (CR).

Regional Patterns

Stream characteristics—Analysis of habitat variables suggested that the streams we sampled in each province were similar. No significant differences were found in width, depth, or pool ratio among provinces (table 4). Streams sampled in the Oregon Cascades had steeper gradients than in the other regions ($P < 0.001$), mostly because of a few streams where very steep reaches (30-45 percent) were sampled. The mean water temperature in Coast Range streams was warmer, perhaps reflecting differences in regional climate. Sites in the interior parts of the Coast Range are in areas that are subject to higher summer temperatures than are streams at higher elevations in the Cascade Range.

Table 5—Mean densities (individuals/m^2) of stream amphibians in each province; subprovinces are listed from northern to southern (see frontispiece)

Province (streams)	Tailed frog	Olympic salamander[a]	Pacific giant salamander	Cope's giant salamander[b]	Dunn's salamander[c]
Oregon Coast Range (23)	0.76	0.29	2.28	–	0.41
Coast (4)	0.86	0.14	1.94	–	0.18
Siuslaw (5)	0.76	0.16	2.41	–	0.24
Umpqua (8)	0.81	0.22	2.28	–	0.57
Coquille (6)	0.65	0.58	2.40	–	0.49
Oregon Cascades (18)	0.25	0.48	0.88	0.40	0.04
Mt. Hood (6)	0.38	1.40	1.75	0.40	0.07
Andrews (6)	0.10	0.07	0.75	–	0.01
Rogue (6)	0.28	0	0.15	–	0.02
So. Washington Cascades (18)	1.72	0.60	0.42	0.31	–
Mt. Rainier (4)	0.35	–	0.10	0.22	–
Cowlitz River (4)	1.11	0.45	0.10	0.83	–
Lewis River (5)	0.70	0.34	1.20	0	–
Wind River (5)	4.32	0.97	0.16	0.29	–

[a] The Olympic salamander does not occur at Mount Rainier.
[b] Cope's giant salamander occurs only in Washington and northern Oregon.
[c] Dunn's salamander does not occur in the Washington Cascades.

For our samples, statistically significant variation was found among provinces in substrate of streams. More boulders and fewer pebble or cobble-sized rocks were found in the streams we studied in the Oregon Cascades than in the other two regions (fig. 7). Some of the Oregon Cascade streams may have been underlaid with bedrock, and the reduction in cover sites may partly explain the generally low abundance of amphibians in some of these streams. Streams we examined in the Washington Cascades had more gravel, pebble, and cobble than those in the Oregon Cascades. The Coast Range sites had more cobble and pebble substrate than either of the Cascade provinces, but the differences were minor.

Amphibian abundance—Considerable variation was found in the abundance of each species among the streams we sampled in the three provinces (table 5). Pacific giant salamanders and Dunn's salamanders were most abundant in the streams we studied in the Oregon Coast Range, and tailed frogs reached their highest densities in streams we sampled in the Washington Cascades. Olympic salamanders were more abundant in the streams we searched in the Washington Cascades than in those we sampled in the Oregon Cascades or Coast Range.

Within each of the provinces, some clinal patterns were found. Abundance of amphibians in the Oregon Cascade sites varied from the southernmost streams that contained only three species in low numbers to streams in the northernmost area (Mount Hood) that had up to five species in moderate to

Table 6—Mean biomass (g/m^2) and density (individuals/m^2) of stream amphibians and salmonid fishes (from Platts and McHenry 1988) in the Pacific Northwest

Species	Number of streams	Density		Biomass	
		Mean	SD	Mean	SD
Tailed frog	59	0.90	1.34	1.56	2.28
Olympic salamander	55	0.43	0.84	0.46	1.24
Giant salamanders	59	1.43	1.53	6.46	6.36
Dunn's salamander	41	0.24	0.43	0.26	0.46
Total amphibians	59	2.90	2.43	8.63	7.25
Salmonid fishes	49	0.29		2.17	

high abundance. Except for Cope's giant salamander, amphibians in Washington streams showed a reverse pattern with the most species and highest abundance in streams to the south. We found few differences from north to south among the streams in the Oregon Coast Range, except that Olympic salamanders were more abundant in the southernmost streams (Coquille River drainage). The four coastal streams in the Coast Range did not differ from inland streams.

Some of these patterns may be due to regional variation in climate or stream productivity. Because of relatively small sample sizes, however, observed differences may also reflect variations in the collecting efficiency of field crews, or simply random variation among the streams sampled. Further work is needed to document possible clinal changes in the occurrence and abundance of species.

Comparison to Salmonid Fishes

Recently, Platts and McHenry (1988) summarized the known literature on density and biomass of salmonid fishes. For streams in the Pacific region, our data indicate that aquatic amphibians are 10 times more abundant with 4 times the biomass than what was reported for salmonids (table 6). We do not have comparable data for other fishes (for example, sculpins). Even if tailed frogs are excluded because their larvae are herbivorous and the adults forage above or out of the water, small streams still harbor populations of aquatic amphibians that exceed any known estimate for coldwater fishes. Several reasons may account for these differences.

Amphibians may reach high densities and biomass because their adults can exploit both aquatic and terrestrial prey (Bury and Martin 1973, Nussbaum and others 1983). Salmonid fishes forage on invertebrates that land on or occur in water. Fish are attack predators and highly active, but amphibians often hide under cover as sit-and-wait predators and thus convert more energy to biomass than do fishes. Amphibians appear to be the predominant vertebrate predator in many headwaters and small streams in the Pacific Northwest.

Managed Stands

Timber harvest increases insolation on waterways and raises stream temperatures (see Beschta and others 1987, Hartman and others 1987). Such effects usually last only until the canopy is reestablished. In the Oregon Coast Range, Andrus and Froehlich (1988) reported that shading over streams may reach 50 percent in less than 5 years after clearcutting and may approach pre-logging cover by age 10. Tailed frogs and Olympic salamanders, however, have low and narrow temperature tolerances, and these species are likely to be negatively affected by the increased water temperature in streams in clearcuts (Bury and Corn 1988b, de Vlaming and Bury 1970). Conversely, Pacific giant salamanders may be more abundant in streams traversing clearcuts than in densely forested stands (Hawkins and others 1983, Murphy and Hall 1981, Murphy and others 1981), possibly because of enhanced populations of invertebrate prey for several years after timber harvest. Invertebrates, salmonids and salamander populations decline once shade is reestablished over streams in western Oregon (Hawkins and others 1982, 1983; Murphy and others 1981).

Logging can cause sedimentation in streams, which eliminates crevices and cover habitat apparently needed by larval salamanders (Bury 1988b, Bury and Corn 1988b, Hall and others 1978). This habitat feature is the most important determinant of the number of amphibians over the long term (Corn and Bury 1989).

Coarse woody debris in and along streams reduces debris torrents and channelization, functions as a sediment trap, and provides sources of nutrients and cover for animals in streams (Franklin and others 1981, Harmon and others 1986, Sedell and Swanson 1984). Timber harvest can also reduce the introduction of new pieces of down wood into the streambed (Bryant 1985, Sedell and Swanson 1984, Swanson and Lienkaemper 1978), and such material helps maintain the ecological role of streams (Meehan and others 1977, Scrivener and Andersen 1984). The juxtaposition and pattern of stand types resulting from forest fragmentation because of logging, furthermore, may influence the occurrence and abundance of stream amphibians. Corn and Bury (1989), for example, suggest that the presence of uncut timber upstream influences the presence and persistence of aquatic amphibians in streams flowing through logged areas downstream.

The response of aquatic amphibians to clearcutting or other disturbances may vary regionally. Hawkins and others (1988) found that tailed frogs were virtually extinct in drainage basins deforested by the eruption of Mount St. Helens, Washington, whereas frog densities were high in partially or completely forested basins. In the Oregon Coast Range, Corn and Bury (1989) reported that the densities and biomass of amphibian species in unlogged streams were 2 to 7 times greater than in logged streams. They suggested that logging severely reduces microhabitats for larval salamanders because streams in logged stands had more fine sediments than control streams. Tailed frogs and Olympic salamanders were especially sensitive to logging, and in some streams these species may experience local extinction immediately after clearcutting (Corn and Bury 1989, Nussbaum and others 1983). Tailed frogs and Olympic salamanders are closely tied to the stream habitats they occupy. These species appear to have limited dispersal abilities that may prevent them from recolonizing altered streams even after the forest canopy has been reestablished. The likelihood of recolonization by tailed frogs is very low in streams surrounded by hot, arid environments (see Daugherty and Sheldon 1982, Hawkins and others 1988, Metter 1967).

There are fewer data on the response of aquatic amphibians to timber harvest in the Cascade Range, on the Olympic Peninsula, or in British Columbia. Aquatic amphibians in these regions may have a higher probability of surviving the effects of clearcutting because northern and higher elevation montane regions are generally cooler than those at lower elevations or lower latitudes.

The response of Pacific giant salamander populations to logging is dependent on stream gradient (Corn and Bury 1989, Hall and others 1978). For several decades after logging, their population numbers remain small in low gradient streams, whereas they appear to be little influenced in high-gradient streams. Logging does not appear to cause local extinction of this species, and timber harvest may even temporarily enhance some giant salamander populations where there are increases in stream productivity related to greater insolation.

Research Needs and Management Recommendations

Additional research is needed on:

- The effects of timber harvest on the occurrence and abundance of aquatic amphibians in the Pacific Northwest;
- The habitat preferences and environmental tolerances of aquatic amphibians, especially the Olympic salamander;
- The life histories, ecology (particularly dispersal abilities), and viable population sizes of tailed frogs and Olympic salamanders;
- The effectiveness of different types and sizes of buffer strips along streams to protect amphibians; and
- The value of different-sized patches of forested habitat in watersheds as reservoirs or source areas for aquatic amphibians.

We recommend that intensive research and improved stream-management practices be directed at the Olympic salamander and the tailed frog, which we consider to be the species most sensitive to the effects of timber harvest. The survival of aquatic amphibian populations in most forested areas of the Pacific Northwest ultimately will depend upon their abilities to persist in streams flowing through managed forests. Comprehensive planning and the protection of small streams during logging are essential components of management strategies aimed at protecting aquatic amphibian populations.

Bury and Corn (1988b) suggested that headwaters should be surveyed for Olympic salamanders and tailed frogs before timber sales, and if these species are present, then protection efforts should be made. Buffer strips have been shown to be effective at protecting stream biota and habitat by maintaining shade and reducing sedimentation (Beschta and others 1987, Hartman and others 1987, Murphy and others 1981, Newbold and others 1980, Raedeke 1988). Costs of buffer strips are higher on smaller streams than on larger streams (Andrus and Froehlich 1988), and it may be difficult to convince land managers that the benefits of buffer strips, and riparian zones outweigh the costs (Bury and Corn 1988b). We therefore need to investigate alternatives for reducing the costs of buffer strips and yet ensure the protection of amphibians, fishes, and other wildlife along headwaters.

Retention of deciduous vegetation (bigleaf maple, alder) and unmerchantable conifers (small or cull trees) may be one inexpensive way to preserve shade. We strongly recommend that natural woody debris (large pieces that are partially buried or decayed) be retained in streams. If merchantable timber is felled away from the stream, the deciduous trees within riparian areas would be left mostly intact. Cull or broken trees that fall across streams or along the streambank during timber harvest provide needed sources of nutrients, sediment traps, shade and cover for wildlife. Moderate amounts of slash and coarse woody debris are best left where they fall. Retention of streamside trees and woody debris also reduces the cost of removing logging debris.

Aquatic amphibians have small home ranges, and the protection of relatively small patches of streamside habitat might provide habitat for viable populations. In the Oregon Coast Range, we found that some species can occur in disturbed reaches if protected waters are present upstream in the same drainage (Corn and Bury 1989). The protection of only part of a drainage (for example, a forest patch containing headwater creeks) or a buffer zone (for example, a 50-m wide strip) may ensure survival of aquatic amphibian populations.

Headwaters and streams comprise less than 5 percent of the total surface area of northwestern forests (Bury 1988). Wise management of this rare and ecologically important resource, however, is essential for maintaining the health and stability of wildlife and fisheries populations in the Pacific Northwest.

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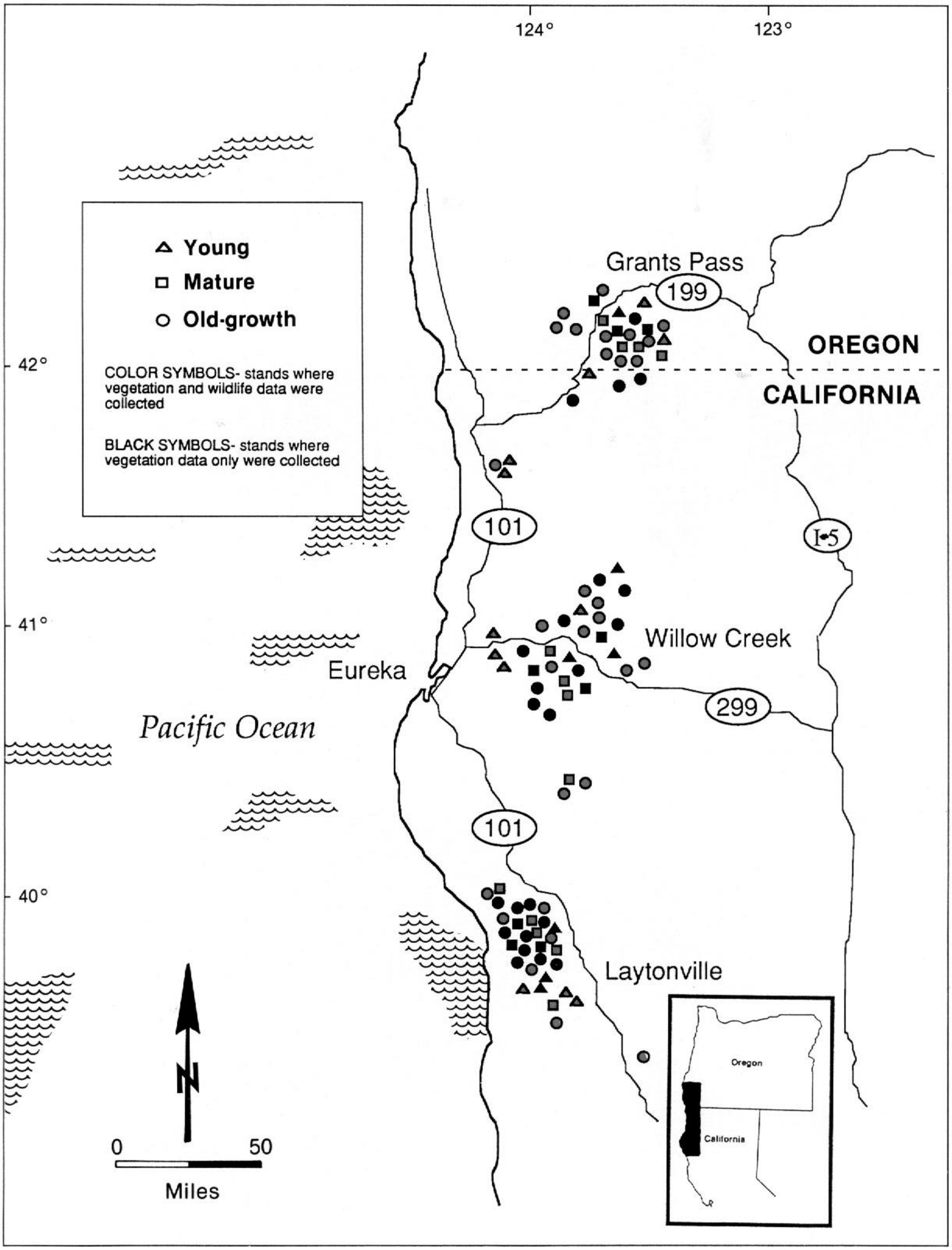
Continue

Part 7

Old-Growth Community Studies in Northern California and Southern Oregon



Location of study sites.

Distinctive Features and Definitions of Young, Mature, and Old-Growth Douglas-Fir/Hardwood Forests

Bruce B. Bingham and John 0. Sawyer, Jr.

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Abstract

We examined the structure of 70 Douglas-fir/hardwood stands ranging from 40 to 560 years old in northwestern California and southwestern Oregon for features that best distinguished among young (40-100 year), mature (100-200 year), and old-growth (>200 year) forests. Separate analyses of 11 groups of variables representing six components of forest structure identified features of trees, understory cover, snags, and logs as important discriminators. Independently, features of understory and dead-wood components were weak-to-moderate discriminators among forest age-classes. The strongest discriminators were features of tree height and diameter components. A discriminant model using features from several components proved to have the greatest overall discriminating power among forest age-classes. This multiple components model included seven variables: the basal area of conifers 240 m tall, the basal area of conifers 290 cm in d.b.h., the basal area of conifers <45 cm in d.b.h., the basal area of hardwoods 45 to 90 cm in d.b.h., the cover of hardwoods 18 m tall, the density of hardwood saplings 1 to 2 m tall, and the density of hardwood snags 220 cm in d.b.h. and 22 m tall. We present definitions for young, mature, and old-growth Douglas-fir/hardwood forests based on a wide range of structural features. In addition, we revise the interim old-growth definition for this forest type introducing new minimum standards along with average values ± 95-percent confidence limits for certain key features.

Introduction

Old-growth Douglas-fir forests display several distinctive structural features (Franklin and others 1981). These features, which include large live trees, large snags, and large logs, play numerous important roles in forest ecosystems. Controversies surrounding the loss of old-growth from the forested landscapes of Washington, Oregon, and California demand the immediate attention of managers and researchers. To assist managers in their planning efforts, the Old-Growth Definition Task Group (1986) developed interim definitions for certain kinds of old-growth forests with minimum criteria for key features. With new data available, their interim definition for old-growth Douglas-fir/hardwood forest should be expanded. For comparison, quantitative definitions for mature and young forests are needed. Such comparisons can help managers develop strategies to recognize and conserve key features when manipulating forests.

In northwestern California and southwestern Oregon, low-elevation (<l200 m) Douglas-fir forests are mixtures of Douglas-fir and hardwood trees. The hardwoods typically account for major percentages of stand basal areas and include tanoak, Pacific madrone, canyon live oak, golden chinkapin, California-laurel, California black oak, and Oregon white oak. Conifers other than Douglas-fir generally account for minor percentages and include redwood, ponderosa pine, incense-cedar, Port-Orford-cedar, sugar pine, western red-cedar, and Pacific yew.

Franklin and Dyrness (1973) refer to these forests as Douglas-fir on mixed evergreen sites. Sawyer and others (1977) used the name Douglas-fir/hardwood to distinguish these forests from others in Oregon and Washington, where, at lower elevations, Douglas-fir dominates with conifer associates instead of hardwoods.

The structural features of Douglas-fir/hardwood forests change with age. These changes ultimately lead to a forest where Douglas-fir and the hardwoods are self-replacing (Sawyer 1980, Thornburgh 1981). This study identified major features of young, mature, and old-growth Douglas-fir/hardwood forests in northwestern California and southwestern Oregon. We used these features and others from a wide range of forest components to develop definitions of young, mature, and old-growth forests. In addition, our results provided data for revising the interim old-growth definition for this vegetation type. We present new minimum standards and average values along with the 95-percent confidence limits for key features such as large trees, snags, and logs.

Location and Environment

Douglas-fir/hardwood forests extend from southwestern Oregon to central California. Along the coast, these forests replace redwood forests on upland and more xeric sites (Stuart 1987). To the south, Douglas-fir dominance dwindles, and evergreen oaks, tanoak, and Pacific madrone become the dominant trees (Sawyer and others 1977, Wainwright and Barbour 1984). In the mountains, the forest type's upper elevational limit occurs when the hardwoods are replaced by conifers, particularly white fir (Sawyer and Thomburgh 1977).

We conducted this study in the Northern California Coast Range and Klamath Mountains provinces (Irwin 1960). The Northern California Coast Range province extends from Oregon as a narrow band of low coastal mountains. The province widens in southern Humboldt and Mendocino counties and continues south to the San Francisco Bay region. The Klamath Mountains province is adjacent to the northern Coast Ranges and includes the Siskiyou Mountains of southwestern Oregon and extends to the Yolla Bolly Mountains of California. Soils supporting Douglas-fir/hardwood forests in both provinces are derived predominantly from metasedimentary rocks.

The climate of northwestern California is generally mild with wet winters and dry summers. Average annual precipitation at coastal and low-elevation mountain locations ranges from 650 to >2000 mm. High summer and low winter temperatures are typically near 38 and -7 °C, respectively.

The Northern California Coast Range and Klamath Mountains provinces are characterized by steep and rugged terrain. Abrupt changes in aspect, slope, soil properties, and localized disturbance regimes result in rapid shifts in tree-species dominance and changes in forest structure. In Douglas-fir/hardwood forests, these shifts are expressed as a forest mosaic with patches of conifers, hardwoods, or diverse mixtures. Canopy openings are common and display various stages of forest regeneration.

Fire has played an important role in the origin and development of Douglas-fir/hardwood forests before and since the arrival of European settlers (Agee, this volume; Johnson 1979). Tree-ring studies in the northern California Coast Range concluded that fires occurred so frequently that settlers, and Native Americans before them, set fires regularly (Anonymous 1983). During settlement, original forest lands were often burned repeatedly after timber harvest as a means of converting the areas to farm or grazing lands (Show and Stuart 1932). For these fires to bum out of control and into adjacent forests was not unusual.

Since the early 1900's, fire management has intensified. The suppression of wildfire has resulted in a scarcity of young stands that originated after naturally ignited fires. Most young stands <100 years old in northwestern California originated after logging. In many of these stands, fire was used as a means of reducing slash accumulations. Large quantities of dead wood often remained, however. These young managed stands do not necessarily possess the same structural features as found in young stands that originated after a catastrophic event other than logging.

Methods

Study Sites

Local ecologists proposed more than 100 candidate study stands with tentative age-class assignments. Each candidate was a forest stand of relatively homogeneous structure, floristic composition, and physiography. We selected 70 Douglas-fir/hardwood stands ranging from 40 to 560 years old and centered in three geographic areas (see frontispiece). Stands were selected to represent three site moisture categories (dry, mesic, or wet) characteristic of each area.

Stand sizes ranged from 5 to about 100 ha. Twenty-two stands were located on the Northern California Coast Range Preserve, a 3200-ha old-growth reserve managed by The California Nature Conservancy and the USDI Bureau of Land Management. Seven stands were located on private lands. The remaining stands were located on lands administered by either the USDA Forest Service or the USDI Bureau of Land Management.

Field Measurements

We sampled 285 plots, each of which consisted of a series of circular plots ranging from 0.002 to 0.2 ha. The smaller plots were systematically positioned within the 0.2-ha plot. Stands <20 ha were sampled by using three (0.2-ha) plots. Larger stands were sampled by using five (0.2-ha) plots. The first plot in each stand was randomly located. Subsequent plots were positioned at 150-m intervals. Plots were placed a minimum of 50 m from the stand edge.

Snags 250 cm in d.b.h. and 215 m tall were sampled in a 0.2-ha plot. Data on live trees 250 cm in d.b.h., snags 210 cm in d.b.h., total canopy cover, and stand physiography (plot aspect, slope, topographic position, and shape) were collected in a 0.l-ha plot. Live trees 25 to 50 cm in d.b.h., saplings 21 m tall and <5 cm in d.b.h., logs 210 cm in diameter, and the percentage cover of trees and large shrubs 18 m tall were sampled in a 0.05-ha plot. Percentage cover estimates of small shrubs, ferns, herbs, and grasses were made in a 0.02-ha plot. Also estimated in the 0.02-ha plot was the percentage cover of mosses, lichens, rocks, and total vegetation cover in three height-classes; 10.5-m, >0.5- to 1.0-m, and >l.0- to 2.0-m. Four 0.002-ha plots were used to sample seedlings cl m tall, litter depth, and soil texture. The distance to streams, ponds, and springs was noted.

Tree ages in stands were collected by increment coring a minimum of three dominant or codominant canopy Douglas-fir trees from at least three plots. Tree ages in old-growth stands were determined from ring counts on stumps along adjacent roads or clearcuts, or from increment cores, or by a combination of both methods. In plots where trees were cored, we selected at least one healthy codominant or dominant tree near plot center. In young stands, these trees were typically <45 cm in d.b.h. In mature stands, codominant and dominant Douglas-fir trees were typically 45 to 90 cm in d.b.h., and 290 cm in d.b.h. in old-growth stands. Each stand was placed in a forest age-class using the mean age as determined from a minimum of three trees. Mean stand ages ranged from 40 to 560 years. Douglas-fir trees determined to be >560 years old *were* rarely encountered, even on the most productive sites.

Vascular plants, snags, and logs were identified to species. Each snag and log was assigned to one of five decay-classes (Cline and others 1980). Later, classes 1 and 2 were combined into a sound wood category, and classes 3 through 5 were combined into a rotten wood category.

Data Analysis

For the purpose of analyses, we defined young stands as those dominated, in terms of relative basal area, by Douglas-fir trees 40 to 100 years old, mature stands as those dominated by Douglas-fir trees 101 to 200 years old, and old-growth stands as those dominated by Douglas-fir trees >200 years old.

Of the 70 stands we selected, we used 56 to determine distinctive features of the three forest age-classes. The 14 young stands had originated after logging. Of 14 mature stands, 7 had originated after logging, and 28 stands were old growth. We reserved 14 stands as a validation set. These stands included 10 old-growth and 4 mature stands. We selected the validation stands to represent the full range of old-growth and mature stand ages and site conditions. We lacked additional managed young stands to include as validation data.

We were interested in identifying features of forest structure that were strong discriminators among young, mature, and old-growth forests. We started our analyses with 60 variables representing six components of forest structure. Because of the importance of certain aspects of forest structure to managers, we viewed dividing the forest into various structural components, such as tree height, tree diameter, snags, and logs as a reasonable approach. Forest components could then be studied separately to reveal important features of each component. Variables were placed into logical groups for analysis. Certain groups were analyzed in terms of more than one unit of measurement (for example, basal area and density). For our analyses, we ended up with 11 groups of variables partitioned into six structural components (table 1). Each group of variables was analyzed independently. Graphical assessment of each variable was used to determine departures from normality. Variables that were not distributed normally were transformed by using a logarithmic or a square-root transformation.

For each group of variables, we used stepwise discriminant analysis (SAS 1985) to assess relative separation among the three age-classes. Each analysis selected a subset of variables that provided maximum discrimination among age-classes. Variables were allowed to enter and to stay in each discriminant function model based on a partial F test with a significance level of 0.1. A moderate-to-low significance level (50.1) helps to ensure that the variables selected are stable and make a significant contribution to the power of the model.

Table l-Eleven groups of variables (features) representing 6 forest structure components included in the discriminant function analyses (each group was analyzed independently of all other groups)

I. Component: Tree height
Group: basal area (m^2/ha) of trees 25 cm in d.b.h. (1.37 m above ground)
1 * hardwoods <12m tall
2 * hardwoods 12-40 m tall
* conifers <12 m tall
4 * conifers 12-40 m tall
5 * conifers 140 m tall

Group: density (stems/ha) of trees ≥ 5 cm in d.b.h.
1 hardwoods <12 m tall
2 * hardwoods 12-40 m tall
3 * conifers <12 m tall
4 * conifers 12-40 m tall
5 conifers MO m tall

II. Component: Tree diameter
Group: basal area (m*/ha) of trees 25 cm in d.b.h.
1 * hardwoods <45 cm in d.b.h.
2 * hardwoods 45-90 cm in d.b.h.
* conifers <45 cm in d b h
4 * conifers 45-90 cm in d.b.h.
5 conifers 290 cm in d.b.h.

Group: density (stems/ha) of trees ?5 cm in d.b.h.
1 * hardwoods <45 cm in d.b.h.
2 * hardwoods 45-90 cm in d.b.h.
3 * conifers <45 cm in d.b.h.
* conifers 45-90 cm in d.b.h.
5 conifers 290 cm in d.b.h.

III. Component: Small trees
Group: density (stems/ha) of saplings l-8 m tall and <5 cm in d.b.h.
1 * hardwoods l-2 m tall
2 * hardwoods ≥ 2-4m tall
3 * hardwoods 24 m tall
4 * conifers l-2 m tall
5 * conifers > 2-4 m tall
6 * conifers 24 m tall

Group: density (stems/ha) of seedlings <l m tall
1 * hardwoods <25 cm tall
2 * hardwoods 25-50 cm tall
3 * hardwoods 250 cm tall
4 * conifers <25 cm tall
5 * conifers 25-50 cm tall
6 * conifers ≥ 50 cm tall

IV. Component: Understory cover
Group: shrubs and trees 58 m tall (percent)
1 * shrub cover
2 * cover of hardwoods
3 * cover of conifers

Group: ground cover (percent)
1 * herb, grass, and fern cover
2 * moss and lichen cover
3 * vegetation cover <0.5 m tall
4 * vegetation cover 0.5-2 m tall
5 * vegetation cover 22 m tall

V. Component: Snags (standing dead trees)
Group: density (snags/ha) of snags ≥ 10 cm in d.b.h. or top diameter
1 * sound snags
2 * rotten snags
3 * hardwood snags 14 m tall
4 * hardwood snags 120 cm in d.b.h. and 12 m tall
5 * hardwood snags 240 cm in d.b.h. and >4 m tall
* conifer snags 24 m tall
7 * conifer snags 220 cm in d.b.h. and 22 m tall
8 * conifer snags 140 cm in d.b.h. and 24 m tall

VI. Component: Logs (dead wood on the ground)
Group: density (pieces/ha) of logs 210 cm in diameter at larger end
1 * sound logs
2 * rotten logs
3 * logs >22 cm in diameter and 22 m long
4 * logs >44 cm in diameter and 24 m long
5 * logs 250 cm in diameter and of any length
6 * logs 250 cm in diameter and ≥ 15 m long

Group: biomass (tons/ha) of logs 210 cm in diameter at larger end
1 * sound logs
2 * rotten logs
3 * logs >22 cm in diameter and 22 m long
4 * logs >44 cm in diameter and 24 m long
5 * logs 250 cm in diameter and of any length
6 * logs 250 cm in diameter and 115 m long

* = variables that were transformed to attain normality

We used Wilks' lambda, which is an inverse measure of class separation ranging from 0 to 1, to assess the discrimination among age-classes. Structure coefficients, which are correlations between variables and canonical variate scores, were used to assess the importance of each variable. Variables with structure coefficients <0.30 were treated as of minor importance and were not used for interpretation of the canonical variates. Eigenvalues were reported as a measure of the relative contribution of each canonical variate to the discriminatory power of each model. The significance of each canonical variate was tested using a decomposition approach to Bartlett's V statistic (Bartlett 1947). Canonical variates that were not significant at the 0.05 level or better were disregarded. With equal prior probabilities, the percentage of training stands (the 56 stands used in the discriminant analyses) correctly assigned to their respective age-classes was used as a measure of classification success.

The variables retained by the 11 stepwise discriminant analyses were combined and analyzed in a final stepwise analysis. This final analysis selected variables representing several structural components. The classification error rate for the multiple components model was determined for old-growth and mature stands using the validation data set. We further tested the model for its ability to correctly assign young, mature, and old-growth stands to their respective age-classes using a jackknife classification procedure (Lachenbruch and Mickey 1968).

Results

Distinctive Features Within Individual Components

Tree height (basal area)—Most of the discrimination among age-classes was due to differences in the basal area of conifers ≥40 m tall (table 2). Conifers <12 m tall was of moderate importance. The basal area of tall conifers increased with forest age-class (fig. 1). The basal area of short conifers was highest in the young age-class, which resulted in strong discrimination of young stands from the other two age-classes (fig. 1).

Tree height (density)—Conifers 12 to 40 m tall and conifers ≥40 m tall were both important to the discriminant model (table 2). The higher density of confers 12 to 40 m tall provided strong discrimination of the young age-class from mature and old-growth forests (fig. 2). Young stands were characterized by a dense layer of conifers intermediate in height, and a very low density of tall conifers. Mature stands generally had a moderately dense lower layer of conifers 12 to 40 m tall and relatively high densities of tall conifers. In old-growth forests, the density of conifers 12 to 40 m tall was typically low compared to young and mature stands. The density of tall conifers in old growth was similar to that of mature forests. The analysis of basal area data indicates, however, that the diameters of conifers >40 m tall are, on the average, considerably larger than the diameters of tall conifers in mature stands.

Tree diameter (basal area)—The basal area of conifers ≥90 cm in d.b.h. and the basal area of conifers <45 cm in d.b.h. were the most important features separating age-classes (table 2). The basal area of large-diameter conifers increased with age-class (fig. 3) and was more than two and a half times greater in old-growth than it was in mature stands. Conifers with large diameters were rare in young stands that were dominated by conifers <45 cm in d.b.h.

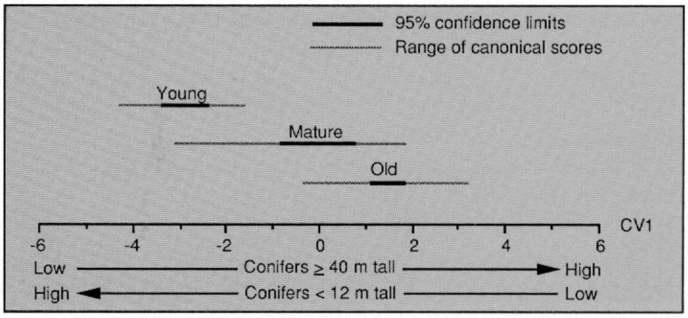

Figure 1—Ordination of forest age-classes according to basal area within tree height-classes (see tables 1 and 2). Significant separation of age-class means was restricted to the first canonical variate (CV1).

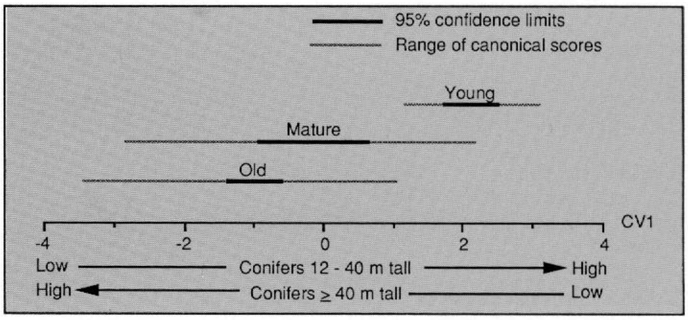

Figure 2—Ordination of forest age-classes according to density within tree height-classes (see tables 1 and 2). Significant separation of age-class means was restricted to the first canonical variate (CV1).

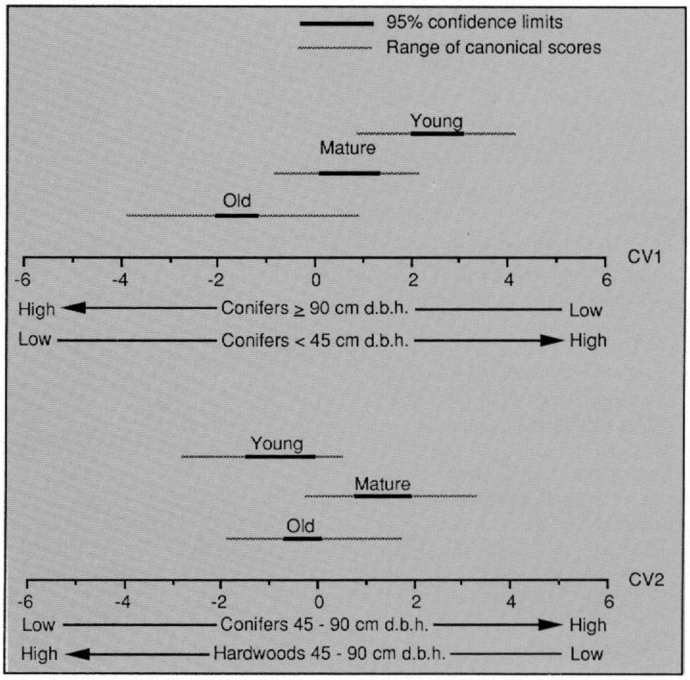

Figure 3—Ordination of forest age-classes according to basal area within tree diameter-classes (see tables 1 and 2). Significant separation of age-class means occurred for both canonical variates (CV1 and CV2).

Table 2—Variables selected by stepwise discriminant analyses on 11 groups of variables representing six forest structure components. Data reported for forest age-classes are means with standard errors in parentheses

Variable selected		Forest age-class			Structure coefficient	
		Young	Mature	Old growth	CV1	CV2[a]
I. Component: Tree height						
group: basal area of trees ≥5 cm in d.b.h.						
Conifers ≥40 m tall		3.2 (1.1)	25.7 (4.0)	40.1 (2.4)	0.97	
Conifers <12 m tall		1.1 (.2)	.8 (.2)	.3 (.1)	–.61	
Wilks' lambda	0.227			Eigenvalue	3.31	
Exact *F* statistic (df = 4, 104)						
(significant at *P* < 0.001)	28.62			(%)	99	
Classification success (%)		100	57	82		
group: density of trees ≥5 cm in d.b.h.						
Conifers 12-40 m tall		321.2 (54.0)	138.6 (27.3)	38.8 (7.3)	.82	
Conifers ≥40 m tall		8.4 (3.1)	48.3 (7.7)	43.5 (2.1)	–.79	
Wilks' lambda	.297			Eigenvalue	1.69	
Exact *F* statistic (df = 4, 104)						
(significant at *P* < 0.001)	21.74			(%)	87	
Classification success (%)		93	72	68		
II. Component: Tree diameter						
Group: basal area of trees ≥5 cm in d.b.h.						
Conifers ≥90 cm in d.b.h.		1.1 (.6)	12.5 (2.5)	34.8 (2.4)	–.94	–.13
Conifers 45-90 cm in d.b.h.		7.8 (1.5)	19.3 (1.9)	8.4 (1.1)	.09	.94
Conifers <45 cm in d.b.h.		14.4 (2.5)	6.7 (1.5)	2.0 (.4)	.82	–.09
Hardwoods 45-90 cm in d.b.h.		5.3 (1.3)	2.8 (1.0)	5.4 (.7)	–.12	–.43
Wilks' lambda	.139			Eigenvalue	3.22	.70
Exact *F* statistic (df = 8, 100)						
(significant at *P* < 0.001)	21.00			(%)	82	18
Classification success (%)		100	71	89		
Group: density of trees ≥5 cm in d.b.h.						
Conifers ≥90 cm in d.b.h.		1.1 (.6)	13.5 (2.9)	28.9 (1.7)	–.97	.03
Conifers 45-90 cm in d.b.h.		31.1 (6.1)	56.9 (6.3)	21.7 (2.7)	.29	.94
Conifers <45 cm in d.b.h.		501.3 (80.9)	233.9 (53.0)	74.8 (13.8)	.80	–.05
Wilk's lambda	.190			Eigenvalue	2.67	.43
Exact *F* statistic (df = 6, 102)						
(significant at *P* < 0.001)	21.97			(%)	86	14
Classification success (%)		86	79	89		
III. Component: Small trees						
Group: density of saplings 1-8 m tall and <5 cm in d.b.h.						
Hardwoods 1-2 m tall		322.3 (53.4)	274.5 (76.3)	633.0 (70.6)	.58	.76
Conifers ≥4 m tall		67.9 (19.3)	19.0 (9.6)	17.6 (4.9)	–.78	.45
Conifers 1-2 m tall		175.7 (68.1)	123.8 (47.8)	114.7 (32.1)	–.25	–.03
Wilks' lambda	.483			Eigenvalue	.54	.34
Exact *F* statistic (df = 6, 102)						
(significant at *P* < 0.001)	7.46			(%)	61	39
Classification success (%)		79	64	61		

Table 2—continued

		Forest age-class			Structure coefficient	
Variable selected		Young	Mature	Old growth	CV1	CV2[a]
III. Component: Small trees (continued)						
Group: density of seedlings <1 m tall						
Hardwoods 25-50 cm tall		1307.1 (305.0)	1370.4 (314.2)	1496.7 (144.3)	0.30	
Hardwoods ≥50 cm tall		783.1 (150.1)	617.5 (148.4)	1050.3 (102.0)	.79	
Wilks' lambda	0.776			Eigenvalue	.28	
Exact F statistic (df = 4, 104) (significant at $P < 0.02$)	3.52			(%)	97	
Classification success (%)		36	57	64		
IV. Component: Understory cover (percent)						
Group: shrubs and trees ≤8 m tall						
Cover of hardwoods		12.5 (2.3)	16.8 (4.3)	25.0 (2.2)	.82	
Cover of conifers		5.2 (1.3)	3.1 (.9)	2.3 (.4)	−.60	
Wilks' lambda	.684			Eigenvalue	.43	
Exact F statistic (df = 4, 104) (significant at $P < 0.002$)	5.43			(%)	95	
Classification success (%)		57	36	68		
Group: ground cover						
Moss and lichen cover		5.3 (2.2)	13.7 (4.8)	18.0 (3.4)	.89	
Vegetation cover 0.5-2 m tall		15.9 (2.2)	15.2 (4.2)	24.0 (2.5)	.69	
Wilks' lambda	.750			Eigenvalue	.27	
Exact F statistic (df = 4, 104) (significant at $P < 0.01$)	4.01			(%)	86	
Classification success (%)		50	43	68		
V. Component: Snags (standing dead trees)						
Group: density of snags ≥10 cm in d.b.h.						
Sound snags		43.1 (9.1)	46.4 (8.2)	14.2 (1.7)	.82	.33
Hardwood ≥20 cm in d.b.h. and ≥2 m tall		6.7 (2.3)	20.0 (5.1)	5.1 (1.2)	.31	.92
Rotten snags		46.1 (7.8)	39.2 (7.4)	17.6 (2.0)	.79	.05
Conifer ≥40 cm in d.b.h. and ≥4 m tall		1.6 (.5)	1.4 (.5)	4.9 (1.0)	−.48	.22
Wilks' lambda	.394			Eigenvalue	.99	.27
Exact F statistic (df = 8, 100) (significant at $P < 0.001$)	7.41			(%)	78	22
Classification success (%)		50	57	82		
VI. Component: Logs (dead wood on the ground)						
Group: density of logs ≥10 cm in diameter at largest end						
Logs >44 cm in diameter and ≥4 m long		29.1 (8.1)	7.2 (2.4)	24.7 (3.0)	.48	
Logs ≥50 cm in diameter		129.1 (24.8)	100.3 (12.1)	81.8 (5.7)	−.35	
Sound logs		59.2 (12.3)	61.8 (16.4)	80.1 (8.8)	.40	
Wilks' lambda	.526			Eigenvalue	.67	
Exact F statistic (df = 6, 102) (significant at $P < 0.001$)	6.45			(%)	83	
Classification success (%)		50	57	71		

Table 2—continued

Variable selected		Forest age-class Young	 Mature	 Old growth	Structure coefficient CV1	 CV2[a]
VI. Component: Logs (continued)						
Group: biomass of logs ≥10 cm in diameter at larger end						
Logs >44 cm in diameter and ≥4 m long		16.2 (5.1)	3.5 (1.1)	18.2 (3.6)	1.00	
Wilks' lambda	0.828			Eigenvalue	.21	
Exact F statistic (df = 2, 53) (significant at $P < 0.02$)	5.49			(%)	100	
Classification success (%)		21	71	54		

[a] Structure coefficients not shown where CV2 was not significant ($P > 0.05$).

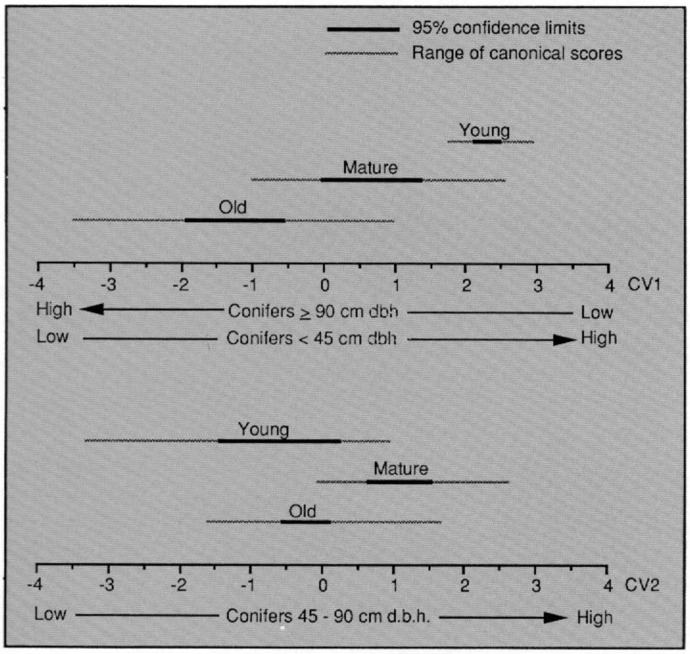

Figure 4—Ordination of forest age-classes according to density within tree diameter-classes (see tables 1 and 2). Significant separation of age-class means occurred for both canonical variates (CV1 and CV2).

Two other variables, the basal area of conifers 45 to 90 cm in d.b.h. and hardwoods 45 to 90 cm in d.b.h. were important in discriminating mature stands from young and old-growth (table 2). Mature stands were further distinguished from young and old-growth stands by having higher basal area of conifers 45 to 90 cm in d.b.h. and lower basal area of hardwoods 45 to 90 cm in d.b.h. The basal area values of medium-sized conifers and medium-sized hardwoods in the young age-class were very similar to old growth. As stands advance to a mature stage, hardwoods become overtopped by taller conifers, resulting in an increase in hardwood mortality. As mature stands develop further, the upper tier of conifers undergoes natural thinning and the hardwoods typically return.

Tree diameter (density)—Three diameter-classes of conifers were important to the discriminant model (table 2). Separation of the three age-classes was strong (fig. 4) and very similar to that provided by the basal-area model. The density of conifers ≥90 cm in d.b.h. increased with age-class, and the density of conifers <45 cm in d.b.h. decreased. Mature forests had the greatest densities of conifers 45 to 90 cm in d.b.h., which was important in discriminating mature from the other two age-classes.

Small trees (saplings)—Two sapling variables, the density of conifers ≥4 m tall and the density of hardwoods 1 to 2 m tall were important to the model (table 2). They provided moderate separation of the forest age-classes (fig. 5). The young age-class was the most distinct because of the high density of conifer saplings ≥4 m tall. Mature and old-growth forests were similar in their densities of conifer saplings. The most important feature distinguishing old growth was a high density of hardwood saplings 1 to 2 m tall. Discrimination of the mature age-class was due to densities of hardwood saplings that were typically lower than the densities found in young and old-growth forests.

Small trees (seedlings)—The analysis of seedling variables selected hardwoods ≥50 cm tall and hardwoods 25 to 50 cm tall (table 2). Overall, discrimination was weak. Old-growth was the most distinct age-class (fig. 6). The separation was primarily due to the density of hardwoods ≥50 cm tall, which was typically highest in old growth and lowest in mature forests.

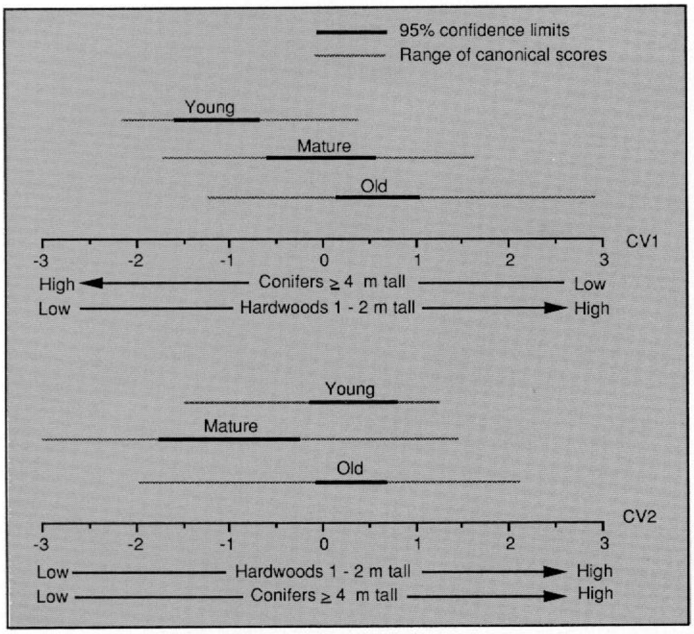

Figure 5—Ordination of forest age-classes according to density within height-classes of small trees 1 to 8 m tall (see tables 1 and 2). Significant separation of age-class means occurred for both canonical variates (CV1 and CV2).

Understory cover (shrubs and small trees)—Two variables, the cover of hardwoods ≤8 m tall and the cover of conifers ≤8 m tall, were important to the model (table 2). Discrimination was moderate. The cover of hardwoods increased with age-class, and the cover of conifers decreased (fig. 7). Old growth was the most distinct age-class. The cover of hardwoods in old growth averaged twice that of young stands, and the cover of conifers in young stands averaged twice that of old growth.

Understory cover (ground cover)—The analysis selected the combined cover of mosses and lichens, and the total vegetation cover from 0.5 to 2 m tall (table 2). Discrimination between young and mature stands was weak. Old growth was the most distinct age-class (fig. 8). Old growth showed the greatest development of moss and lichen cover, the more important variable in the model. Old growth also had the highest cover of vegetation 0.5 to 2 m tall.

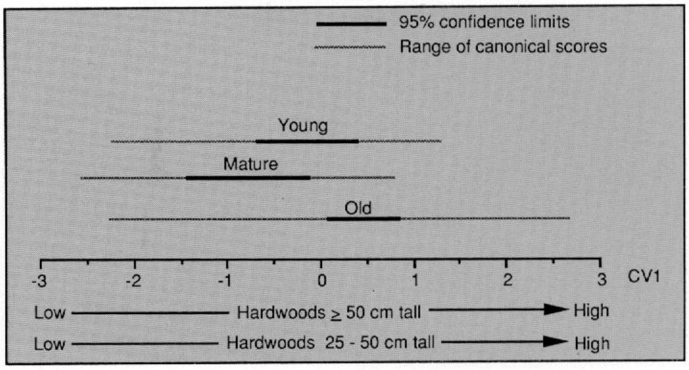

Figure 6—Ordination of forest age-classes according to density within height-classes of small trees <1 m tall (see tables 1 and 2). Significant separation of age-class means was restricted to the first canonical variate (CV1).

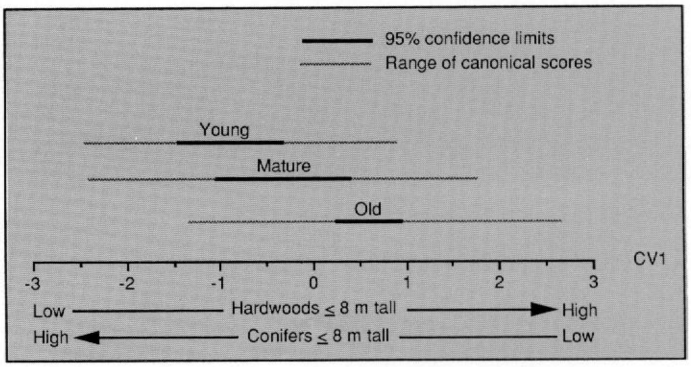

Figure 7—Ordination of forest age-classes according to understory cover of shrubs and small trees ≤8 m tall (see tables 1 and 2). Significant separation of age-class means was restricted to the first canonical variate (CV1).

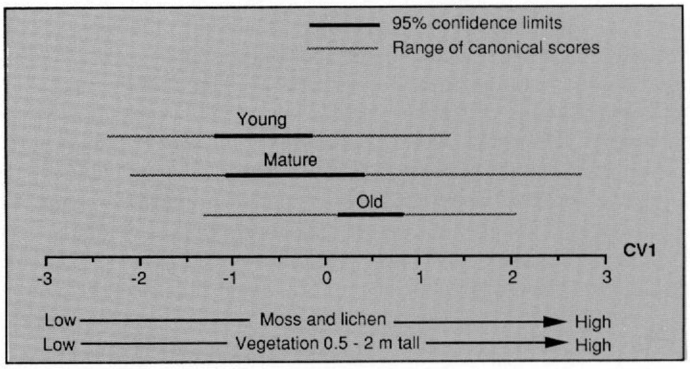

Figure 8—Ordination of forest age-classes according to ground cover variables (see tables 1 and 2). Significant separation of age-class means was restricted to the first canonical variate (CV1).

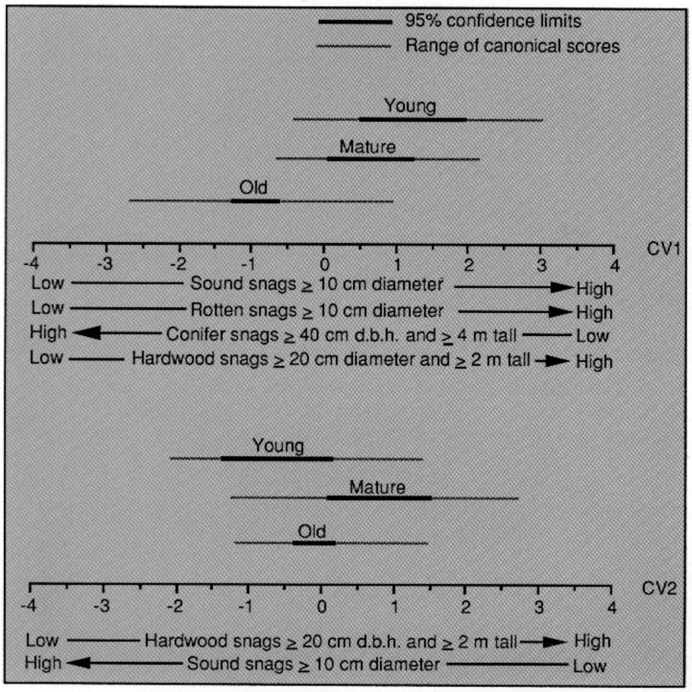

Figure 9—Ordination of forest age-classes according to density within size- and decay-classes of snags (see tables 1 and 2). Significant separation of age-class means occurred for both canonical variates (CV1 and CV2).

Snags (density)—The density of sound snags and the density of rotten snags were the two most important variables to the model (table 2). The model was strongest in discriminating old-growth from young and mature stands. Old growth was characterized by having the lowest densities of sound and rotten snags (fig. 9). A higher density of large conifer snags ≥40 cm in d.b.h. and ≥4 m tall also contributed to the discrimination of old growth. Young and mature forests were similar to one another in their densities of sound, rotten, and large conifer snags. A fourth variable, the density of hardwood snags ≥20 cm in diameter and ≥2 m tall was important in discriminating mature stands. In young, mature, and old-growth forests, hardwoods are typically an important contributor to the snag component. Hardwoods can be especially important in mature stands, however, where they often account for up to 90 percent of the total snag density.

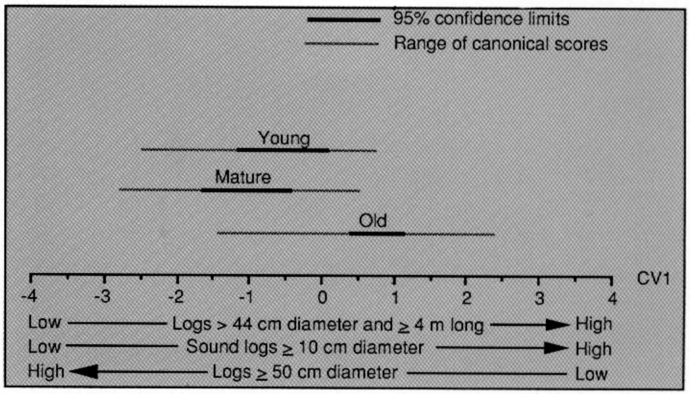

Figure 10—Ordination of forest age-classes according to density within size- and decay-classes of logs (see tables 1 and 2). Significant separation of age-class means was restricted to the first canonical variate (CV1).

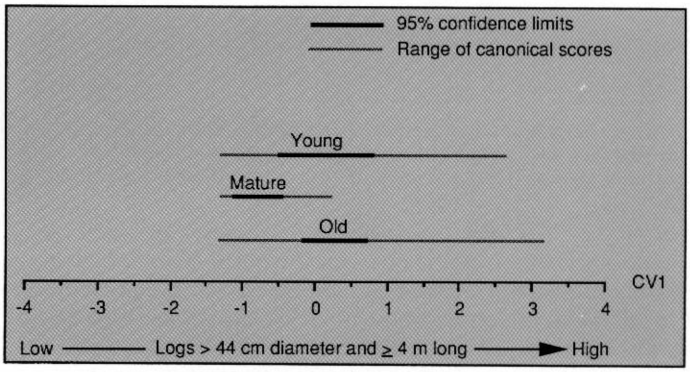

Figure 11—Ordination of forest age-classes according to biomass within size- and decay-classes of logs (see tables 1 and 2). Significant separation of age-class means was restricted to the first canonical variate (CV1).

Logs (density)—Three variables were selected, all of similar importance to the model (table 2). Although separation between the young and mature age-classes was poor, discrimination of old growth was fairly strong (fig. 10). Old growth was distinguished from the two younger classes by having the highest density of sound logs and the lowest density of logs ≥50 cm in diameter. Mature stands typically had low densities of large logs >44 cm in diameter and ≥4 m long. Young and old-growth stands had similar densities of logs >44 cm in diameter and ≥4 m long. In young stands, the abundance of large pieces of wood on the ground was evidently an artifact of the logging methods practiced more than 40 years ago.

Logs (biomass)—Only one variable was selected by the analysis of log biomass (table 2). The biomass of logs ≥44 cm and >4 m long provided essentially no power in distinguishing old growth from the young age-class (fig. 11); both of which showed similar averages. A low biomass of large logs, however, clearly separated mature from the young and old-growth classes.

Distinctive Features Based on Multiple Components

Stepwise discriminant analyses of the 11 groups of variables representing six forest-structure components (table 1) selected 28 variables (table 2). A final stepwise analysis selected 8 of the 28 variables and produced a model that was very

Continue

Table 3—Multiple components model representing 5 forest structure components (data are forest age-class means with standard errors in parentheses)

Variable selected		Forest age-class Young		Mature		Old growth		Structure coefficient CV1	CV2
Basal area of conifers ≥40 m tall		3.2	(1.1)	25.7	(4.0)	40.1	(2.4)	0.93	–0.15
Basal area of conifers ≥90 cm in d.b.h.		1.1	(.6)	12.5	(2.5)	34.8	(2.4)	.88	.20
Basal area of conifers <45 cm in d.b.h.		14.4	(2.5)	6.7	(1.5)	2.0	(.4)	–.79	–.03
Density of hardwood saplings 1-2 m tall		322.3	(53.4)	274.5	(76.3)	633.0	(70.6)	.42	.41
Percentage cover of hardwoods ≤8 m tall		12.5	(2.3)	16.8	(4.3)	25.0	(2.2)	.47	.19
Density of hardwood snags ≥20 cm in d.b.h. and ≥2 m tall		6.7	(2.3)	20.0	(5.1)	5.1	(1.2)	–.10	–.56
Basal area of hardwoods 45-90 cm in d.b.h.		5.3	(1.3)	2.8	(1.0)	5.4	(.7)	.09	.34
Density of hardwood seedlings 25-50 cm tall		1307.1	(305.0)	1370.4	(314.2)	1496.7	(144.3)	.18	.07
Wilks' lambda	0.048					Eigenvalue		4.97	2.48
Exact *F* statistic (df = 16, 92) (significant at $P < 0.001$)	20.45					(%)		67	33
Classification success (%)		100		100		100			

powerful in discriminating among the forest age-classes. The variables selected represented five of the six forest components (table 3). No down-wood (log) variables were retained.

The most important variables discriminating the age-classes were the basal areas of conifers ≥40 m tall, ≥90 cm in d.b.h., and <45 cm in d.b.h. The density of hardwood saplings 1 to 2 m tall, the percentage cover of hardwoods ≤8 m tall, the basal area of hardwoods 45 to 90 cm in d.b.h., and the density of hardwood snags ≥20 cm in d.b.h. and ≥2 m tall were of moderate importance. The eighth variable, the density of hardwood seedlings 25 to 50 cm, made a very minor contribution to the model.

Features most distinctive of old growth (fig. 12) were high basal areas of conifers ≥40 m tall and conifers ≥90 cm in d.b.h., and a low basal area of conifers <45 cm in d.b.h. A high cover of hardwoods ≤8 m tall and a high density of hardwood saplings 1 to 2 m tall also contributed (table 3). Young forests were distinguished by low basal areas of conifers ≥40 m tall and conifers ≥90 cm in d.b.h., along with a high basal area of conifers <45 cm in d.b.h. Mature forests were typified by basal area values that were all intermediate to old-growth and young forests. Another feature of the mature age-class was a relatively high density of hardwood snags ≥20 cm in d.b.h. and ≥2 m tall. Two other features, the density of hardwood saplings 1 to 2 m tall, and the basal area of hardwoods 45 to 90 cm in d.b.h. were both lower in mature stands than in young and old-growth forests.

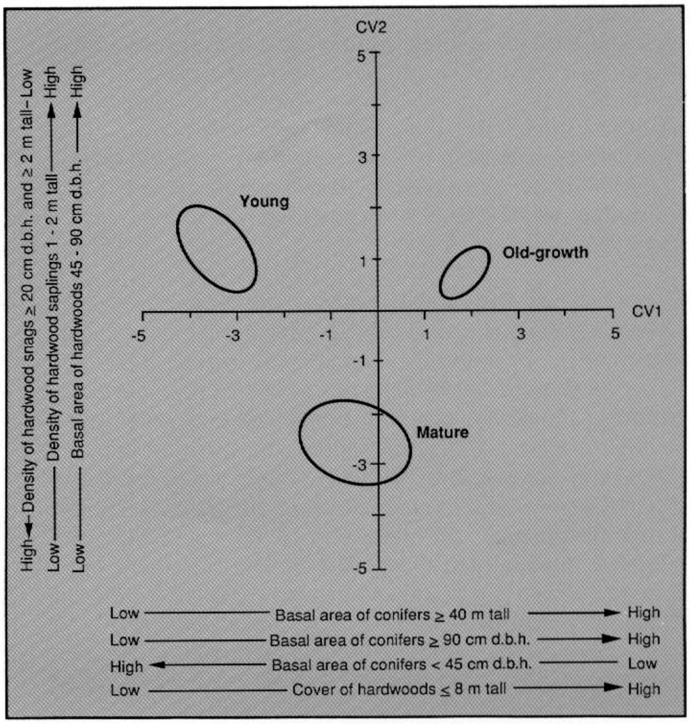

Figure 12—Ordination of forest age-classes according to seven variables. Significant separation of age-class means occurred for both canonical variates (CV1 and CV2). Plotted are the 95 percent confidence elipses around age-class centroids.

Of the 14 validation stands used to test the model, all 10 old-growth and three of the four mature stands were correctly assigned. One mature stand dominated by trees ≥ 185 years old and on a productive site was incorrectly assigned to old growth.

The jackknife classification of the training set (56 stands) correctly assigned 100 percent of the old-growth stands, 79 percent of the mature stands, and 100 percent of the young stands. One mature stand, about 135 years old, was incorrectly assigned to the young class. It was an unmanaged stand characterized by a considerably higher density of hardwoods, and a lower density of conifers 45 to 90 cm in d.b.h. than was typical of mature stands. Another mature unmanaged stand, 190 years old, was incorrectly assigned to old-growth. It had a moderate density of large conifers ≥ 90 cm in d.b.h. and high densities of hardwoods ranging from seedlings to large trees. The third stand was also incorrectly assigned to the old-growth class. The stand was logged 115 years ago but retained several residual large conifers per hectare and had a high density of hardwoods.

Discussion

As indicated by our multiple components model and by our analyses of individual forest components, features associated with tree size provide the strongest discrimination among different-aged Douglas-fir/hardwood forests. In the multiple components model, the most distinctive features of old-growth forests were a high basal area of very large Douglas-fir trees and a low basal area of small Douglas-fir trees. The reverse was true of young forests and intermediate values were typical of mature forests.

The four discriminant models based on variables representing the tree height and tree diameter components were the most powerful of the 11 individual-components models. The remaining models indicated that features of tree reproduction, understory, and dead-wood components, on their own, provide little-to-moderate discrimination. The variation in such features, between stands as well as within a stand, can be extreme. Changes in microhabitat conditions affect seedling and sapling densities, and understory cover values. Tree reproduction, especially of Douglas-fir, varies from scattered individuals to densely populated patches associated with canopy openings regardless of forest age. The influences of total canopy cover on tree reproduction and understory growth are similar for different-aged forests. Regardless of age-class, hardwood reproduction is mainly from crown sprouts. Reproduction from seed is variable, showing patterns in distribution similar to those of Douglas-fir. As a result, seedling and sapling densities, and understory cover can each include a wide range of stand values that typically overlap among different-aged forests.

The accumulation and distribution of coarse woody debris are affected by environment, disturbance, decay rates, and topography (Harmon and others 1986). Wet sites typically have greater amounts of coarse wood than do dry sites (Spies and others 1988). Recruitment of coarse woody debris as snags and logs often occurs in waves related to some event. Stands with histories of hot or frequent fire can contain small quantities of dead wood. Managed stands can inherit large quantities of wood on the ground as slash. Low numbers of large snags, and higher numbers of stumps are also carried over. Decay progresses at different rates depending on species, size, microclimate, and cause of mortality. Topography affects accumulations and distributions by influencing storm patterns, the direction of tree-fall, and the movement of material by gravity. Such influences are important regardless of stand age, and help explain similarities among different-aged forests in certain features of coarse woody debris.

Our multiple components model provides forest managers with a set of features that, in combination, are distinctive of young, mature, and old-growth Douglas-fir/hardwood forests. Together, these features act as a powerful tool for discriminating among the forest age-classes. The models composed of variables selected by analyses of individual forest components can further assist managers in identifying important features of each forest age-class. For example, the analysis of the snag component showed that managed young forests generally have higher sound-snag and rotten-snag densities than does old growth. Old-growth forests, however, typically have higher densities of large conifer snags > 40 cm in d.b.h. and > 4 m long. As another example, analyses of the features of the log component showed that managed young stands and old growth generally have relatively high densities and biomasses of logs >44 cm in diameter and ≥ 4 m long, while mature stands typically contain low quantities.

Testing our model with the validation data set and the jackknife classification helps confirm certain ideas about the development of old-growth features. Age alone may be a poor indicator of old-growth structure. Old-growth conditions develop gradually, with the rate related to the environmental conditions and the disturbance history of the stand (Spies and Franklin 1988). Certain features of old growth, such as a high density of very large trees, do appear on productive sites before 200 years. Stands on sites that are poor at producing large conifers may require much longer periods or may never develop certain features commonly associated with old growth. On managed sites, logging practices can retain large conifers and hardwoods at densities more characteristic of old growth than younger stands.

Forest Definitions

We define young, mature, and old-growth Douglas-fir/hardwood forests by using ranges of means observed in the majority of the stands we sampled in each age-class. The ranges, therefore, represent typical stand values and not minimums or maximums. To provide the most thorough descriptions, we included features beyond those selected by our stepwise discriminant analyses. The major features we used to define each forest age-class, such as tree densities for dominant height- and diameter-classes, and total snag and log densities, all exhibited standard errors that were < ± 20 percent of the age-class mean. Other features, such as those of seedling densities and understory cover, are more affected by changes in microhabitat conditions and tend to show greater variation.

Young Douglas-fir/hardwood forests

Canopy <40 m tall, single-tiered, total cover 65 to 80 percent.

Trees 12 to 40 m tall, conifers 105 to 525 per ha and hardwoods 160 to 660 per ha. Dominant stems, conifers <45 cm in d.b.h., 260 to 780 per ha; hardwoods <45 cm in d.b.h., 225 to 1215 per ha. Stand basal area, 30 to 75 percent hardwoods.

Saplings 1 to 8 m tall, conifers 150 to 450 per ha and hardwoods 300 to 1200 per ha.

Seedlings <1 m tall, conifers 100 to 2500 per ha and hardwood seedlings or sprouts 1500 to 7000 per ha.

Understory cover ≥ 8 m tall, conifers 2 to 10 percent and hardwoods 5 to 20 percent.

Ground cover < 2 m tall, 10 to 25 percent. Moss and lichen cover including epiphytes on the ground, 1 to 5 percent.

Snags ≥ 10 cm in d.b.h., 45 ***to*** 135 per ha. Hardwood snags 20 to 60 percent of snag density. Large snags >40 cm in d.b.h. and >4 m tall, 0.5 to 5 per ha.

Logs ≥ 10 cm in diameter, 200 to 530 per ha. Hardwood logs 20 to 65 percent of log density. Large logs >44 cm in diameter and ≥ 4 m long, 7 to 48 per ha.

Biomass of snags and logs, 10 to 50 metric tons per ha.

Mature Douglas-fir/hardwood forests

Canopy <55 m tall, two-tiered but indistinct, total cover 65 to 80 percent.

Trees 12 to 40 m tall, conifers 60 to 215 per ha and hardwoods 120 to 330 per ha; ≥ 40 m tall, conifers 30 to 60 per ha. Dominant stems, conifers 45 to 90 cm in d.b.h., 40 to 70 per ha: hardwoods <45 cm in d.b.h. 255 to 760 per ha. Stand basal area, 15 to 45 percent hardwoods.

Saplings 1 to 8 m tall, conifers 50 to 400 per ha, and hardwoods 30 to 1100 per ha.

Seedlings <1 m tall, conifers 250 to 1200 per ha and hardwood seedlings or sprouts 3000 to 9000 per ha.

Understory cover ≤ 8 m tall, conifers 1 to 5 percent and hardwoods 5 to 35 percent.

Ground cover <2 m tall, 5 to 55 percent. Moss and lichen cover including epiphytes on the ground, 1 to 20 percent.

Snags 210 cm in d.b.h., 35 to 125 per ha. Hardwood snags 20 to 90 percent of snag density. Large snags ≥ 40 cm in d.b.h. and ≥ 4 m tall, 0.5 to 4 per ha.

Logs ≥ 10 cm in diameter, 225 to 385 per ha. Hardwood logs 45 to 75 percent of log density. Large logs >44 cm in diameter and ≥ 4 m long, 0.5 to 16 per ha.

Biomass of snags and logs, 5 to 30 metric tons per ha.

Old-growth Douglas-fir/hardwood forests

Canopy >55 m tall, two-tiered and well to defined, total cover 65 to 80 percent.

Trees 12 to 40 m tall, conifers 15 to 55 per ha and hardwoods 105 to 280 per ha; 240 m tall, conifers 35 to 50 per ha. Dominant stems, conifers ≥ 90 cm in d.b.h. 20 to 40 per ha; hardwoods <45 cm in d.b.h. 425 to 690 per ha. Stand basal area, 15 to 40 percent hardwoods.

Saplings 1 to 8 m tall, conifers 30 to 300 per ha and hardwoods 650 to 1500 per ha.

Seedlings <1 m tall, conifers 150 to 1100 per ha and hardwood seedlings or sprouts 3500 to 9900 per ha.

Understory cover ≤ 8 m tall, conifers 1 to 5 percent and hardwoods 15 to 30 percent.

Ground cover <2 m tall, 10 to 65 percent. Moss and lichen cover including epiphytes on the ground, 5 to 25 percent.

Snags ≥ 10 cm in d.b.h., 20 to 40 per ha. Hardwood snags 15 to 75 percent of snag density. Large snags ≥ 40 cm in d.b.h. and ≥ 4 m tall, 0.5 to 11 per ha.

Logs ≥ 10 cm in diameter, 215 to 385 per ha. Hardwood logs 20 to 55 percent of log density. Large logs >44 cm in diameter and ≥ 4 m long, 14 to 38 per ha.

Biomass of snags and logs, 10 to 110 metric tons per ha.

Old-growth Douglas-fir/hardwood forest overstories are strongly two-tiered. The hardwoods attain maximum heights roughly half the height of Douglas-fir and dominate the lower tier. In the upper tier, Douglas-fir dominates as widely spaced individuals or as groups of trees. Within the forest, the prevalence of either tier shifts from place to place. Forest openings with hardwood and conifer regeneration at various stages add to the high spatial diversity.

In addition to the forest canopy, the hardwood element of Douglas-fir/hardwood forest influences other forest components. Hardwoods contribute importantly to snag and log densities, but because of the smaller dimensions of hardwoods, along with several other factors (such as different climatic and disturbance regimes), snag and log biomasses are low in comparison to Douglas-fir forests farther north where other conifers share dominance. Densities of large snags and large logs are also typically lower.

New Standards for Old-Growth Douglas-Fir/Hardwood Forests

Our research indicates that the minimum standards prepared by the Old-Growth Definition Task Group (1986) for old-growth Douglas-fir/hardwood forests require revision (table 4). We introduce standards for some additional features not included in the interim definition, but identified as key features by our analyses. Along with new minimum standards, we present average values ± 95-percent confidence limits for each key feature.

The most diagnostic feature of nonmanipulated old-growth Douglas-fir/hardwood forests is the presence of large old trees in densities adequate to form an upper tier that dominates over a hardwood layer. Stands that fail to meet minimum standards for other features, such as those for large snags and large logs can qualify as old growth. For example, wet and mesic sites are more likely to exceed the minimum values, and dry sites are more likely to approach or even drop below the minimum criteria. We believe that the new minimum standards will include the majority of old-growth Douglas-fir/hardwood stands in northwest California and southwest Oregon.

Table 4-Interim and new standards for old-growth Douglas-fir/hardwood forests in northwestern California and southwestern Oregon

Stand characteristic	Interim minimum standards from Old-Growth Definition Task Group 1986[a]	New minimum standards	New average standards ± 95% confidence limits
Live trees	Douglas-fir and evergreen hardwood (tanoak, Pacific madrone, and canyon live oak) associates (40 to 60 percent of canopy)	Douglas-fir and evergreen hardwood associates (e.g. tanoak, Pacific madrone, and canyon live oak), hardwoods account for ≥ 10 percent of the total stand basal area	Basal area of hardwoods average 30 ± 5 percent of the total stand basal area
	Douglas-fir or sugar pine ≥ 15 per ha of trees >80 cm in diameter or >200 years old	Douglas-fir or minor conifers (e.g. sugar pine, Port-Orford-cedar, iucense-cedar, or redwood) ≥ 14 per ha of trees ≥ 90cm diameter or >200 years old	Douglas-fir or minor conifers average 29 ± 3 per ha of trees ≥ 90 cm in diameter or >200 years old
	Intermediate and small size-classes may be evergreen hardwoods or include a component of conifers (e.g., Douglas-fir or white fir)	Intermediate and small size-classes of hardwoods and Douglas-fir, >lO percent total cover of trees ≤ 8 m tall, may include minor conifers	Intermediate and small size-classes with high numbers of hardwoods and moderate numbers of Douglas-fir or minor conifers, small sires ≤ 8 m tall average 25 ± 5 percent cover of hardwoods and 2 ± 1 percent cover of conifers

Table 4—continued

Stand characteristic	Interim minimum standards from Old-Growth Definition Task Group 1986[a]	New minimum standards	New average standards ± 95% confidence limits
Canopy	Douglas-fir emergent above evergreen hardwood canopy	Distinct two-tiered canopy with an upper tier of Douglas-fir with trees reaching heights >40 m and a lower tier of conifers and hardwoods <40 m tall and a total canopy cover of >60 percent	Conifers ≥ 40 m tall average 44 ± 2 trees per ha, conifers 12 to 40 m tall average 39 ± 15 trees per ha, hardwoods 12 to 40 m tall average 221 ± 43 trees per ha, and an average total canopy cover of 71 ± 3 percent
Snags	Conifer snags >4 per ha that are >50 cm in diameter and >4.5 m tall	Conifer or hardwood snags >13 per ha that are ≥10 cm in diameter including >0.25 per ha of conifer snags that are ≥40 cm in diameter and ≥4 m tall	Conifer or hardwood snags ≥10 cm diameter average 32 ± 6 per ha including 5 ± 2 per ha of conifer snags that are ≥40 cm diameter and ≥4 m tall
Logs	Logs >22 metric tons per ha including 5 pieces per ha >60 cm in diameter and >15 m long	Logs >2.5 metric tons per ha including >1 piece per ha >44 cm in diameter and ≥4 m long, of which >0.25 piece per ha are >15 m long	Logs average 26 ± 8 metric tons per ha including 25 ± 6 pieces per ha that are >44 cm in diameter and ≥4 m long, of which 5 ± 2 pieces per ha are >15 m long

[a] The Old-Growth Defiinition Task Group uses the name Douglas-fir on mixed evergreen sites in their interim definition. Values from the interim minimum standards have been converted to metric equivalents.

The new minimum standards are intended to assist managers in identifying nonmanipulated and manipulated stands that contain key old-growth features. Additionally, the minimum standards can be used as guidelines for retaining features associated with old growth when manipulating stands. We view the mean values and 95 percent confidence limits as being more appropriate for identifying optimal old-growth conditions. We also suggest that the new old-growth definition be used to supplement the minimum and average standards. The old-growth definition goes beyond the standards for large trees, snags, and logs in providing criteria for additional understory features. The definitions for young and mature stands will also assist managers when making age-class comparisons over a wide range of structural features.

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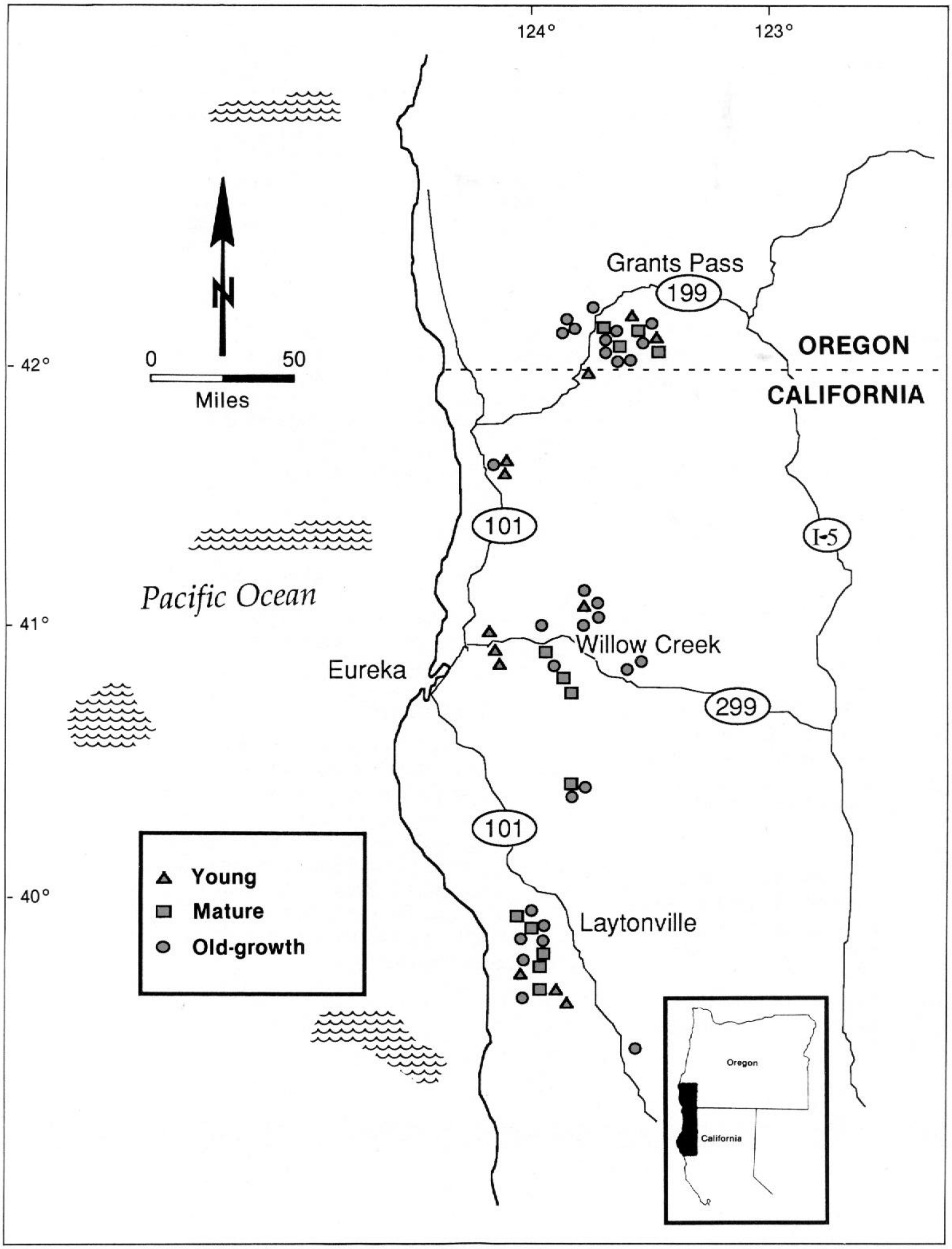

Location of study sites.

Habitat Association Patterns of Breeding Birds and Small Mammals in Douglas-Fir/Hardwood Stands in Northwestern California and Southwestern Oregon

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Abstract

We surveyed birds and small mammals in 45 forest stands from southern Oregon, near Cave Junction, south into northern California, near Branscomb. Over this 350-km distance, we found 71 species of birds and 7 species of mammals that were common enough for detailed analysis. Fourteen species of birds and two mammals reached peak abundances in older (mature and old-growth) forests; however, none appeared limited to these forests. The species were: Allen's hummingbird, hairy woodpecker, pileated woodpecker, Hammond's flycatcher, western flycatcher, gray jay, chestnut-backed chickadee, red-breasted nuthatch, brown creeper, winter wren, golden-crowned kinglet, wrentit, hermit warbler, black-headed grosbeak, Douglas' squirrel, and the California red-backed vole. In addition, about half of the species were correlated with total conifer or hardwood stems. The abundance of many species also differed among the three geographic regions we sampled. These differences could also be associated with elevation because our northern stands tended to be at higher elevations than were the southern stands. Our community analysis of the birds showed separations between different regions, and between the avian communities of young forests and those of older (mature and old-growth) forests. The mature and old-growth bird communities were not readily separable from each other.

Introduction

The Douglas-fir forests of northwestern California are a major source of timber products in the United States, with almost half of the Nation's timber supply contained in the old-growth forests of the West (Society of American Foresters Task Force 1983: 1). Clearcutting has been the primary method of harvesting timber in the region for the past 30 years. Morrison (1988) has documented the great reduction of old-growth timber in many forests of the Pacific Northwest, which includes Washington, Oregon, and northern California.

Present management guidelines state that the USDA Forest Service shall "maintain viable populations" of all vertebrates found on each National Forest (National Forest Management Act 1976, 16 U.S.C. 1600-1614), yet the impacts of the decline of old-growth forests on vertebrate populations in northwestern California are uncertain, with only a few studies on the subject (Hagar 1960, Raphael 1984, Raphael and others 1988). Our study's goal is better understanding of the association patterns of flora and fauna across a chronosequence of forests in the Northwest; it was conducted as a part of research that extends north into Washington (Carey and Spies, this volume; Ruggiero and Carey 1984).

We studied the relative abundance of small mammals and diurnal birds along an age gradient of selected forest stands in northwestern California and southwestern Oregon during the summers of 1984 and 1985. We surveyed the entire diurnal avian community and trapped small mammals to determine if the relative abundance of each species differed between the stands, and to determine which habitat variables correlated with the abundances of each species. We detected **23** small mammal species and 102 bird species over 2 years of field work; in this paper, we concentrate on the more common species.

Methods

Study **Areas**

We selected 45 principal study stands (table 1) in three regions of northwestern California and southwestern Oregon to represent a successional gradient typical of the Douglas-fir communities (see frontispiece). We selected stands nonrandomly based on accessibility by road, presence of a representative age-class of trees, and moderate topography. The stands were conveniently divided into three geographical regions of 15 stands each (table 1): Cave Junction in the north, Willow Creek in the central area, and Branscomb in the south. Stands ranged in elevation from about 400 m to 1550 m, and most were dominated by Douglas-fir in association with tanoak and madrone. Six low-elevation plots had some redwood, and four high-elevation stands in the Cave Junction region were dominated by white fir.

Bird Counting Techniques

Diurnal birds were counted in 1984 and 1985 during the breeding seasons from May to June. Each stand was visited 5 to 7 times each field season, with counts conducted over the entire breeding season at the rate of about once per week for each stand. We minimized observer bias by rotating observers at each stand. In 1984, we had 5 to 6 observers per region, so each stand was usually counted once per observer. During the 1985 field season, we had only 3 to 4 observers in each region, so stands were usually visited on the average of twice per observer. Counts were conducted on 12 fixed stations placed 150 m apart at least 100 m from adjoining habitat types. Observers counted at each station for 8 minutes, recording horizontal distance to each bird seen or heard. All counts were initiated within 15 minutes of official sunrise and took approximately 3.5 hours to complete, to minimize time-of-day bias.

We used the number of individuals detected per station as a relative index of population abundance, which corrects for differences in effort. We did not establish an arbitrary distance from the observer beyond which detection would be excluded because the unit of analysis was the stand as a whole, not individual stations within the stand. Double registrations of an individual consequently would not affect the conclusions. We include in this report only those species that we recorded more than about 10 times during the survey in abundances greater than or equal to a total of 0.001 birds per station, which included all but the rarest species.

Mammal Trapping

For the mammalstudies, we included an additional two stands at Butte Creek, near Dinsmore, California. A single trapping-grid for snap and livetrapping was laid out in each stand in a pattern of 12 rows with 12 trap stations per row. Trap stations were placed at 15-m intervals in a 165-m x 165-m grid.

In 1984, two Museum Special snaptraps were placed at each trap station within 1.5 m of the grid coordinate in all 47 stands. We trapped in six stands simultaneously (two in each region) for 5 days (4 nights) until all stands were sampled (July 3 to August 31). In 1985, a single Sherman livetrap (**7.6** cm x 8.9 cm x 22.0 cm) was used at the same stations in **43** of the stands, and we trapped again in six stands during each 5-day session from July 9 to August 30. We did not livetrap in four stands (two in Branscomb area and two in Cave Junction area). We also used pitfall traps to sample small mammal populations in all 47 stands during both 1984 and 1985. A pitfall grid consisted of six rows of six pitfall traps per row spaced at 15-m intervals in each stand. Snap and pitfall grids were usually separated by more than 100 m. Traps were constructed from two No. 10 cans taped together and sunk until the top was flush with the ground. A funnel collar prevented animals from escaping. We propped a cedar shake 3 to 4 cm above the opening of each pitfall trap to act as a cover, and examined the traps at 5-day intervals for 50 days in October and November 1984, and for 30 days in October 1985. In the analyses below, we used the number of mammals captured, without standardizing the data for effort (table 4). Total trap nights were adjusted for inoperative traps.

Table 1-List of study stands by region, with stand abbreviation, elevation, mean age, age-class, and mean density in stems per 1000 m^2 of hardwood and conifer trees

Region	Stand	Elevation	Canopy trees		Mean density of trees	
			Age	Age-class	Hardwoods	Conifers
Cave Junction						
(AC)	Althouse Flat	427	107	Mature	0.531	1.890
(BP)	Buck Peak	1366	60	Young	.034	.919
(CG)	California Gray Back	1556	265	Old	.000	1.352
(FR)	Frog Pond	1439	196	Mature	.000	3.141
(GG)	Galagy Grove	1334	259	Old	.000	2.639
(HC)	Happy Camp Road	1053	179	Mature	.179	1.879
(HO)	Holcomb Peak	1411	235	Old	.042	3.235
(LG)	Little Grayback	1205	72	Young	.016	1.359
(LH)	Left Hand	1362	96	Young	.044	2.997
(OC)	Oregon Caves Road	872	192	Mature	.316	1.157
(PM)	Page Mountain	1519	204	Old	.007	3.450
(SK)	Skag Hope	1305	267	Old	.011	3.890
(TU)	Tunnel Site	624	65	Young	.368	1.679
(UH)	Upper Horse	1502	91	Young	.013	1.581
(WC)	Waters Creek	614	240	Old	.246	1.338
Willow Creek						
(BA)	Bald Mountain East	846	43	Young	.862	0.701
(BE)	Brannon Mountain	750	236	Old	.597	1.379
(BM)	Beartooth Mountain	1144	327	Old	.383	2.176
(BR)	Brush Mountain	1050	116	Mature	.420	1.773
(CC)	Cedar Creek	665	347	Old	.396	1.728
(EB)	East Fork Big Creek	1134	246	Old	.589	1.383
(FN)	Fawn Prairie	750	44	Young	.983	.945
(GR)	Gray II	972	101	Mature	.292	1.481
(HP)	Hennessy Peak	949	100	Mature	.172	1.700
(LE)	Lord Ellis	778	48	Young	1.366	1.024
(LR)	Ladder Rock	805	319	Old	.828	2.072
(SF)	South Fork	659	289	Old	.470	1.291
(SH)	Sharber	747	283	Old	.673	.932
	Tish Tang	680	204	Old	.888	1.484
(WR)	Waterman Ridge West	633	85	Mature	1.091	1.140
Branscomb						
(AP)	Alpine	444	210	Old	.730	1.899
(BT)	Barnes	467	53	Young	.357	.329
(DP)	Darby	587	240	Old	.317	1.021
(EC)	Elder Creek	555	155	Mature	.402	2.361
(EH)	Elkhorn Ridge Hydric	518	137	Old	.230	.603
(EX)	Elkhorn Ridge Xeric	518	140	Mature	.487	.291
(FC)	Fox Creek	543	187	Old	.576	1.757
(FP)	Fanny's Place	445	122	Mature	.375	1.372
(HN)	Harwood's Ninty	695	118	Mature	1.010	.424
(HT)	Homestead	726	40	Young	1.071	1.300
(MS)	Mud Springs	689	70	Young	.691	.678
(SC)	Skunk Creek	529	291	Old	.278	1.223
(SG)	Standley Grove	481	450	Old	.082	3.555
(TM)	Ten Mile	445	241	Old	.317	1.718
(WH)	White House	427	136	Mature	.655	1.451

Vegetation Sampling

Vegetation was quantified on each of the 12 bird-count stations in each stand. On the snap-livetrap grid we measured 16 plots overlaying the 144 trap stations. Nine vegetation plots were also uniformly distributed among the 36 pitfall stations. For this analysis, we used the mean number of all hardwood and conifer stems greater than 50 cm in d.b.h. within 15 m of each mammal-trapping station and 25 m for bird observations. We reasoned that, for this study, individual plant species would be too detailed for our analysis.

Stand ages were based on data supplied by B. Bingham (pers. comm.) from core samples of three to five dominant Douglas-firs on each of three plots in each young and mature stand (up to about 180 years). In old-growth stands, tree cores could not always be taken because trees were so large and had rotten cores; thus, some stand ages were estimated from rings counted on stumps in adjacent clearcuts or beside nearby roads, or they were based on ages provided by local Forest Service offices.

We minimized the number of variables for the small mammal community by comparing the capture rates associated with logs that have fallen relatively recently, hard logs of decay-classes 1 and 2 of Thomas (1979: 80), and soft logs of decay classes 3 to 5.

Data Analysis

The objective of this analysis was to estimate how much variation in bird abundance among stands could be explained by stand age or geographical region, and whether abundance was affected by interaction between stand age and region. For most analyses, stand age was considered as a continuous variable, and entered into calculations as a square-root transformation. Region was considered a categorical variable. A probability level of $P < 0.05$ was used to signify statistical significance.

We considered that the bird counts, as discrete variables, approximated normal distributions with means linear on the independent variables and with equal variances.

A general linear model (GLM) in SAS (Freund and others 1986: 145) was used to compare relations between the abundance of each bird species with stand age and region. This comparison was treated as an analysis of covariance with interaction between age and region, with region as the covariate. The interaction term determines if the relation (the slope of the line describing the relation between age and abundance) was statistically different among regions.

The SAS procedure “GLM,” produces two sets of statistics, Type I and III Sums of Squares, which we used in constructing table 2. If the interaction between age and region was not significant, then we used the statistics from Type I (the unadjusted treatment sums of squares), where age was entered into the model after region. If the interaction term was significant, then we used Type III (adjusted treatment sum of squares), which takes into account the other variables before calculating the effect of the variable under consideration. For example, if an age and region interaction was significant, then the statistic appearing in table 2 was the effect of age **after** accounting for the effects of both region and the interaction of age and region.

We also treated stand age as a classification variable when separating the sites into young, mature, or old-growth, based on a discriminant function analysis of vegetation data sampled from the entire stand (Bingham and Sawyer, this volume). These classifications, based on vegetative structure and composition, sometimes differed from stand age as determined by counting tree rings. Bird abundances are presented in table 2 according to the stand-age classifications of Bingham and Sawyer. A least-squares test (Freund and others 1986) determined significant differences in bird abundances between age-classes and regions.

We compared numbers of species and individuals detected between years and habitat types by using Pearson product-moment correlation coefficients.

Our analysis of the data aggregated the various stands according to similarities in the abundance of bird species found in each stand. For this, we used Ward’s method of cluster analysis (SAS 1982: 423), but only for the commoner species, which we defined as the 29 species with average abundances greater than 0.1 birds per station in either 1984 or 1985 (table 3). We acknowledge that this analysis is only an approximation because it is not based on actual densities, but we believe that the figures were indicative of the relative abundance of most species.

Table 2—Comparison of the number of individuals of each bird or mammal species detected or captured per station in the three regions; the significance (*P* <) of region alone as a contribution to a model; the number of individuals per station in young, mature, and old-growth stands; the significance of age alone as a contribution to a model; the significance of the interaction of age and region; and the amount of variance explained by the model (R^2)

		Region				Age of stands					
Species		Branscomb	Willow Creek	Cave Junction	Region significance	Young	Mature	Old-growth	Age significance	Age*Region significance	R^2
Turkey vulture		0.008	0.001	0.000	0.0369	0.000	0.003	0.005	0.3124	0.5512	0.1951
Northern goshawk		.001	.003	.001	.4094	.000	.001	.003	.1561	.7576	.1030
Red-shouldered hawk		.006	.000	.000	.3800	.000	.000	.005	.4709	.5607	.0864
Red-tailed hawk		.004	.006	.008	.7967	.001	.009	.006	.2979	.9966	.0389
Blue grouse		.000	.000	.051	.0001	.033	.002	.021	.9224	.9369	.3848
California quail		.014	.001	.009	.3832	.027	.004	.001	.0128	.4107	.2137
Mountain quail		.325	.075	.071	.0001	.116	.169	.169	.9229	.9037	.3844
Band-tailed pigeon		.002	.013	.003	.0606	.015	.001	.005	.2360	.9301	.1635
Mourning dove		.019	.001	.025	.4213	.013	.024	.008	.4902	.6863	.0717
Flammulated owl		.000	.001	.003	.0932	.000	.002	.002	.1831	.3008	.1936
Northern pygmy-owl		.030	.256	.005	.0828	.005	.025	.024	.2228	.3939	.1834
Anna's hummingbird		.011	.003	.003	.0262	.004	.005	.007	.1425	.0036	.3402
Allen's hummingbird	+	.046	.002	.006	.0013	.003	.007	.036	.0008	.0001	.5540
Acorn woodpecker		.075	.066	.066	.9853	.030	.093	.069	.9610	.4755	.0381
Red-breasted sapsucker		.025	.031	.030	.9042	.020	.031	.032	.6857	.1850	.0908
Downy woodpecker	–	.003	.001	.002	.1922	.001	.002	.002	.8319	.8798	.0876
Hairy woodpecker	–	.055	.048	.054	.8133	.034	.036	.076	.0133	.2767	.2007
White-headed woodpecker		.000	.001	.003	.2019	.000	.000	.003	.0562	.0900	.2403
Northern flicker		.426	.193	.159	.0001	.230	.253	.280	.2669	.3135	.5251
Pileated woodpecker	–	.152	.110	.089	.0880	.051	.127	.144	.0285	.9227	.2124
Olive-sided flycatcher	+	.016	.038	.119	.0003	.063	.025	.082	.0890	.5924	.3788
Western wood-pewee		.078	.009	.082	.0259	.044	.064	.056	.2404	.4916	.2185
Hammond's flycatcher		.000	.104	.374	.0001	.091	.157	.198	.0377	.2185	.4611
Dusky flycatcher		.000	.005	.053	.0001	.042	.008	.016	.2122	.2818	.4594
Western flycatcher	+	1.780	1.175	.520	.4531	.543	1.230	1.420	.0001	.0480	.8194
Ash-throated flycatcher		.015	.000	.000	.2297	.019	.002	.000	.1010	.0752	.2264
Gray jay		.000	.000	.011	.2236	.003	.000	.007	.0360	.0257	.3881
Steller's jay		.978	.748	.555	.0007	.651	.850	.743	.8193	.8286	.3187
Scrub jay		.011	.004	.000	.0116	.010	.005	.002	.0772	.5351	.2720
American crow		.000	.001	.006	.1604	.001	.005	.000	.3631	.3815	.1459
Common raven		.373	.086	.083	.0001	.075	.213	.209	.3174	.4458	.5036
Mountain chickadee		.000	.000	.041	.0031	.016	.002	.022	.3456	.1819	.3149
Chestnut-backed chickadee	+	.609	.548	.317	.0001	.339	.533	.535	.0113	.9390	.5574
Bushtit		.013	.008	.001	.1262	.005	.010	.006	.7712	.0667	.2083
Red-breasted nuthatch		.264	.544	.830	.0001	.335	.514	.684	.0047	.1853	.5344
White-breasted nuthatch		.000	.014	.002	.1906	.001	.010	.004	.7786	.9520	.0854
Brown creeper	–	.528	.218	.222	.0001	.118	.313	.438	.0001	.0001	.8521
Bewick's wren		.001	.000	.004	.0783	.004	.001	.001	.1569	.2103	.2164
House wren		.000	.005	.005	.4594	.005	.005	.002	.3365	.7833	.0720
Winter wren		.084	.160	.235	.0452	.173	.068	.229	.0134	.0319	.3381
Golden-crowned kinglet	+	.013	.270	.774	.2346	.417	.242	.411	.1560	.0301	.6618
Townsend's solitaire		.003	.050	.149	.0018	.139	.034	.057	.0710	.0291	.4630
Hermit thrush	+	.382	.671	.453	.0413	.551	.422	.543	.9865	.9476	.1528
Swainson's thrush		.000	.023	.008	.1541	.016	.001	.016	.8395	.7464	.1046
American robin	–	.251	.086	.124	.0024	.053	.195	.173	.1515	.2447	.3293

Table 2—continued

Species		Region			Region significance	Age of stands			Age significance	Age*Region significance	R^2
		Branscomb	Willow Creek	Cave Junction		Young	Mature	Old-growth			
Varied thrush		0.000	0.057	0.008	0.0132	0.081	0.001	0.008	0.1871	0.0413	0.2756
Wrentit	+	.222	.085	.009	.0118	.054	.079	.155	.0063	.1002	.3728
Solitary vireo	–	.462	.306	.148	.0078	.110	.453	.284	.9630	.6651	.2331
Hutton's vireo	–	.186	.126	.045	.0005	.123	.137	.102	.0931	.3535	.3776
Warbling vireo	+	.781	.291	.147	.0001	.359	.582	.283	.0090	.0001	.6070
Orange-crowned warbler		.109	.011	.000	.0010	.073	.029	.032	.2956	.6806	.3204
Nashville warbler	–	.144	.148	.495	.0021	.306	.280	.224	.3731	.3871	.3060
Yellow-rumped warbler		.001	.037	.321	.0001	.155	.062	.150	.5975	.3089	.4645
Black-th. gray warbler	–	.772	.220	.357	.0030	.484	.632	.279	.0200	.0036	.4468
Townsend's warbler	–	.000	.003	.021	.0001	.011	.008	.006	.5187	.6717	.4841
Hermit warbler	+	1.306	2.279	1.695	.0032	1.155	1.761	2.078	.0040	.0247	.4630
MacGillivray's warbler	+	.000	.009	.033	.0001	.027	.010	.011	.0880	.0964	.5076
Wilson's warbler	+	.550	.205	.022	.0001	.165	.259	.309	.0466	.1203	.5021
Western tanager	–	1.089	.677	.367	.0002	.319	.933	.730	.4929	.2290	.3833
Black-headed grosbeak	–	.537	.583	.242	.0414	.204	.552	.503	.8691	.0235	.3260
Lazuli bunting		.000	.005	.000	.0095	.001	.002	.003	.3790	.8622	.2295
Rufous-sided towhee	–	.350	.007	.009	.0001	.097	.156	.106	.5147	.3277	.6540
Fox sparrow		.000	.000	.013	.0119	.005	.001	.008	.4914	.3890	.2407
Song sparrow		.000	.016	.001	.1153	.017	.002	.003	.1152	.1683	.1998
Dark-eyed junco	–	.490	.374	.600	.1137	.401	.554	.478	.9428	.0791	.2045
Brown-headed cowbird		.001	.006	.040	.0473	.010	.034	.004	.4290	.5470	.1784
Purple finch		.043	.097	.099	.0966	.052	.084	.091	.2313	.2122	.1987
Red crossbill		.011	.015	.031	.0728	.026	.013	.021	.5273	.0249	.2474
Pine siskin		.004	.075	.395	.0001	.164	.127	.182	.0802	.1588	.7240
Lesser goldfinch		.004	.001	.006	.2265	.004	.004	.003	.9962	.8748	.0792
Evening grosbeak		.000	.002	.053	.0001	.031	.012	.017	.4127	.8730	.6541
Chipmunks		.007	.007	.035	.0003	.020	.016	.014	.9837	.9731	.3408
Douglas' squirrel		.072	.315	.443	.0001	.180	.235	.362	.0363	.0755	.4589
Western gray squirrel		.050	.007	.030	.0004	.017	.037	.028	.9808	.8263	.3340

Note: When a significant difference was found between the abundance of a species by age-classes or regions, those that were statistically indistinguishable by a least-squares test are joined by an underline. For nonadjacent, indistinguishable column values (for example, young and old-growth) the underline is disjunct. If all three differ significantly from each other, each is underlined. A plus (+) or minus (–) after the species' name indicates a significantly positive or negative relation to stand age according to the analysis of Raphael (1984).

Results

Bird Abundances

Overall abundance patterns—Seventy-one bird species (table 3) were found in the study plots in both years in numbers greater than 0.001 birds per station. The most abundant species was the hermit warbler, with over 1.7 birds per station in both years. The western flycatcher was next in abundance with more than 1.1 birds per station.

Some birds began to reach the limit of their distributions within the geographic range of this study. For instance, blue grouse and gray jay were only found at Cave Junction in the north, and Hammond's flycatcher was not found at Branscomb in the south. These species could be found in areas we did not count to the north or south, but in limited numbers. They also probably were largely limited by the altitudinal gradient between study stands. The Cave Junction stands were generally at higher elevations and Branscomb tended to be lower.

We divided the species into three groups: year-round residents, short-distance migrants (birds wintering in the United States), and long-distance migrants. More than half (59 percent) of the species were residents, 11 percent were short-, and 30 percent long-distance migrants. By contrast, only 42 percent of individuals (birds per station) were residents, 6 percent short, and the majority (52 percent) long-distance migrants.

Comparison between years—We compared, by correlation, the abundance of each species between years in each stand to determine the concordance of the 2 years' data. The closer the agreement between the 2 years, the greater the likelihood (but, by no means, certainty) that some aspect of the habitat was important in determining the abundance of that species at any sampling point. The less the agreement, the greater the likelihood that stochastic events in the population could be responsible for the abundance of the species.

Table 2—continued

		Region				Age of stands					
Species		Brans-comb	Willow Creek	Cave Junction	Region signif-icance	Young	Mature	Old-growth	Age signif-icance	Age*Region signif-icance	R^2
Varied thrush		0.000	0.057	0.008	0.0132	0.081	0.001	0.008	0.1871	0.0413	0.2756
Wrentit	+	.222	.085	.009	.0118	.054	.079	.155	.0063	.1002	.3728
Solitary vireo	–	.462	.306	.148	.0078	.110	.453	.284	.9630	.6651	.2331
Hutton's vireo	–	.186	.126	.045	.0005	.123	.137	.102	.0931	.3535	.3776
Warbling vireo	+	.781	.291	.147	.0001	.359	.582	.283	.0090	.0001	.6070
Orange-crowned warbler		.109	.011	.000	.0010	.073	.029	.032	.2956	.6806	.3204
Nashville warbler	–	.144	.148	.495	.0021	.306	.280	.224	.3731	.3871	.3060
Yellow-rumped warbler		.001	.037	.321	.0001	.155	.062	.150	.5975	.3089	.4645
Black-th. gray warbler	–	.772	.220	.357	.0030	.484	.632	.279	.0200	.0036	.4468
Townsend's warbler	–	.000	.003	.021	.0001	.011	.008	.006	.5187	.6717	.4841
Hermit warbler	+	1.306	2.279	1.695	.0032	1.155	1.761	2.078	.0040	.0247	.4630
MacGillivray's warbler	+	.000	.009	.033	.0001	.027	.010	.011	.0880	.0964	.5076
Wilson's warbler	+	.550	.205	.022	.0001	.165	.259	.309	.0466	.1203	.5021
Western tanager	–	1.089	.677	.367	.0002	.319	.933	.730	.4929	.2290	.3833
Black-headed grosbeak	–	.537	.583	.242	.0414	.204	.552	.503	.8691	.0235	.3260
Lazuli bunting		.000	.005	.000	.0095	.001	.002	.003	.3790	.8622	.2295
Rufous-sided towhee	–	.350	.007	.009	.0001	.097	.156	.106	.5147	.3277	.6540
Fox sparrow		.000	.000	.013	.0119	.005	.001	.008	.4914	.3890	.2407
Song sparrow		.000	.016	.001	.1153	.017	.002	.003	.1152	.1683	.1998
Dark-eyed junco	–	.490	.374	.600	.1137	.401	.554	.478	.9428	.0791	.2045
Brown-headed cowbird		.001	.006	.040	.0473	.010	.034	.004	.4290	.5470	.1784
Purple finch		.043	.097	.099	.0966	.052	.084	.091	.2313	.2122	.1987
Red crossbill		.011	.015	.031	.0728	.026	.013	.021	.5273	.0249	.2474
Pine siskin		.004	.075	.395	.0001	.164	.127	.182	.0802	.1588	.7240
Lesser goldfinch		.004	.001	.006	.2265	.004	.004	.003	.9962	.8748	.0792
Evening grosbeak		.000	.002	.053	.0001	.031	.012	.017	.4127	.8730	.6541
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Table 3—Mean number of detections of each bird and mammal species per station in 1984 and 1985, the linear correlation (R^2) between years and its sign, and the linear correlation (R^2) between the number of detections and the abundance of hardwood and conifer trees and its sign (significant correlations are indicated as: * = $P \leq .05$, ** = $P \leq .01$, and *** = $P \leq .001$)

	Year				Tree type	
Species	1984	1985	R^2	*P*	Hardwood (R^2)	Conifer (R^2)
Turkey vulture	0.003	0.003	0.47	0.0011	0.01	−0.16
Northern goshawk	.001	.002	−.06	.7017	.03	.11
Red-shouldered hawk	.000	.004	.00	1.0000	−.05	−.11
Red-tailed hawk	.007	.006	−.06	.6836	−.17	−.23
Blue grouse	.020	.014	.37	.0122	−.52***	.27
California quail	.011	.006	.90	.0001	.24	−.24
Mountain quail	.160	.154	.68	.0001	.05	−.12
Band-tailed pigeon	.007	.005	.37	.0115	.29*	−.23
Mourning dove	.012	.018	.88	.0001	.03	−.03
Flammulated owl	.001	.001	−.06	.7208	−.24	.40**
Northern pygmy-owl	.019	.022	.26	.0796	.04	−.29
Anna's hummingbird	.009	.003	−.10	.4978	.00	.19
Allen's hummingbird	.027	.009	.09	.0001	−.17	.32*
Acorn woodpecker	.055	.082	.88	.0001	.15	−.10
Red-breasted sapsucker	.023	.346	.65	.0001	−.31*	.10
Downy woodpecker	.001	.003	−.08	.5931	.07	.00
Hairy woodpecker	.061	.044	.24	.1112	−.29	.27
White-headed woodpecker	.001	.002	−.04	.8022	−.18	.26
Northern flicker	.269	.250	.63	.0001	.08	−.26
Pileated woodpecker	.136	.098	.71	.0001	−.03	−.10
Olive-sided flycatcher	.041	.074	.62	.0001	−.58***	.53***
Western wood-pewee	.045	.068	.63	.0001	−.29	.42**
Hammond's flycatcher	.154	.165	.92	.0001	−.44**	.46**
Dusky flycatcher	.015	.023	.55	.0001	−.48***	.20
Western flycatcher	1.138	1.177	.91	.0001	.17	−.12
Ash-throated flycatcher	.005	.005	.98	.0001	.00	−.26
Gray jay	.005	.003	.21	.1611	−.41**	.33*
Steller's jay	.791	.730	.61	.0001	.12	−.37*
Scrub jay	.005	.005	.21	.1639	.25	−.34*
American crow	.002	.002	.54	.0001	.01	.03
Common raven	.152	.209	.88	.0001	.08	−.21
Mountain chickadee	.014	.013	.76	.0001	−.41**	.13
Chestnut-backed chickadee	.501	.482	.52	.0003	.36*	−.20
Common bushtit	.011	.004	.05	.7498	.21	−.15
Red-breasted nuthatch	.492	.600	.89	.0001	−.51***	.53***
White-breasted nuthatch	.010	.001	.86	.0001	−.10	.00
Brown creeper	.337	.308	.93	.0001	−.19	.28
Bewick's wren	.001	.002	.36	.0144	−.21	.00
House wren	.001	.006	.13	.4139	−.25	.09
Winter wren	.194	.125	.74	.0001	−.33*	.54***
Golden-crowned kinglet	.374	.331	.91	.0001	−.56***	.60***
Townsend's solitaire	.057	.077	.70	.0001	−.52***	.22
Hermit thrush	.447	.557	.71	.0001	.40**	−.31*
Swainson's thrush	.013	.007	.15	.3250	.19	.11
American robin	.165	.143	.69	.0001	−.15	.06
Varied thrush	.020	.024	.67	.0001	.43**	−.12
Wrentit	.090	.121	.96	.0001	−.09	.06
Solitary vireo	.279	.331	.78	.0001	.23	−.19
Hutton's vireo	.109	.129	.65	.0001	.66***	−.50***
Warbling vireo	.447	.366	.91	.0001	.43**	−.28
Orange-crowned warbler	.040	.040	.88	.0001	.09	−.23

Table 3—continued

	Year				Tree type	
Species	1984	1985	R^2	*P*	Hardwood (R^2)	Conifer (R^2)
Nashville warbler	0.236	0.288	0.85	0.0001	−0.27	−.09
Yellow-rumped warbler	.090	.149	.86	.0001	−.59***	.37*
Black-th. gray warbler	.354	.545	.84	.0001	.29	−.40**
Townsend's warbler	.003	.013	.20	.1873	−.36*	.31*
Hermit warbler	1.729	1.791	.86	.0001	−.22	.43**
MacGillivray's warbler	.011	.017	.37	.0199	−.40**	.15
Wilson's warbler	.206	.312	.94	.0001	.00	−.14
Western tanager	.702	.720	.84	.0001	.28	−.27
Black-headed grosbeak	.407	.501	.81	.0001	.40**	−.32*
Lazuli bunting	.003	.001	−.07	.6561	.18	−.07
Rufous-sided towhee	.081	.163	.94	.0001	.01	−.11
Fox sparrow	.001	.007	.50	.0005	−.37*	.17
Song sparrow	.008	.003	.95	.0001	.23	−.09
Dark-eyed junco	.509	.466	.88	.0001	−.44**	.22
Brown-headed cowbird	.021	.011	.80	.0001	−.10	.04
Purple finch	.068	.091	.31	.0359	−.11	.14
Red crossbill	.007	.031	.56	.0001	−.16	.09
Pine siskin	.162	.154	.83	.0001	−.63***	.42**
Lesser goldfinch	.003	.003	.55	.0001	−.09	−.05
Evening grosbeak	.018	.019	.81	.0001	−.48**	.39**
Chipmunks	.014	.019	.57	.0001	−.49***	.32***
Douglas' squirrel	.228	.325	.84	.0001	−.42***	.44***
Western gray squirrel	.031	.027	.60	.0001	−.02	.18

Although the majority of species had similar detection rates between years, 15 (21 percent) species showed significant differences (table 3). Most of these were rare species that undoubtedly varied because of the low numbers that were detected; only five were fairly abundant, having detection rates in either year in excess of 0.01 birds per station. Common species with abundances that changed significantly between years were the northern pygmy-owl, common bushtit, hairy woodpecker, Swainson's thrush, and Townsend's warbler. No common thread (such as food habits or foraging methods) unites these species; changes such as these are to be expected in a study of several species.

Geographic differences—Geographical variation in abundance is a pattern that overlies the species' response to changes in the amount and suitability of its habitat. Even though the habitat may be suitable, factors that are related to geography (such as climate or competition with existing species) may preclude or severely limit the species' presence, and mute its response to habitat.

By comparing the average number of species recorded on the 15 stands making up each region (fig. 1), we found that the northern Cave Junction stands averaged 37.3 species per stand, the Willow Creek stands averaged 32.4, and the Branscomb stands 32.6. The Cave Junction stands had significantly greater species richness than the southern stands (Duncan's Multiple Range Test).

We also found distinct patterns in the abundances of individual species in the northern and southern study sites. The majority of the species that showed differences between geographic regions were on a north-south cline (table 2). This cline was also of higher elevation with more true fir in the north, and more hardwoods in the south (table 1). When region was the only significant variable selected in a GLM model, 12 species were more abundant in northern stands, and 14 were more abundant in southern stands. Among the species more abundant in either the north or the south were species with geographic affinities in either direction. Significantly more common to the north were the more montane species, such as blue grouse, olive-sided flycatcher, dusky flycatcher, mountain chickadee, MacGillivray's warbler, Nashville warbler, yellow-rumped warbler, fox sparrow, pine siskin, and evening grosbeak. The brown-headed cowbird and Townsend's warbler were also more abundant in the northern regions. More abundant southern species included turkey vulture, mountain quail, Anna's hummingbird, northern flicker, Steller's jay, scrub jay, common raven, American robin, Hutton's vireo, solitary vireo, orange-crowned warbler, Wilson's warbler, western tanager, and rufous-sided towhee.

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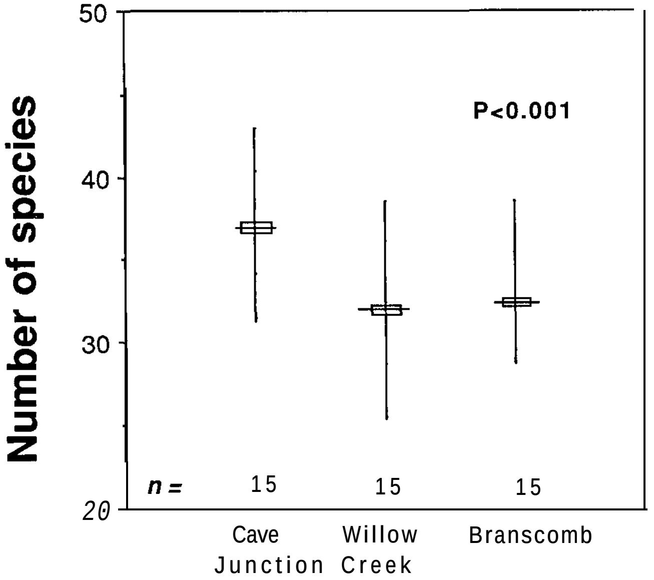

Figure 1—Comparison of the number of bird species by region. The means, standard errors, and ranges are shown for stands in each region. Sample size is shown below.

Few species showed other geographical patterns. Only two species were more abundant at the central Willow Creek stands: the lazuli bunting and hermit thrush. Only the western wood-pewee was less abundant in these central stands than in either the northern or southern stands.

Relation of abundance to stand age—By comparing the average number of species recorded in a stand by stand age (fig. 2), we found no difference among mature (33.5), young (33.7), and old-growth (34.7) forests (Duncan's Multiple Range Test). A correlation between stand age and average number of species also showed no relation ($r = 0.13$; $P = 0.132$), in contrast to results of Manuwal and Huff (1987), who found an increase in richness in their old-growth stands.

Stand age was an important factor in the abundance of many species in the community. For three species, the California quail, hairy woodpecker, and pileated woodpecker (fig. 3), age was selected as the sole significant contributor to our model (table 2). The quail was found in younger forests, and the two woodpeckers in greater numbers in older forests. When we used stand age as a classification variable in a separate analysis, three species (the hairy woodpecker, western flycatcher, and brown creeper) were significantly more abundant in old-growth forests than either the mature or young stands. Except for their occurrence in modest numbers in younger stands, these birds could be considered old-growth species.

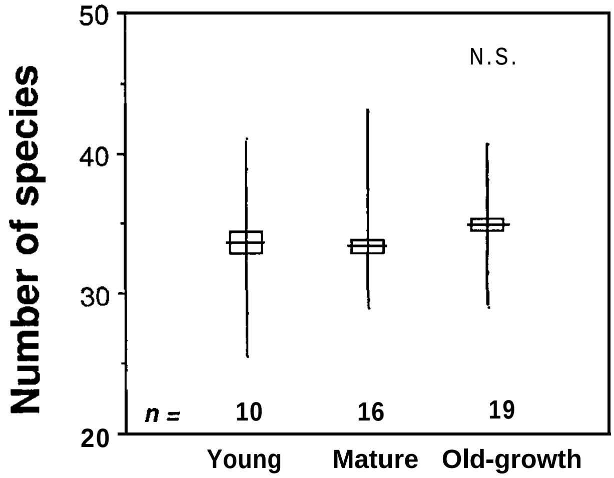

Figure 2—Comparison of the number of bird species by age-class. The means, standard errors, and ranges are shown for stands in each age-class. Sample size is shown below.

For 17 species, or 24 percent of the 71 species total, both stand age and region were selected in the linear model as affecting the numbers of individuals recorded. The abundances of four species (chestnut-backed chickadee, Hammond's flycatcher, red-breasted nuthatch, and wrentit) were special in that they showed a consistent, positive relation with age among all three regions. That is, the interaction between age and abundance was not significantly different between regions. These species, along with the two woodpeckers mentioned above, showed the strongest affinity between abundance and age of forest.

Eight of the 17 species' abundances were positively related to stand age, and occurred most commonly in older forests: Allen's hummingbird, western flycatcher (fig. 3), gray jay, brown creeper (fig. 3), winter wren, golden-crowned kinglet, hermit warbler (fig. 3), and black-headed grosbeak. Only four species were more common in younger stands and also had their numbers influenced by region: Townsend's solitaire, varied thrush, warbling vireo, and black-throated gray warbler. The red crossbill was influenced by both region and stand age, but the effect of age was not clear. Although the abundances of many species were influenced by geography, these data showed that stand age was an important determinant for a large proportion of the species.

Selection of Forest Types

Comparing the stands as to their recorded number of species indicated that the richness of bird species was higher in stands with more conifers ($r = 0.28$; $P < 0.05$) and lower in stands with more hardwoods ($r = -0.53$; $P < 0.001$).

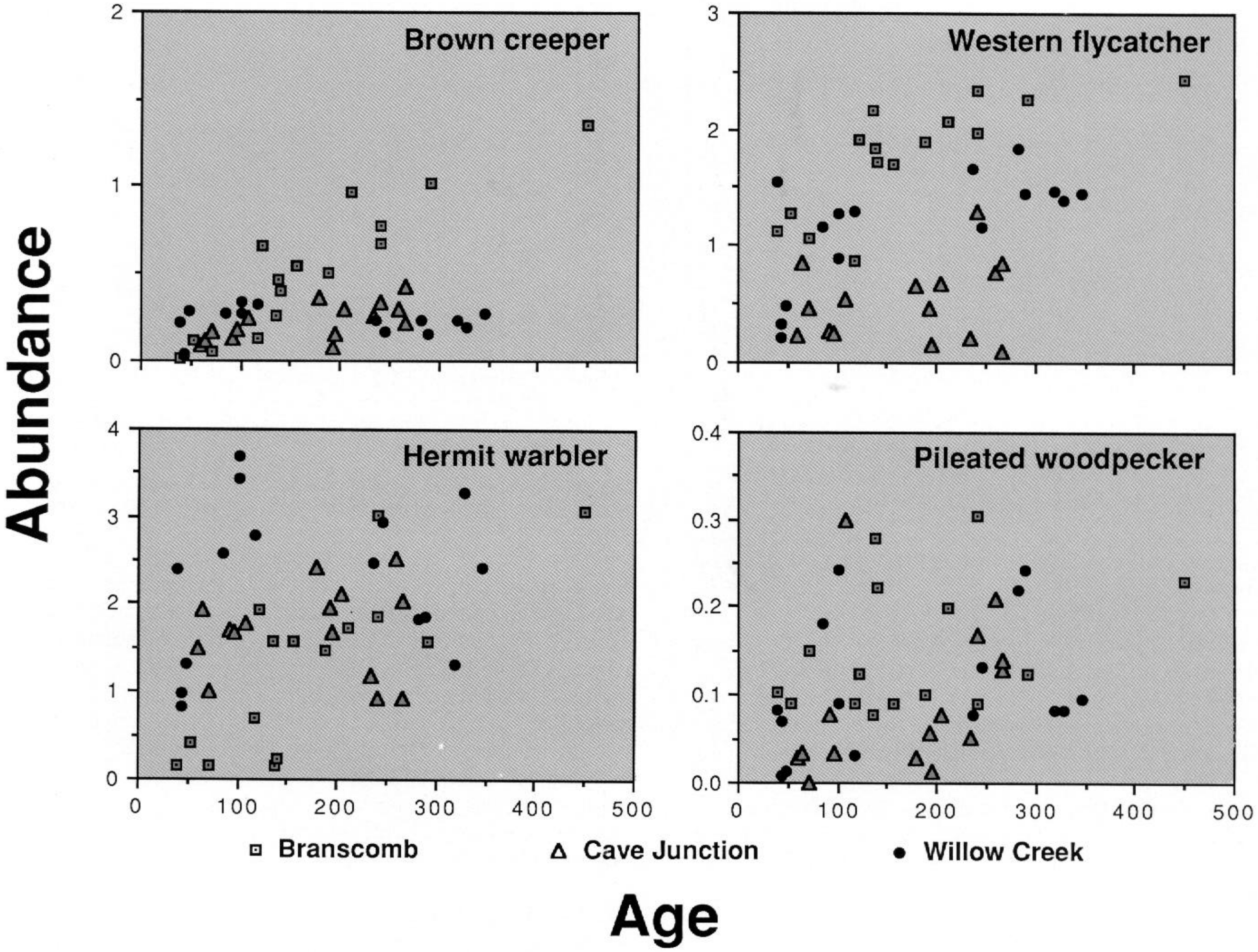

Figure 3—A comparison of the mean abundance of four bird species by stand and region with the square root of stand age as a continuous variable.

The abundance of many species was strongly correlated with the number of conifer or hardwood trees in the plots (table 3). In many of these species, we expected a positive correlation with one type and a negative with the other. Fourteen species were positively associated with conifers, which was the commonest association: flammulated owl, Allen's hummingbird, olive-sided flycatcher, western wood-pewee, Hammond's flycatcher, gray jay, red-breasted nuthatch, winter wren, golden-crowned kinglet, yellow-rumped warbler, Townsend's warbler, hermit warbler, pine siskin, and evening grosbeak. Three species apparently had a negative association with conifers, but were not positively associated with hardwoods: Steller's jay, scrub jay, and black-throated gray warbler. Only seven species were positively associated with hardwoods: band-tailed pigeon, chestnut-backed chickadee, hermit thrush, varied thrush, Hutton's vireo, warbling vireo, and black-headed grosbeak. Finally, eight species were negatively correlated with hardwoods, but were not positively associated with conifers: blue grouse, red-breasted sapsucker, dusky flycatcher, mountain chickadee, Townsend's solitaire, MacGillivray's warbler, fox sparrow, and dark-eyed junco.

In all of these species, a more detailed, species-by-species analysis of habitat association patterns by plant species, as well as actual habitat use, is needed to determine the actual environmental factors that limit their distribution and abundance.

Table 4—Number of mammal captures by species and trapping technique within each study area[a] (for each technique, significant differences among captures in each study area are indicated by different letters after the totals)

	Technique								
	Pitfalls			Snap traps			Live traps		
Species	CJ	WC	BR	CJ	WC	BR	CJ	WC	BR
Trowbridge's shrew	349	296	247	146	124	84	27	57	17
Pacific shrew	14	16	3	19	40	5	6	2	3
Vagrant shrew	—	1	—	—	1	—	—	—	—
Marsh shrew	—	1	—	—	—	—	—	—	—
Shrew-mole	11	21	8	6	17	5	—	2	3
Coast mole	—	1	—	—	—	—	—	—	—
Chipmunks	2	—	—	25	3	1	171	39	72
Golden-mantled ground squirrel	—	—	—	—	—	—	1	—	—
Northern flying squirrel	6	—	—	—	1	—	2	5	1
Botta's pocket gopher	5	—	—	2	—	—	—	—	—
Deer mouse	51	36	27	72 A	212 B	209 B	41 A	204 B	159 B
Piñon mouse	1	7	8	25 A	67	113 B	113 A	76	124 B
Dusky-footed woodrat	—	2	—	1	—	3	4	6	18
Bushy-tailed woodrat	—	—	—	—	—	—	5	—	—
Western red-backed vole	341 A	186 A	45 B	73	49	35	28	32	41
Red tree vole	5	9	8	—	—	—	—	—	—
California vole	—	5	9	2	—	10	—	—	5
Long-tailed vole	2	—	—	—	—	—	—	—	—
Creeping vole	2	2	2	1	3	—	1	1	8
Black rat	1	—	—	—	—	—	—	—	—
Pacific jumping mouse	1	1	1	3	8	—	—	—	—
Ermine	—	—	—	—	—	—	5	—	1
Number of trap-nights[b]									
Cave Junction		43,200			19,275			7,263	
Willow Creek		48,960			18,559			8,289	
Branscomb		48,960			17,450			7,815	

[a] The three study areas are Cave Junction, Oregon (CJ), Willow Creek, California (WC), and Branscomb, California (BR).

[b] Totals were adjusted for traps damaged by bears.

Bird Community Organization

Using the number of individuals observed for each of the 29 most-common species as an approximation of the composition of the avian communities in a cluster analysis, we found some divisions (fig. 4). The divisions were largely geographical and probably depend on major vegetation types related to altitude. A secondary division occurred between the young stands and the combined group of mature and old-growth categories. No clear distinction could be made, judging from the bird community, between old-growth and mature communities.

The first division was a separation of the younger Branscomb stands, which contained a great deal of chapparal. The second division was between the upper elevation Cave Junction stands that had a substantial amount of true fir, and the young Willow Creek stands. The third major separation was between the Branscomb and Willow Creek stands with mature and old-growth being intermixed. The TU stand that Bingham (pers. comm.) classed as young did have some remnant old-growth trees, and the bird species associated with these trees apparently increased the stand's similarity to the older stands.

These patterns confirm the information from the individual species: that clear geographical separations are present, and that, although young forests differ from older forests, mature and old-growth forests are much alike.

Mammal Abundance Comparisons

Twenty-three species of small mammals were captured during the study, though several were represented by only a few individuals (table 4). The three techniques differed in their effectiveness for capturing different species of mammals. Six species or species groups had sufficient captures (≥100 individuals or more, by one or more of the trapping techniques) to permit intensive analyses. These were the western

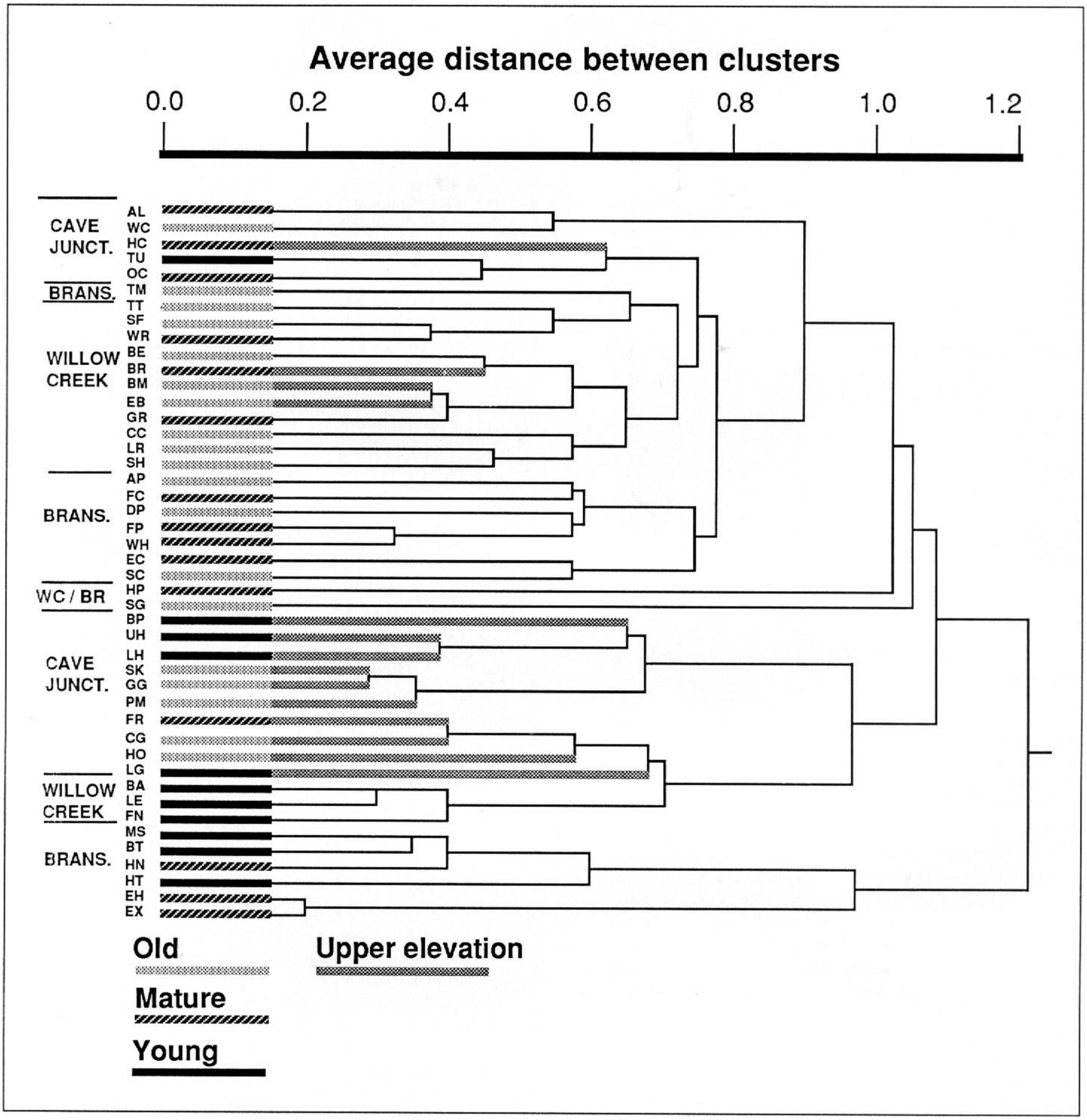

Figure 4—Cluster diagram of the 45 stands based on the abundance of the 21 most common bird species.

Table 5—Comparison of the correlation[a] between the abundance of small mammal captures and the age of the stand, amount of conifers, amount of hardwoods, and amount of hard and soft logs

Species	Age	Conifer	Hardwood	Hard log	Soft log
Snap traps					
Western red-backed vole	0.350*	0.302	–0.163	0.161	0.172
Deer mouse	.171	–.125	.114	.129	–.129
Pacific shrew	.236	.303	.333*	.242	.497*
Trowbridge's shrew	–.113	.010	–.222	.010	.466*
Piñon mouse	–.248	–.462*	.369*	–.048	–.026
Live traps					
Western red-backed vole	.600*	.204	–.181	.091	.045
Deer mouse	.223	–.123	.030	.053	–.254
Trowbridge's shrew	–.203	–.117	–.124	–.209	.370*
Piñon mouse	–.117	–.445*	.449*	.021	–.117
Chipmunks	.265	–.461*	.419*	.138	.046
Pitfall traps					
Western red-backed vole	.158	.266	–.231	–.151	.307
Deer mouse	–.045	.290	–.193	–.153	.212
Pacific shrew	.112	.281	–.134	.185	–.146
Trowbridge's shrew	.141	.355*	.498*	–.032	.303
Piñon mouse	–.142	–.083	–.210	–.130	.241

[a] Significant linear correlations ($P \leq 0.05$) are indicated with an asterisk.

red-backed vole, deer mouse, piñon mouse, Pacific shrew, Trowbridge's shrew, and the combined chipmunk species. In addition, two squirrels and the chipmunks were counted during the bird counts.

We captured most species of mammals in all three areas, and by all three techniques, with the exception of some of the rarer species (table 4). We have discussed at length the strong differences among the different capture methods (Taylor and others 1988). Among the mammals, the western red-backed vole had significantly fewer captures in the more southerly Branscomb region than in the central and northern regions. We have reported (Taylor and others 1988) that the vole's abundance was significantly correlated with true firs found on 11 stands in the north and none in the south. The two mice species were significantly more abundant in the south than in the north. The shrews were equally common in all regions, and the sample sizes of other species, including the chipmunks, were perhaps too small to demonstrate the effect of region.

The western red-backed vole was the only captured species that had a significant positive association with the age of the forest stand ($P < 0.05$; table 5), which confirms previous studies (Raphael 1988, Raphael and Barrett 1984) in the Willow Creek area. Bird count data indicates that Douglas' squirrel was also positively associated with stand age, and this greater abundance in older stands was consistent among the regions (table 2). The abundance of the chipmunk species and gray squirrel were related to region. Chipmunks and Douglas' squirrel were more common at Cave Junction, and the gray squirrel was more common at Branscomb.

The piñon mouse had the clearest association with hardwood density and clearly lacked association with stands that included conifers (table 5), judging from captures in both snap and live traps. The Pacific shrew was positively associated with hardwoods and soft logs, and Trowbridge's shrew was also positively associated with soft logs. The combined chipmunk species were positively associated with hardwoods, and negatively with conifers.

Discussion

Total species richness of birds in our stands is much higher than for stands discussed elsewhere in this volume that are located farther north in Oregon and Washington. We suspect this results from the much greater diversity of vegetation in our stands (Bingham and Sawyer, this volume) that resulted from a greater abundance of hardwood. Indeed, a few of our bird species showed a close association with hardwoods in general. A matter of concern is that present logging practices in our region are directed towards eliminating hardwoods as an important component of the commercial forests. As Raphael (1987) has shown, and our data reaffirm, the numbers of many species would probably be greatly reduced if this strategy was successful. Perhaps fortunately for the wildlife, silviculture is an imperfect art and many harvested conifer stands are regenerating into stands with a high per-

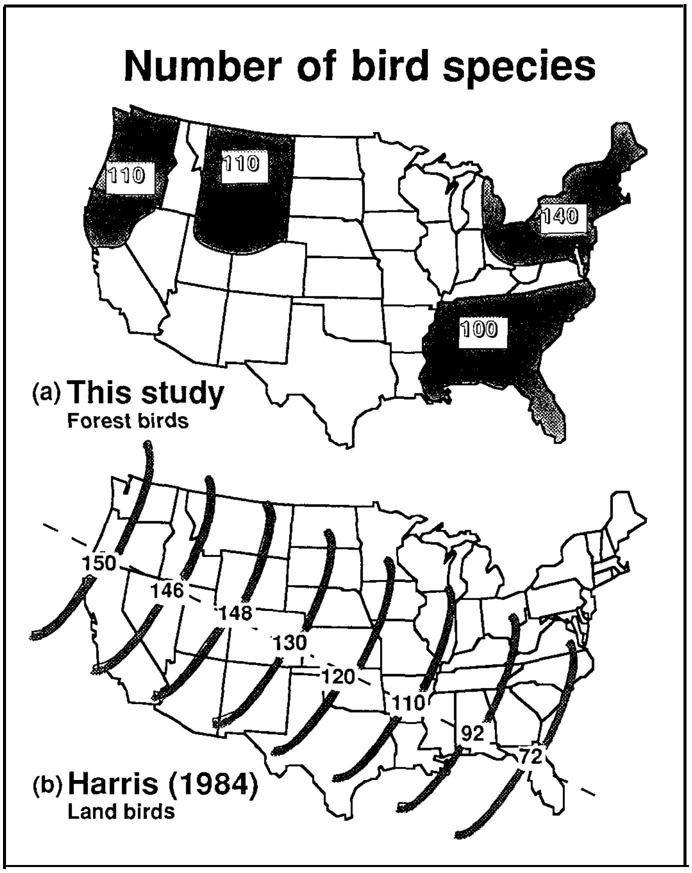

Figure 5—Number of breeding forest birds by geographic region, (a) taken from Blom (National Geographic Society [1987]), and (b) Harris (1984).

centage of hardwoods. We are experiencing a permanent loss of mature hardwoods, however, which may profoundly affect some animal species.

Harris (1984) points out that Pacific Northwest forests were the richest in North America in terms of bird species, based on MacArthur and Wilson's data (1967) (reproduced in fig. 5b). MacArthur and Wilson, however, were discussing all breeding birds, not just forest birds. Our recalculation of the number of breeding forest birds (fig. 5a) showed that the northeastern United States is the richest area in the North America, with about 140 species, and the Rocky Mountain area and the Pacific Northwest are tied at about 110 species each.

Although the Pacific Northwest is not particularly rich in forest-bird species, it does have many species endemic to the area. A comparison (based on the range maps of the National Geographic Society 1987) of the endemic species largely confined to the four regions of figure 5a showed a striking contrast. The Rocky Mountain area has no species confined to that region's forests. The northeastern region of the United States has only the golden-winged warbler. Only the southeast and the northwest have a significant number of endemic forest birds. The southeast has six (red-cockaded woodpecker, ivory-billed woodpecker, brown-headed nuthatch, Swainson's warbler, Bachman's warbler, and Bachman's sparrow) and the northwest has seven (Vaux's swift, rufous hummingbird, white-headed woodpecker, red-breasted sapsucker, hermit warbler, and chestnut-backed chickadee). That most of the endemics in the southeast are now extinct, rare, or declining, may not be irrelevant because that region's old-growth forest was essentially eliminated during the last century.

Many species in our study showed affiliations with stand age. Three birds were significantly more abundant in old-growth forests than either the young or mature stands: the hairy woodpecker, western flycatcher, and brown creeper. Many other birds were more common in the mature and old-growth stands than in the young stands. For these species, older forests are probably a preferred, but perhaps not required, forest configuration. Age was a major factor only when the difference between the young forests on the one hand, and the combined mature and old-growth forests on the other is considered. Between the two older categories, the species composition was quite similar.

Raphael (1984, 1987) and Raphael and Barrett (1984) conducted a study of forest birds and mammals and their stand-age associations in one of our study regions near Willow Creek, California. Raphael (1984), compared stand age with the abundance data from a single year for birds in the Willow Creek area. He found 25 significant relations (see table 2). Of the 25 species, our data agreed for 8 species, but disagreed for 7 species. In these seven cases, Raphael (1984) found a negative relation with stand age, and we found a positive relation. We found no significant relation for the remaining 10 species. We are not certain of the reason for this disparity of results, although methods did vary because our study covered a wider geographical range over a period of 2 years, and Raphael's (1984) study used 136 study plots from a single year.

Of the mammals we studied, only the abundance of western red-backed voles and Douglas' squirrels were positively associated with the age of the forest stand. Raphael (1988) found both species associated with older stands. He found 10 mammals that were positively correlated with stand age. Voles had by far the strongest relation to stand age. Perhaps the techniques we used did not adequately sample the larger carnivores that he found associated with stand age.

The stands chosen to represent different age-classes occurred naturally in the Cave Junction and Branscomb regions; that is, the young stands originated from fire or other catastrophic events, rather than as the result of timber harvests, and often were heterogeneous, with some structural and floristic comportents that resembled old-growth stands. Scattered old trees and abundant dead-and-down material were sometimes present in young stands. These characteristics, which are usually absent from young stands that originated from clearcut timber harvests, may be important factors that affect patterns of bird abundance. Results from even-aged stands regenerating from a clearcut may be very different. The cluster analysis did, however, group the bird community of the natural, young Branscomb stands with the young Willow Creek stands that resulted from timber harvesting.

Our study area was fire-prevalent, and for that reason, it may have been a poor area for examining species that become dependent on old-growth stands. The stands in this southern area of Douglas-fir are subject to drier conditions and more frequent fires than their counterparts to the north. Many species may have developed more flexibility in the southern portion of the range of their habitat type.

When a species is more common in older forests, we cannot make a statement about the species' reliance on older stands without information on the activities of that species in younger stands. The three bird species of significantly greater abundance in old-growth forests (the hairy woodpecker, western flycatcher, and brown creeper) are a case in point. Some evidence (van Home 1983) indicates that a species' density is not necessarily correlated with habitat suitability. Thus, although these three species do attain moderate numbers in young and mature forests, those stands may include habitat that is unsuitable for breeding.

By far the most common habitat association pattern we detected was a positive association with conifers. The next most common, perhaps the converse, was a lack of association with hardwoods. Only seven bird and no mammal species were positively correlated with hardwoods. The association with conifers, both direct and indirect, might not be surprising given the conifer dominance of these forests. As we have suggested above, however, greater abundance of hardwood could be a factor in the increased species richness of the southern Douglas-fir forests. Raphael (1987) also found some species strongly associated with tanoak, an important hardwood species. This association included six positively correlated ($P < 0.05$) species, some of which were in agreement with our data. Raphael found one, the olive-sided flycatcher, positively correlated with tanoak, but our data indicated a negative correlation with all hardwoods. He also found the western flycatcher and hermit warbler positively associated with hardwood, but we did not. Our results agreed with Raphael's for only three species: the hermit thrush, varied thrush (only in the winter), and warbling vireo. The differences quite likely result from our method of combining all hardwood species, and Raphael's concentration on tanoak. They may, however, be related to the much larger geographic region included in our study.

The strong geographic influence on patterns of species abundance within our study area has important management implications. We found that species abundances often differed significantly between regions in their relation to age (the age-region interaction shown in table 2); that is, in one region the relation might be positive, in another negative, and in the third, have no pattern. These differences are to be expected because at the periphery of its range or habitat, a species is most likely to be constrained to a narrower range of environmental conditions than at the center. Land managers might find that, to maintain a species in a given region, quite different strategies of land use from those used in other regions might well be necessary.

Because many species' abundances are related to stand age and composition, further alterations of the landscape will likely result in profound changes in the abundance patterns of many of the species in the study area. This, however, will probably not result in any extinctions in the foreseeable future. For the great majority of the species in this study, the pervasive influence of stand age and composition on population levels should warn us that close monitoring of some species may be necessary. At the very least, periodic sampling should be conducted to determine the population status of species in the area.

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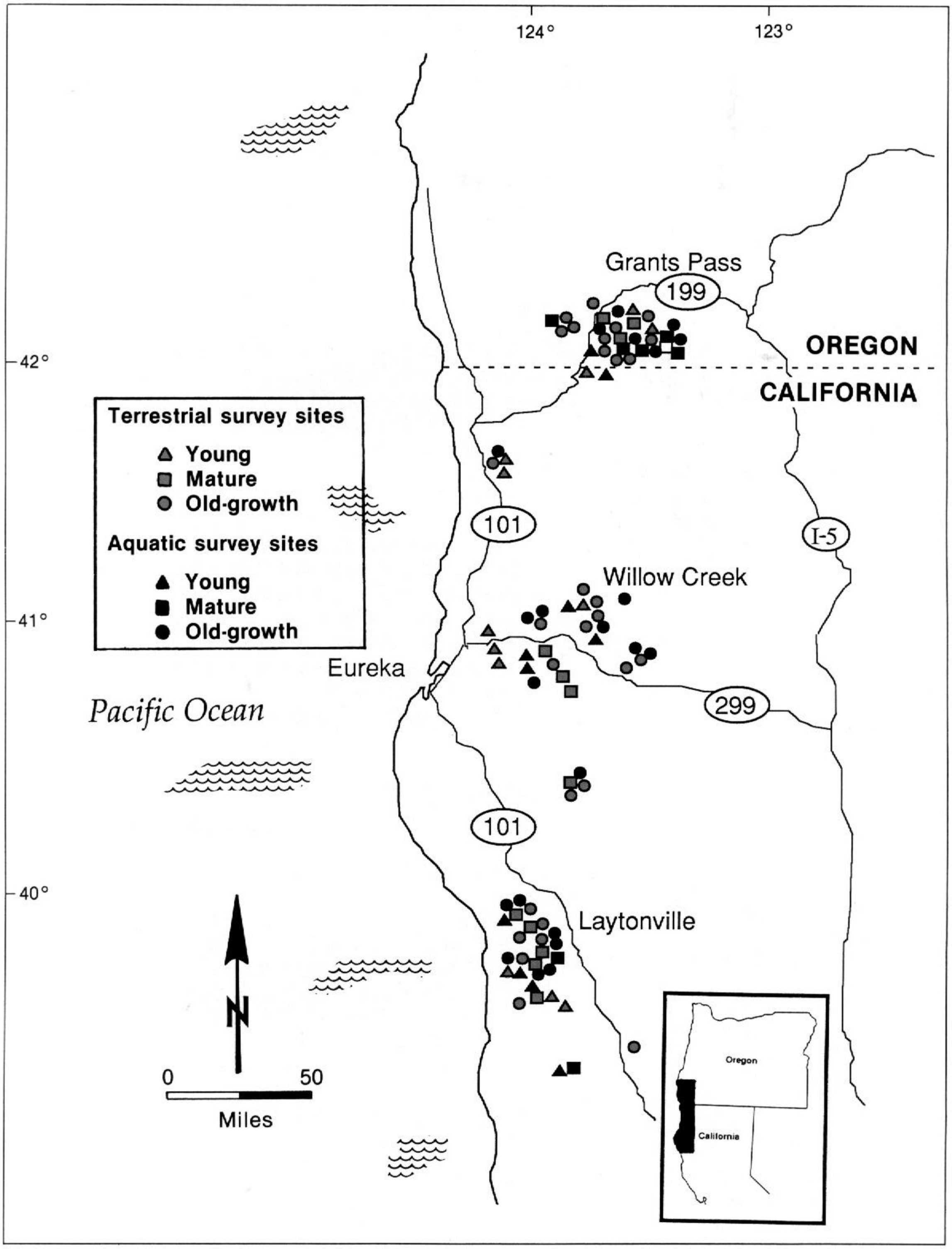

Location of terrestrial and aquatic study sites.

The Structure of the Herpetofaunal Assemblage in the Douglas-Fir/Hardwood Forests of Northwestern California and Southwestern Oregon

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Abstract

Terrestrial and aquatic herpetofauna were sampled by three methods, time-constrained searches, pitfall traps, and area-constrained searches from 1984 to 1986 in northwestern California and southwestern Oregon. The 54 terrestrial and 39 aquatic study sites were in Douglas-fir/hardwood forest stands that ranged in age from 30 to 560 years. Results of these surveys are presented in terms of species richness, equitability, relative abundance, relative biomass, and macrohabitat and microhabitat associations.

Although species richness did not differ among forest age-classes, the composition of the herpetofauna was notably different. Old and wet sites had proportionately more amphibian species, and young and dry sites had proportionately more reptile species. Terrestrial salamanders were more abundant on old-growth than on young sites. We also found that structural components associated with older forests were the best predictors of increased numbers of salamanders. Analyses of microhabitat associations indicated that large, well-decayed logs were the most heavily used woody debris, though use of particular size- and decay-classes varied among salamander species.

Harvesting forests without immediately affecting herpetofauna is probably not possible; however, strategies can be developed to minimize long-term adverse effects. We provide a summary of management recommendations designed to assure long-term viablity of herpetofauna in areas subject to logging.

Introduction

Old-growth forests are a unique and complex ecosystem where many life forms occur in numbers disproportionate to their occurrence in other parts of their range (Thomas and others 1988), but the nature of the ecological dependencies (Ruggiero and others 1988) between these species and the ancient forest ecosystem are only beginning to be understood. More knowledge about the spatial and temporal distributions of species in old-growth and in younger natural and managed forests, and an understanding of habitat requirements and ecological interdependencies are required to make sound decisions that assure healthy forests in the future.

We describe the species composition and relative abundance of members of the herpetofaunal assemblage in the southern portion of the Douglas-fir region, with a focus on how presence and abundance are related to forest age and structural aspects of the forest habitat.

Heatwole (1982), in a review of available literature on the structure of temperate and tropical herpetofaunal assemblages, noted how little is known about them and their relation to the larger community of organisms that constitute a complete ecosystem.

Pough (1980, 1983) outlined some of the unique adaptations of herpetofauna that illuminate their critical role in ecosystem dynamics and place them in a larger ecological context. Their small body size and elongate body form, energetically unfeasible for endotherms, permits them to use space and exploit food resources unavailable to other vertebrates. Their ectothermic nature facilitates a life of low energy demand. They are better suited than endotherms to periods of limited food, water, or oxygen. Endotherms are generally viewed in terms of the energy they consume, but reptiles and amphibians are more realistically considered in terms of the biomass they produce and make available to other trophic levels (Pough 1980: 104). These small vertebrates comprise an essential trophic level in the ecosystem, where invertebrate biomass is converted to vertebrate biomass far more efficiently than by endotherms. Pough, comparing the efficiency of secondary production of endotherms and ectotherms, noted that the "...net long-term conversion efficiencies of amphibians and reptiles are many times greater than those of birds and mammals. The ecological significance of this efficient biomass production is enormous" (Pough 1980: 102).

Methods

Study Area

The study was conducted in Douglas-fir/hardwood forests of the Klamath Mountains and Coast Range of northwestern California and southwestern Oregon; the southern portion of the Oregonian Province (Udvardy 1975). Fifty-four terrestrial study sites, ranging in size from 21 to 150 ha, and 39 aquatic study sites (15-m lengths of second- or third-order streams) were sampled (see frontispiece and appendix table 9). For site selection procedures see Bingharn and Sawyer (this volume). Forests at the terrestrial sites ranged in age from 40 to 450 years; forests at the aquatic sites ranged in age from 30 to 560 years.

Herpetofauna Sampling

Four methods were used to sample the species composition, abundance, and biomass of the herpetofauna; time-constrained searches (timed searches), pitfall traps (pitfall), area-constrained searches (area searches), and opportunistic observations. These methods are described in more detail elsewhere (Bury and Raphael 1983, Corn and Bury 1990, Raphael and Rosenberg 1983, Welsh 1987). **Timed searches** recorded the search effort of two to three persons while they moved about the forest at random examining all microhabitats encountered, raking through litter, turning rocks and logs, tearing open decomposed logs, probing in vegetation, and so on. The clock was stopped when animals were encountered and while data were gathered. Our timed searches differed from those of Corn and Bury (1990) in that we searched seeps and springs in addition to rocks, logs, bark, and litter. **The pitfall** method consisted of trap grids with 36 traps spaced at 15-m intervals in a 6 x 6 arrangement. Traps were made of two, number 10 tins taped together and buried with the lip at the groundline and concealed by a cover of bark or cedar shake propped above the ground.

Terrestrial sites were sampled with timed searches, pitfalls, and opportunistic observations. We conducted four person-hour timed searches on each of 54 sites from April to June of 1984 and 1985, and on a subset of 30 sites from April to May of 1986. Our combined effort for timed searches totaled 552 person-hours. We ran 36-trap pitfall grids on 49 sites in October and November of 1984 for 50 nights and October of 1985, for 30 nights. The total pitfall effort equaled 141,120 trap-nights. Twenty-six amphibians and reptiles were recorded by opportunistic observation during sampling for other vertebrate groups or while vegetation data were collected.

Area searches were only done at aquatic sites. Our sampling of aquatic habitats consisted of area-constrained searches of 39 second- or third-order streams (Strahler 1952) on or near the terrestrial sites. We selected three 5-m reaches 1 to 3 m wide along each stream by walking 50 m upstream from the nearest trail or road access for the first reach, and 50 m from the top of the previous reach for subsequent reaches. Stream searches occurred during the summers of 1984 and 1985. The method consisted of mapping each reach to scale in order to plot captures, then methodically and sytematically searching all substrates, with catch nets placed downstream to capture dislodged animals.

Measurements of Forest Landscape, Structure, and Composition

Forest age- and moisture-classes-Sites were grouped into three forest age-classes: young, mature, and old-growth; and old-growth sites were classified into three moisture-classes: wet, mesic, and dry. Forest age was determined by tree

Continue

coring, ring counts, and accessing structural characteristics (Old-Growth Definition Task Group 1986). An average of three Douglas-fir trees in the dominant size-class were cored on each site (Bingham and Sawyer, this volume). Age of trees on young sites ranged from 24 to 99 years, on mature sites from 100 to 200, and on old-growth sites 7200 years.

Eight of the young forest stands that we sampled had been logged, and three were naturally regenerated after fire. All mature sites were unmanaged. Moisture classification of old-growth terrestrial sites was based on mean percentage cover values and the absolute constancy of particular shrub and herb species (B. Bingham, pers. comm.). Only the old-growth mesic sites were used for analysis of the terrestrial herpetofauna relative to forest age-class.

Landscape and macrohabitat variables-We use the term **landscape** to describe variables that incorporated a broad spatial scale (for example, elevation and distance from the coast). We used the term **macrohabitat** for aspects of forest structure and composition in general proximity to where animals were sampled.

Plant species composition, structural features, and forest age on terrestrial sites were gathered from three to five, 0.l-ha circular plots in accordance with the methods described in detail in Spies and others (1988) and Bingham and Sawyer (this volume). All dead and down woody material with a diameter 210 cm was measured. Values were averaged among plots at each site and the means used to represent that variable for the entire site. These data are reported as macrohabitat associations.

Microhabitat variables-with each timed-search capture we recorded type of substrate, vertical postion relative to that substrate, the width and length of substrate objects (for example, rocks, logs, or bark slabs), and the decay state of logs and snags under 5 categories of decay from sound to rotten (Maser and others 1979). Decay-class 1 was defined as a newly fallen tree with intact bark, limbs, and twigs. Decay-class 2 logs were sagging slightly, had intact bark, with some large branches, but no twigs. Decay-class 3 logs were sagging near the ground, with sloughing bark and no large branches. Decay-class 4 logs were completely on the ground, had little or no bark, and the wood was punky. Decay-class 5 logs are well-decayed with soft, powdery wood and massive invasion of roots and seedlings.

We estimated relative abundance of downed woody material by size (based on surface area) and decay-class for our sites by pooling data across vegetation sampling plots within the same stands sampled for herpetofauna (data from B. Bingham). These estimates included only woody material, not bark, and were calculated separately for hardwood and conifer species. These aspects of the habitat are reported as **microhabitat** associations, and the data are presented as frequencies of occurrence.

Sites Used for Analyses of Landscape and Habitat Parameters

We used data from 42 terrestrial forest sites to compare species richness, species equitability, relative biomass, relative abundance by forest age- and moisture-class, and structural aspects of habitat use. We omitted nine higher-elevation, white fir-dominated sites and three sites on serpentine soils because they differed greatly from our remaining sites (appendix table 9). The high-elevation sites were at the upper limit of the range of Douglas-fir and contained a depauperate herpetofauna; the three serpentine sites were open, dry, and brushy with abundant lizards, characteristic of early successional clearcuts. Of the **42** sites, half occurred in the Coast Range (coastal area) and half were inland in the Klamath/Siskiyou Mountains (inland area) (appendix table 9). Differences in species numbers and relative abundance of the total herpetofauna, salamanders, frogs, and reptiles, among forest age- and moisture-classes, were analyzed by geographic area (coastal vs. inland). Although the coastal and inland sets of sites also showed a latitudinal gradient, most of the species we examined range across this gradient, therefore, we assumed no effect.

We used 39 stream sites for analyses of the aquatic herpetofauna relative to forest age and habitat variables (appendix table 9). Captures from all three reaches on each stream were totaled for this analysis.

Statistical Methods

No significant differences were found between years for numbers of captures per site for either the pitfall or timed-search data (Welsh and Lind 1988) so we combined years for these data. Comparisons of mean species richness among forest age-classes were based on the combined pitfall and timed-search data. We used mass data taken during pitfall sampling to compare biomass among forest age- and moisture-classes. In all other analyses of terrestrial herpetofauna we used data from the timed searches.

We tested the null hypotheses of equality of animal (or species) abundance and biomass among forest age- and moisture-classes by geographic area (coastal and inland), and a lack of association between numbers of animals and habitat variables.

We used a 2-factor analysis of variance (ANOVA) to test for differences in species numbers and relative abundance of higher taxa (orders) among age- and moisture-classes in each area (Dixon 1985:BMDP, 2V). Analysis of the relation of individual species to forest age- and moisture-classes were restricted to those that were found on at least one-third of sites. We incorporated results from an earlier analysis of these data where relationships with forest age- and moisture-classes within and among coastal and inland areas were examined using one-way analysis of variance followed by multiple comparisons (Welsh and Lind 1988). Two species were restricted primarily to either our coastal (California slender salamander) or inland area (Del Norte salamander); their relations to habitat were analyzed only within the appropriate area.

We used Jaccard's similarity coefficient to compare species composition among forest age- and moisture-classes (Sneath and Sokal 1973: 131):

$$Sj= \frac{a}{a + b + c} ,$$

in which, for any two classes, a = number of species in common, b = number of species in the first class only, and c = number of species in the second class only.

Mean biomass for the most common species and higher taxa is reported by forest age-class (coastal and inland areas combined), based on combined fall pitfall samplings from 1984 and 1985-a total of 115,200 trap-nights. We have no way of estimating the actual area sampled by our pitfall grids; however, we assumed that they sampled the same area on all sites regardless of slope or topography. We emphasize that these are not density data. We recognize that many species are not effectively sampled by pitfalls (for example, snakes, clouded salamanders, and treefrogs) and we do not assume, even for those species sampled effectively, that all individuals in the grid area were captured. We present these data as relative biomass. We used a l-factor analysis of variance (ANOVA) to test for differences in biomass among forest age- and moisture-classes (Dixon 1985:BMDP, IV).

Correlation and all-possible-subsets regression analysis were used to examine the relationships of the herpetofauna to forest vegetation, structure, and landscape characteristics (Dixon 1985: BMDP, 9R; Neter and others 1989). Forest age and geographic area (distance from coast) were included as continuous variables in this analysis. We analyzed a total of 36 biologically relevant variables relative to captures per person-hour (timed search) of salamanders (all species combined), reptiles (all species of lizards and snakes combined), and the four most abundant species of salamander. We selected the 36 variables from an independently derived data set of over 60 measures of forest structure and composition (Bingham and Sawyer, this volume) that we judged biologically relevant to the herpetofauna, and that reduced redundancy (such as selecting hardwood log volume over hardwood log weight). All-possible-subsets regression was performed on subsets of 15 variables that were most highly correlated with each species or species group but that were not highly intercorrelated ($R < 0.80$). For each species or group, we report the best univariate and multivariate models with up to five variables, based on maximum adjusted R^2.

Chi-square goodness-of-fit tests were used to examine the relation between the size, type, and decay-class of downed wood available and the microhabitat associations of the total herpetofauna and selected salamander species.

We emphasize that our inferences are drawn from observations and not experimental manipulations. Although our results are described in the context of hypothesis-testing, our study was primarily exploratory. Because the total number of sites we sampled in each age- or moisture-class was small, we caution against broad inferences. We report actual P-values for our analyses so that readers may judge the level of significance of any particular test result. For purposes of discussion, we use alpha level ≤ 0.05 to indicate significance.

Results and Discussion

Composition of the Herpetofauna

We captured 6419 individuals by all sampling methods combined from the 54 terrestrial and 39 aquatic sites; 97.6 percent were amphibians and 2.4 percent reptiles (table 1). Most captures (88.1 percent) were salamanders, clearly the dominant group among the forest herpetofauna of this region. Bury and Corn (1987), using pitfall/drift-fence arrays in similar forested habitats in the Oregon and Washington Cascades, also found salamanders to comprise a high proportion (51.9 percent) of the herpetofauna. Their data also indicated a high proportion of frogs (42.5 percent) but most of these captures resulted from intercepting groups of dispersing young-of-the-year at a few stands. Using these data to estimate the relative abundance of frogs in the Cascade forests would probably give inflated values, although we would expect frogs are probably more abundant there than here because of the higher and more consistent precipitation in Oregon and Washington.

We suspect that our sampling regime probably underestimated the reptile component of the herpetofauna because of timing. The timed searches were performed in early to mid-spring, and the pitfalls were run in mid- to late fall corresponding with the fall rains. Both periods would favor the capture of amphibians, but are, respectively, early and late for the best reptile sampling. Combining total captures from our timed-search and pitfall data, we found 2.4 percent were reptiles. Bury and Corn (1987) ran their arrays from late

Table 1-A comparison of numbers of captures by order for herpetofauna collected by 4 sampling methods in Douglas-fir/hardwood forests of northwestern California and southwestern Oregon from 1984 to 1986

Method	Taxa					
	Salamanders	Frogs	Lizards	Snakes	Turtles	All species
Pitfall traps	1580	48	13	1	0	1642
Time-constrained searches	3156	49	95	29	0	3329
Area-constrained aquatic searches	914	508	0	0	0	1422
Opportunistic observations	8	4	4	9	1	26
All methods combined	5658	609	112	39	1	6419
Percentage of total	88.1	9.5	1.7	0.6	<0.01	100

May through the dry summer months and into the fall; they reported 5.6 percent of captures were reptiles. Also, they used funnel traps with their pitfall arrays, which significantly increased their capture of snakes.

Relations of the Herpetofauna to Forest Age, Moisture, and Geographic Area

Species richness and species similarity-Combining all methods, we found 31 species, 16 reptiles and 15 amphibians, on the 54 terrestrial and 39 aquatic sites (table 2); the number of species per site ranged from 1 to 13.

Analysis (ANOVA) of numbers of terrestrial species among geographic areas and forest age- and moisture-classes for 42 terrestrial sites (appendix table 9) indicated no significant differences in species richness among age- or moisture-classes, but a significant difference between coastal and inland areas and a significant interaction effect between forest age and area (table 3). We found greater species richness in the Coast Range, Four of the five species detected in the coastal area but not inland (four snakes species) are known to occur in the vicinity of our inland sites. Only the fifth species, the arboreal salamander, has not been reported from this part of California (Stebbins 1985). Consequently, differences in geographic areas do not appear to reflect true biogeographic differences but are probably best explained as an artifact of the difficulty of sampling for snakes (Welsh 1987, Welsh and Lind 1988). The significant interaction effect between forest age and area results from detecting more species in the mature age-class in the coastal area only. We consider that the greater richness found on the coastal mature stands is a result of these sites being generally closer to ponds and streams than other sites. This proximity to riparian areas tended to increase the number of species (particularly amphibians) detected relative to sites farther from water.

Although we did not find significant differences in species richness among forest age- or moisture-classes, we did find notable differences in species composition. Using presence-absence data, we calculated Jaccard's similarity index for 10 randomly selected sites in each forest age-class. These results (table 4) indicated higher similarity among species for the mature and old-growth sites and lower similarity between the young sites and both of the older age-classes.

These differences among age-classes are attributable to the loss, after logging, of certain amphibian species that occur in the older age-classes and the addition of several lizard species that prefer the open, drier, and warmer areas resulting from clearcut logging. Bury and Corn (1988a), Raphael (1988c), and Raphael and Marcot (1986) also found more lizards in early successional stages after timber harvest.

Using the similarity index for four randomly selected sites in each moisture-class indicated lowest similarities between the wet and dry sites. Differences in species composition among moisture-classes are also attributable to amphibian species being replaced by reptile species on the relatively more xeric and generally more open old-growth dry sites (table 4).

Species equitability-We examined species evenness or equitability by plotting the numbers of captures for the 10 most abundant species vs. species rank, with data (timed-search) from 10 sites in each forest age-class (only the mesic sites from the old-growth set). We ranked the species from most to least abundant along the x-axis. Results indicated that the herpetofaunal assemblage of this area, like other herpetofaunal communities both temperate and tropical (Scott 1982), is dominated by a few species and hence displays low equitability (fig. la). We found little difference among forest age-classes. A similar analysis for four randomly selected sites in each old-growth moisture-class indicated no apparent differences (fig. lb).

Relative abundance-Analysis (ANOVA) of the number of captures (timed-search data-total herpetofauna) by geographic area and forest age- and moisture-class indicated significant differences in total numbers of individuals among forest age-classes (table 3). In a previous analysis of the same data, we found that these differences were significant only between the young and the old-growth sites (old > young, $P < 0.05$: Welsh and Lind 1988) but not between the two older age-classes.

Table 2—Total captures from all sampling methods and summary of analyses of relative abundance by forest age-class of herpetofaunal species in Douglas-fir/hardwood forests of northwestern California and southwestern Oregon

Species	Sampling method(s)[a]	Total captures[b]	Mean relative abundance among forest age-classes[a, c]			P-value[d]
			Young	Mature	Old	
Frogs and toads						
Tailed frog	AC,PF,TC,OP	501	0.111	0.555	0.810	0.001 A
Western toad[e]	PF,TC	4	0	2	1	—
Pacific treefrog	TC,PF,OP	55	.049	.166	.117	.366
Foothill yellow-legged frog	PF,AC	48	.316	.058	.579	.392
Red-legged frog[e]	OP	1	0	0	1	—
Salamanders						
Northwestern salamander[e]	PF,TC,OP	6	1	3	2	—
Pacific giant salamander	AC,PF,TC	936	19.2	18.1	25.67	.254 B
Olympic salamander	TC,AC,OP,PF	48	.000	.038	.192	.001 B
Roughskin newt	TC,PF,AC	97	.038	.140	.192	.377
Del Norte salamander[f]	TC,PF	471	.278	.396	2.278	.016 B
Ensatina	TC,PF	2751	2.265	2.595	4.508	.036
Black salamander	TC,PF,AC	62	.099	.121	.050	.701
Clouded salamander	TC,PF,OP	240	.496	.390	.725	.495
Arboreal salamander[e]	PF	1	1	0	0	—
California slender salamander[f]	TC,PF	1046	2.718	5.533	5.542	.014
Turtles						
Western pond turtle[e]	OP	1	0	1	0	—
Lizards						
Western fence lizard[e]	TC,PF,OP	26	1	4	21	—
Sagebrush lizard[e]	TC,	14	0	0	14	—
Western skink[e]	TC,PF	20	1	7	12	—
Southern alligator lizard[e]	TC	4	0	1	3	—
Northern alligator lizard	TC,PF,OP	48	.095	.167	.042	.239
Snakes						
Rubber boa[e]	TC	1	1	0	0	—
Sharptail snake[e]	TC,OP	10	1	1	8	—
Ringneck snake[e]	TC	11	0	7	4	—
Racer[e]	TC,OP	3	2	0	1	—
California mountain kingsnake[e]	TC	1	0	0	1	—
Common garter snake[e]	TC	1	0	0	1	—
Western terrestrial garter snake[e]	TC	2	2	0	0	—
Western aquatic garter snake[e]	TC	1	0	1	0	—
Northwestern garter snake[e]	TC,PF	5	2	1	2	—
Western rattlesnake[e]	OP	4	0	1	3	—

[a] Data from 1st method listed were used to calculate mean relative abundance and for statistical tests: AC, area-constrained search (aquatic sites only); PF, pitfall traps, TC, time-constrained search; OP, opportunistic observations (terrestrial sites only).

[b] Data were from 54 terrestrial sites and 39 aquatic sites.

[c] Tests based on 42 terrestrial sites (only old-mesic sites were used for age analysis) or 39 aquatic sites (9 young, 9 mature, and 21 old). Young means ≤100 years old; mature, 100-200 years; old, >200 years old. Some results were previously reported in Welsh and Lind (1988) and Welsh (1990).

[d] P-values are from analysis of variance (no letter), Tukey tests (proportions) (A), or regression analysis (B). A dash indicates no test was performed.

[e] These species are too uncommon for subsequent analysis; actual captures are reported for these species.

[f] Sites used for forest age analysis were those within the geographic range of the species.

Table 3—*F*-statistics and *P*-values from 2-factor analyses of variance of species richness (timed-search and pitfall data) and relative abundance of higher taxa of herpetofauna (timed-search data) by forest age- and moisture-class in coastal and inland areas

Group definition	Forest age	Area	Interaction	Forest moisture	Area	Interaction
Total number of species	1.48 (.25)	12.83 (.001)	3.36 (.05)	0.75 (.49)	0.50 (.49)	2.98 (.08)
Total herpetofauna[a]	3.33 (.05)	.00 (.99)	.24 (.79)	2.42 (.12)	1.14 (.30)	0.85 (.45)
All salamanders[a]	3.08 (.04)	.28 (.60)	.13 (.88)	2.24 (.14)	1.07 (.32)	.84 (.45)
All frogs	1.01 (.38)	1.48 (.23)	2.84 (.08)	7.41 (.006)	2.33 (.15)	7.72 (.006)
All reptiles	2.68 (.09)	2.87 (.10)	.56 (.57)	2.88 (.09)	.81 (.38)	1.76 (.21)

[a] Two species of salamander were not included here because of obvious differences in distributions between coastal and inland areas; the California slender salamander occurred primarily on coastal sites and the Del Norte salamander occurred primarily on inland sites.

Table 4—Jaccard similarity index values[a] for species of herpetofauna in 3 age-classes and 3 moisture-classes of Douglas-fir/hardwood forest

Age-class	Young	Mature	Old growth
Mature	0.54		
Old-growth	.48	0.71	
Total number of species	16 (.62)[b]	21 (.62)	15 (.73)
Moisture-class	**Old-wet**	**Old-mesic**	**Old-dry**
Old-mesic	.64		
Old-dry	.50	.67	
Total number of species	10 (.80)	13 (.69)	17 (.59)

[a] Values are based on data from 10 randomly selected sites in each age-class (mesic old-growth sites only) and 4 sites in each moisture-class, with equal numbers from coastal and inland areas where possible. Greater JSI values indicate greater similarity in species composition.

[b] Proportion of amphibians.

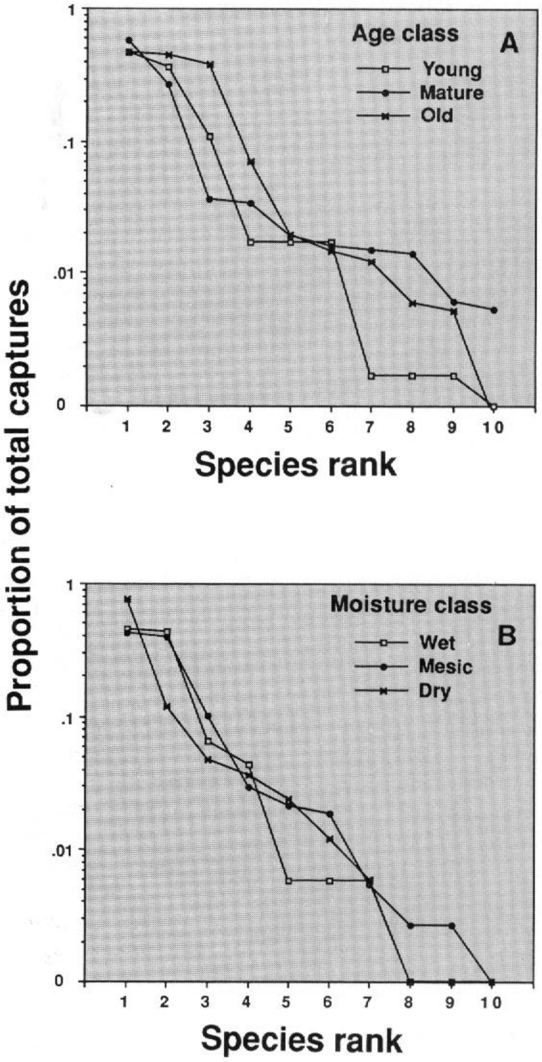


Figure 1—Proportion of total herpetofaunal captures, by ranked species, from (A) 10 sites in each forest age-class and (B) 4 sites in each forest moisture-class. The first ranked species is the most abundant. Capture data are from timed searches and plotted on a logarithmic scale.

Salamanders (timed-search data, all species combined) showed a significant difference among age-classes (table 3), also occurring in greater numbers on old-growth forest sites (old > young, $P < 0.05$: Welsh and Lind 1988). Of the eight species of salamanders sampled in sufficient numbers for statistical analyses, half were significantly more abundant on old-growth forest sites: Olympic salamander, Del Norte salamander, ensatina, and California slender salamander (table 2).

Although this analysis failed to detect significant differences among moisture-classes for the total herpetofauna or salamanders (table 3), in a previous analysis of these data, using the Games and Howell modification of the Tukey test, we found significant differences between the mesic and dry categories for both of these groupings (Welsh and Lind 1988).

Frogs detected by terrestrial sampling (timed-search data, all species combined) were not significantly more abundant in any forest age-class (table 3). We did find significant moisture-class effects and moisture-class and area interaction effects, however, these results reflect the fact that terrestrial anurans (mostly Pacific treefrogs) were significantly more abundant on our mesic sites within the Coast Range (mesic > wet, $P = 0.02$: Welsh and Lind 1988). This result may be due to the fact that the mesic sites were generally closer to appropriate breeding habitat for treefrogs. Terrestrial anurans were absent from most of our inland sites, probably because the inland area is drier than the coastal area. These climatic differences between areas probably account for the significant interaction effect between moisture-class and area indicated for frogs (table 3).

The forest age-class analysis did not yield significant relations for species of terrestrially sampled frogs (table 2). Interpreting our results for the abundance of frogs and aquatic-breeding salamanders relative to forest age- and moisture-class is confounded because we did not gather data on distances from our forest sites to suitable breeding habitat for these species. Proximity of breeding habitat is probably the single most important factor in determining the presence and relative abundance of these species. Bury and Corn (1988a) reported marked increases in numbers of these amphibians on sites near appropriate breeding habitat, regardless of forest age- or moisture-class.

Our aquatic sampling (area searches) detected two species of frogs, the foothill yellow-legged frog and the tailed frog. The tailed frog was significantly more abundant in streams associated with old-growth forests (table 2).

Reptiles as a group did not appear to be significantly influenced by geographic area, forest age, or forest moisture (table 3), but our samples were small for these taxa.

The only reptile species for which we had adequate numbers to compare abundances among forest age-classes was the northern alligator lizard. It was detected in similar numbers in all forest age-classes (table 2).

Table 5—Mean relative biomass, in grams, from pitfall sampling in different age- and moisture-classes of Douglas-fir/hardwood forests in northwestern California and southwestern Oregon

	Young (10)[a]	Mature (11)	Old-wet (6)	Old-mesic (9)	Old-dry (4)
All frogs	1.52[b]	2.67	0.63	4.63	3.23
	±4.53	±5.46	±1.01	±8.81	±3.73
Salamanders					
Black salamander	.09	3.91	.00	1.11	1.55
	±.28	±11.88	—	±2.25	±3.10
California slender salamander[c]	.69	5.11	.86	5.49	1.20
	±.95	±3.07	±.76	±3.37	—
Pacific giant salamander	18.50	8.90	53.80	18.17	.00
	±37.70	±16.46	±47.90	±28.67	—
Ensatina	70.10	93.00	53.20	81.90	118.80
	±43.90	±81.80	±37.40	±64.80	±82.10
Del Norte salamander[c]	6.41	1.00	8.66	73.80	.00
	±9.40	±2.45	±12.90	±145.60	—
Roughskin newt	2.86	4.09	2.27	7.82	1.87
	±4.46	±4.69	±5.03	±17.37	±3.75
All salamanders[d]	94.50	112.70	114.00	152.50	122.60
	±67.40	±76.00	±64.30	±116.00	±85.70
All reptiles	1.65	.50	.57	.95	1.47
	±5.22	±1.15	±1.38	±1.95	±1.99

[a] Number of sites.

[b] Mean ±1 standard deviation.

[c] Stands within the geographic range only; slender salamander: n = young, 7; mature, 5; old-wet, 3; old-mesic, 4; old-dry, 1. Del Norte salamander: n = young, 3; mature, 6; old-wet, 3; old-mesic, 5; old-dry, 3.

[d] Sum of biomass of above 6 species only; incidental records of other species omitted.

Mean biomass—We found a pattern of increasing biomass of terrestrial amphibian species from young to old-growth forest age-classes (table 5). Because of high variances among sites within both age- and moisture-classes, however, analysis (1-factor ANOVA) indicated only one species, the California slender salamander, to have significantly higher biomass on older stands ($F = 6.99$, $P = 0.009$).

Ensatina accounted for 67 percent of the relative biomass (all sites combined) followed by the Pacific giant salamander at 16 percent. Some notable differences were found in some species' relative contributions to abundance and biomass. The Pacific giant salamander had low mean relative abundance (0.182/1000 trap-nights), but its mean biomass exceeded that of the more abundant California slender salamander (1.23/1000 trap-nights) and the Del Norte salamander (3.65/1000 trap-nights) in most forest age- and moisture-classes (table 5). These two smaller salamanders accounted for 1 percent and 9 percent of the biomass, respectively.

Differences between the Coast Range and the Klamath Mountains-Although we consider the difference in mean number of species between coastal and inland areas (table 3) to be an artifact of sampling difficulties rather than a reflection of true biogeographical differences, we did find some evidence of real differences between these areas. For example, we found significantly more black salamanders and a pattern of higher abundance for many other species in the Coast Range, although differences were not statistically significant for the other species (Welsh and Lind 1988). We think that the explanation for these results lies in differences in the suitability of habitats for the herpetofauna. Progressing from the influences of the Pacific Ocean eastward toward interior California is a pronounced environmental gradient characterized by high precipitation, both rain and fog, and mild temperatures along the coast, to lower precipitation and more extreme temperatures-both highs and lows-farther inland (Kahrl 1979:5, 13). Conditions along the coast create more suitable conditions for forest-dwelling herpetofauna, particularly amphibians, than do conditions inland. This climatic gradient may have affected the number of species (table 3), the increasingly patchy distribution of their populations, and their relative abundance (see below). For example, we found the black salamander on 43 percent of coastal stands versus 19 percent of inland stands (also see Lynch 1981). Either actual densities of individuals of many but not all species are greater in coastal areas, or more equable coastal habitats tend to increase the likelihood of detection of individuals and of less-common species because of more accessible retreats (near or on surface vs. subsurface cover).

Forest Landscape and Habitat Structure: Macrohabitat Associations

Herpetofaunal abundances (timed-search data) were related to macrohabitat characteristics of the forest by using correlation and regression analyses for 36 variables (table 6). We report the five "best" single predictor-variables of animal abundance, and the best multivariate models (up to five variables) for the most common species of salamanders and for salamanders and reptiles as a whole (table 7).

Salamanders-As a group, salamanders were significantly related to macrohabitat variables associated with late-successional stages of the forest (table 7): increasing densities of large trees, particularly hardwoods, and large snags, and a decreasing density of small conifers. Also of importance in predicting salamander numbers were landscape variables (table 6) indicative of relative moisture in the habitat-distance from coast (negative correlation) and presence of seeps. The third type of variable that entered into our predictive models for salamanders were ground layer variables: percentage cover of rock, a significant indicator of protective cover, and percentage vegetation cover from 0 to 0.5 m high.

Table 6-Macrobabitat variables used for multiple regression analysis

Landscape variables
- Forest age (years)
- Elevation (m)
- Solar (KgCal/cm^2[Langleys]/year)
- Presence of streams
- Presence of seeps
- Distance from coast

Tree variables
- Small conifers (all tree variables are stems/ha)
- Large conifers (>80 cm diameter at breast height [d.b.h.])
- Small hardwoods
- Large hardwoods (>50 cm d.b.h.)
- Small trees
- Large trees
- Basal area conifers (m^2/ha)
- Basal area hardwoods
- Total basal area
- Conifer importance (number of stems + basal area)
- Hardwood importance
- Canopy cover (ocular percentage cover estimate; mean of 3-5 200 m^2 plots/stand)

Coarse woody debris variables
- Large snags (>50 cm d.b.h. & >4.5 m tall)
- Small snags
- Large conifer logs (>50 cm diameter & >15 m long; pieces/ha)
- Small conifer logs
- Small hardwood logs
- Large logs
- Small logs
- Large-log weight (metric tons/ha)
- Small-log weight
- Conifer-log volume (m^3/ha)
- Hardwood-log volume
- Sound-log volume
- Decayed-log volume
- All-log volume

Ground layer variables
- Litter depth (mm; average of 36-60 profiles/stand)
- Rock (ocular percentage-cover estimate; mean of 3-5 200 m^2 plots/stand)
- Ferns (ocular percentage-cover estimate; mean of 3-5 200 m^2 plots/stand)
- 0-.5 m vegetation cover (ocular percentage-cover estimate; mean of 3-5 200 m^2 plots/stand)

Vegetation cover was negatively correlated with salamander abundance, but this may be a sampling artifact. Given equal search time on otherwise comparable sites (timed-search method), the site with the thicker understory might yield fewer salamanders because of increased difficulty in finding obscured cover materials (Welsh and Lind 1988).

Table 7—Results of multiple regression analysis for abundance of selected herpetofauna (timed-search data) relative to macrohabitat variables (the 5 best single variables and the best multivariate models are given)

Variables in model	C[a]	R^2 (adj.)	*F*	*P*
All salamanders:				
Large hardwoods	+	0.286	16.22	0.0003
Small conifers	–	.270	15.11	.0004
Large trees	+	.259	14.32	.0005
Distance from coast	–	.222	11.87	.001
Basal area of hardwoods	+	.204	10.77	.002
Small conifers, 0-0.5 m cover	–,–	.458	17.07	<.0001
Large trees, distance from coast, 0-0.5 m cover	+,–,–	.519	14.68	<.0001
Large trees, distance from coast, large snag numbers, seeps present	+,–,–,+	.565	13.33	<.0001
Large trees, distance from coast, large snag numbers, seeps present, rock	+,–,–,+,+	.603	12.56	<.0001
Ensatina:				
0-0.5 m cover	–	.232	12.51	.001
Large hardwoods	+	.180	9.32	.004
Seeps present	+	.171	8.85	.005
Small hardwood logs	+	.150	7.74	.008
Large trees	+	.143	7.33	.010
0-0.5 m cover, large trees	–,+	.406	13.99	<.0001
0-0.5 m cover, large trees, seeps present	–,+,+	.486	12.96	<.0001
0-0.5 m cover, large trees, seeps present, distance from coast	–,+,+,+	.512	10.97	<.0001
0-0.5 m cover, large trees, seeps present, distance from coast, small conifers	–,+,+,+,–	.523	9.33	<.0001
Del Norte salamander:				
Small conifers	–	.257	6.89	.018
Forest age	+	.247	6.56	.021
Rock	+	.246	6.55	.021
Basal area of hardwoods	+	.232	6.13	.025
Large trees	+	.226	5.95	.027
Basal area hardwoods, small-log weight	+,–	.491	9.19	.002
Seeps present, hardwood-log volume, small-log weight	+,–,–	.668	12.41	.0003
Seeps present, hardwood-log volume, small-log weight, rock	+,–,–,+	.803	18.29	<.0001
California slender salamander:				
Elevation	–	.693	46.08	<.0001
Distance from coast	–	.449	17.31	.0005
Large trees	+	.312	10.09	.005
Rock	+	.201	6.05	.024
Small conifers	–	.175	5.24	.034
Distance from coast, small trees	–,–	.833	50.74	<.0001
Distance from coast, small trees, elevation:	–,–,–	.849	38.48	<.0001
California slender salamander (without elevation and distance from coast):				
Large trees	+	.312	10.09	.005
Rock	+	.201	6.05	.024
Small conifers	–	.175	5.24	.034
Large hardwoods	+	.120	3.74	.068
Forest age	+	.077	2.68	.118
Large trees, rock	+,+	.404	7.78	.004
Large trees, sound-log volume, seeps present	+,+,–	.438	6.19	.005

Table 7—continued

Variables in model	C[a]	R^2 (adj.)	F	P
Clouded salamander:				
Small-log weight	+	.257	14.18	.0006
Decayed-log volume	+	.133	6.88	.013
Canopy cover	+	.119	6.14	.018
Small conifer logs	+	.118	6.10	.018
Seeps present	+	.076	4.14	.049
Small-log weight, canopy cover	+,+	.280	8.42	.001
Small-log weight, elevation, basal area of hardwoods	+,+,+	.294	6.28	.002
Small-log weight, elevation, basal area of hardwoods, solar	+,+,+,–	.331	5.71	.001
All reptiles:				
Seeps present	–	.102	5.31	.027
Large snags	–	.101	5.29	.027
Elevation	–	.085	4.54	.040
Canopy cover	–	.085	4.54	.040
Conifer-log volume	–	.076	4.11	.050
Large snags, canopy cover	–,–	.159	4.61	.017
Seeps present, solar, conifer importance	–,+,–	.213	4.42	.010
Small snags, seeps present, large-log weight, solar	–,–,–,+	.237	3.95	.010
Solar, litter depth, seeps present, elevation, conifer importance	+,–,–,–,–	.270	3.81	.008

[a] Partial correlation (positive or negative).

Ensatina—We captured more ensatina, by both timed search and pitfalls than any other species (table 2; Welsh and Lind 1988). Significant relationships with large-tree and large-hardwood densities (positive correlations) and small conifers (negative correlation) (table 7) are consistent with significantly higher abundances of ensatina on old-growth sites (table 2). Also significant in our predictive models for this species are variables indicative of protective cover: density of small hardwood logs (positive correlation), and vegetation cover from 0 to 0.5 m tall (negative correlation—see explanation above, under salamanders). Presence of seeps, possibly an indication of relatively moister soils, was also important for ensatina. Previously (Welsh and Lind 1988), we found significantly more ensatina in the inland area. The appearance here in two of our models of a positive correlation with "distance from coast" (table 7) is consistent with our earlier result. This finding contrasts with the negative correlation for salamanders as a whole (table 7). Despite its ubiquity in the moist, cool forests of the Pacific Northwest and in contrast to other native salamanders, ensatina appears to have greater tolerance of the higher temperatures and lower moisture that are characteristic of interior forested areas of northern California. This tolerance is further evidenced by its distribution in other parts of California, particularly the Sierra Nevada, and the mountains of southern California (Stebbins 1985).

Del Norte salamander—This species was found primarily on sites in the Klamath/Siskyou mountains, and a subset of sites within their geographic range was used in the analysis (n = 18). Del Norte salamander abundance varied positively with forest age, basal area of hardwoods, and large trees, and negatively with small conifers (table 7), a pattern indicative of late-successional forest. Percentage cover of rock was also important. This species was always found on sites with rocky soils, and most captures occurred in direct association with rock or under woody debris in contact with rock. The reason for the addition of two negatively correlated variables describing downed woody material in the multivariate models for this species (table 7) is not clear.

California slender salamander—This species was found primarily on sites in the Coast Range, and a subset of sites within their geographic range was used in the analysis (n = 21). The greatest amount of variation in numbers was accounted for by the landscape variables of elevation and distance from coast (negative correlations; table 7). A single cover variable—percentage cover of rock—and several variables indicating late-successional forest also proved to be significant. Significance of the late-sucessional forest variables is consistent with earlier analyses that found the slender salamander to occur in greater abundance on old-growth sites (table 2; Welsh and Lind 1988).

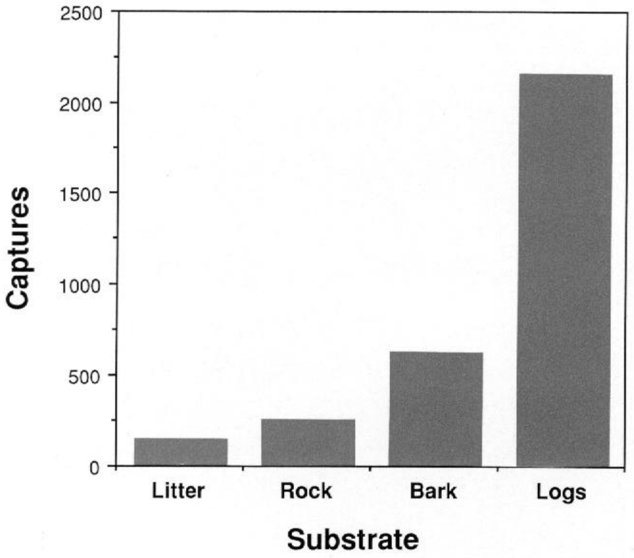


Figure 2—Captures of herpetofauna (all species combined from timed searches) by substrate type.

We performed a second multiple regression on the slender salamander data to determine the importance of forest structural factors apart from the overriding factors of elevation and distance from coast (table 7). The second analysis brought in additional variables that covaried positively with late-successional forest, such as forest age and large hardwoods, but these variables were not significant. The cover variable sound-log volume and the presence of seeps were significant in our second multivariable model, however. Bingham and Sawyer (this volume) found sound-log volume to be greater on old growth than young or mature sites, and the positive correlation with abundance of slender salamanders once again indicates an association with older forests. The negative correlation with presence of seeps is difficult to explain and may be spurious.

Clouded salamander—Our analysis of data for this species indicated an association with cool, moist forest with positive correlations with increasing canopy cover and presence of seeps. Its abundance was also related to decayed woody debris (significant positive correlations with small-log weight, decayed-log volume, and small conifer logs). The remaining variables entering models are consistent with these associations (table 7). The low adjusted R^2 for our best model (0.331) explained less than half the variation in abundance, however.

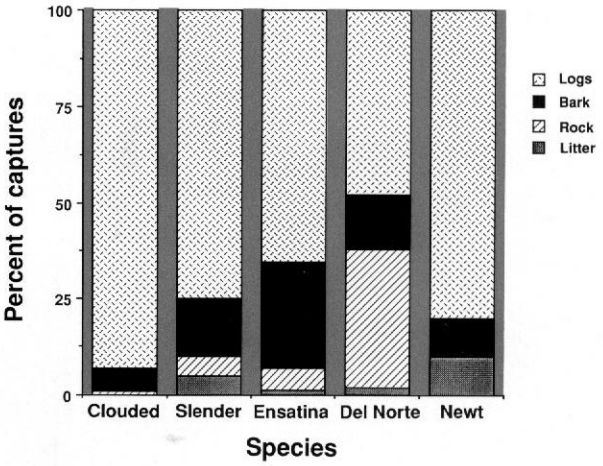


Figure 3—Captures of common salamanders (timed search) by substrate type.

Reptiles—Our analysis of reptiles is based on a total sample of 151 captures of 15 species, including both snakes and lizards (table 2). Lumping such a diverse array of species has obvious shortcomings, but it offers an informative contrast to macrohabitat use by the salamanders which dominate the forest herpetofauna of this region. Five significant variables entered the model; reptile abundance was negatively correlated with all of them (table 7). Collectively, high values of these variables indicated cool, moist, late-successional forests—clearly not optimal habitat for most reptiles. Additional variables that entered the regression models were also indicative of late-successional forests and negatively correlated with reptile abundance. The only variable that showed a positive correlation with reptile abundance was "solar," a measure of incident radiation (Frank and Lee 1966), as would be expected with a group of heliothermic species. The adjusted R^2 for our best model (0.270) indicated these variables explained little of the observed variation in reptile abundance.

Forest Landscape and Habitat Structure: Microhabitat Associations

Substrates—We analyzed all timed-search captures by substrate, combining them into four categories (fig. 2). Of 2769 total captures, 87.5 percent were associated with dead, woody plant material—logs, snags, and bark. We analyzed the distributions of the five most commonly captured salamanders relative to these substrate categories (fig. 3). Ninety-nine percent of clouded salamanders, 89 percent of slender salamanders, 93 percent of ensatina, and 90 percent of roughskin newts were captured in association with dead, woody plant material. The slender salamander was more commonly encountered in the litter layer, and the Del Norte salamander more commonly captured among rocks, than any of the other salamander species (fig. 3).

Continue

Table 8—Results (*P*-values) of chi-square analyses comparing logs where salamanders were captured to the distributions of logs in different size- and decay-classes[a]

	Size-class (conifers)[b]							Size-class (hardwoods)							
Species	1	2	3	4	5	6	7[c]	1	2	3	4	5	6[c]	7[c]	Total
Clouded salamander	*** -	*** -	0.35	* +	* +	* +	—	*** -	*** -	0.36	*** +	*** +	—	—	***
California slender salamander	*** +	*** -	*** -	* -	*** +	*** +	—	*** +	0.09	.72	0.47	*** +	—	—	***
Ensatina	0.31	*** -	** -	0.30	*** +	*** +	—	*** +	** -	.22	*** +	*** +	—	—	***
Del Norte salamander	*** +	*** -	** -	* -	.36	.27	—	*** +	.41	.13	.27	.73	—	—	***
Total herpetofauna	* +	*** -	*** -	.71	*** +	*** +	—	*** +	*** -	.85	*** +	*** +	—	—	***

	Decay-class (conifers)					Decay-class (hardwoods)					
	1	2	3	4	5	1	2	3	4	5	
Clouded salamander	* -	** -	*** +	.25	*** -	* -	.07	** -	* -	.46	***
California slender salamander	** -	*** -	*** -	*** +	.07	*** -	*** -	.66	*** +	.29	***
Ensatina	*** -	*** -	*** -	*** +	.37	*** -	*** -	*** -	*** +	*** +	***
Del Norte salamander	.12	*** -	.05	* +	.13	.12	* -	** -	*** +	*** +	***
Total herpetofauna	*** -	*** -	*** -	*** +	* -	*** -	*** -	*** -	*** +	*** +	***

[a] Expected values were calculated from an independent data set of structural variables measured on the stands where herpetofaunal sampling occurred. Species captured in significantly greater (+) or smaller (-) numbers than expected for each class are indicated by *'s (* = 0.05 > P > 0.01; ** = 0.01 > P > 0.001; *** = P < 0.001).

[b] Size-classes of downed woody debris are presented in square meters and defined as follows: 1, 0 - 0.5; 2, 0.5 - 1; 3, 1 - 2.5; 4, 2.5 - 5; 5, 5 - 10; 6, 10 - 25; and 7, 25 - 50.

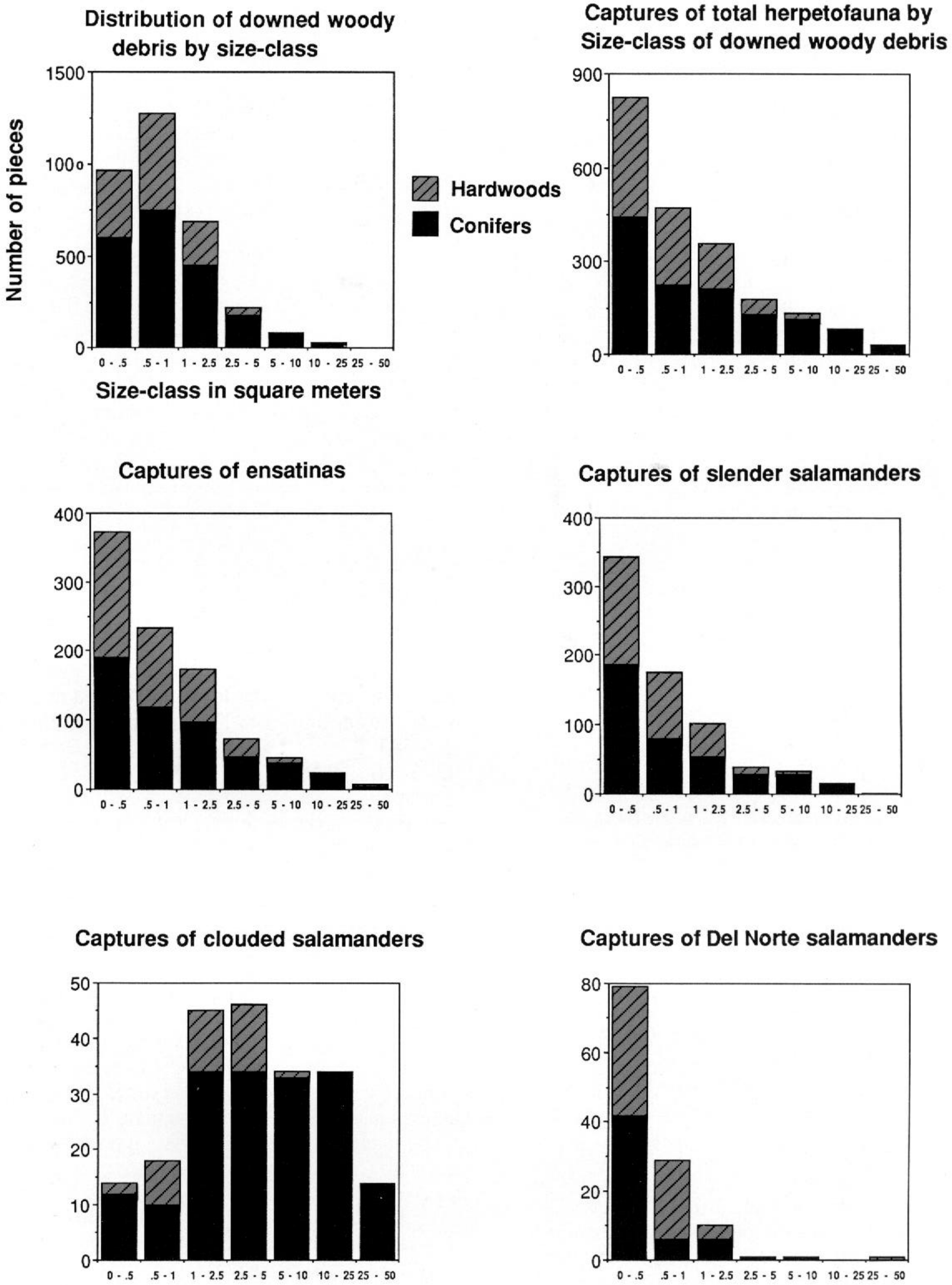
[c] Not tested; no expected values available.

Herrington (1988) reported the Del Norte salamander as essentially restricted to talus habitat. We concur that rocky habitats are important for this species (see macrohabitat section, above), but we believe some clarification is warranted. All of our captures for the Del Norte salamander occurred on sites with talus, rock outcrops, or rocky soils. Within these areas, however, we also found this species using downed woody debris for cover. Sixty-two percent of our captures were associated with such material (fig. 3), and 5 percent were within decayed logs.

We have almost no knowledge of the importance of below-surface habitat use for forest salamanders (N. Scott, pers. comm.); however, our data indicate that large numbers of salamanders use the subsurface, surface, and above-surface habitats provided by downed woody debris. Similar results from other studies in comparable habitats (Aubry and others 1988; Bury and Corn 1988a; Corn and Bury, this volume b) support the conclusion that these habitat features are probably essential for many species of forest salamanders.

Size of woody debris cover—The highest capture rates of all species combined were in the smallest and the next two larger size-classes of both conifer and hardwood logs (fig. 4). Captures were significantly lower than expected in several of the intermediate size-classes and did not vary from expected captures in others (table 8). The most abundant downed woody materials on our sites were pieces in the 0.5- to 1-m^2 size-class (fig. 4), but the frequency of captures of herpetofauna for this size-class was significantly less than expected (table 8). Although we captured salamanders in the largest size-classes of both conifers and hardwoods, the independent data set from which we derived our expected values lacked sufficient numbers of logs in these classes to allow for statistical tests (fig. 4, table 8).

The slender salamander and ensatina occurred in patterns similar to that described for the total herpetofauna (table 8). The clouded salamander, however, apparently chooses the larger classes (table 8), particularly of conifer logs (fig. 4), consistent with the findings of Corn and Bury (this volume b). The


Distribution of downed woody debris by size-class

Captures of total herpetofauna by Size-class of downed woody debris

Captures of ensatinas

Captures of slender salamanders

Captures of clouded salamanders

Captures of Del Norte salamanders

Figure 4—A comparison of the distribution of size-classes of hardwood and conifer downed woody debris (B. Bingham, pers. comm.), with the use of size-classes by the total herpetofauna (timed search) and the five most abundant salamander species.

Del Norte salamander occurred more often than expected under the smallest size-class of both hardwood and conifer debris, less than expected in intermediate conifer debris, and showed no deviation from expected in large conifer and all other hardwood classes (table 8).

Decay-class of woody debris-Our estimates for the amount of downed woody material (logs and branches-snags were not included) by decay-class indicated a nearly normal distribution from sound to rotten, with more conifer than hardwood pieces (fig. 5). Decay-class 3, characterized by logs with bark exfoliating and heartwood beginning to rot, contained the most pieces. In contrast, captures of the total herpetofauna by decay-class indicated significantly more captures than expected for class 4 conifer and class 4 and 5 hardwood logs, and fewer captures than expected in class 1, 2,3, and 5 conifer logs, and class 1,2, and 3 hardwood logs (table 8).

The slender salamander and ensatina occurred in patterns similar to those of the total herpetofauna with two differences. Both occurred as expected in class 5 conifer logs, and the slender salamander also occurred as expected in class 3 and 5 hardwood logs (table 8). The clouded salamander showed a strong preference for conifer logs (82 percent of all captures; fig. 5), and was captured more often than expected in decay class 3 (table 8). The Del Norte salamander was captured more often than expected under class 4 and 5 hardwood and class 4 conifer logs, and significantly less often in association with many of the sound-log classes (table 8).

Conclusions

Although we found 31 species of amphibians and reptiles over the course of this study, with 1 to 13 species per site, the herpetofauna of the region demonstrated low equitability, being dominated by a few species of salamanders. Species richness did not differ by forest age- or moisture-class, but species composition did. Several species of amphibian were rare or absent from young sites, while reptiles were relatively more abundant on these sites and on the old-growth dry sites.

We captured over 6400 individuals, of which 97.6 percent were amphibians, with salamanders comprising 88.1 percent. Terrestrial salamanders were more plentiful on old-growth sites, with four of eight species sampled at greater than incidental levels, significantly more abundant on these sites. Concurrently, we found greater relative biomass of amphibians on old-growth mesic sites and greater relative biomass of reptiles on young and dry sites.

We found that structural components (multiple regression analysis; macrohabitat variables) associated with older forests (Franklin and Spies, this volume) were the best predictors of increased numbers of salamanders.

Our analysis of microhabitat associations indicated that large, well-decayed logs, both hardwood and conifer, were the most heavily used downed woody debris. We found that the pattern of use of woody debris varied considerably, both in size- and decay-class, by species of salamander.

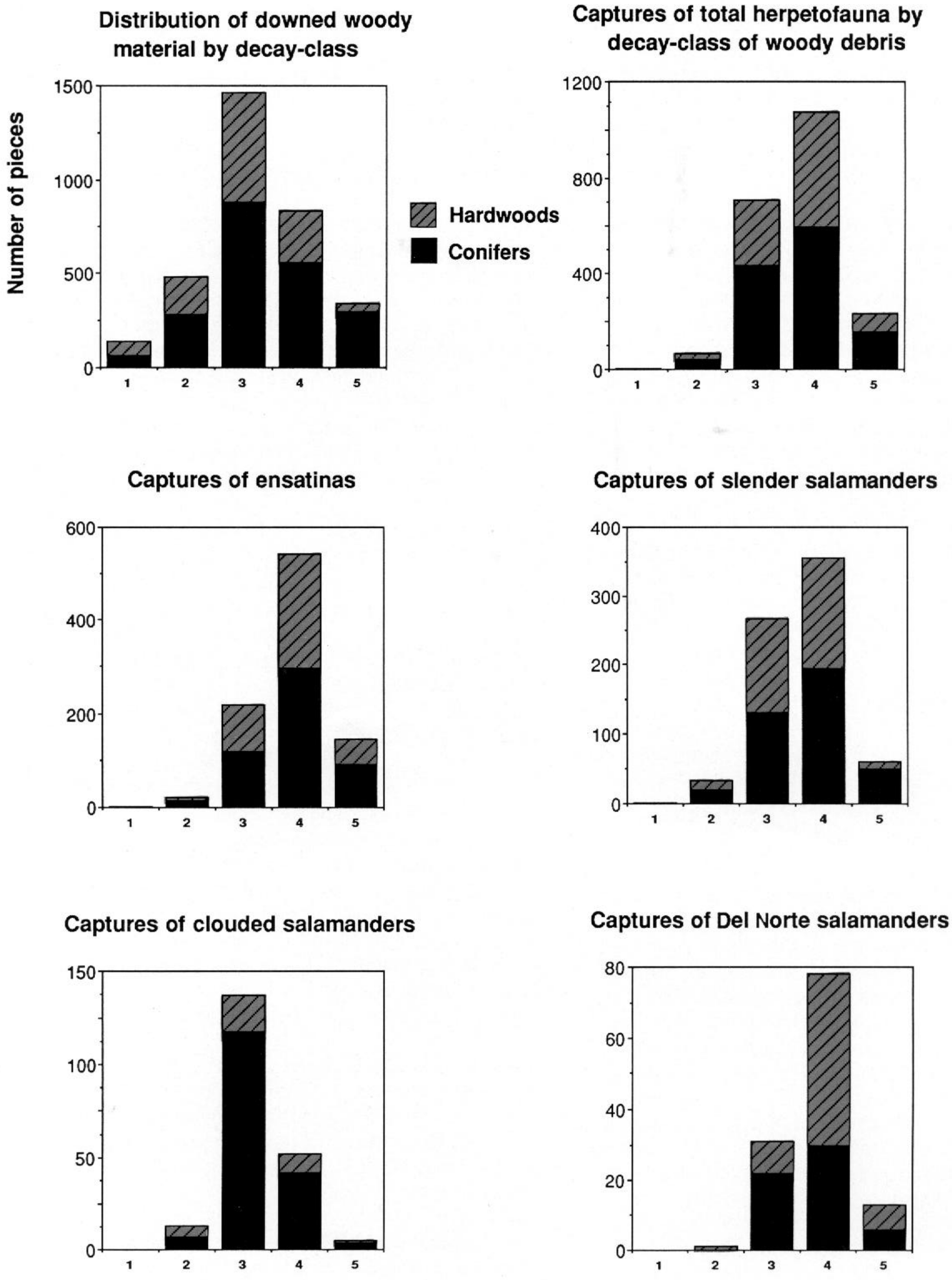
Nineteen of the 31 species we detected were captured at incidental levels (table 2). Some of these species may be considered secondary elements of the forest herpetofauna-for example, the sagebrush lizard that invades open areas subsequent to harvesting. Others, however, were captured rarely, either because they were uncommon or because we lacked adequate methods to sample them-for example, snakes. We know little about these species' life histories, their relation with the forest environment, what constitutes a viable population, or how these populations respond to the conversion of old-growth forests to young, managed stands.

Management Strategies To Maintain a Viable Herpetofauna

An increasing body of evidence from research in forested habitats indicates a change in herpetofaunal species composition, reduction of numbers of species, and reduced abundance within species after logging (Bennett and others 1980; Blymer and McGinnes 1977; Buhlmann and others 1988; Bury 1983; Bury and Corn 1988a, 1988b; Bury and Martin 1973; Corn and Bury 1989; Enge: and Marion 1986; Gordon and others 1962; Herrington and Larsen 1985; Pough and others 1987; Ramotnik and Scott 1988; Welsh and Lind 1988). Forests cannot be harvested without affecting the herpetofauna, but we believe that it is possible to reduce long-term adverse effects. Area-specific strategies can be developed that take into account the natural history of local species of reptiles and amphibians and the particular habitat requirements of these species. With this knowledge, the timing and potential effects of harvest activities can be modified to ensure minimal impact and thus maintain the long-term viability of the herpetofauna.

Based on data reported here and previously (Welsh and Lind 1988) for northwestern California and southwestern Oregon and summarizing ideas presented by other authors cited above, we propose a four-part strategy to ensure the long-term viability of all elements of the local herpetofauna in areas subjected to logging.

Avoid riparian zones-Riparian zones are often the most species-rich (for all wildlife, not just herpetofauna), and their protection with no-cut buffer zones could maintain source populations and corridors for gene flow that would promote rapid repopulation once regeneration has created suitable habitat in harvested upland areas (see Bury and Corn 1988b Bury and others, this volume b; Gilbert and Allwine, this volume c).


Distribution of downed woody material by decay-class

Captures of total herpetofauna by decay-class of woody debris

Captures of ensatinas

Captures of slender salamanders

Captures of clouded salamanders

Captures of Del Norte salamanders

Figure 5—A comparison of the distribution of decay-classes of hardwood and conifer downed woody debris (B. Bingham, pers. comm.), with the use of decay-classes by the total herpetofauna (timed search) and the five most abundant salamander species.

Protect special habitats-Protecting special habitats includes springs, seeps, and other headwater habitats; large rock outcrops; talus slopes; ponds, and unique patches of habitat that are critical to certain highly sensitive species (for example, the red-legged frog, Olympic salamander, tailed frog, and Del Norte salamander) (see also Bury 1988; Bury and Corn 1988b; Bury and others, this volume a, b; Corn and Bury 1989; Gilbert and Allwine, this volume c; Herrington 1988).

Provide microhabitat-For forest herpetofauna, providing microhabitat means managing for downed woody debris. Almost all species of forest herpetofauna use woody debris at some stage, and many species use it throughout their existence, for cover, foraging, or nesting. After logging, an abundant amount of woody debris should be left, in all sizes and decay-classes, including both hardwoods and conifers when present, to facilitate the recovery of the terrestrial herpetofauna and other small vertebrates (see also Aubry and others 1988; Bury and others, this volume a; Corn and Bury, this volume b). The simplest approach is to leave all downed woody debris that was present before harvesting.

Minimize direct Bogging effects--Restricting tractor logging would minimize compaction of the soil, and cable logging in winter would have far less effect on hibernating herpetofauna (Ramotnik and Scott 1988). As much canopy as possible should be left to prevent drying of the soil and alteration of understory vegetation.

Acknowledgments

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Appendix

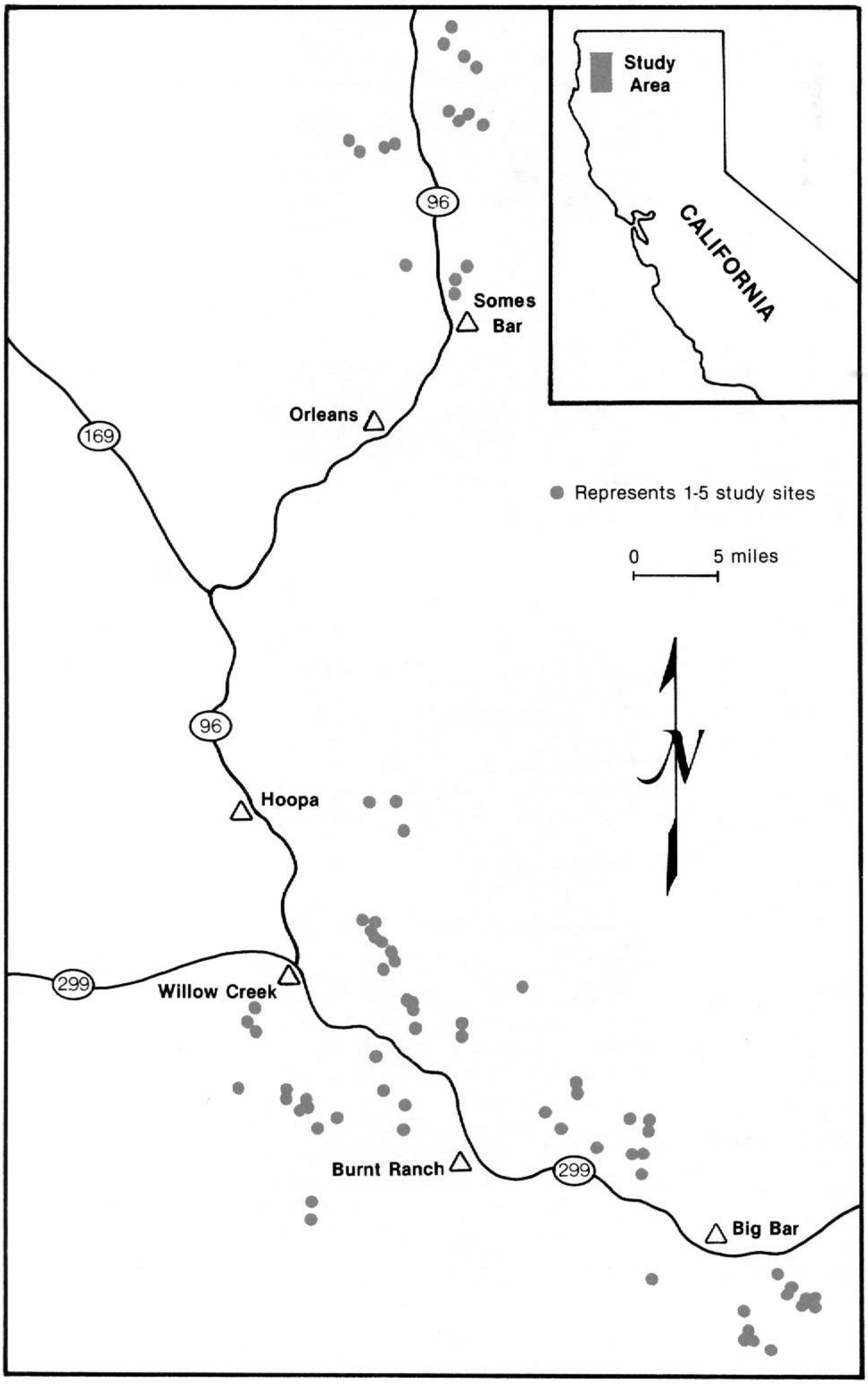
Table 9—Study sites in mixed evergreen forests of northwestern California and southwestern *Oregon* **(sites marked with an asterisk were included for total capture counts but omitted from further analyses—see text)**

Sites	Age-class[a]	Moisture-class[b, c]	Location	County, State[d]	Elevation (m)
Terrestrial:					
Inland—					
Little Greyback	Y	M	T39S,R6W,S8	Jos,OR	1205
Tunnel	Y	M	T18N,R4E,S3&4	Del,CA	624
Waterman Ridge	Y	M	T7N,R5E,S15	Hum,CA	633
*Buck Peak	Y	M	T39S,R6W,S33	Jos,OR	1366
Althouse	M	M	T40S,R8W,S3	Jos,OR	427
Brush Mountain	M	M	T6N,R5E,S18	Hum,CA	1050
Gray	M	M	T5N,R6E,S4&5	Tri,CA	972
Hennessey Peak	M	M	T5N,R6E,S8&9	Tri,CA	949
Oregon Caves	M	M	T39S,R6W,S31	Jos,OR	872
Shelterwood	M	M	T1N,R4E,S34	Hum,CA	1022
*Left Hand	M	M	T40S,R6W,S23	Jos,OR	1362
*Upper Horse	M	M	T40S,R6W,S16	Jos,OR	1502
Beartooth Mountain	O	W	T6N,R7E,S34	Tri,CA	1144
Brannon East	0	W	T6N,R4E,S13&24	Hum,CA	750
Cedar Creek	0	W	T7N,R5E,S30	Hum,CA	665
*California Greyback	0	W	T19N,R6E,S32	Del,CA	1556
*Frog Pond	O	W	T41S,R7W,S14	Jos,Or	1539
*Holcomb Peak	O	W	T39S,R6W,S9	Jos,OR	1411
*Serpentine Wet	0	W	T41S,R9W,S4	Jos,OR	549
Big Creek-East	O	M	T6N,R7E,S36	Tri,CA	1134
Clouded	O	M	T1S,R4E,S2	Hum,CA	961
Ladder Rock	0	M	T8N,R6E,S32	Hum,CA	805
spotted Owl	0	M	T1S,R4E,S2&3	Hum,CA	981
Tish Tang	O	M	T8N,R5E,S35	Hum,CA	680
Sharber	O	M	T6N,R6E,S7	Tri,CA	747
*Galleghy Grove	O	M	T41S,R7W,S8,9,17,18	Jos,OR	1334
*Page Mountain	O	M	T41S,R7W,S8	Jos,OR	1519
*Serpentine Mesic	0	M	T38S,R9W,S25	Jos,OR	527
*Skag Hope	O	M	T41S,R7W,S7	Jos,OR	1305
Happy Camp	O	D	T40S,R7W,S29&30	Jos,OR	1053
South Fork	0	D	T6N,R6E,S31	Tri,CA	659
Waters Creek	0	D	T36S,R7W,S28,29,32,33	Jos,OR	614
*Serpentine Dry	0	D	T38S,R8W,S29	Jos,OR	544
Coastal—					
Bald Mountain	Y	M	T6N,R3E,S17&20	Hum,CA	846
Barnes Thirty	Y	M	T22N,R16W,S29&32	Men,CA	467
Fawn Prairie	Y	M	T7N,R2E,S25	Hum,CA	750
Homestead	Y	M	T21N,R16W,S13&24	Men,CA	726
Lord Ellis	Y	M	T6N,R3E,S8&17	Hum,CA	778
Mud Springs	Y	M	T21N,R15W,S13&24	Men,CA	689
Seed Tree	Y	M	T14N,R1E,S21&22	Del,CA	120
Shelterwood Leave	Y	M	T14N,R1E,S27	Del,CA	120
Elder Creek	M	M	T22N,R16W,S28	Men,CA	555
Elkhom Xeric	M	M	T22N,R16W,S17	Men,CA	518
Fanny's Place	M	M	T22N,R16W,S21	Men,CA	445
Harwood's 90	M	M	T21N,R15W,S23	Men,CA	695
White House	M	M	T22N,R16W,S21	Men,CA	427
Old Growth	O	W	T14N,R1E,S21&28	Del,CA	53
Skunk Creek	O	W	T22N,R16W,S29	Men,CA	529
Standley Grove	0	W	T21N,R16W,S26	Men,CA	481
Alpine	0	M	T22N,R16W,S20&21	Men,CA	444
Elkhom Hydric	0	M	T22N,R16W,S17	Men,CA	518
Fox Creek	0	M	T22N,R16W,S21&22	Men,CA	543
Ten Mile Creek	0	M	T22N,R16W,S15&16	Men,CA	445
Darby's Place	0	D	T18N,R13W,S1&2	Men,CA	587

Table 9—continued

Sites	Age-class[a]	Moisture-class[b, c]	Location	County, State[d]	Elevation (m)
Aquatic:					
Ammon—North	Y		T5N,R5E,S11	Hum,CA	549
Barnwell Creek	Y		T22N,R16W,S21	Men,CA	427
Bybee Creek	Y		T19N,R5E,S33	Del,CA	671
Coon Creek	Y		T7N,R5E,S15&16	Hum,CA	213
Four Mile Creek	Y		T6N,R5E,S20	Hum,CA	671
Hawkins Tributary	Y		T6N,R6E,S15&16	Tri,CA	488
Kenny Creek	Y		T21N,R16W,S14&15	Men,CA	472
Sixteen Gulch	Y		T18N,R15W,S31	Men,CA	171
Sugar Creek	Y		T22N,R16W,S29&32	Men,CA	466
Althouse—Main	M		T41S,R7W,S11	Jos,OR	1341
Althouse—West	M		T41S,R7W,S16	Jos,OR	1158
Bolan Creek	M		T40S,R6W,S31	Jos,OR	975
Chamberlin Creek	M		T18N,R15W,S27&28	Men,CA	244
Days Gully	M		T38S,R9W,S25&36	Jos,OR	526
Lefthand Creek	M		T40S,R6W,S23	Jos,OR	1361
Limestone Creek	M		T40S,R6W,S21	Jos,OR	1067
McKinley Creek-Upper	M		T22N,R16W,S21	Men,CA	445
Page Creek	M		T41S,R8W,S2	Jos,OR	561
Barney Creek	O		T5N,R5E,S32	Hum,CA	823
Big Creek—East	O		T6N,R7E,S36	Tri,CA	1133
Big Creek—Main	O		T6N,R7E,S24	Tri,CA	1067
Brannon Creek	O		T6N,R4E,S13&24	Hum,CA	750
Butte Creek	O		T1S,R4E,S2&3	Hum,CA	980
Campbell Creek	O		T7N,R4E,S23	Hum,CA	884
Cedar Creek	O		T7N,R6E,S26	Hum,CA	1006
Elder Creek	O		T22N,R16W,S34	Men,CA	533
Elk Creek	O		T40S,R5W,S12	Jos,OR	1463
Elkhorn Creek—Upper	O		T22N,R16W,S17	Men,CA	518
Elkhorn Creek—Lower	O		T22N,R16W,S17	Men,CA	518
Fox Creek	O		T22N,R16W,S21&22	Men,CA	543
Frog Pond Creek	O		T41S,R7W,S14	Jos,OR	1539
Happy Camp Creek	O		T40S,R7W,S29&30	Jos,OR	1053
High Prairie	O		T14N,R1E,S21&28	Del,CA	53
Horse Linto—East	O		T7N,R7E,S7	Hum,CA	1280
Little Creek	O		T40S,R5W,S6	Jos,OR	1402
Little Greyback Crk.	O		T39S,R6W,S8	Jos,OR	1205
McKinley Creek—Lower	O		T22N,R16W,S21	Men,CA	445
Paralyze Canyon	O		T22N,R16W,S34	Men,CA	533
Skunk Creek	O		T22N,R16W,S29	Men,CA	529

[a] Age-class: Y - young, M - mature, O - old.
[b] Moisture-class: W - wet, M - mesic, D - dry.
[c] Aquatic sites were not assigned a moisture-class.
[d] County, State: Del - Del Norte, CA; Hum - Humboldt, CA; Jos - Josephine, OR; Men - Mendocino, CA; Tri - Trinity, CA.



Location of study sites.

Vertebrate Species Richness Within and Among Seral Stages of Douglas-Fir/Hardwood Forest in Northwestern California

Martin G. Raphael

Author

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Abstract

One objective of wildlife management programs in National Forests is maintaining diversity, often thought of as the number of species or "species richness." Regional (multistand or landscape) species diversity varies in relation to species richness within stands and by similarity of species composition among stands. To evaluate numbers of species of terrestrial vertebrates in Douglas-fir forests of various ages in northwestern California, I systematically sampled at 166 sites representing clearcut (<20 years old) through old-growth (>250 years) forest. Mean numbers of mammalian species differed among seral stages and was lowest in mid-aged stands. Reptilian species richness declined with stand age. Amphibian and avian species richness did not differ among stages. Mean similarity values of all taxa did not differ significantly when sites within stages or sites among stages were compared. Thus, landscape-wide species richness was independent of the arrangement of seral stages. These results suggest that maximizing population sizes of selected species is a more useful management objective than maximizing species diversity.

Introduction

The National Forest Management Act of 1976 made maintaining biological diversity a prime consideration in multiple-use management of National Forests. Thus, what has been termed "biodiversity" is now a major national issue, as evidenced by the National Biological Diversity Conservation and Environmental Research Act (H.R. 4335) brought before the 100th Congress in 1988. An important, but by no means the only component of biological diversity is species richness, the total number of species in a given system. Conservation strategies for maintaining biodiversity have ranged between two extremes: managing only for threatened or endangered species and managing whole ecosystems or communities (Scott and others 1987, 1988). Managing to maintain species richness falls under the latter strategy; it is now one of the major goals of USDA Forest Service wildlife management programs (Salwasser and Tappeiner 1981, Siderits and Radke 1977, Thomas 1982).

Managing Douglas-fir forests of the Pacific Northwest is under intense scrutiny because of conflicts between logging and preservation of remaining old-growth stands (The Wilderness Society 1988, Thomas and others 1988). Part of this concern centers on the importance of old-growth forest to biological diversity (Harris 1984, Norse and others 1986). This paper reports the results of a study designed, in part, to investigate the contribution of old-growth forest to local and regional species diversity in northwestern California.

Methods

Study Area

Sites were within a 3900-km^2 area encompassing parts of the Klamath, Six-Rivers, and Shasta-Trinity National Forests in northwestern California. Forest cover-classified as Douglas-fir (Mayer and Laudenslayer 1988)-is described elsewhere (Raphael 1988a). Criteria for site selection included elevation from 400 to 1300 m, road access, freedom from scheduled timber harvest over the 3 years of sampling, location on National Forest land, relatively homogeneous forest cover, and absence of major confounding features such as streams, meadows >l ha, and rock outcrops. In addition, sites were selected to fill an array of stand sizes and age-classes (Raphael 1984).

Stand Classification

Sites were classified into four seral stages based on years since cutting or an index of stand age. Clearcut sites (n = 20) were <20 years old, young sites (n = 37) were 50 to 150 years old, mature sites (n = 56) were 150 to 250 years old, and old-growth sites (n = 53) were >250 years old. The age index was calculated with a weighted average of estimated ages of all softwood trees <90 cm in diameter at breast height (d.b.h.) counted on four 0.04-ha circular plots and softwoods $\geq$ 90 cm counted on one 0.50-ha plot on each site. The average was weighted by multiplying the estimated age of each tree by its basal area, summing the products over all trees, and dividing the sum by total basal area. In this way, the numerous small trees had less influence on stand age than if each tree was counted regardless of diameter. Tree age was estimated from diameter at breast height, based on extensive tree-ring counts on file in District offices. Details of vegetation sampling methods and vegetation characteristics of each stage are reported elsewhere (Raphael 1988c).

Vertebrate Sampling

Vertebrate sampling methods are described elsewhere (Raphael 1984, 1988c; Raphael and Barrett 1984; Raphael and Mamot 1986; Raphael and Rosenberg 1983; Raphael and others 1986; Rosenberg and Raphael 1986; Taylor and Raphael 1988). Field sampling took place from September 1981 through September 1983. A standardized series of techniques was used on each site. Sampling stations were located at or around the center of a site and were separated from adjacent sites by at least 360 m. Birds were counted at each site (only in the three oldest seral stages) in variable-radius circular plots (12 lo-minute counts in each site, season, and year), insectivores and other small mammals were trapped at each site in pitfalls (10 2-gallon buckets per site, 2 x 5 grid, 20-m spacing, run continuously), and larger mammals were detected at each site by using a single smoked-aluminum station deployed in August and September 1981-83. In addition, subsets of sites in each seral stage were more intensively sampled by area- and time-constrained searches for reptiles and amphibians (0.12 ha per site in 1981,4 person-hours per site in 1982, 1983), livetrap grids for small mammals (usually 100 25-cm Sherman traps per site, 10 x 10 grid, 20-m spacing, operated 5 nights in July 1981-83), and drift fence arrays for snakes (two 5-gallon buckets, connected by a 7.6-m x 50-cm fence with two 20- x 76-cm cylindrical funnel traps on each side of the fence center).

Data Analysis

Species richness-All observations were reduced to the presence or absence of each vertebrate species at each site, pooled over all years of study (1981-83). A matrix of 166 rows (= sites) and 218 columns (= species, including separate entries for birds in spring and winter) was constructed so that each cell (combination of site and species) contained a 1 if the species had been detected at that site or a 0 if it had not. Based on stand age, each site was also classified into one of four seral stages for calculating species richness in each seral stage. Total species richness in a stage was calculated by summing numbers of species detected at any site within each stage. Mean species richness by stage was calculated by counting all species occurrences for each site, then calculating mean counts per site within each stage.

Species accumulation curves were computed to evaluate the effects of sample size (numbers of sites) on species richness. A bootstrap procedure (Efron 1982) was used to generate pseudosamples of increasing numbers of sites from 1 to 50. At any particular sample size y, a site (row) was randomly drawn from the site-by-species matrix. Data were stored, then replaced, and a new row was randomly drawn and data were accumulated. This process was repeated y times, accumulated cell values > 1 were recoded to 1, and cells were summed across all species to calculate species richness. The entire cycle was repeated for a desired number of pseudoreplications, usually 500. The mean and standard deviation were calculated over all pseudoreplicates and a standard error of the mean was calculated (which equals standard deviation under bootstrap theory).

Mean species richness was plotted against number of sites for various combinations of taxa and seral stages. Nonlinear regression (SPSS/PC+, Version 3.0, Norusis 1988) was used to estimate parameters of the species-area curve $S = CA^z$, where S was species richness, A was the number of sites sampled, and C and z were regression parameters (Connor and McCoy 1979, Higgs and Usher 1980, Usher 1985). Equality of regression parameters was tested among curves for each age-class using Extra Sum of Squares (Draper and Smith 1966: 67).

Species similarity-To compare occurrences of species between sites or groups of sites, I computed Jaccard's index of similarity,

$$RI = 100 \frac{a}{a + b + c} ,$$

where a was the number of species present at both i and j, b was the number present at site i only, and c was the number at site j only (Pielou 1984: 57). This index has many desirable properties (see Bloom 1981, Huhta 1979, Wolda 1981): it is easy to interpret (the index value is the percentage of species common to both sites), it takes no account of species absent from both sites (presence data are unambiguous, whereas absence could mean the species could not survive at the site or it was absent merely by chance), and it is metric (similarity values behave like distances in Euclidian space).

Similarities were computed between all possible pairs of plots and then sorted into site-by-site comparisons within each age-class and comparisons across age-classes. Means and standard errors were calculated for each grouping. I also computed similarities for each within and between age-class comparison using a bootstrap procedure in which a site was randomly drawn, replaced, and compared with another randomly drawn site. Similarity was computed, and a mean and standard error were computed over the total number of pseudoreplications used in an analysis (usually 200). To evaluate the effects of sample size (number of sites) or similarity, I used bootstrap procedures based on increasing numbers of subsets of sites from two to the maximum number of sites in an age-class.

All bootstrap analyses were conducted with a PC-based FORTRAN program, available on request (Raphael and Brink, documentation on file).

Table 1—Total numbers of species detected in 4 age-classes of Douglas-fir forest, northwestern California, 1981-83

Group	Age-class[a]				
	Clearcut	Young	Mature	Old-growth	Total
Amphibians	9	12	11	10	12
Reptiles	12	13	13	11	16
	NA				97
Wintering birds	NA	44	45	47	55
Mammals	26	28	33	29	38

NA = not available (see Marcot 1984).

[a] Age-classes and number of sites sampled were clearcut stands (<20 years, n = 20); young stands (<150 years, n = 37 for amphibians, reptiles, and mammals; n = 27 for birds); mature stands (<250 years, n = 56); and old-growth stands (>250, n = 53).

Results

Species Richness

Observers detected 167 vertebrate species over all sites and years. Recorded numbers of species varied within species groups among age-classes (table 1), but these values are difficult to interpret because of differences in sampling effort (number of sites) among age-classes. A more meaningful measure is mean species richness (fig. 1), the average number of species detected per site in each age-class.

Number of amphibian species averaged 2.7 species per site; means did not differ among age-classes (Welch's $F = 0.22$, $P = 0.89$, fig. 1). Numbers of reptilian species averaged 2.6 species per site and varied among age-classes (Welch's $F = 25.6$, $P < 0.01$, fig. 1), declining from youngest to oldest sites. Multiple comparisons of means (Dunnett's (1980) T^3, $P < 0.05$) showed significantly more species in clearcut, fewer in old growth, and no difference between young and mature sites. An average of 10.8 mammalian species were detected at each site, and mean numbers of species varied among age-classes (Welch's $F = 9.1$, $P < 0.01$). Lowest mean numbers were detected in clearcuts and young stands; means were significantly greater in mature and old-growth stands (Dunnett's T^3, $P = 0.05$). Numbers of breeding avian species averaged 32.3 species per site; means did not differ among age-classes ($F = 0.13$, $P = 0.88$). Avian species richness averaged 15.0 species per site in winter, and means also did not differ among age-classes ($F = 0.96$, $P = 0.39$).

In comparing differences between age-classes, I found large numbers of species that were infrequently detected. Of 218 vertebrates (including birds in two seasons), 88 (40 percent) were observed on 5 percent or fewer sites (fig. 2). Thus, estimated species richness at any particular site was influenced by chance occurrence of rare species. To alleviate this problem, I calculated species accumulation curves across successively larger sets of sites within each age-class (fig. 3).

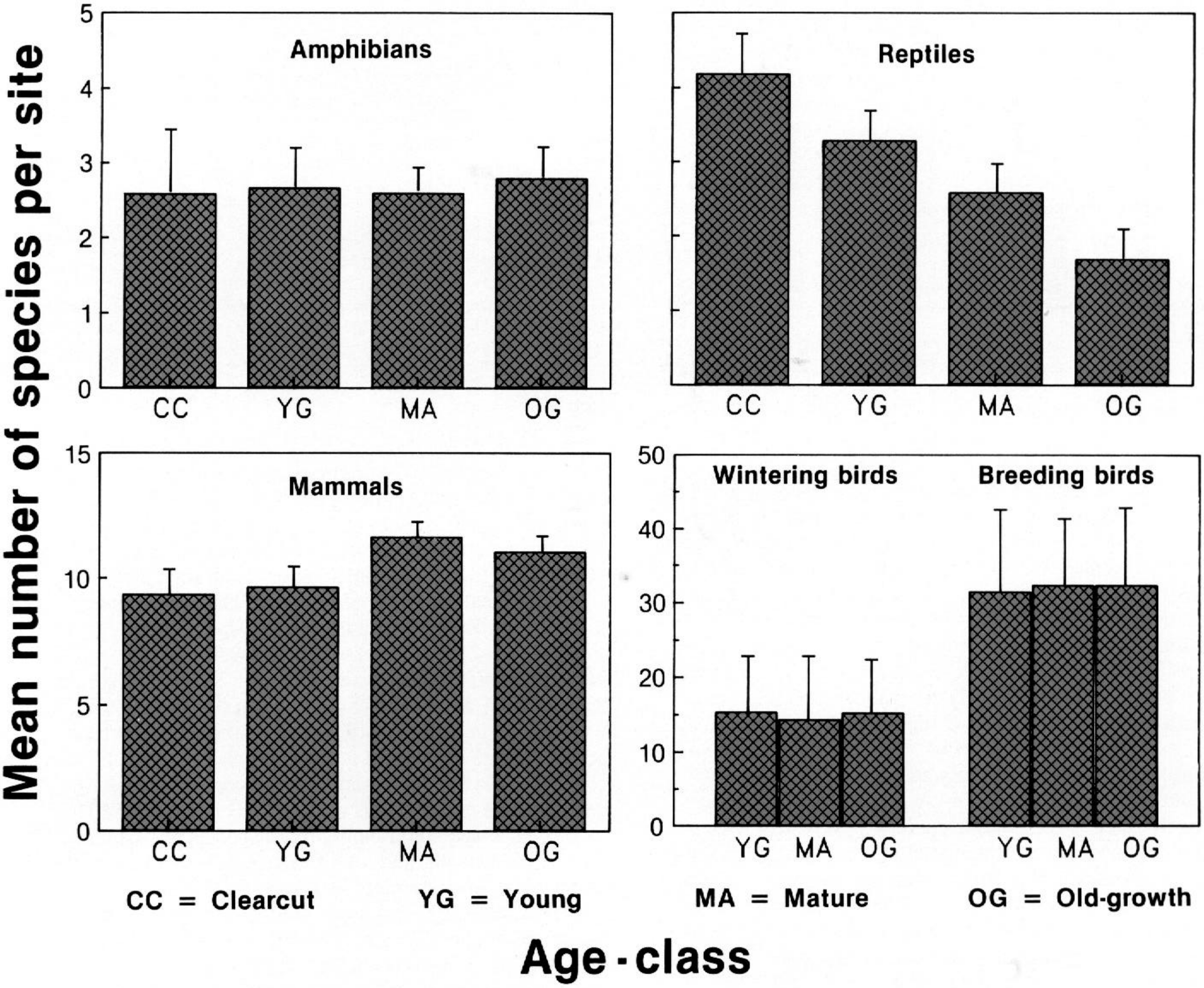

Figure 1—Mean numbers of vertebrate species detected in four age-classes of Douglas-fir forest, northwestern California, 1981-83. Age-classes are CC (clearcut stands, <20 years), YG (young stands 20 < x ≤150 years), MA (mature stands 150 < x ≤250 years), and OG (old-growth stands, >250 years); sample sizes are given in table 1.

For each species group, curves differed among age-classes (table 2). Extra sums-of-squares analyses for each species group rejected hypotheses of similar regression curves among age-classes (table 3). These analyses showed that, for each species group, C, z, or both differed significantly among two or more age-classes. Thus, rates that species accumulated as numbers of sites increased differed among at least two age-classes.

A more direct comparison, however, was to test differences in mean species richness at larger numbers of sites, illustrated for $n = 10$ sites (fig. 4). Means and standard errors were derived from a sample of 500 pseudoreplications of sites representing each age-class. For each species group, 95-percent confidence intervals around the mean for any age-class overlapped the means of each other age-class. This pattern held for each sample size tested up to the maximum number of sites.

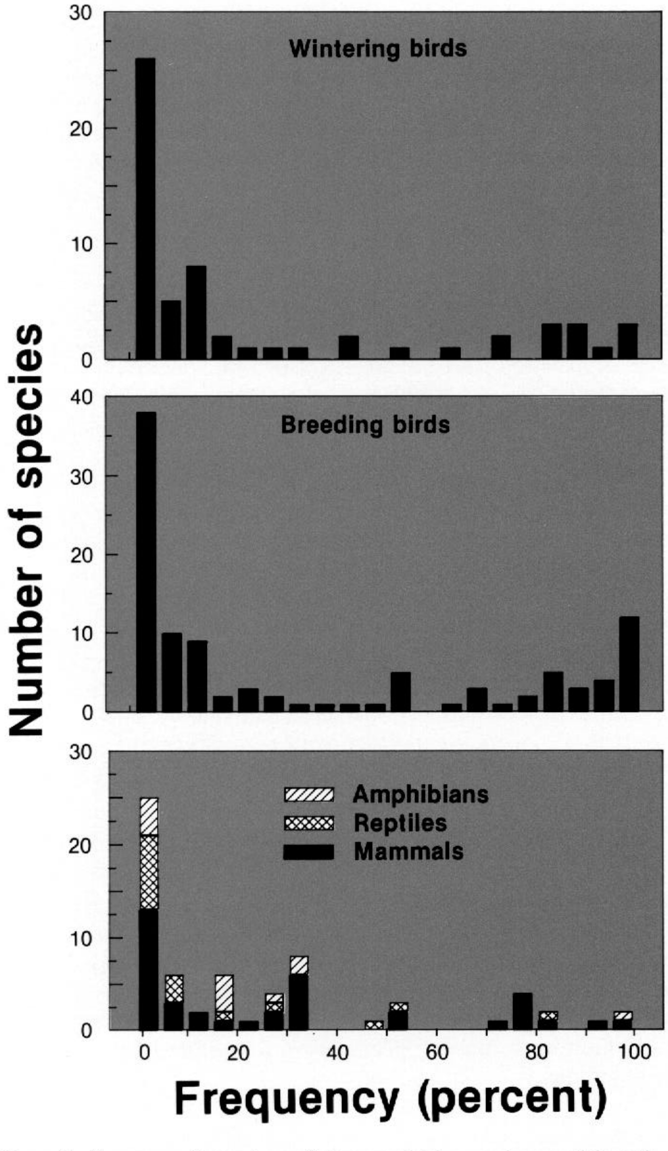

Figure 2—Frequency (percentage of sites on which a species was detected) of avian, amphibian, reptilian, and mammalian species on study sites (n = 136 for birds, n = 166 for all other groups) in Douglas-fir forests of northwestern California, 1981-83.

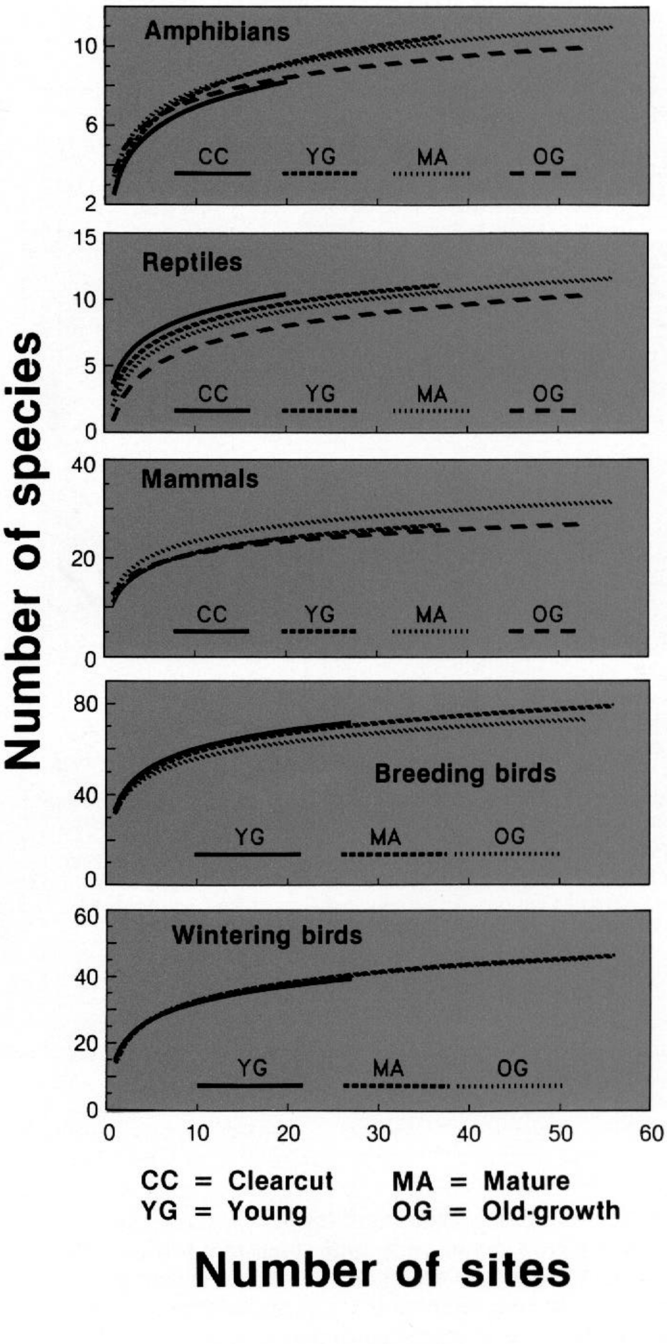

Figure 3—Species accumulation curves derived from bootstrapped samples of successively larger numbers of sites grouped into four age-classes of Douglas-fir forest, northwestern California.

Table 2-Regression parameters from nonlinear model relating species richness[a] to numbers of sites among age-classes of Douglas-fir forest, northwestern California

Group	Age-class[b]	Parameter (SE)[a]		
		C	Z	r^2
Amphibians	Clearcut	3.31 (0.15)	0.31 (0.02)	0.96
	Young	3.76 (0.12)	0.29 (0.01)	0.97
	Mature	4.70 (0.19)	0.21 (0.01)	0.90
	Old growth	4.79 (0.20)	0.20 (0.01)	0.91
Reptiles	Clearcut	4.32 (0.05)	0.30 (0.00)	1.00
	Young	3.97 (0.07)	0.29 (0.01)	0.99
	Mature	3.69 (0.08)	0.29 (0.01)	0.98
	Old growth	2.80 (0.10)	0.34 (0.01)	0.97
Breeding birds[c]	Young	34.69 (1.20)	0.22 (0.01)	0.98
	Mature	35.33 (0.81)	0.20 (0.01)	0.99
	Old growth	34.01 (0.53)	0.19 (0.01)	0.99
Wintering birds[c]	Young	17.70 (0.55)	0.25 (0.01)	0.99
	Mature	18.72 (0.81)	0.23 (0.01)	0.97
	Old growth	18.61 (0.71)	0.22 (0.01)	0.97
Mammals	Clearcut	11.82 (0.42)	0.24 (0.01)	0.95
	Young	12.93 (0.33)	0.20 (0.01)	0.96
	Mature	15.10 (0.27)	0.18 (0.01)	0.97
	Old growth	14.14 (0.16)	0.16 (0.01)	0.96

[a] $S = CA^z$, where S was number of species and A is number of sites in sample. A varied from 1 to 20, 37, 56, or 53 in clearcuts, young, mature, or old growth, respectively.

See table 1 for description of age-classes.

[c] Birds were not sampled in clearcut stands.

Table J-Results of analyses testing equality of nonlinear regression lines relating species richness to numbers of sites in different age-classes of Douglas-fir forests, northwestern California (see fig. 3)

Group	F-ratio	df	P
Amphibians	25.46	6,156	<0.001
Reptiles	223.56	6,156	<0.001
Breeding birds	96.48	4,130	<0.001
Wintering birds	3.21	4,130	<0.010
Mammals	103.91	6,156	<0.001

Inspection of the species-area curves (fig. 3) showed that 20 to 25 sites were required to include at least 90 percent of all species sampled in any age-class. Given a z-value (equivalent to slope coefficient) of about 0.25 (average from table 2), 10 sites would be expected to include about 79 percent and 67 percent of the species that would be expected in 25 and 50 sites, respectively.

Species Similarity

How did species composition differ among age-classes? Species similarity (Jaccard coefficients) averaged 42 percent for amphibians, 37 percent for reptiles, 60 percent for breeding birds, 54 percent for wintering birds, and 44 percent for mammals between randomly drawn pairs of sites, regardless of age-class. Mean similarity between sites within age-classes and between age-classes was strikingly similar within species groups, especially considering the wide confidence intervals about each mean (fig. 5). Pairs of sites within age-classes were just as likely to share species as pairs of sites between age-classes.

As in analyses of species richness, Jaccard's measure of species similarity was sensitive to the presence of rare species. Therefore, examining similarity based on larger subsets of sites to offset the influence of rare species had more meaning. As larger numbers of sites were included in samples, between-age-class similarity increased for each species group (fig. 6). At larger sample sizes, regression curves predicted nearly equal similarity values among age comparisons for breeding birds, wintering birds, and amphibians. Similarity of reptilian faunas between age-classes tended to converge at sample sizes >10 sites. Similarity of mammalian fauna was consistently lower in clearcut vs. older age-class comparisons than in other comparisons (fig. 6). Bootstrapped estimates of mean similarity, however, had large standard errors, and none of the between-class comparisons could be considered statistically significant, as is evident when 95-percent confidence intervals are plotted around mean values, illustrated for samples of 10 sites (fig. 7).

Discussion

Species richness (alpha diversity) of birds and amphibians did not vary significantly among age-classes of Douglas-fir forest, especially when the effects of rare species were reduced by pooling sites. Reptilian species richness did vary; more species occurred in younger than in older stands. Slightly more mammalian species were found in older than in younger stands.

Total species diversity did not vary much between age-classes. Species similarity (beta diversity) did not vary significantly for any species group, whether comparing sites within age-classes or sites among age-classes. These observations of similar alpha and beta diversities among age-classes led to a conclusion that as area (number of sites) increased, species accumulated at nearly the same rate regardless of age-class. In other words, landscapes composed entirely of clearcuts, old-growth, young forest, or any combination of ages would support similar numbers of vertebrate species. I demonstrated this for amphibians, reptiles, and mammals that I sampled in all four age-classes by comparing species accumulation curves derived for each age-class with the curve derived by randomly drawing sites without regard to age-class (fig. 8). At n = 10 sites, mean species richness (± 95-percent C.I., experimentwise) varied

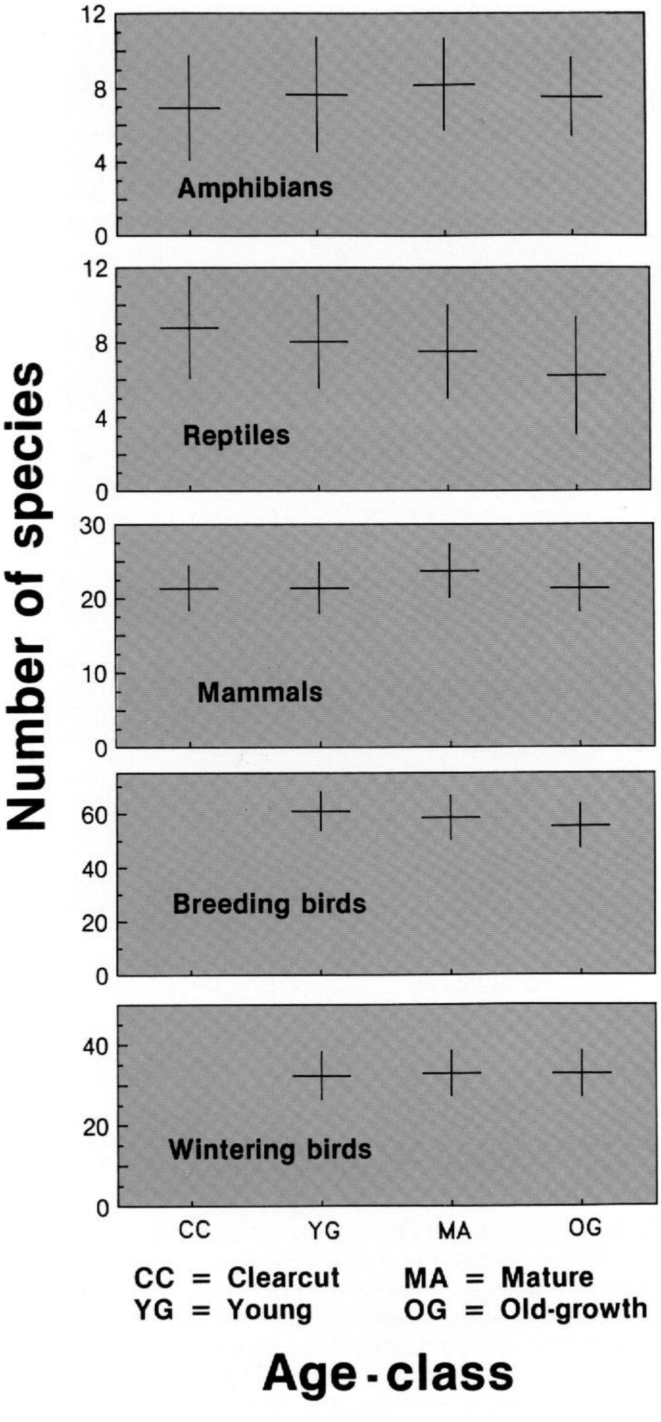

Figure 4—Comparisons of mean species richness (± 95-percent confidence intervals) estimated from randomly drawn subsets of 10 sites in each of four age-classes of Douglas-fir forest, northwestern California.

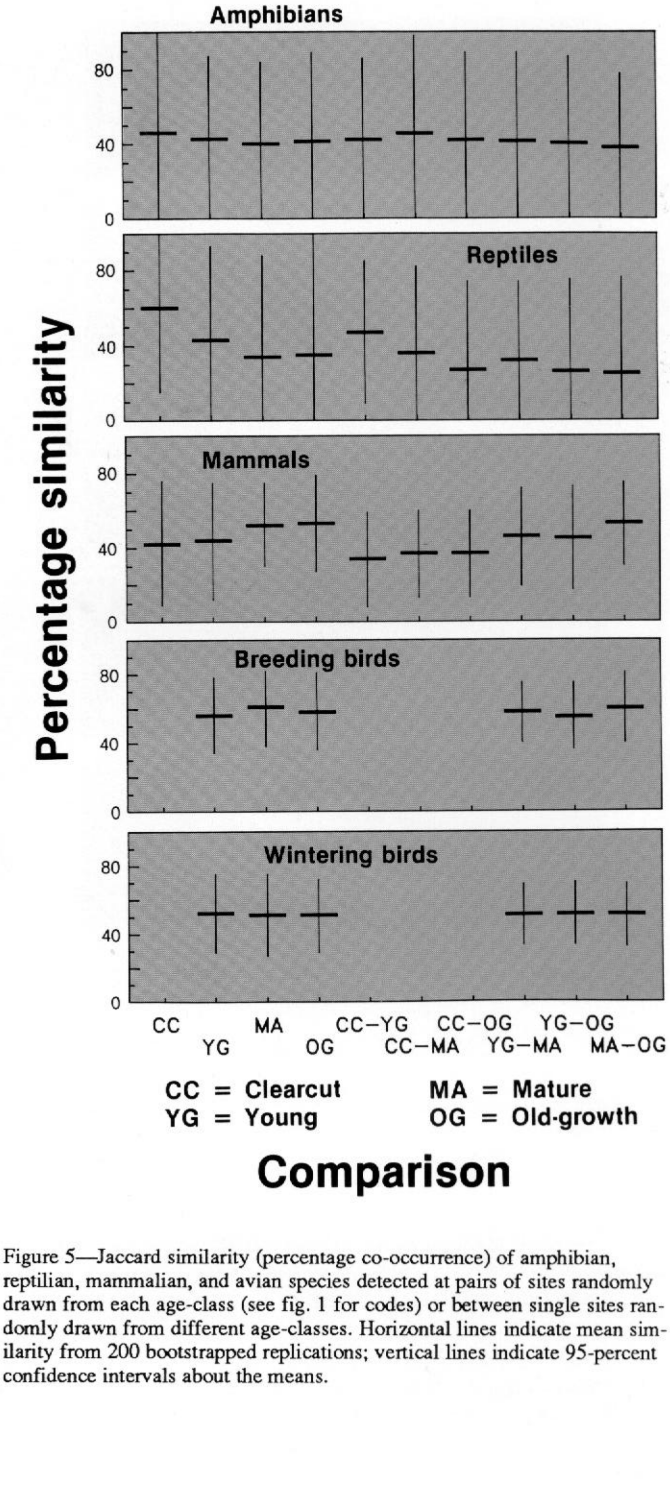

Figure 5—Jaccard similarity (percentage co-occurrence) of amphibian, reptilian, mammalian, and avian species detected at pairs of sites randomly drawn from each age-class (see fig. 1 for codes) or between single sites randomly drawn from different age-classes. Horizontal lines indicate mean similarity from 200 bootstrapped replications; vertical lines indicate 95-percent confidence intervals about the means.

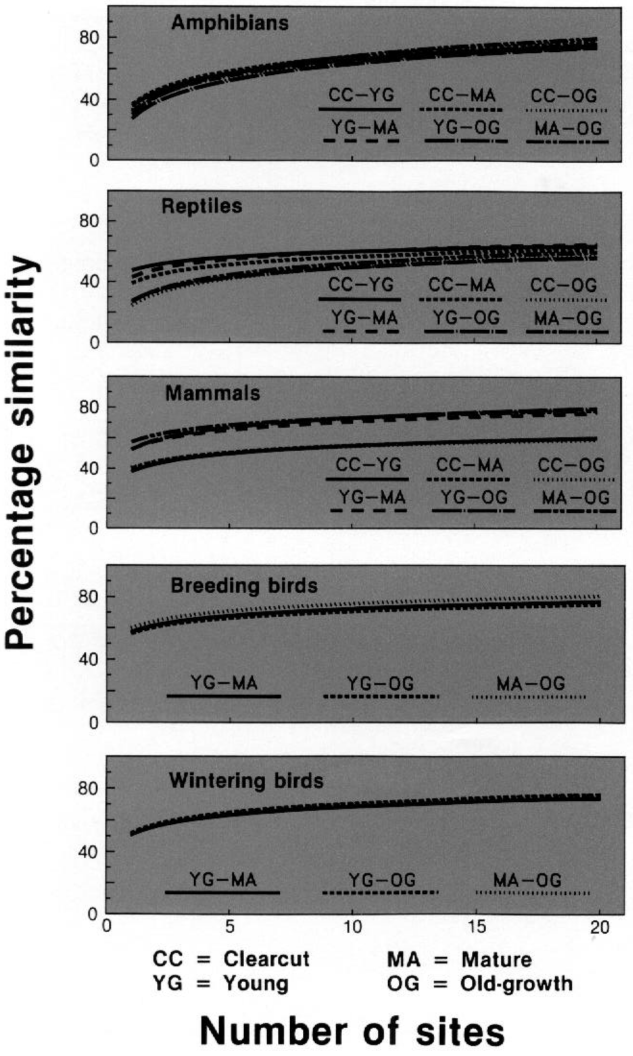

Figure 6—Relation between similarity and numbers of sites for all comparisons between age-classes for each group. Lines are curves fitted to mean similarity calculated for successively larger subsets of sites (up to *n* = 20) by use of a bootstrap procedure.

from 32 ± 8.2 (age-class 1) to 40 ± 9.2 (all age-classes). Thus, confidence intervals overlapped means for all comparisons, indicating insufficient evidence that means differed significantly.

Do these results suggest that all old growth could be eliminated without negative effects on biodiversity? The answer is yes, but only if the number of species is all that counts. As shown elsewhere in these proceedings and by other analyses of these data (Raphael 1988c, Raphael and others 1988), a substantial proportion of species are significantly more abundant in certain age-classes. Loss of preferred age-classes may

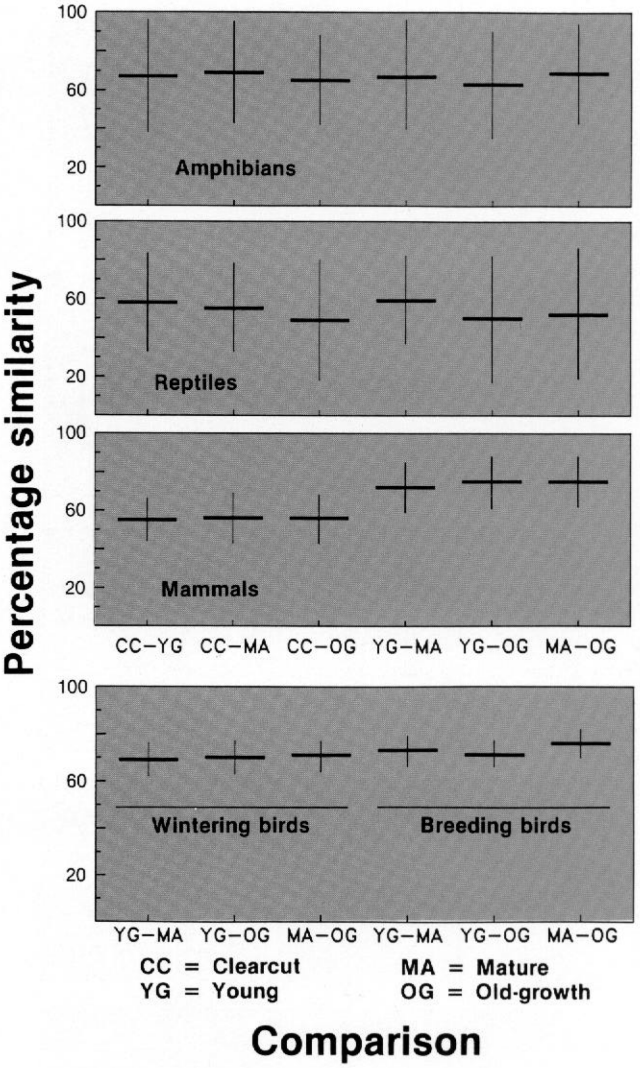

Figure 7—Comparisons of mean similarity (± 95-percent confidence intervals) estimated from 200 bootstrap replications of 10 randomly selected sites for all possible comparisons between age-classes for each group.

reduce the population viability of these species. Species richness is only one component of biodiversity and, for terrestrial vertebrates of Douglas-fir forests in northwestern California, species richness is not a sensitive indicator of habitat value. Results of my analyses indicate that species richness is independent of age-class, yet other analyses reported in this volume indicate that the abundance of certain species is quite dependent on age-class. For this reason, I agree with conclusions of Samson and Knopf (1982) and suggest that species richness should not be used as a basis for allocating distributions of land base among age-classes. Rather, I suggest that such decisions should be based on more sensitive,

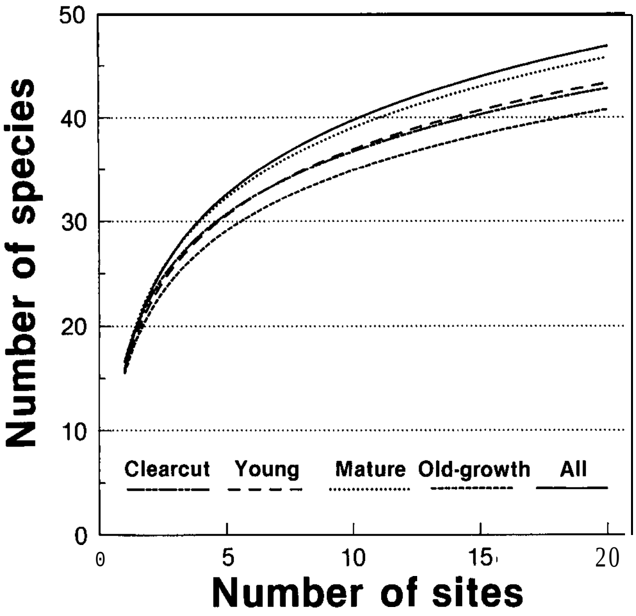

Figure 8—Accumulation of amphibian, reptilian, and mammalian species with increasing numbers of sites for each of four age-classes and for all age-classes combined from Douglas-fir forests of northwestern California.

abundance-based measures. Raphael and Hof (unpubl. data), for example, suggest a MAXMIN approach by use of linear-programming techniques to compute the optimum mix of age-classes to maximize the minimum population sixes of all species of interest. If probabilities of population viability can be maximized, then probabilities of extinction can be minimized and species richness will be maintained.

Acknowledgments

I thank Glen Brink and Marilyn Whitfield for writing bootstrap programs and Rudy King for statistical advice. I also thank my field assistants whose hard work permitted these analyses. Field studies and subsequent analyses were supported by the Pacific Southwest Region and Pacific Southwest Forest and Range Experiment Station of the USDA Forest Service and by the University of California Agricultural Experiment Station, Project 3501 MS. I am indebted to Barry R. Noon and C. John Ralph for comments on earlier drafts.

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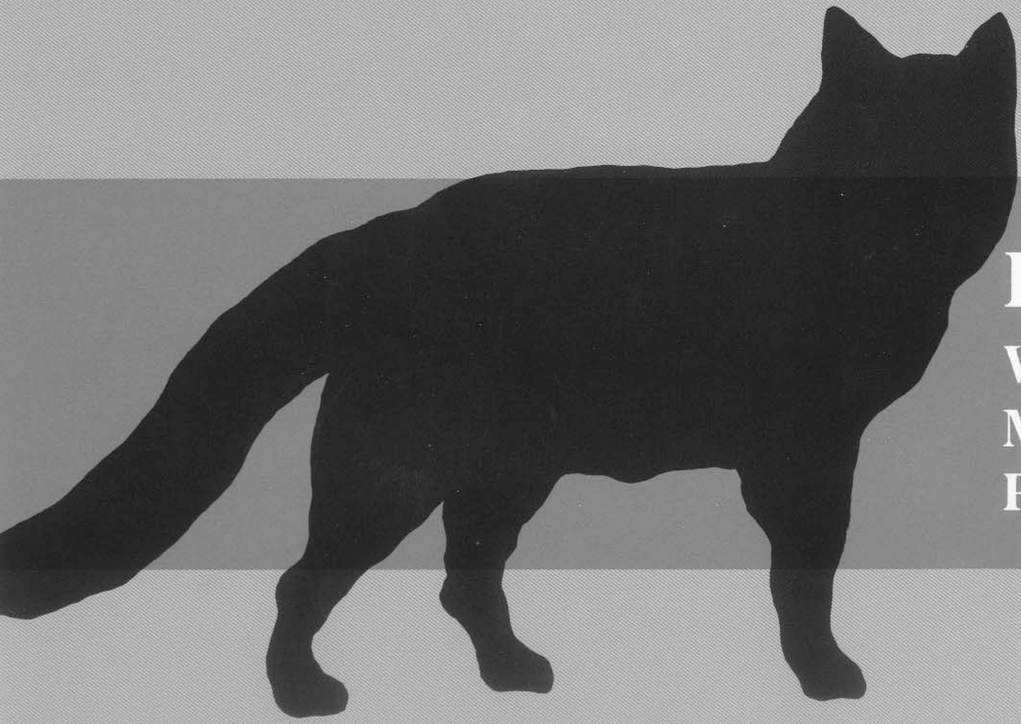

Part 8

Wildlife and Forest Management in the Pacific Northwest

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Landscape-Scale Patterns of Forest Fragmentation and Wildlife Richness and Abundance in the Southern Washington Cascade Range

John F. Lehmkuhl, Leonard F. Ruggiero, and Patricia A. Hall

Authors

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Abstract

The richness and abundance of birds, small mammals, and amphibians in the community-study stands of Douglas-fir in southern Washington were examined in relation to their surrounding landscapes. We also compared landscape patterns with the Franklin and Forman (1987) model of forest-landscape dynamics. Forest and nonforest habitats in 2025-ha landscapes were mapped around the center of old-growth study stands from current forest-type maps and aerial photographs. Map data were analyzed with geographic information systems. Vertebrate richness and abundance in study stands and their relation to landscape variables were analyzed at four scales: stand area and configuration, the habitat composition of the stand's neighborhood, the habitat composition of the entire 2025-ha landscape, and relative to indices of landscape pattern. Correlations indicated that landscape variables were weakly ($R^2 \leq 0.15$) associated with richness and abundance in young to old stands. Regression models suggested that bird richness increased from conventional edge effects associated with clearcut logging in the surrounding landscape. Bird abundance was highest in large old stands in clearcut landscapes, suggesting that logging displaced birds, which were then packed into remaining old stands. Packing also was implicated as one explanation for amphibian abundance, but elevation proved the strongest influence. Mammal richness and abundance showed little relation to landscape variables. A source-sink phenomenon between young and old forest was suggested by the higher abundance of cavity-nesting birds and the greater mammal richness in young stands surrounded by old growth. We concluded that fragmentation probably has not yet reached the critical threshold that would initiate a decline in biotic diversity, and the opportunity remains for pro-active management.

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Introduction

Forest fragmentation is the loss of late-successional forest habitats to timber harvest or other disturbances, and the isolation of remaining forest patches and wildlife populations. Legal mandates for public land-management agencies, and popular sentiment favoring the protection of threatened or endangered species and maintaining populations of other species has generated interest in the effects of forest fragmentation on biotic diversity (Lehmkuhl and Ruggiero, this volume; Nelson and Salwasser 1983; Nelson and others 1983; Salwasser and others 1984). Management and research on forest fragmentation have been guided by studies that describe the effects of habitat isolation in the context of island biogeographic theories of vertebrate extinction and colonization on oceanic and land-bridge islands (Diamond 1972, 1984, Faaborg 1979, MacArthur and Wilson 1967, Simberloff 1974, Terborgh 1974, Wilcox 1978) and on habitat islands in terrestrial landscapes (Brown 1971,1978, Forman and others 1976, Freemark and Merriam 1986, Galli and others 1976, Soule and others 1988, Van Dorp and Opdam 1987, Whitcomb and others 1977, Whitcomb and others 1981; also see Biological Journal of the *Linnean Society* 1986, volume 28). Extinction and colonization on habitat islands, however, may be only one of many biotic or environmental processes that determine biotic diversity in fragmented forest landscapes (Haila 1986, Haila and Jarvinen 1981, Simberloff and Abele 1982, Williamson 1981). Population viability theory (see Soule 1986 and papers in Soule and Wilcox 1980) and landscape ecology, with its emphasis on patch structure, context, and edge or boundary effects (Forman and Godron 1986, Urban and others 1987) have expanded the theoretical basis for studying the effects of fragmentation on biotic diversity (Lehmkuhl and Ruggiero, this volume).

The loss and fragmentation of old-growth Douglas-fir forest in the Pacific Northwest that results from clearcut logging exemplifies forest fragmentation. During the last 40 years, logging in Oregon and Washington has converted 80 to 90 percent of the original mature and old-growth forest into a mosaic of early and late-successional forest (Harris 1984, Meslow and others 1981, Spies and Franklin 1988). Similar cutting in coastal northern California has accomplished the same transformation in about 50 percent of the original forest there (Rosenberg and Raphael 1986). The situation varies within the region, however. Fragmentation of industrial forest is a minor issue because high harvest rates have resulted in the near-complete conversion of old forests to plantations (Spies and Franklin 1988), and the practice of cutting square-mile blocks leaves few forest fragments. Fragmentation, however, is a critical issue on public forest lands where much of the remaining pristine forest in the region is located because the more conservative harvest rates and the prevailing practice of staggered-set clearcutting of small patches have resulted in a high degree of fragmentation in the remaining forest habitats and wildlife populations (Franklin and Forman 1987; Harris 1984; Lehmkuhl and Ruggiero, this volume).

Research on wildlife in fragmented landscapes has been conducted largely in areas of relatively simple patch dynamics such as woodlots in agricultural landscapes and mountaintop habitat islands. Managed forests differ from woodlots or mountaintop islands in several respects, however. Pattern in a managed forest is spatially dynamic. Undisturbed forest initially forms the matrix (rather than the patch, as with woodlots) until a threshold is reached where disturbed area exceeds forest area (Franklin and Forman 1987, Verner 1986). Pattern in a managed forest is also temporally dynamic. Boundaries between the forest and clearcuts initially are distinct, but with secondary succession, boundaries later become increasingly ambiguous (Rosenberg and Raphael 1986). Only a few studies in northern California (Raphael 1984, Rosenberg and Raphael 1986) have examined the effects of fragmentation in such dynamic managed-forest landscapes. The need for more research is critical.

Our research has analyzed the effects that forest fragmentation and spatial patterns of habitat availability have on wildlife diversity and abundance in western Oregon and Washington. The goals of our research were to extend the interpretation of data on the old-growth vertebrate community (this volume) beyond the stand to include the context of the landscape, to examine pattern in managed-forest landscapes and advance the theory of forest landscape dynamics, and to assess the impact of current forest management practices. Our analysis was guided by four basic questions about the richness and abundance of birds, small mammals, and amphibians. Each question addressed a succeeding, higher, landscape-scale of analysis:

- Do species richness and abundance decline with decreasing area of community-study stands as predicted by insular ecology theory? How does the length of stand edge affect richness and abundance?
- How do the proportions of habitats immediately adjacent to the community-study stands (the neighborhood context) affect species richness and abundance?
- How does the habitat composition of the entire landscape (the landscape context) affect species richness and abundance in the community-study stands?
- Can variations in species richness and abundance in the community-study stands be associated with indices of landscape pattern that convey properties of dominance, point diversity, and patch shape (fractal dimension)?

Table 1-Cross-tabulation of sample stands by age-classes assigned by Spies and Franklin (SF) (this volume) and the types assigned for this study through aerial photograph interpretation and ground-truthing

	Photo interpreted types[a]		
Ages	Young	Mature	Old-growth
Young	90 (9)	10(1)	-
Mature	20 (2)	80 (8)	
Old-growth	--	7 (2)	93 (26)

[a] SF values are percentages of types correctly typed by photo interpretation.
Number Number of stands are in parenthesis.

Table 2-Habitat types mapped in the southern Washington Cascade Range for landscape-scale studies of old-growth communities

Nonforest types	Forest types
(1) Nonvegetated	(10) Clearcut
(2) Human habitation	(11) Clearcut-forb
(3) Agriculture	(12) Clearcut-shrub
(4) Water	(13) Sapling-pole, d.b.h. 0-25 cm trees
(5) Rock	(13.1) Clearcut-sapling
(6) Wetland	(13.2) Clearcut-pole
(7) Grassland	(13.3) Natural pole
(8) Subalpine meadow	(14) Young, d.b.h. 26-51 cm trees
(9) Brush	(15) Mature, d.b.h. 52-81 cm trees
	(16) Old growth, d.b.h. (>81 cm and multistory canopy)
	(17) Hardwood-conifer
	(18) Hardwood
	(19) Riparian
	(20) Special feature

Our paper is more of a progress report than a presentation of final results. We present results for the southern Washington Cascades province; similar studies in the Oregon Cascade and Coast Range provinces are still in progress.

Methods

Mapping Procedures

Study landscapes were circular 2025-ha areas around the 45 community-study stands of old growth in the southern Washington Cascade Range. We defined landscapes by drawing a circle of radius 2.54 km from the center of the stand. Forest stands 24 ha and nonforest stands >0.4 ha initially were mapped and typed, from Forest Service Total Resource Inventory (TRI) maps, as homogeneous forest patches with similar crown diameters and canopy closure. We then updated and corrected the maps by examining color aerial photographs taken during 1982, by consulting with field personnel, and by conducting field reconnaissance. We digitized, managed, and analyzed map data with vector and raster geographic information systems (GIS) for personal computers.

Random samples of 14 percent (N = 171) of the mapped forest polygons and 6 percent (N = 76) of the nonforest polygons were ground-truthed to assess the accuracy of types determined from the TRI maps and photo-interpretation. Field crews visually truthed nonforest sites and examined forested stands with plotless sampling techniques to estimate tree frequencies, densities, and basal areas in five diameter-classes (sapling $\leq$ 13 cm d.b.h, pole 14-25 cm d.b.h, small sawtimber 26-51 cm d.b.h, large sawtimber 52-81 cm d.b.h, and old-growth >81 cm d.b.h with a multistory canopy). They also estimated the extent of multistory canopy, number of snags, and canopy closure. Ground-truthing determined that nonforest types concurred with 95 percent of the mapped types. Misclassification was much greater with the forested types, however. An initial comparison of mapped and ground-truthed forest types (on the basis of measured basal areas in the five diameter-classes that were used to map the stands) showed only 68 percent concurrence between mapped types and ground-truthed types. This percentage was unacceptable, so we first reclassified mapped stands by grouping the ground-truth plots with k-means clustering (Wilkinson 1988). Cluster groups and types were initially assigned to truthed stands from photo interpretation, and then cross-tabulated to determine which mapped types characterized each cluster. This procedure formed the basis for reassigning all of the original mapped types to one of four new forest types that were defined (through cluster anlaysis) by the dominant tree diameter-classes. The new forest types were sapling-pole, young, mature, and old-growth types. The forest types assigned to the community-study stands by this method corresponded very well (90 percent) to the age-classes assigned by Spies and Franklin (this volume) on the basis of increment coring (table 1). These were the only stands in the landscapes for which age data were available. Old-growth stands showed the highest consistency with Spies and Franklin's classification, followed by young stands, and mature stands.

Map Variables

Community-Study Stand Variables

We determined the elevation, age, area, perimeter, and shoreline edge index (Patton 1975) for each community-study stand. The proportion of clearcut area, old-growth forest area, and late-successional forest (types 14, 15, 16, 17, and 19 in table 2) area were calculated for a 400-m buffer zone around the periphery of the stand. Four-hundred meters was chosen as a likely limit of edge effects (Wilcove and others 1986). Habitat patches within the study stand, such as clearcuts, were included in the buffer zone.

Landscape Variables

We characterized the composition of each 2025ha landscape by the area of clearcuts, old-growth forest, and late-successional forest. Landscape pattern was measured with several indices proposed by O'Neill and others (1988) as standard measures of landscape pattern. We measured **dominance** of habitat types as the deviation from maximum evenness according to the equation,

$$D = \log_e (n) + \Sigma (Pi \log_e Pi)$$

where *Pi* equals the proportion of the ith habitat type and n is the total number of types in a particular landscape. The highest possible value was slightly less than $\log_e(20) = 3$.

We measured **point diversity** not as contagion per O'Neill and others (1988), but with a raster GIS algorithm for measuring map diversity. The GIS scanned the map and determined for each 0.25-ha grid cell the total number of cells of different habitat types within a 150-m radius or "window." The mean of this frequency distribution was used as an index of point diversity, an inverse measure of contagion. High point diversity indicated a complex landscape pattern.

We calculated **the fractal dimension as two times the slope** of log(perimeter) over log(area) of all the habitat polygons in a landscape (Lovejoy 1982, O'Neill and others 1988). This index measured the complexity of polygon shapes within a range of 1 to 2. An index of 1 indicated very regular polygon shapes, such as a circle or square, whereas an index of 2 indicated highly complex polygon boundaries. A **disturbance index** was calculated as the ratio of clearcut area to late-successional forest area (O'Neill and others 1988). Indices less than one indicated relatively more forest than clearcut.

Vertebrate Data

We analyzed the common data set used for the cross-province analyses of bird (Huff and Raley, this volume), small mammal (Aubry and others, this volume), and amphibian (Bury and others, this volume a) communities. Bird occurrence was based on those individuals observed within a 50-m variable-circular-plot radius and observed on 2 or more of an average 6 sample-days per stand. Only small mammal and amphibian pitfall-data taken during autumn were analyzed. Average daily detections rather than density estimates were used to measure wildlife use. Sampling effort was the same for each stand, regardless of area, and between years.

Richness and abundance were analyzed separately for each taxon. We calculated species richness as the total number of species detected in the community-study sample-stand at each landscape's center. Total abundance in a taxon or functional group was calculated as the sum of average daily detections for all species in that group. Species richness and abundance from 1984 and 1985 were averaged for the analysis. Associations of individual species' abundance with landscape variables were examined for those species occurring in $\geq$ 10 percent of the stands in either year.

Analytical Procedure

We visually screened the dependent variables of vertebrate species richness and total abundance for normality by examining the frequency distributions with fitted normal curves and testing with the Kolmogorov-Smimov test (Wilkinson 1988). The log of total abundance was used to approximate a normal frequency distribution. We examined the linearity of dependent-variable responses to independent map variables by fitting smoothed curves to scatterplots (Wilkinson 1988). We did not observe nonlinear responses requiring data transformations.

The univariate associations of species richness and abundance with stand, stand-buffer, landscape-composition, and landscape-pattern variables were analyzed by partial correlation holding stand elevation and age constant to separate natural from human-caused fragmentation effects as was done by Rosenberg and Raphael (1986). We used stepwise regression with an enter and removal P-value of 0.15 (Wilkinson 1988) as a multivariate exploratory technique to select a subset of variables that explained the most variation (highest R^2) in species richness or abundance. Stepwise regression is often criticized as too dependent on the correlation structure of the independent variables, but we found few strong correlations between dissimilar variables that would complicate the interpretation of stepwise regressions. Moreover, selected variables were not later removed from any of the models, so little ambiguity existed in the selection of the "best" set of variables.

The significance of stepwise regression models was tested with probabilities adjusted for stepwise regression (Wilkinson 1979 in Tabachnick and Fidel1 1983). Assumptions for regression were valid for all models: we found residuals to be normally distributed and homoscedastic from an examination of the probability plots of residuals and by plotting residuals against expected values (Wilkinson 1988). No outliers for regression models were detected from an examination of leverage statistics and standardized residuals (Sokal and Rohlf 1981). We were liberal in noting the significance of statistical relationships at $P \leq 0.10$ in tables, but generally were conservative in interpreting and discussing relationships that were significant only at $P \leq 0.05$.

Lines were fitted to data in scatterplot figures by the Lowess algorithm. Lowess smoothing is useful for examining relations between variables because it does not presuppose the shape of the function, but calculates predicted Y values from a weighted average of nearby Y values (Wilkinson 1988).

Table 3-Summary statistics for sample stand and landscape variables used in landscape-scale analysis of vertebrate community patterns in the southern Washington Cascade Range

	summary statistics			
Variable	Min	Max	Mean	Std error
Sample stand				
Area (ha)	51.0	1,689.0	488.0	49.6
Perimeter (km)	3.0	65.6	25.0	1.9
Edge index	121.0	550.0	322.0	11.8
Elevation (m)	404.0	1,218.0	762.0	31.4
Age	55.0	730.0	297.0	30.0
Stand buffer proportions				
Clearcut	**0**	0.61	0.15	0.026
Old-growth	.006	.55	.19	.020
Late-successional forest	.16	.94	.47	.025
Landscape composition (ha)				
Clearcut	0	.48	.13	.018
Old-growth	.03	.86	.31	.025
Late-successional forest	.39	.99	.77	.017
Landscape pattern indices				
Fractal	1.09	1.27	1.20	.0056
Dominance	.33	1.66	.93	.036
Point diversity	1.14	2.06	1.72	.026
Disturbance	0	1.22	.20	,035

Species-area curves, however, were fitted with straight lines to conform to the theoretical distribution (MacArthur and Wilson 1967, Wilcox 1980).

Results

Landscape Characteristics

Community-study stands-Community-study stand-areas ranged from 51 ha to 1690 ha, with a mean of 488 ha (table 3). Old-growth stands were generally larger (mean of 546 ha) than young (mean of 486 ha) or mature (mean of 352 ha) stands (table 3), but the differences were not significant by analysis of variance ($P \leq 0.05$). The mean proportion of clearcut in stand buffers was 15 percent, ranging from 0 to 60 percent. Young and mature sample stands averaged no more than 9 percent clearcut area in their buffers, but old-growth stands averaged 20 percent clearcut.

Composition of Landscapes

Clearcut area ranged from 0 to 48 percent of the total landscape area (table 3), but most landscapes had relatively small amounts of clcarcut area (<15 percent) (fig, 1A). Old-growth area was more normally distributed (fig. lB), with an average of 31 percent old-growth (table 3). Late-successional forest area was generally less variable (fig. 1C) than old-growth with most landscapes comprised of 70 to 90 percent late-successional forest. Late-successional forest and clearcut areas showed a strong reciprocal relationship (fig. 2), which conforms to Franklin and Forman's (1987) checkerboard model of forest-landscape dynamics under a clearcutting regime. The relation indicated a 50-percent cutover threshold where dominance of the landscape matrix switches from forest to clearcut habitats. Most landscapes remained well under this 50 percent threshold, where forest-clearcut edge reaches an apex. The relation was much different with respect to old growth. The regression of old-growth area against the clearcut proportion was not significantly different than zero (fig. 2). Residual variation around the regression line was consistently high, within the observed range of 0 to 50 percent clearcut.

Patch Sizes

Over 90 percent of the clearcut patches were <30 ha, with a few very large cuts on private lands of up to 150 ha. Old-growth patch size was extremely skewed toward small stands (fig. 3). Despite their greater number, the cumulative area of patches ≤ 10 ha accounted for only 4 percent of the summed old-growth area for all landscapes, and patches ≤ 20 ha totaled about 10 percent of the old-growth area. Most old-growth patches were ≤ 50 ha, but the maximum patch-size was 1741 ha. Late-successional forest generally occurred as larger patches (fig. 3). Late-successional patches ≤ 10 ha accounted for only 0.5 percent of the summed area for all landscapes, and patches ≤ 20 ha totaled 0.8 percent.

As the proportion of clearcut area in a landscape increased, clearcut patch-size initially increased slightly, but then remained nearly constant (fig. 4A). Old-growth patch-size increased rapidly up to about 10 percent cutover, then decreased steadily to the 50 percent clearcut point, the maximum observed in our landscapes (fig. 4B). The linear trend was not significant by regression ($P = 0.33$). Late-successional forest patch-sizes showed a small initial increase up to about 8 percent cutover, then a steady decline in patch size as with old growth (fig. 4C). The linear trend was significant by regression ($P = 0.009$), but with low explained variation ($R^2 = 0.14$).

Pattern Indices

Patch shapes were not complex as measured by the fractal index (table 3). Within the possible range of 1 to 2, our maximum index value was 1.27. Fractal dimension showed a strong negative correlation ($r = -0.72$) with clearcut area: the complexity of patch boundaries decreased as the number of regular-shaped clearcuts increased. Dominance indices suggested low habitat dominance in most landscapes, with a mean of 0.93 and a maximum value little more than half the

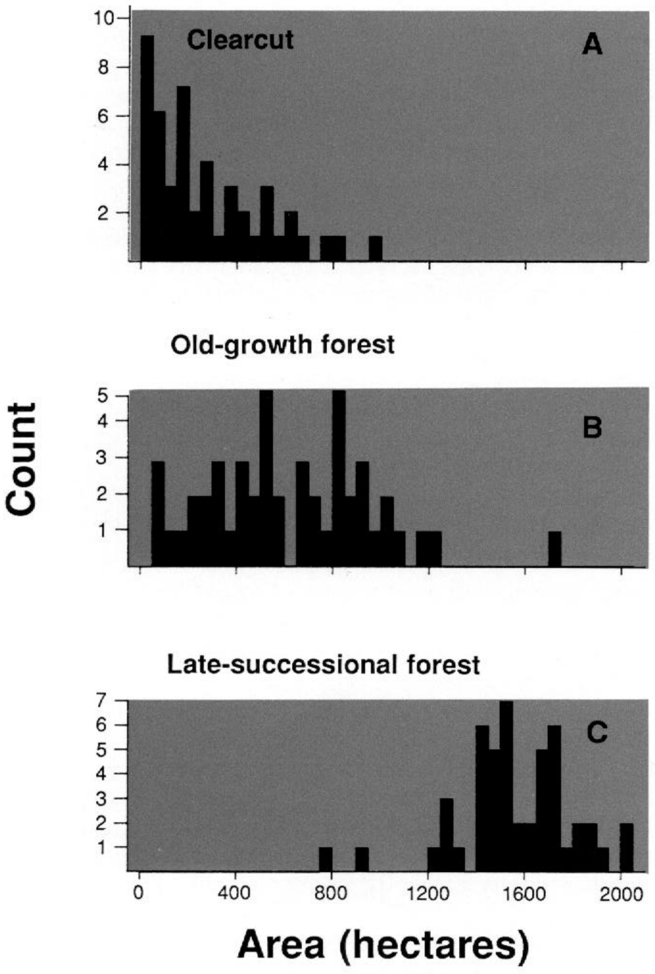

Figure 1—Frequency distributions of mean landscape clearcut, old-growth forest, and late-successional forest area in 48 landscapes around sample stands in the southern Washington Cascade Range.

theoretical maximum of 3 (table 3). Landscapes showed little habitat point diversity at the scale of 12 ha patches: the maximum possible index was 20 habitat-type transitions, whereas our landscapes had a maximum of 2.1 transitions and an average of 1.7 transitions in a 12-ha area. The disturbance index, the ratio of clearcut to late-successional forest, showed a relatively low amount of disturbance (table 3). Clearcuts in the majority of the landscapes were less than 40 percent the area of late-successional forest, with a mean of 20 percent.

Landscape-Vertebrate Relationships

Species Richness

All sample stands—Partial correlations, holding stand elevation and age constant, revealed few significant or strong relations between species richness and landscape variables

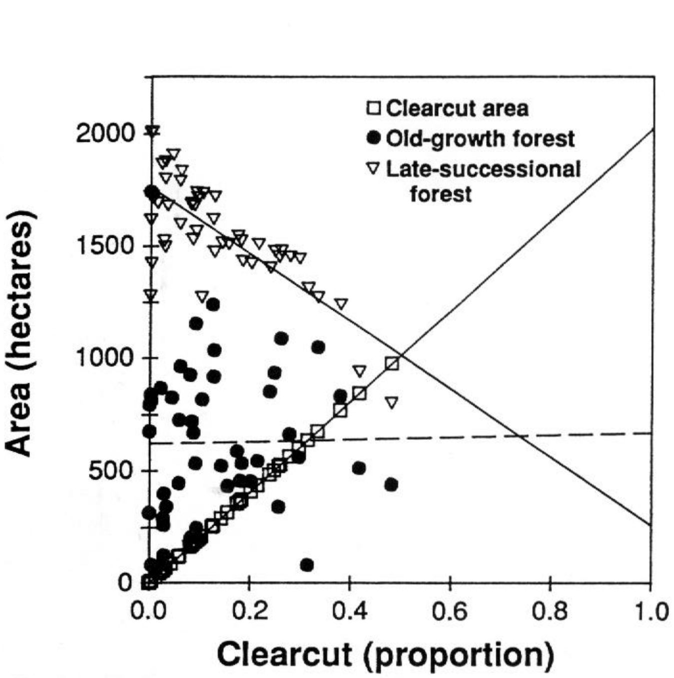

Figure 2—Relation of clearcut, old-growth forest, and late-successional forest area to the proportion of the landscape clearcut. Solid lines are linear regression lines for clearcut and late-successional forest data; dotted line is linear regression line for old-growth data.

(table 4). Correlations were mostly weak ($R^2 \leq 0.37$), indicating ≤14 percent shared variation. The strongest relations were with bird and amphibian species richness. Bird richness was positively associated with the proportion of clearcut area within the buffer, and negatively correlated with the amount of late-successional forest in the buffer. Amphibian richness was most strongly correlated with the dominance index, indicating association with relatively homogeneous landscapes. Small mammal richness was not even weakly associated with any landscape variable.

We graphically examined four questions about the relation of species richness to landscape variables:

- Does richness increase with the size of the sample stand?
- Is richness in young stands greater when surrounded by old growth (may richness in young stands be "subsidized" by adjacent old forest)?
- Does richness increase from local edge effects in stands that have a clearcut buffer area?
- Does richness increase from landscape edge effects in stands located in clearcut landscapes?

Island biogeographic theory predicts a positive relation between species richness and stand area, but species-area curves revealed no significant relation between stand area and richness (fig. 5). Richness in young stands increased, as hypothesized, with the area of old growth in the neighbor-

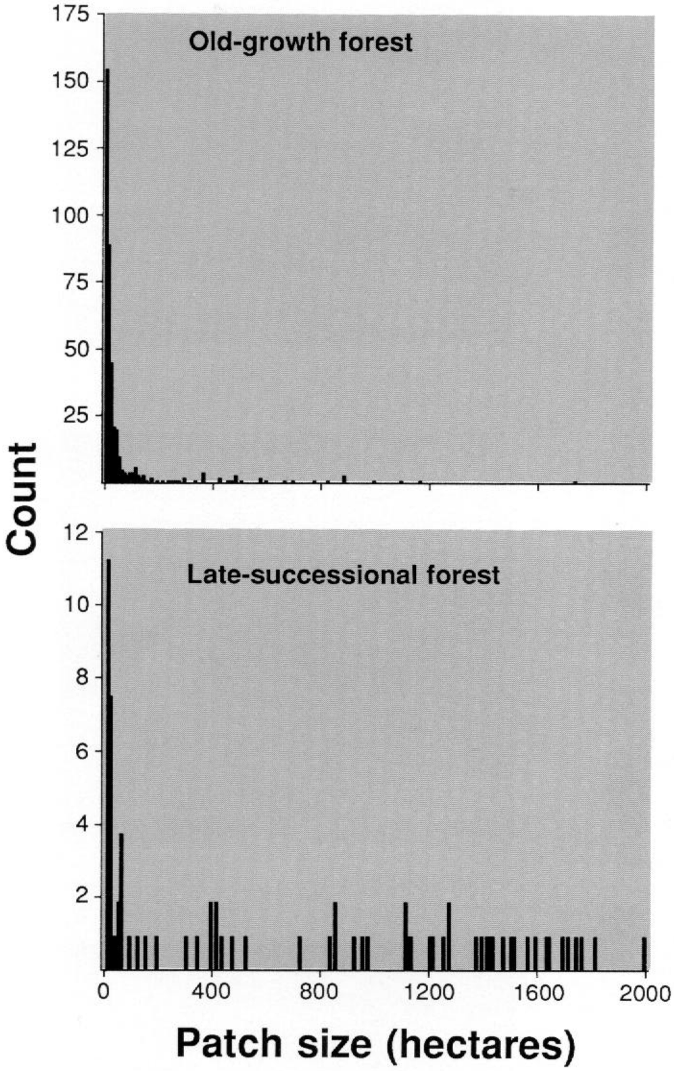

Figure 3—Patch-size distributions for old-growth and late-successional forest. Bars represent 10-ha classes.

hood, in a significant linear relation ($P = 0.085$; $R^2 = 0.36$) only for small mammals (fig. 6B). An opposite relation was evident for birds and amphibians (fig. 6A, 6C). A linear regression model for birds was significant ($P = 0.006$), but weak ($R^2 = 0.16$). The line fitted to the amphibian data indicated a slight negative relation up to a threshold of 30 percent old growth, beyond which richness declined rapidly. A linear model was not significant.

Clearcut area in the buffer of sample stands of all ages was positively but weakly associated with bird richness (fig. 7A). The linear regression model was significant ($P = 0.006$), but with low explained variation ($R^2 = 0.162$). A similar relation was indicated for bird richness and the total area of

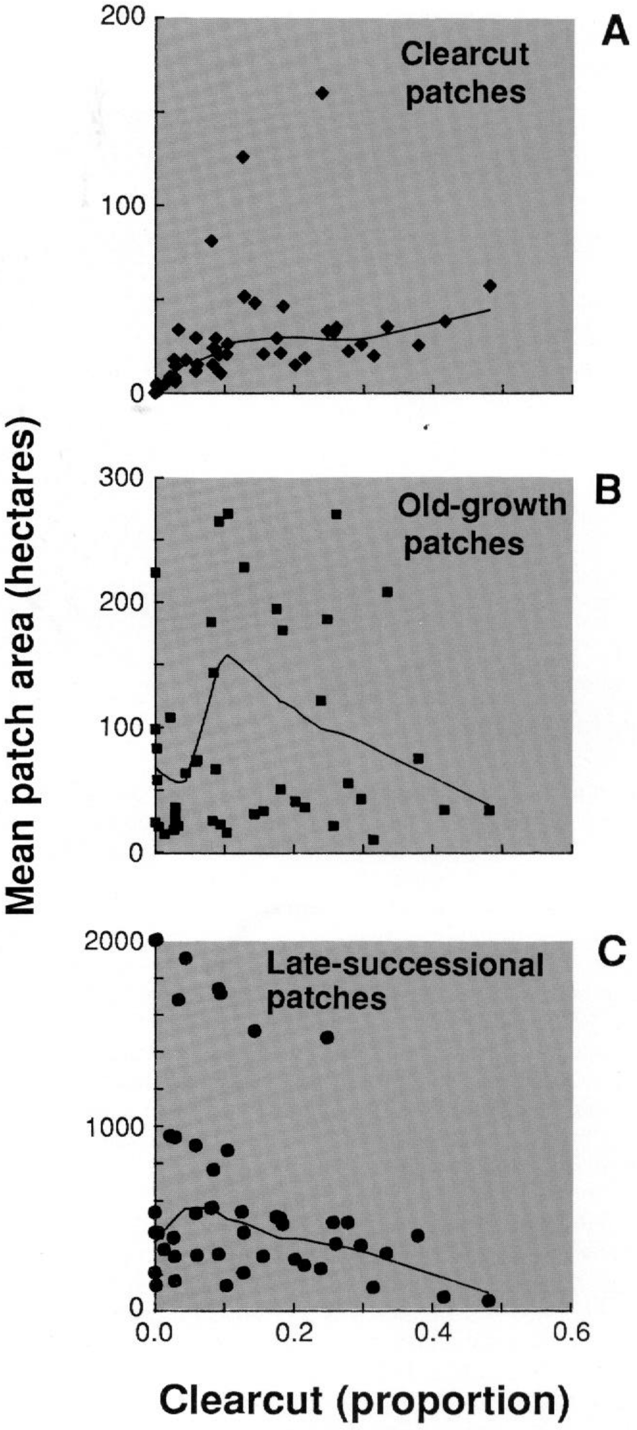

Figure 4—Relation of mean area of clearcut, old-growth, and late-successional forest patches to proportion of the landscape clearcut. Old-growth patch size was truncated at 300 ha, eliminating one outlying patch of 600 ha.

Table 4—Partial correlations (stand age and elevation constant) of bird, small mammal, and amphibian species richness and abundance with landscape variables

	Species richness			Abundance		
	Birds	Small mammals	Amphibians	Birds	Small mammals	Amphibians
Sample stand						
Area	0.05	–0.05	0.22	0.07	0.04	0.07
Perimeter	.12	.00	.27*	.18	.01	.08
Edge index	.19	.08	.29*	.15	–.01	.00
Stand buffer composition						
Clearcut	.37**	–.17	.11	.13	.07	.24
Old-growth	–.11	.00	–.09	–.16	.11	–.29*
Late-successional forest	–.36**	.24	–.10	–.09	–.02	.05
Landscape composition						
Clearcut	.21	–.23	–.22	.15	–.24	.06
Old-growth	–.16	–.07	.13	–.31**	.04	–.14
Late-successional forest	–.14	.20	.23	–.11	.24	.02
Landscape pattern indices						
Fractal	–.12	.23	.05	–.01	–.06	–.28*
Dominance	.01	.02	.47**	–.07	.32**	.28*
Point diversity	.08	.00	–.23	.15	–.18	–.02
Disturbance	.17	–.22	–.16	.08	–.18	.06

* $P \le 0.10$; ** $P \le 0.05$; *** $P \le 0.01$; **** $P \le 0.001$.

clearcut in the landscape (fig. 8A), but it was not significant ($P = 0.107$). Both relations showed little change in bird richness up to about 18 percent clearcut, then a rising trend in richness with increasing clearcut area. The similarity of responses to clearcut area at both scales may be due to the moderate correlation between clearcut in the buffer and landscape ($R^2 = 0.78$). No associations between small mammal richness and clearcuts in the buffer (fig. 7B) or landscape (fig. 8B) were observed. Amphibian richness initially decreased as clearcut area in the buffer (fig. 7C) and landscape (fig. 8C) approached 15 percent, but beyond that percentage, richness increased steadily. The relations were weak, however, as suggested by the large residual variation. Linear regression models were not significant.

Stepwise regression models including stand age and elevation were consistent with the results of partial correlation and were significant for birds and amphibians (table 5). Bird richness was best predicted as a positive function of stand area and clearcut area in the buffer zone, and a negative function of elevation and old-growth area in the landscape. These variables accounted for 37 percent (R^2) of the variation in bird richness. The model for amphibian richness was most-strongly influenced by a negative elevation gradient, but positively influenced by habitat dominance (table 5). The amphibian model was the strongest of the three taxa ($R^2 = 0.56$).

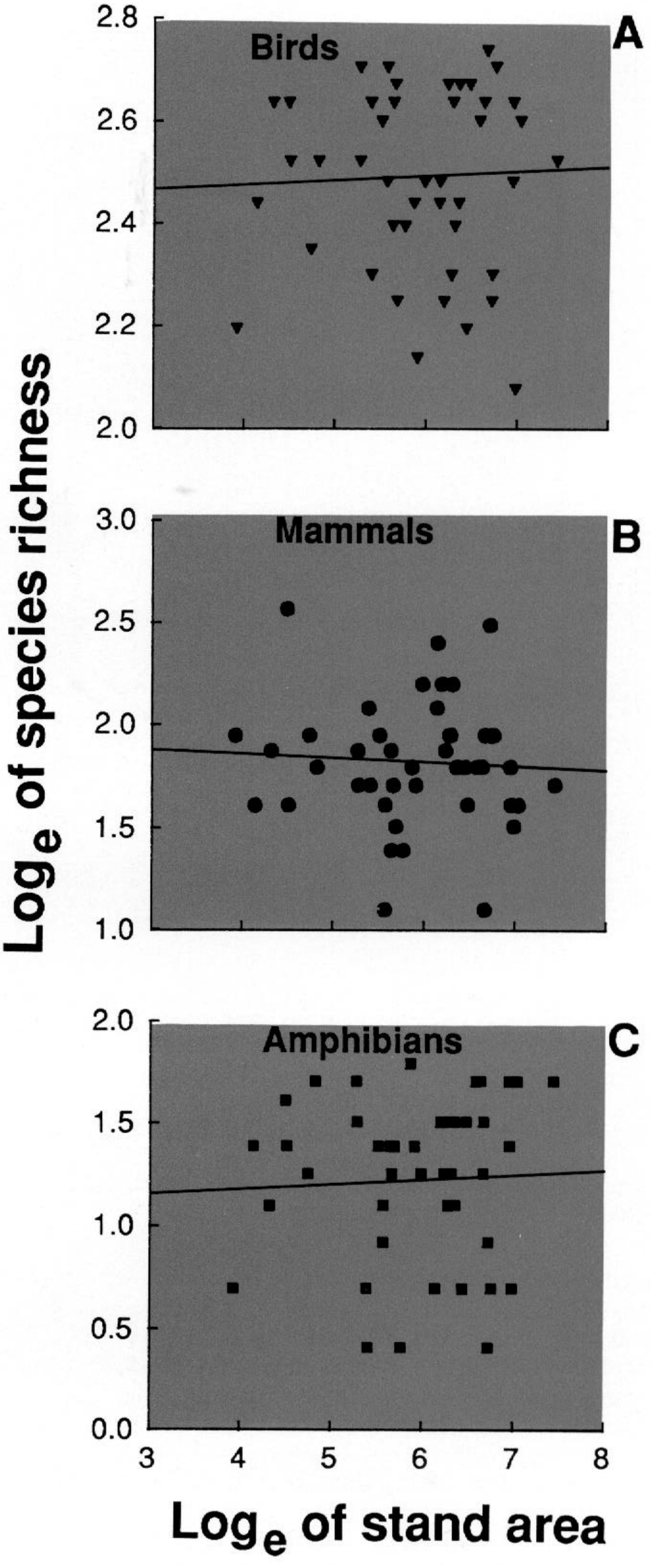

Figure 5—Species-area curves for birds, small mammals, and amphibians.

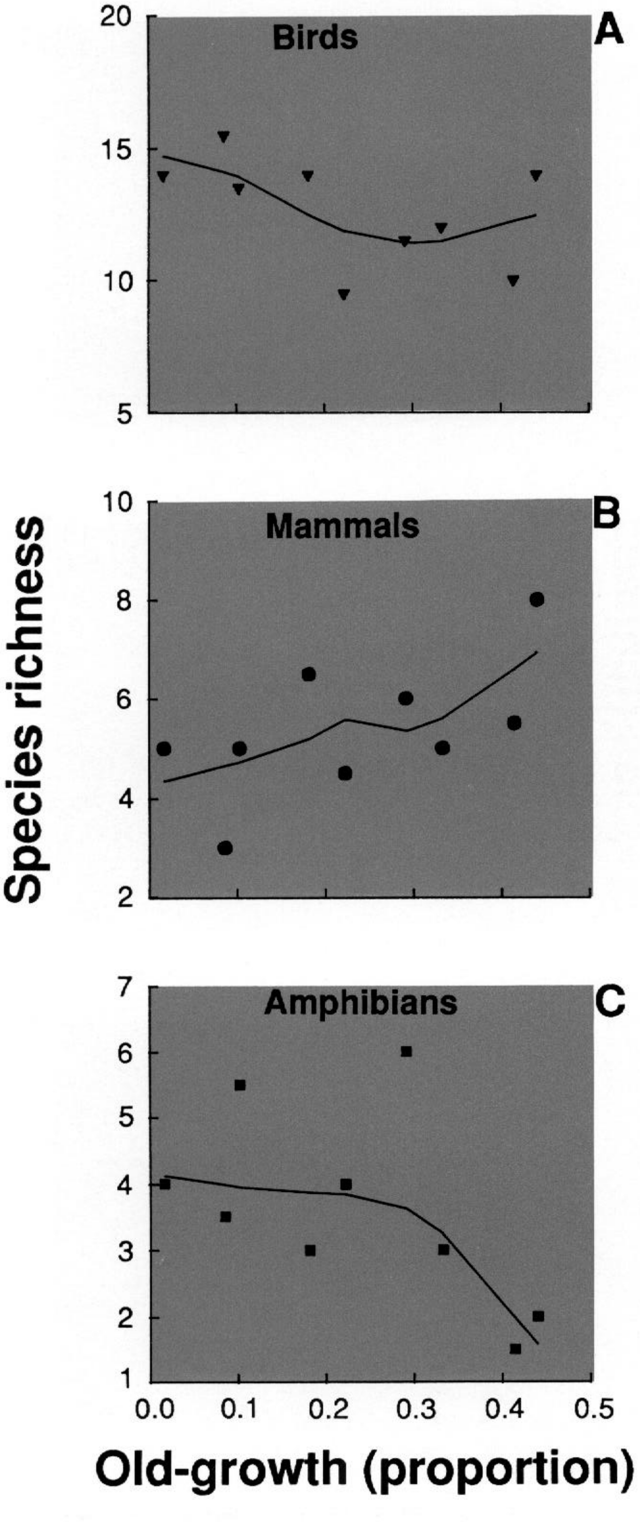

Figure 6—Relation of species richness of birds, small mammals, and amphibians sampled in young stands only to the proportion of old-growth forest in a 400-m buffer zone around the sampled stand.

Old-growth sample stands—The associations between landscape variables and bird richness in the sample stands classified as old growth were consistent with stepwise regression models for all stands (table 6). Bird richness increased with landscape disturbance at neighborhood and landscape scales as indicated by a positive correlation with clearcut area in buffer zones and landscapes, and a negative correlation with fractal dimension. Bird richness in old-growth stands also showed a negative relation to elevation. In contrast to previous analyses with data from all stands, small mammal richness in old-growth stands was associated with complex patch shapes (fractal dimension). As with the regression model for all stands, amphibian richness in old-growth stands had a strong negative correlation with elevation.

Species Abundance

All sample stands—Vertebrate abundance was weakly associated through partial correlation with few landscape variables (table 4). As with bird richness in the regression model, bird abundance was negatively associated with old growth in the landscape. Small mammal abundance was correlated with habitat dominance. Amphibian abundance was not significantly correlated with any variable.

Stepwise regression suggested a model of bird abundance increasing with age and size of stands, with old growth in the immediate buffer, and with increasing clearcut area and decreasing old-growth area in the landscape (table 5). Stepwise regression was not able to select a statistically significant model of small mammal abundance. The amphibian-abundance model indicated a strong positive influence of habitat dominance, and negative influences of complex patch shape (fractal index), old-growth area in the landscape, and elevation.

Old-growth sample stands—Spearman correlations of bird abundance in old-growth sample stands contradicted the regression model for all stand ages by suggesting a negative relation with stand area (table 6). The negative associations of bird abundance with old-growth area in the landscape and with habitat dominance, however, were consistent with the regression model. Small mammal abundance in old-growth stands surprisingly showed some relatively strong correlations not evident in previous statistics: abundance was negatively associated with clearcut area in the landscape (and its related disturbance index), and was positively associated with habitat dominance. Amphibian abundance in old stands declined with elevation as in the regression model, but also with complex patch shapes in the landscape (fractal index); abundance also increased with clearcut area in the stand buffer.

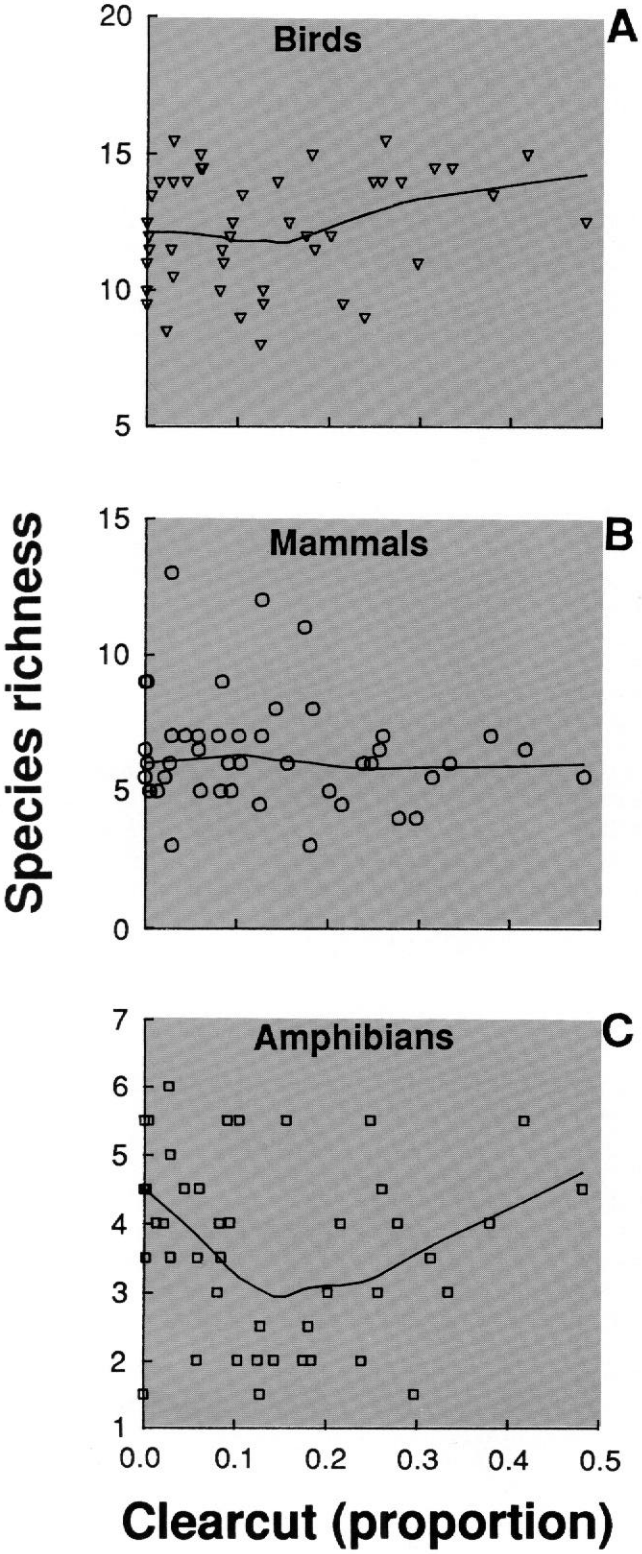

Figure 7—Relation of species richness of birds, small mammals, and amphibians to the proportion of clearcut in a 400-m buffer zone around the sampled stand.

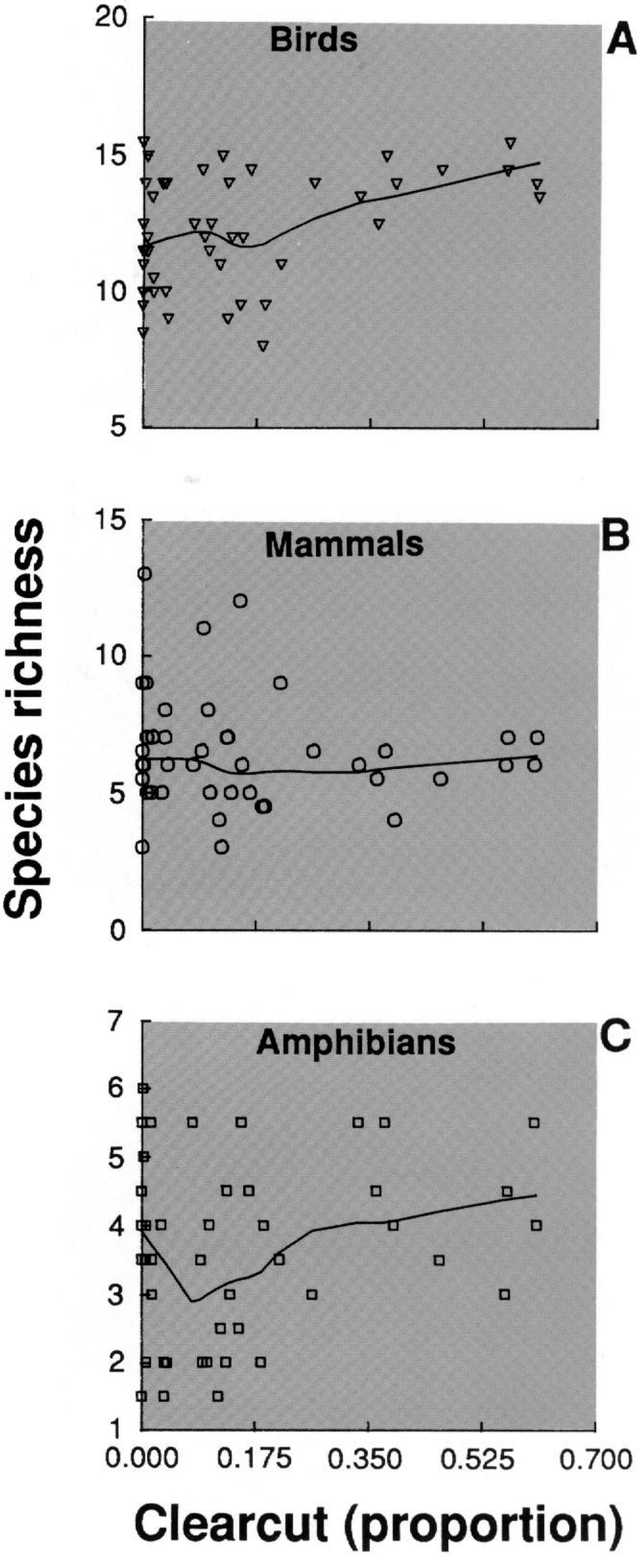

Figure 8—Relation of species richness of birds, small mammals, and amphibians to the proportion of clearcut in the entire 2025-ha landscape.

Table 5—Contribution of landscape variables to squared multiple R (R^2 change) in stepwise regressions of vertebrate richness and $\log_e$ (abundance) with stand and landscape variables (alpha to enter and remove in regression = 0.15)

Selected variables	Richness			Abundance			
	Birds	Mammals	Amphibians	Birds	Mammals	Amphibians	N[a]
Model R^2	0.352	0.191	0.562	0.475	0.159	0.370	—
Regression P	**	ns	**	**	ns	**	—
Sample stand							
Area	.283*	..	..	.739****	–.350	..	2
Perimeter	..	..	..	..	..	..	0
Edge index	..	..	..	..	..	..	0
Elevation	–.227**	..	-.689**	..	..	–.339**	3
Age	..	.137	..	.768****	..	..	1
Stand buffer composition							
Clearcut	.455**	..	..	..	..	..	1
Old growth	..	..	..	.335*	..	..	1
Late successional forest	..	..	-.174	..	..	..	0
Landscape composition							
Clearcut	..	.054	..	1.432***	..	..	1
Old growth	–.394**	..	..	–.893****	..	–.384**	3
Late successional forest	..	..	..	..	..	..	0
Landscape pattern indices							
Fractal	..	..	..	..	..	– .475**	1
Dominance	..	..	.403**	..	.548	.653**	2
Point diversity	..	..	..	..	..	.358	0
Disturbance	..	..	..	–1.156***	..	..	1

* $P \le 0.10$; ** $P \le 0.05$; *** $P \le 0.01$; **** $P \le 0.001$.

[a] Number of significant regression coefficients.

Table 6—Spearman correlations of bird, small mammal, and amphibian species richness and abundance in old-growth stands with landscape variables

	Species richness			Abundance		
	Birds	Mammals	Amphibians	Birds	Mammals	Amphibians
Sample stand						
Area	–0.19	–0.26*	–0.10	–0.42***	–0.19	–0.13
Perimeter	–.13	–.24	–.07	–.35**	–.16	–.15
Edge index	–.05	–.02	–.27*	–.03	–.30*	–.25*
Elevation	–.39***	.28*	–.63****	–.22	.24	–.33**
Stand buffer composition						
Clearcut	.51****	–.30	.21	.15	–.07	.30**
Old growth	.01	.01	–.00	.07	.24	–.18
Late successional forest	–.33**	.29*	–.08	–.15	.12	–.05
Landscape composition						
Clearcut	.30**	–.21	–.07	.28*	–.35**	.00
Old growth	–.07	–.30*	–.08	–.34**	–.03	–.12
Late successional forest	–.08	.07	.23	–.25*	.29*	.27*

Table 6-continued

	Species richness			Abundance		
	Birds	Mammals	Amphibians	Birds	Mammals	Amphibians
Landscape pattern indices						
Fractal	-.44***	.41***	-.29*	-.03	-.10	-.40***
Dominance	-03	-.20*	.15	-.33**	.42***	.19
Point diversity	.08	.16	-.03	.39**	-.14	-.14
Disturbance	.29*	-.22	-.09	.28*	-.37**	.00

* P ≤ 0.10; ** P ≤ 0.05; *** P ≤ 0.01; **** P ≤ 0.001.

Individual bird species-Few strong associations between the abundance of 22 bird species and landscape variables were revealed by partial correlation (table 7). Most correlations were ≤ 0.50, indicating a weak association with less than 25 percent shared variation. Moreover, the number of significant correlations may not be different than expected by chance alone ($P \leq 0.10$). Dark-eyed juncos were the only species that showed an association with stand-scale variables: abundance increased with stand area, perimeter, and edge, which were all somewhat collinear. Red-breasted nuthatches and rufous hummingbirds were associated with clearcuts in the buffer and negatively associated with complex patch-shapes measured by the fractal index. Consistent with these neighborhood relations, red-breasted nuthatches increased with clearcut area in the landscape. Rufous hummingbirds however, were positively correlated with old-growth area in the landscape.

The abundance of winter wrens was associated with undisturbed buffer zones: abundance decreased with clearcut area and increased with late-successional-forest area in stand buffers. Their abundance was not associated with the whole-landscape variables. Black-throated gray warbler abundance showed a very strong negative correlation with late-successional forest in stand buffer-zones. The combined abundance of hermit and Townsend's warblers was similarly associated with young forest: abundance decreased with old-growth area at the buffer and landscape scales. Hermit and Townsend's warblers were grouped into one functional species because hybridization in southern Washington made them indistinguishable in the field (see Manuwal, this volume).

Cavity-nesting birds-Several abundance relations were graphically examined for cavity-nesting birds (hairy woodpecker, red-breasted nuthatch, chestnut-backed chickadee, brown creeper) based on the hypothesis that these birds would be negatively affected by the loss of vertical structural diversity from clearcut logging and snag-reduction policies in remaining forest stands (Manuwal, this volume).

Our questions were:

- Does abundance increase with the size of the sample stand?
- Is abundance in young stands greater when surrounded by old growth (may abundance in young stands be subsidized by adjacent old forest)?
- Is abundance less in stands that have a clearcut neighborhood (buffer zone)?
- Is abundance less in stands embedded in a clearcut landscape?

Cavity-nesting bird abundance showed no significant relation to stand area (fig. 9A). Abundance increased with clearcut area in the buffer in a weak ($R^2 = 0.102$), but significant ($P = 0.033$), linear relationship (fig. 9B). The linear relation between abundance and total clearcut area (fig. 9D) was not significant ($P = 0.127$), however. The hypothesis that abundance is higher in young stands surrounded by old growth is supported (fig. 9C) with a significant linear regression ($P = 0.011$) and high $R = 0.76$, if the apparent outlier in the top left comer is deleted.

Individual small mammal species-Some strong partial correlations were found between individual small mammal species' abundance and stand or landscape variables, but these correlations could have occurred by chance ($P \leq 0.10$) (table 8). The creeping vole was the only species showing an association with stand variables: abundance was negatively correlated with stand perimeter and the edge index. Northern flying squirrels and marsh shrews both were negatively associated with late-successional forest in the buffer zones, but the water shrew was very strongly associated with late-successional forest in the buffer. Marsh shrew abundance also was positively correlated with landscape clearcut area and the disturbance index, and negatively associated with late-successional-forest area. Ermine were associated with high point diversity.

Table 7—Partial correlation coefficients (stand age and elevation constant) of bird species' abundance with landscape variables (data for 1984 and 1985 were combined)

	Sample stand			Stand buffer composition			Landscape composition			Landscape pattern				
Birds[b]	Area	Perim[a]	Edge	CC	OG	LSF	CC	OG	LSF	Fract	Domin	Point	Dist	N
AMRO[c]	0.31	0.24	0.03	–0.32	0.03	0.31	-0.31	0.27	0.29	0.24	0.07	-0.22	-0.34	15
BGWA[c]	–.16	–.34	–.50	–.06	–.26	-.92***	-.05	-.24	-.56	.24	-.21	-.29	-.04	8
BRCR	.08	.02	–.04	.20	.08	-.05	.03	.23	.10	-.33	.06	-.20	-.03	88
CBCH	–.01	–.01	–.04	–.14	.01	.07	-.15	-.07	-.02	.13	-.15	.08	-.15	91
DEJU	.39****	.45****	.35***	.05	–.11	-.09	.03	.00	.07	-.03	.28***	-.15	.03	83
EVGR[c]	.45	.34	.20	–.23	–.10	.25	-.29	.11	.38	.03	.34	-.57*	-.30	12
GCKI	.04	.10	.13	.06	.06	-.09	.03	-.07	.06	.12	.10	-.04	.01	92
GRJA	.02	.10	.11	.07	–.02	-.15	.04	-.14	-.09	-.05	.01	.14	.04	64
HAFL[c]	–.22	–.20	–.24	–.20	–.08	.41*	-.16	-.23	.11	.12	.09	.07	-.16	23
HAWO[c]	.05	.09	.07	.04	–.06	-.09	.05	-.10	.04	-.12	.28	-.09	.07	26
HETH[c]	–.12	–.16	–.18	–.04	.10	-.12	.18	-.22	-.24	-.21	-.23	.19	.16	39
HETO	.12	.17	.11	–.01	–.23**	.07	.10	-.26**	-.10	.07	.03	.13	.10	78
PISI[c]	–.07	–.05	–.05	.24	.16	-.32*	.34*	.03	-.16	-.39**	-.14	.03	.30	31
RBNU	.08	.13	.13	.32***	–.03	-.26	.25**	.05	-.13	-.25**	.07	-.01	.19	72
RUHU[c]	.23	.25	.19	.55***	-.05	-.27	.26	.37**	-.07	-.50***	.20	-.23	.16	31
STJA	–.01	–.01	.07	–.14	.02	.07	-.04	.09	-.02	.27	-.13	.16	-.04	22
SWTH[c]	–.43*	–.35	–.13	.42	-.17	-.21	.23	-.38	-.26	-.16	-.18	.39	.20	17
VATH	–.07	–.11	–.15	.03	.05	-.02	.16	-.05	-.06	-.16	-.14	.09	.07	87
WEFL	–.16	.01	.10	.02	-.12	.01	-.08	-.33****	.00	.11	.06	.20	-.07	84
WETA[c]	.16	.04	–.11	–.18	-.47	.19	-.10	-.37	.05	.07	.36	-.28	.02	9
WIWA[c]	.05	.03	.03	.26	.02	-.08	.23	.31	-.03	-.21	.17	-.11	.20	24
WIWR	–.08	–.02	–.01	–.23**	-.07	.22**	-.05	-.17	.00	.24	-.03	.19	-.06	91

[a] Variables: Perim = perimeter; CC = clearcut; OG = old-growth; LSF = late-successional forest; Fract = fractal; Domin = dominance; Point = point diversity; Dist = disturbance.

[b] Species: AMRO, American robin; BGWA, black-throated gray warbler; BRCR, brown creeper; CBCH, chestnut-backed chickadee; DEJU, dark-eyed junco; EVGR, evening grosbeak; GCKI, golden-crowned kinglet; GRJA, gray jay; HAFL, Hammond's flycatcher; HAWO, hairy woodpecker; HETH, hermit thrush; HETO, hermit-Townsend's warbler; PISI, pine siskin; PUFI, purple finch; RBNU, red-breasted nuthatch; RUHU, rufous hummingbird; STJA, Steller's jay; SWTH, Swainson's thrush; VATH, varied thrush; WEFL, western flycatcher; WETA, western tanager; WIWA, Wilson's warbler; WIWR, winter wren.

[c] Species with frequency of 10 to 50 percent of stands for 1984-85 combined; other species >50 percent frequency.

* $P \leq 0.10$; ** $P \leq 0.05$; *** $P \leq 0.01$; **** $P \leq 0.001$.

Individual amphibian species—A few significant partial-correlations were strong enough to be unlikely due to chance (table 8). Amphibians responded more strongly to stand-scale variables and more weakly to neighborhood- and landscape-scale variables than birds or small mammals. Abundance of the western redback salamander was associated with more variables than other species: abundance was positively correlated with stand area and the associated variables of perimeter and edge, and negatively associated with old growth in the buffer. The abundance of western redback salamanders was also correlated with habitat dominance. The abundance of tailed frogs was negatively correlated with stand edge and complex patch-shapes represented by the fractal index.

Pond-breeding amphibians—We hypothesized that the abundance of pond-breeding amphibians (northwestern salamander, roughskin newt, red-legged frog, Cascades frog) would decline with fragmentation as a result of the increased isolation of subpopulations and postbreeding dispersal mortality in clearcut barriers. The abundance-area relationship was not significantly different from zero (fig. 10A). Abundance appeared to increase with clearcut area in the buffer zone, but the linear relation was not significant. Abundance also was not associated with clearcut area in the landscape in a significant linear fashion. Abundance in young stands, however, showed a strong negative relation to buffer-zone old-growth, with a significant linear regression model ($P \leq 0.05$; $R^2 = 0.55$).

Discussion

Limitations of the Data Set

The stand-scale vertebrate data set is limited in several ways for a landscape-scale analysis. The criterion that study stands be larger than 40 ha restricted the examination of species-area relations to relatively large stands, where the effects of size may be less important. Rosenberg and Raphael (1986) found that forest stands <20 ha in northern California had less than the full complement of species. The minimum-size criterion also may have resulted in the selection of landscapes with less fragmentation than might have occurred had selection been unconstrained.

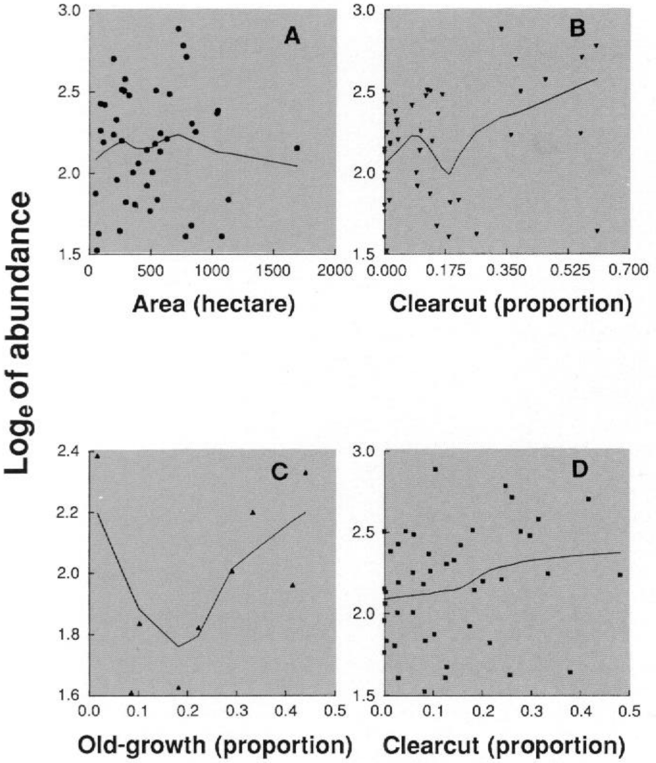

Figure 9—Relation of abundance of cavity-nesting birds to selected landscape variables: (A) stand area; (B) proportion of clearcut in a 400-m buffer zone; (C) in young stands only, the proportion of old-growth forest in a 400-m buffer zone; and (D) total area of clearcut in the landscape.

Sampling bias for relatively large stands may have excluded highly fragmented areas from the analysis, resulting in conservative estimates of fragmentation. Study landscapes on National Forest land ranged from 0 to 48 percent clearcut, with most landscapes less than 30 percent cutover. The mean cutover percentage was 16 percent. The mean percentage cutover for the entire Forest, based on data from the TRI database (G. Gruelich, unpubl. data), was also 16 percent, with a range of 14 to 19 percent cutover by Ranger District. The similarity of the means may be misleading, however, because Forest-wide estimates are averages made for a larger District scale of measurement. Proper comparison requires estimates from a random sample of 2025-ha landscapes across the Forest, which is a project beyond the scope of our study.

The vertebrate sampling design also had limitations for detecting uncommon and medium- to large-bodied species that may be most influenced by fragmentation (Diamond 1984; Lehmkuhl and Ruggiero, this volume; Pimm and others 1988; Terborgh and Winter 1980). The nine species suggested by Rosenberg and Raphael (1986) as most sensitive to fragmentation are all uncommon with medium-to-large body-size for their taxa: we examined data for only three of these species. Also, sampling area for vertebrates was constant in all stands so that large stands had relatively less area sampled than small stands. An attempt was made to distribute the sampling effort throughout the stand, but our sampling in large stands with high habitat-heterogeneity and associated heterogeneous species distributions may not have detected all of the species present (Robbins and others 1989). Thus, species-area relations may be more underestimated by the relatively smaller sampling areas in large stands than in small stands (Wilcox

Table 8—Partial correlation coefficients (stand age and elevation constant) of small mammal and amphibian species' abundance with landscape variables (data for 1984 and 1985 were combined)

	Sample stand			Stand buffer composition			Landscape composition			Landscape pattern				
	Area	Perim[a]	Edge	CC	OG	LSF	CC	OG	LSF	Fract	Domin	Point	Dist	N
Mammals[b]														
SRBV	0.00	0.02	0.05	0.15	0.16	–0.15	–0.02	0.05	0.08	–0.10	0.23	–0.08	–0.03	83
FLSQ[c]	–.29	–.12	.29	.24	.17	–.52**	–.07	–.13	–.20	.10	–.12	.27	–.01	18
CRVO[c]	–.38	–.60**	–.63**	–.12	.32	.05	.04	–.02	.05	–.24	–.50*	–.17	.02	15
ERMI[c]	–.44	–.40	–.37	–.10	.13	–.03	–.13	–.12	–.28	.09	–.36	.63**	–.07	15
SHMO	–.11	–.08	–.03	–.02	.14	.00	–.13	–.07	.22	.14	.14	–.14	–.15	42
DEMO	.03	–.01	–.05	.15	–.16	–.06	.12	.07	–.17	–.22	–.08	–.10	.11	50
FDMO	.10	.09	.08	–.12	.22	–.10	–.20	.13	.19	.06	.20	–.15	–.08	56
COMO[c]	–.53*	–.55*	–.36	–.04	–.26	.22	.20	–.36	–.24	.28	–.28	.29	.14	13
MASH[c]	–.29	–.24	–.07	.19	.14	–.45**	.43**	–.20	–.45**	.11	–.37*	.32	.53**	25
MOSH	.09	.00	–.10	–.17	–.07	.13	–.22	–.12	.14	.03	.18	–.11	–.18	83
WASH[c]	–.20	–.29	–.36	.01	.27	.99****	–.34	.10	.79	–.14	.47	–.58	–.40	6
TRSH	.14	.10	.02	–.07	.06	.13	-.17	.09	.22	.00	.20	–.10	–.15	87
VASH[c]	.05	.05	.13	.18	.17	-.39*	.00	.36	.21	–.06	.11	–.28	–.03	21

Table 8—(continued)

	Sample stand			Stand buffer composition			Landscape composition			Landscape pattern				
	Area	Perim[a]	Edge	CC	OG	LSF	CC	OG	LSF	Fract	Domin	Point	Dist	N
Amphibians[d]														
NWSA	–.04	–.07	–.06	.03	–.04	.03	–.09	–.06	.14	.05	.13	–.08	–.12	43
TLFR	–.15	–.28**	–.40****	.04	–.12	.22*	.06	–.04	–.04	–.26**	–.09	.10	.0367	
ENSA	.17	.24**	.20*	.02	–.18	.01	.01	–.11	–.02	–.03	.21	.02	.07	69
RBSA[c]	.65***	.63***	.53**	–.14	–.46**	–.02	–.29	–.38	.21	.26	.51**	–.04	–.23	20
RLFR[c]	–.09	–.05	.04	.26	–.20	–.02	.21	–.21	–.11	.09	.00	.16	.14	33
CAFR[c]	–.38	–.26	–.18	–.03	–.49	.62	.23	–.13	.04	.22	–.07	.31	.16	9
RASP[c]	.07	.18	.17	–.13	–.15	.19	–.23	–.20	.28	.07	.32	–.02	–.24	25
RSNE[c]	.29*	.25	.07	.21	–.11	.06	–.18	.27	.30	–.23	.32*	–.45	–.29*	34

[a] Variables: Perim = perimeter; CC = clearcut; OG = old-growth; LSF = late-successional forest; Fract = fractal; Domin = dominance; Point = point diversity; Dist = disturbance.

[b] Mammal species: SRBV, southern red-backed vole; FLSQ, northern flying squirrel; CRVO, creeping vole; ERMI ermine; SHMO, shrew-mole; DEMO, deer mouse; VASH, forest deer mouse; COMO, coast mole; MASH, marsh shrew; MOSH, montane shrew; WASH, water shrew; TRSH, trowbridge shrew; VASH, vagrant shrew.

[c] Species with frequency of 10 to 50 percent of stands for 1984-85 combined; other species >50 percent frequency.

[d] Amphibian species: NWSA - northwestern salamander; TLFR - tailed frog; ENSA - ensatina; RBSA - western redback salamander; RLFR - red-legged frog; CAFR - Cascades frog; RASP - frog *(Rana)* spp.; RSNE - roughskin newt.

* $P \le 0.10$; ** $P \le 0.05$; *** $P \le 0.01$; **** $P \le 0.001$

1980). Finally, interpretations of abundance in young or mature stands was constrained by sample sizes less than half (n = 11) the number of old-growth stands (n = 26).

Despite these limitations, we believe our studies provide valuable insight for examining the effects of landscape context on vertebrate richness and abundance in the community-study stands.

Landscape Dynamics

Habitat-Area Relations

The reciprocal relation of late-successional forest and clearcut areas in the landscape conformed to the Franklin and Forman (1987) checkerboard model: the composition of the landscape matrix switched from late-successional forest to clearcut at 50 percent cutover (fig. 1). The model did not hold for old-growth and clearcut areas, however: clearcut area exceeded old-growth area earlier in the harvest regime when the landscape was 30 percent cutover. Timber harvest apparently was not restricted to old-growth stands, and the amount of clearcutting in an area did not indicate the loss of old-growth forest, but rather the loss of late-successional forest. The 30-percent cutover threshold means that old-growth patches and populations of closely associated species will be isolated more rapidly than will late-successional forest patches and animals as cutting continues.

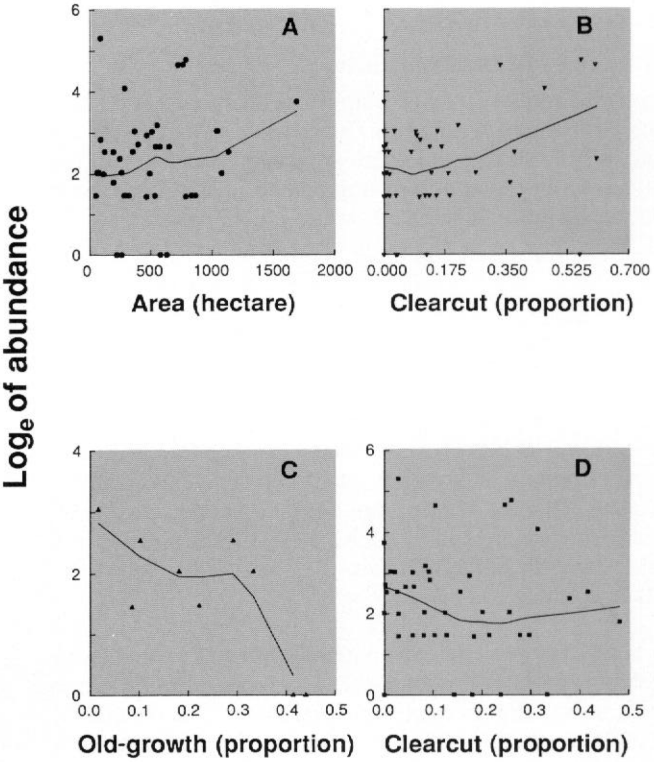

Figure 10—Relation of the abundance of pond-breeding amphibians to selected landscape variables: (A) stand area; (B) proportion of clearcut in a 400-m buffer zone; (C) in young stands only, the proportion of old-growth forest in a 400-m buffer zone; and (D) total area of clearcut in the landscape.

Continue

Patch Size

Clearcut patch size conformed to the Franklin-Forman model by remaining constant up to 50 percent cutover, except for a small anomalous increase in patch-size up to 10 percent cutover. Individual clearcuts had not coalesced into larger clearcuts within the areas sampled: this pattern follows from the standard procedure of not locating new cuts immediately adjacent to existing ones. Old-growth and late-successional-forest patch-sizes, however, did not conform to the model: patch-size decreased linearly instead of remaining constant within the range of 0 to 30 percent cutover as predicted by Franklin and Forman.

Franklin and Forman described forest patch-size as remaining constant during the initial stages of fragmentation, although patches become "increasingly porous" with progressive clearcutting. This rationale for calculating patch-size ignores the fact that forest patch-size as measured by area will always decline with conversion of some part of the patch to clearcut. An absolute loss of habitat occurs, a reduction in the habitat "core area" (Temple 1986) devoid of edge effects, and a decline in the connectivity of remaining forest, however contiguous the external boundaries of the patch may be.

Landscape-Vertebrate Relationships

Importance of Landscape Scale

Birds, small mammals, and amphibians responded differently to the three scales of analysis. Birds were influenced by stand, neighborhood, and whole-landscape variables. Stand area, primarily a function of fragmentation, was an important influence on bird abundance, and, to a lesser extent, on richness. Stand elevation and stand age (variables that are not influenced by fragmentation) also had strong effects on bird richness and abundance, respectively. Larger-scale factors of neighborhood and landscape proportions of clearcut or forest also strongly influenced bird richness and abundance. The richness and abundance of small mammals and amphibians in sampled stands was closely associated with few stand or landscape variables related to fragmentation. Elevation also was an important determinant of amphibian richness and abundance. Habitat features are likely to be important determinants of variations in the richness and abundance of birds, small mammals, and amphibians that are not explained by landscape features.

The landscape indices alone had little power for predicting vertebrate richness or abundance. Dominance did show some significant relation to small mammal abundance and amphibian richness and abundance, and the fractal dimension was associated with bird and small mammal richness in old-growth stands. These relations were relatively weak, however. We believe that these variables alone would have little utility as indices for management in tracking trends in richness or abundance. They will have some value, however, in providing information on the spatial characteristics of the whole landscape to support the interpretation of other more specific variables describing habitat composition. The fractal index, for example, was most strongly correlated with clearcut area and may be a useful index of logging disturbance, although the correlation was only moderately strong ($r = 0.60$).

Response of Species to Fragmentation

Bird richness showed a clear response to fragmentation. Richness in all stands was associated with clearcutting in the immediate neighborhood of the stand, and also in old-growth stands with clearcuts in the landscape. These phenomena were not entirely unexpected: they conform to the conventional edge-effect of richness increasing with disturbance from the influx of early successional and edge species (Leopold 1933, Raphael and Barrett 1984, Raphael and others 1988, Rosenberg and Raphael 1986, Verner 1986). Among the four generalist species well represented in the data set (American robin, black-throated gray warbler, dark-eyed junco, and rufous hummingbird), however, only rufous hummingbird abundance showed a clear correlation with clearcuts in the surrounding area. Black-throated gray warbler abundance had a negative relation with late-successional forest in the buffer, which can be construed as a preference for young forest as found by Huff and Raley (this volume). If the edge effect drives bird richness, we would expect future studies to show bird richness to peak at 50 percent cutover, when the areas of late-successional forest and clearcuts are equal and edge length peaks.

The regression model predicted high bird abundance in old, large, stands surrounded by old growth in the buffer zone, and in landscapes with a high proportion of clearcut area and a low proportion of old-growth area. Similar results were found in old-growth stands where abundance increased with the reduction of surrounding old-growth and late-successional forest, and with the addition of more clearcuts in the landscape. We believe this phenomenon is a result of the conventional edge effects described earlier and the "packing" (Rosenberg and Raphael 1986, Whitcomb and others 1981) of late-successional-forest birds displaced from adjacent logged forest into remaining old-growth stands. Abundance data for red-breasted nuthatches and pine siskins, two common birds normally associated with late-successional forest habitats (Huff and Raley, this volume), support our packing hypothesis with greater abundance in stands surrounded by clearcuts.

The pattern of associations that indicate packing were not entirely clear for all forest birds, however. The common winter wren was more abundant in stands surrounded by late-successional forest with few clearcuts. Negative correlations between the abundance of black-throated gray warblers, hermit-Townsend's warblers, and western flycatchers and old-growth or late-successional forest surrounding the stand might be construed to support packing, but are probably a consequence of these birds' affinities for younger stands (Huff and Raley, this volume) rather than a negative response to clearcutting.

Small mammal richness and abundance, and the abundance of individual small mammal species, showed little response to fragmentation. Marsh shrews were more abundant in stands in disturbed landscapes with relatively more clearcut than in late-successional forest. Water shrews, however, showed a strong association with late-successional forest in the neighborhood of stands.

Amphibian richness and abundance were mainly influenced by stand-scale variables, primarily elevation, but also showed an affinity for landscapes with high habitat-dominance. Interpreting the relation to habitat dominance in terms of habitat components is difficult, except to say that dominance was moderately correlated ($r = 0.68$) with late-successional forest in the landscape. That relation is somewhat contradicted, however, by the negative correlation between amphibian abundance and old growth (a component of late-successional forest) in the landscape.

A somewhat weaker packing-effect than seen with birds could be inferred for amphibian abundance by a negative association with old growth in the buffer, as indicated by partial correlation and regression, and the positive correlation between abundance in old-growth stands and surrounding clearcut area. The western redback salamander was the only species with an abundance consistent with that pattern, showing a positive correlation with stand size and a negative correlation with old growth in the buffer zone. The negative association with buffer old growth, however, is consistent with its greater abundance in young rather than old stands (Aubry and Hall, this volume). No strong relation were found for other amphibian species.

Management Implications

The greater richness of birds in stands situated in clearcut landscapes does not mean that clearcutting is the preferred practice to maintain biotic diversity on forest lands. The increase in species diversity is caused by the influx of generalist species adapted to human-disturbed landscapes. Generalist species will likely persist in forest landscapes regardless of management practices, but late-seral species will decline with conversion of late-successional forest to early seral stages. Increasing local diversity by adding generalist species is less important than maintaining the quality of biotic diversity regionally through retention of specialist or endemic species (Murphy 1989, Samson and Knopf 1982, Van Horne 1983, Verner 1986).

Why did we not detect strong relations between species richness or abundance and habitat fragmentation? An optimistic assessment is that we have not yet reached the threshold of fragmentation where populations begin to decline. Rosenberg and Raphael (1986) made a similar assessment of the situation in northern California. Models of vertebrate response to fragmentation suggest that species diversity will begin to decline when 50 to 75 percent of the landscape is cutover (Franklin and Forman 1987, McLellan and others 1986) within a short enough period that late-successional forest will not have been replaced by succession. Our study areas and much of the Western public forest lands have not yet reached that stage of fragmentation. Other interpretations, however, suggest various processes operating beyond the scope of our study to mask the potentially negative effects of fragmentation on biotic diversity.

The packing displayed by birds and amphibians suggests that some animals associated with late-successional forest are at artificially high populations in some stands. Whitcomb and others (1981) found that populations of forest birds packed into remnant patches were later greatly reduced or eliminated from those areas. This finding has important implications for interpreting ecological research, monitoring populations, and assessing habitat relations.

A lag in resident-species population decline after isolation caused by fragmentation may further complicate interpretations of abundance. Populations of long-lived species may not show instantaneous responses to isolation because the relaxation time may be long (Shaffer 1981). A source-and-sink effect suggested by higher small mammal richness and the abundance of cavity-nesting birds in young stands surrounded by old-growth may also confound evaluation of habitat use and the effects of patch size and isolation. Our results suggest that the value of early-successional communities as wildlife habitat may be overestimated where adjacent habitats are possible sources of immigrants. The same relation may occur between small sink-patches and large source-patches of the same habitat. Populations may appear high in sink-patches, but net reproduction is negative and the population is maintained only through immigration from nearby sources (Pulliam 1988, Van Home 1983). A related process is the "rescue effect" (Brown and Kodric-Brown 1977), in which immigrants from large, viable habitat patches rescue declining or extirpated populations in intermittently viable patches and present a false impression of viability.

Finally, extinctions caused by fragmentation are influenced by stochastic demographic, environmental, and genetic processes (Gilpin and Soule 1986, Shaffer 1981) that may not have been active during the study period. Long-term studies are necessary to account for all these unpredictable controls on population viability.

The prudent manager will realize that fragmentation-that is, habitat loss and isolation of remaining fragments-will nearly reduce the populations of species associated with late-successional forest and possibly result in their extirpation. Declining population trends are evident in some areas for forest birds (Jarvinen and Vaisanen 1978, Raphael and others 1988), and for small mammals and amphibians (Raphael 1988). The ability of populations that have been reduced by habitat loss to cope with the effects of habitat isolation is determined by the life history and population structural characteristics of the species, and by the success of land managers in implementing low-fragmentation alternatives to current logging practices and managing the landscape as an interacting network of habitats. The absence of strong negative responses to forest fragmentation in our study optimistically suggests that we have not yet reached the threshold of decline for most vertebrates, and still have the management opportunity to ensure the integrity of vertebrate communities in Pacific Northwest Douglas-fir forests.

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Wildlife Habitat Relationships and Viable Populations

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The issue that has provided the greatest impetus for research on wildlife habitat relationships on Federal lands has been concern about preserving biological diversity-that is maintaining viable populations of native plants and animals. Some animals, like wolves, grizzlies, and spotted owls, have exciting and dramatic natural histories and charismatic appeal to the general public, so we hear a lot about them. But the statutes and regulations that guide public land management clearly direct land managers to maintain viable populations of all native species as efforts are made to preserve, and sometimes enhance, biological diversity.

To maintain viable populations, the kinds, amounts, and arrangements of environments necessary for populations to survive over long periods-not just for the next few years-must be met. The knowledge that these environments are essential comes from ecological theory and applied research in plant and animal ecology, including wildlife habitat studies. The many different terms commonly used in discussions about habitat relationships are important because they influence the way we think about very complex ecological interactions.

One frequently used term that has been the focus of attention ever since the importance of old-growth Douglas-fir forests to wildlife emerged as an issue is “dependency” (Carey 1984). The term is uncommon in the literature of ecology and wildlife management, and no definition of dependency or explicit practical criteria for determining whether a population is dependent on a particular environment had been published until recently (Ruggiero and others 1988). The concept of dependency involves an extremely complex and dynamic array of ecological interactions. Ecology is defined as “. ..the scientific study of interactions that determine the distribution and abundance of organisms” (Krebs 1985). Because studying dependencies also includes studying the interactions that determine the distribution and abundance of organisms, the Krebs’ definition (and common sense) suggests that the concept of dependency includes virtually all aspects of ecology. I find this realization rather sobering, yet in spite of its implications, the terms dependent and dependency are used freely and rather casually by the media, in political debate, and in discussions among biologists about wildlife and old growth. This broad usage has, I believe, led to some confusion about the nature of wildlife habitat relationships.

Most people define dependency in fairly simple terms-a habitat or habitat element that is required for a population to exist. But given the complexity of ecological systems, such requirements are not always recognizable. Ecological requirements are not necessarily the same across the entire geographic range of a species. Most important, ecological requirements may change over time as environmental conditions change. Because requirements can change over time, the focus of research should not only be on the features of the environment that are required for a population to exist under a given set of conditions, but also on the requirements necessary for the population to persist over time under varying environmental conditions. The profound difference between **existence** and **persistence** must be clearly recognized.

Ecological dependency describes the relationship between a population and the environment or environments required for its persistence. Populations will persist only if sufficient kinds, amounts, and patterns of environments are available to meet the biological needs of individuals within populations and if these environments provide sufficient resources to sustain populations over time as environmental, genetic, and demographic conditions fluctuate (Ruggiero and others 1988).

Population persistence is likely to involve complex and often subtle interactions that may vary over time (season, year, or longer) or with chance events that may affect environments and populations in dramatic ways. So, although all organisms in some way depend on the environment in which they exist, dependency is best thought of as an ecological concept rather than as a precisely or readily measurable state of nature. The term “ecological dependency” emphasizes the dynamic and interactive nature of the concept in both space and time. Discussions about wildlife habitat in general and about dependency in particular sometimes fail to consider this perspective. I am convinced that meaningful scientific and political discussions about maintaining viable wildlife populations require that participants understand the concept of ecological dependency, and then come to grips with some very real problems with the way people generally think about dependency. This understanding will mean sharing a common perspective about ecological requirements.

As a further example, when the ecological requirements of wildlife are assessed, populations should be the focus rather than individuals or species. The concepts of dependency and population viability both focus on the issue of **population** persistence (Ruggiero and others 1988, Shaffer 1981). Yet observations of one or a few individuals are too often generalized to the species or to the population scale of biological organization. The debate over whether spotted owls depend on old growth is a good illustration of how focusing on individuals can confuse the issue and lead to misunderstandings about habitat requirements. Anecdotes about individual owls observed in unusual environments do not adequately represent the behavior of the population in selecting habitat. Statistical analyses determine when enough individuals from a population have been observed to reliably estimate the mean and variance associated with a particular attribute. Until a population has been studied in this way, how well the behavior of one or more individuals reflects the ecological requirements of the population to be maintained is unknown. Thus, questions about dependency must address population attributes, not the attributes of individuals. A similar danger exists in overgeneralizing about the ecological requirements of populations based on broad observations of a species, which can happen when discrete, ecologically meaningful populations are not identified. It can also result in confusion about population versus species attributes and about ecotypic variation within species.

The concept of ecotypes has been around for a long time, but its importance is sometimes overlooked. Ecotypes are populations adapted to a set of local conditions-in other words, populations of a particular species that are adapted to some part of the species’ geographic range (Odum 1971). Defining populations too broadly can result in generalizations about ecological requirements that fail to meet the needs of locally adapted populations. Simply because a given species exists as a set of ecotypes across a range of environments does not mean that any given ecotype is equally plastic and can quickly “adapt” to drastically altered environments. Adaptations exhibited by one ecotype cannot be assumed to be within the range of genetic potential of another ecotype. The spotted owl serves once again as a practical example: the habitat associations and ecological requirements of the northern spotted owl must not be confused with those of its southern relatives.

When wildlife habitat requirements are being assessed, degrees of association should be recognized, rather than two simple states of naturedependent or not dependent. Some species and some environments may have no association at all. Others may have an exclusive association, and the species will occur in only that one environment. Answering questions about dependency at these extremes is relatively easy. But at what point along a gradient of increasing association a population becomes dependent on some habitat is not known. When a population is substantially more abundant in a given habitat than in any other-when it is “closely associated” with that habitat-it should be assumed **to require** that habitat for long-term persistence.

Such close associations can be inferred from patterns of species abundance (for example, when a population is abundant in old growth but rarely found in younger forests), from measures of how well a population reproduces in a particular habitat, and from observations of when the habitat is used (for example, in instances where a population reaches its highest reproductive attainment in a particular habitat or when the habitat is selected during a critical period). But intensive study of individual species is required to determine how various amounts and arrangements of the habitat in question will influence the probability of population persistence. For example, although the loss of old growth would be expected to result in a significant decline in numbers of a closely associated population, predictions cannot be more precise until intensive studies are conducted to better understand why the population exhibits a close association with old growth.

Nevertheless, a close association with a habitat should be interpreted to indicate ecological requirements for persistence. This condition must be accepted as indicating dependency unless more intensive research supports a different interpretation. Equivocating and insisting on "absolute proof of dependency before committing to the appropriate management actions is inappropriate. The scientists who provide research results and the managers who use those results must recognize that such absolute knowledge is usually not attainable.

One of the major accomplishments of the studies reported in this volume is that they have identified species that are closely associated with old-growth Douglas-fir forests (see Ruggiero and others, this volume, for a summary). The principal limitation in these studies is that without additional research, recommendations for managing most of these species cannot be very precise. In addition, several species were found to be more abundant in old-growth than in young and mature forests, but still occurred in high numbers in earlier stages of unmanaged forests. We remain uncertain to what extent this group would be affected by eliminating old growth.

Although old-growth forests are unique and potentially critical components of Western Hemlock Zone ecosystems, a related but broader issue is emerging. This new issue is about managed versus natural or unmanaged forest landscapes, and the importance of all developmental stages of unmanaged forests in meeting the ecological needs of wildlife.

Under certain conditions, undisturbed Douglas-fir-dominated forests can occupy a site for over 1000 years and are in old-growth condition for 80 percent or more of their lifespan (Spies and Franklin 1988). But 80 years is a common rotation age for managed forests in the Pacific Northwest. How will wildlife respond as the predominant forest type shifts toward these younger, generally less complex forests? Will short-rotation landscapes containing islands of dedicated old growth be better for late-successional wildlife than landscapes managed on a 250-year rotation, but largely devoid of older forests? Such questions are unlikely to be answered in our lifetimes. Society should, therefore, be conservative and recognize the inherent uncertainty in any long-term management strategy. A range of options should be considered for meeting the needs of late-successional forest wildlife, including retaining the largest remaining old-growth tracts within some suitable managed forest matrix (Thomas and others 1988).

The research results presented in this volume demonstrate the ecological diversity found in all developmental stages of unmanaged forests, and establish their importance as wildlife habitat. These results provide a place to start in designing managed landscapes that will provide maximum benefits to wildlife species associated with late-successional forests.

Ecology is a young science. Questions related to maintaining viable populations push this developing science to its limits, and many problems need to be solved before most of these questions can be answered. These problems will not be solved by politicians or lawyers or economists: nor will solutions be found on the pages of the Harvard Business Review or by applying corporate models for risk assessment. Rather, these problems will be solved only by ecologists and through a significant and sustained commitment of time and money in the conduct of scientific research. In the meantime, ecologists should continue to give decision-makers the very best information they can; they should offer interpretations and judgments as part of their professional responsibility; and rather than apologizing for their uncertainty, they should stress the substantial body of ecological understanding upon which they base their opinions.

Although the problems are extremely complex, the most important tools for meeting these challenges are not multivariate analyses nor sophisticated research methods. The most important tools are the creativity, intuition, and judgment of our best ecologists, And to the extent that society demands solutions to ecological problems, these tools must suffice, and those who possess them must have a seat at the decision-making table. □

Plant and Animal Habitat Associations in Douglas-Fir Forests of the Pacific Northwest: An Overview

Leonard F. Ruggiero, Lawrence L.C. Jones, and Keith B. Aubry

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Introduction

This book contains the most comprehensive and detailed research information ever reported for wildlife habitat relationships in the Pacific Northwest, and it is likely that the scope and intensity of this research program (see Carey and Spies, this volume) will not soon be duplicated. The results reported here represent the best information currently available for evaluating the effects of land management decisions on wildlife and vegetation and for identifying the most productive avenues for new research.

The primary objective of the Old-Growth Forest Wildlife Habitat Program was to identify wildlife and plant species that depend upon or find optimal habitat in old-growth Douglas-fir forests (Carey and Spies, this volume). The purpose of this paper is to summarize in tabular form the major patterns of association among forest age-classes for all wildlife and plant species that were adequately studied in at least one physiographic province during this research effort. The information contained in the following matrices was provided by the scientists responsible for collecting, analyzing, and interpreting the data. These designations result from statistical analyses, review of pertinent literature, and the professional judgments of the principal investigators. Unlike similar compendia of wildlife habitat relationships, the information in this chapter is derived primarily from actual field research in the geographic areas listed, and the interpretation of research findings has been done by the scientists who conducted the studies. Detailed descriptions of research methods, data analyses, and interpretive rationales can all be found elsewhere in this volume (see also Carey and Ruggiero, in press).

Wildlife habitat relationships are dynamic, especially over long periods of time, and such relationships are generally not reducible to “obligatory vs. non-obligatory” associations (Ruggiero and others 1988). A species’ ecological and biological requirements may change as a function of its reproductive status, age, and environment, and habitat associations can change accordingly. Moreover, habitat requirements can be subtle and difficult to detect, and can be based upon or modified by interactions with other species (Simberloff 1983). When available information is limited to general patterns of species' abundances derived from extensive community sampling, precise descriptions of each species' habitat requirements are difficult. Even after intensive autecological study, habitat relationships may not be precisely definable.

Nature of the Data

Some attributes of the data upon which this summary information is based should be kept in mind. First, the study stands were preferentially selected to represent a wide range of site conditions occurring in young, mature, and old-growth Douglas-fir forests across a broad geographic area (Carey and Spies, this volume). Consequently, the statistical variation within each age-class makes detecting significant differences among age-classes difficult. In other words, such a selection process is expected to result in greater variation and fewer statistically significant differences in measured parameters among age-classes than if the stands had been selected randomly; these results are therefore conservative. Conversely, ecologically important differences may exist in the absence of statistical significance (see Connor and Simberloff 1986). Thus, we recommend careful consideration of these caveats when interpreting results that fail to demonstrate statistically significant relationships, especially for those species that have been designated as "associated" with a particular age-class (see Summary Matrices).

Second, the influence of stand size and surrounding habitats (stand context) on species' abundances within old-growth study stands was largely uncontrolled. Old-growth stands varied considerably in size. Although the old-growth study stands were relatively large-78 percent were larger than 100 ha-they were often irregularly shaped and located in various contexts within landscapes containing on average only about 25 percent old growth (J. Lehmkuhl, pers. comm.).

Lastly, the survey techniques used were designed to sample the broadest possible assemblage of species within a community. As a result, relatively few data were collected on rare or highly vagile species. Thus, for certain species of special interest or concern to forest managers, such as the red tree vole and pileated woodpecker, the ability to evaluate observed patterns of abundance or occurrence was limited by small sample sizes. More intensive research will be necessary to generate adequate information on the habitat relationships of these species. Other species were either not effectively sampled with our techniques (for example, highly mobile avian and mammalian predators) or were so locally distributed (for example, Larch Mountain salamanders) that insufficient data were collected for any conclusions about their habitat associations to be made. Lack of information, however, should not be equated with a lack of concern about the potential effects of forest management on these species. Further research is urgently needed on at least the following species or species groups: the Larch Mountain salamander, Siskiyou Mountains salamander, Van Dyke's salamander, spotted frog, Keen's myotis, white-footed vole, carnivores (especially the marten), accipiter hawks (especially the goshawk), and numerous nonvascular plant species.

Structural Diversity in Naturally Regenerated Forests

Virtually all of the study stands were naturally regenerated after wildfires. Consequently, these results do not apply to intensively managed forest stands. Because some structural or vegetative components of stands, such as large snags, logs, and live trees, generally survive even catastrophic wildfires, such components often carry over from the preceding mature or old-growth stand to the new, young stand (Spies and others 1988, Spies and Franklin 1988). Intensively managed forest stands, which generally lack such components (Spies and Cline 1988), may not provide suitable habitat for wildlife associated with these features.

Because of these carryover components and variation in establishment patterns, naturally regenerated Douglas-fir stands can be structurally diverse, even in the younger age-classes (Spies and Franklin, this volume). Moreover, the regional pattern of natural disturbances typically created forest mosaics where stands of different ages resulting from a varied history of disturbance were interspersed with relatively old, undisturbed forest (Agee, this volume; Spies and Franklin 1988). This process created widespread habitat conditions that consisted either of late-successional forests or younger forests containing structural or vegetative characteristics of late-successional forests. The structural diversity of naturally regenerated young stands and an interspersed pattern of disturbance probably interacted to maintain high ecological diversity in natural landscapes (Hansen and others, in press).

Given that presettlement landscapes in this region were composed of a wide variety of vegetative conditions, including large expanses of suitable habitat for species adapted to late stages of forest development, some species would logically have become adapted to structurally diverse forests (Thomas and others 1988). Current forest management practices have resulted in extensive simplification of stand structures (Spies and Cline 1988) and fragmentation of natural forests (Lehmkuhl and Ruggiero, this volume; Morrison 1988). Although young plantations that have already been established for timber production can be modified to improve their habitat capability (Spies and others, in press), the ecological values of new approaches to harvesting remaining late-successional forests (Franklin 1989) have not yet been evaluated through field research.

Alternative silvicultural strategies may be needed to maintain populations of species adapted to structurally diverse stands or to unfragmented forest conditions. Perhaps such species can be maintained by aggregating disturbances at the landscape scale and leaving various components of harvested stands to add complexity and important functional elements to managed stands and landscapes (Franklin 1989). The results presented here suggest that such a scenario imitates natural disturbance regimes more closely than traditional silvicultural practices and is more compatible with the goal of maintaining biological diversity. The extent to which such alternative management strategies could functionally replace extensive blocks of relatively undisturbed late-successional habitat is unknown, however.

Summary Matrices

The designations listed in the following matrices are intended to summarize the results of the studies reported in this book. These designations therefore reflect comparisons of indices to abundance among old-growth (200-730 yr), mature (80-195), and young (35-79) age-classes of unmanaged, naturally regenerated, closed-canopy forests in the Douglas-Fir/ Western Hemlock Zone of western Oregon and Washington and northwestern California (Franklin and Dyrness 1973). Although a large percentage of the species listed are primarily forest-dwelling species that occur most commonly in the forest zone we studied, many also occur in other forest types or in precanopy seral stages of Douglas-fir/ western hemlock forest. Consequently, because some species may have closer associations with other habitats not considered here, these designations should be viewed with caution-they only reflect **relative differences** in patterns of abundance among the three seral stages of unmanaged forest we studied. The following designations represent the operational definitions used by the principal investigators to assign degrees of association among age-classes for each species.

* *Closely Associated.* A species was designated as “closely associated” with a seral stage if it was found to be significantly more abundant (based on statistical significance levels set by each investigator) in that seral stage compared to the other seral stages, or if it is known to occur almost exclusively in that seral stage.

\+ *Associated.* A species was designated as “associated” with a seral stage if it was found to be numerically more abundant in that stage compared to the other seral stages. [Note: some species were also designated as associated with old growth if they were determined to require one or more habitat features that are characteristic of that seral stage, such as very large diameter logs, snags, or broken-top live trees.]

P *Present.* A species was designated as “present” in a seral stage if it occurred in that seral stage in numbers lower than or equal to those found in the other seral stages.

? *Unknown.* A species was designated as “unknown” across all seral stages in a given geographic area if the species was not studied or the data collected were insufficient for any designations to be made.

/ A species was designated with a diagonal slash across all seral stages if it does not occur in the geographic area sampled.

For species designated as closely associated with old growth, we predict that a significant reduction in old growth would result in a marked decline in the population numbers of those species. The extent to which such a decline would threaten the persistence of each population will depend on various environmental, demographic, and stochastic factors. The consequences of a significant loss of old-growth habitat on the population viability of species designated as associated with old growth, are unknown.

The principal investigators that provided the designations shown here **are as** follows: **diurnal forest birds:** Andrew B. Carey (Oregon Coast Range), Frederick F. Gilbert (Oregon Cascade Range), David A. Manuwal (Southern Washington Cascade Range), Mark H. Huff (Regional Analyses for Oregon and Washington; Southern Washington Cascade Range-Winter), Richard W. Lundquist and Jina M. Mariani (Southern Washington Cascade Range-Snag-Dependent Birds), C. John Ralph (northern California and southern Oregon); **small mammals:** Paul Stephen Corn and R. Bruce Bury (Oregon Coast Range), Frederick F. Gilbert (Oregon Cascade Range), Stephen D. West (Southern Washington Cascade Range); Keith B. Aubry (Regional Analyses for Oregon and Washington), C. John Ralph (northern California and southern Oregon); **bats:** Donald W. Thomas (Oregon Coast Range; Southern Washington Cascade Range); **amphibians:** R. Bruce Bury and Paul Stephen Corn (Oregon Coast Range; Regional Analyses for Oregon and Washington), Frederick F. Gilbert (Oregon Cascade Range), Keith B. Aubry (Southern Washington Cascade Range), Hartwell H. Welsh, Jr., and Amy J. Lind (northern California and southern Oregon); **vascular plants:** Thomas A. Spies (Oregon and Washington) and Bruce B. Bingham (northern California and southern Oregon); **hypogeous fungi:** Daniel L. Luoma (Oregon Cascade Range).

For birds, mammals, amphibians, and reptiles, all species for which data collected were sufficient for analyses in at least one province are included. For vascular plants, only those species showing an association with a particular age-class in at least one province are included. Hypogeous fungi were only studied in the Oregon Cascade Range. Because sampling for hypogeous fungi was not as intensive nor extensive as for other taxa, the likelihood of not detecting the presence of a species within a particular age-class was high. For this reason, dashes were used in the matrix for hypogeous fungi to indicate that the species was not detected in forests of that age-class.

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Hypogeous Fungi

	Oregon Cascade Range		
Species	**Y**	**M**	**OG**
Alpova trappei Fogel	+	*	P
Destuntzia fusca Fogel & Trappe	–	–	P
Elaphomyces granulatus Fries	P	P	+
Elaphomyces muricatus Fries	–	+	+
Endogone lactiflua Berkeley & Broome	P	P	P
Gautieria gautierioides (Lloyd) Zeller & Dodge	–	–	P
Gautieria monticola Harkness	+	+	P
Genabea cerebriformis (Harkness) Trappe	P	–	P
Genea intermedia Gilkey	–	–	P
Geopora cooperi Harkness	–	–	P
Hydnotrya variiformis Gilkey	–	P	P
Hymenogaster gilkeyae Zeller & Dodge	–	–	P
Hymenogaster parksii Zeller & Dodge	–	–	P
Hymenogaster sublilacinus Smith	P	–	–
Hysterangium coriaceum Hesse	+	P	P
Hysterangium crassirhachis Zeller & Dodge	–	+	+
Hysterangium setchelii Fischer	P	P	+
Leucogaster gelatinosus Fogel	P	–	–
Leucogaster rubescens Zeller & Dodge	P	P	P
Leucophleps magnata Harkness	+	+	P
Leucophleps spinispora Fogel	P	P	P
Martellia brunnescens Singer & Smith	+	–	P
Martellia ellipsospora (Zeller) Singer & Smith	–	–	P
Martellia fallax Singer & Smith	–	P	–
Martellia oregonensis (Zeller) Singer & Smith	–	–	P

Hypogeous Fungi	Oregon Cascade Range		
Species	**Y**	**M**	**OG**
Martellia parksii Singer & Smith	–	–	P
Martellia vesiculosa Singer & Smith	–	P	–
Modicella malleola (Harkness) Gerderman & Trappe	–	–	P
Picoa carthusiana Tulasne & Tulasne	–	–	P
Radiigera atrogleba Zeller	P	–	–
Radiigera taylorii (Lloyd) Zeller	P	–	P
Rhizopogon atroviolaceus Smith	–	–	+
Rhizopogon clavitisporus Smith	–	–	P
Rhizopogon parksii Smith	P	P	P
Rhizopogon subcaerulescens Smith	P	P	P
Rhizopogon truncatus Linder	–	–	P
Rhizopogon villosulus Zeller	P	–	P
Rhizopogon vinicolor Smith	P	P	P
Thaxterogaster pingue (Zeller) Singer & Smith	–	P	P
Truncocolumella citrina Zeller	+	P	P
Truncocolumella sp. nov.	–	–	P
Tuber asa Tulasne & Tulasne	P	–	–
Tuber californicum Harkness	–	–	P
Tuber gibbosum Harkness	P	–	P
Tuber monticola Harkness	–	–	P
Tuber rufum Pico ex Fries	–	–	+
Tuber shearii Harkness in Murrill	–	–	P

Vascular Plants	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Northern California and Southern Oregon		
Species	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**
Understory Trees												
Cascara buckthorn	*	*	P	*	*	P	*	*	P	*	+	P
Pacific yew	P	P	*	P	P	*	P	P	*	P	P	*
Shrubs												
Alaska huckleberry	?	?	?	P	P	P	P	P	+	/	/	/
Common pipsissiwa	?	?	?	P	+	+	P	P	+	P	P	P
Dwarf rose	P	P	P	P	+	P	P	P	P	P	P	P
Little pipsissiwa	P	P	P	+	P	P	P	P	P	P	P	P
Red huckleberry	P	P	P	P	P	P	P	P	+	P	P	P
Thimbleberry	P	P	P	P	P	P	+	+	P	?	?	?
Thin-leaved huckleberry	?	?	?	P	P	P	P	P	+	/	/	/
Herbs and Grasses												
Achlys triphylla	P	P	+	P	*	*	P	P	P	P	+	+
Adenocaulon bicolor	P	+	+	P	+	P	+	+	P	P	P	+
Allotropa virgata	?	?	?	?	?	?	?	?	?	P	+	+
Anemone deltoidea	P	+	P	P	+	P	+	+	P	?	?	?
Anemone lyallii	?	?	?	+	P	P	P	P	P	/	/	/
Arenaria macrophylla	?	?	?	P	*	P	P	P	P	?	?	?
Asarum caudatum	P	P	P	P	P	P	P	P	P	P	+	+
Asarum hartwegii	P	P	+	P	P	+	/	/	/	P	+	+
Aster canescens	?	?	?	P	P	P	+	P	P	/	/	/
Calypso bulbosa	?	?	?	?	?	?	?	?	?	P	+	+
Campula scouleri	P	P	P	P	+	P	+	P	P	P	P	P
Clintonia uniflora	?	?	?	P	P	P	P	P	+	P	+	+

Vascular Plants	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Northern California and Southern Oregon		
Species	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**
Collomia heterophylla	P	P	P	P	+	P	?	?	?	P	P	P
Coptis laciniata	P	P	P	P	P	+	?	?	?	P	P	+
Corallorhiza mertensiana	P	P	P	P	P	P	P	P	+	P	P	+
Cornus canadensis	?	?	?	P	P	+	P	P	*	?	?	?
Festuca occidentalis	P	P	P	P	+	P	P	P	P	P	P	P
Fragaria vesca	P	P	P	P	+	P	P	P	P	P	P	P
Galium triflorum	P	P	P	P	+	P	+	+	P	P	P	P
Galium oreganum	?	?	?	P	+	P	P	P	P	?	?	?
Goodyera oblongifolia	P	P	+	P	+	+	P	+	+	P	+	+
Hypericum perforatum	+	P	P	P	P	P	?	?	?	+	P	P
Linnaea borealis	P	P	*	P	P	*	P	P	*	P	P	P
Montia sibirica	P	P	P	+	+	P	P	P	P	P	P	P
Osmorhiza chilensis	P	P	P	P	P	P	+	+	P	P	P	P
Pityopus californica	?	?	?	?	?	?	?	?	?	P	+	+
Plagiobothrys figuratos	?	?	?	+	P	P	?	?	?	/	/	/
Pleuricospora fimbriolata	?	?	?	?	?	?	?	?	?	P	+	+
Pyrola aphylla	P	P	P	+	P	P	P	P	P	P	P	P
Pyrola asarifolia	?	?	?	P	P	+	P	P	P	P	P	P
Pyrola picta	P	P	P	+	P	P	+	+	P	P	P	P
Synthyris reniformis	P	P	+	P	P	P	?	?	?	P	P	P
Tiarella trifoliata	P	P	P	P	P	+	P	P	P	P	P	P
Vancouveria hexandra	P	P	P	P	+	+	P	P	P	P	+	+
Ferns												
Pteridium aquilinum	+	+	P	*	*	P	*	P	P	+	P	P

Vascular Plants	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Northern California and Southern Oregon		
Species	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**
Lichens												
Lobaria oregona	?	?	?	?	?	?	?	?	?	P	P	*
Lobaria pulmonaria	?	?	?	?	?	?	?	?	?	P	+	+
Lobaria oregana and/or *L. pulmonaria*	P	P	*	P	P	*	P	P	*	?	?	?

Birds	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Regional Analyses for Oregon and Washington			Northern California and Southern Oregon			Endemic[a]	Broadly endemic[b]
Species	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**		
Blue grouse	P	P	P	+	P	+	+	P	+	P	P	P	?	?	?		
Ruffed grouse	P	P	P	P	P	P	P	P	+	?	?	?	?	?	?		
Mountain quail	P	P	P	?	?	?	?	?	?	?	?	?	P	P	P		
Marbled murrelet[c]	P	P	*	/	/	/	/	/	/	/	/	/	P	P	*		
Band-tailed pigeon	P	P	P	P	P	P	P	P	P	?	?	?	?	?	?		
Barred owl[c]	?	?	?	?	?	?	P	P	P	?	?	?	?	?	?		
Northern pygmy-owl	P	+	+	?	?	?	P	P	P	P	P	P	?	?	?		
Northern spotted owl[c]	P	P	*	P	P	*	P	P	*	P	P	*	P	+	*	×	
Allen's hummingbird	/	/	/	/	/	/	/	/	/	/	/	/	P	P	+		
Rufous hummingbird	P	P	P	P	+	+	P	P	P	P	P	P	/	/	/		
Vaux's swift	P	P	*	P	P	*	P	P	*	P	P	*	?	?	?		×
Downy woodpecker	P	P	P	?	?	?	?	?	?	?	?	?	?	?	?		
Hairy woodpecker (spring)	P	P	+	P	+	+	P	P	+	P	P	+	P	P	*		
Hairy woodpecker (winter)	?	?	?	?	?	?	P	P	P	?	?	?	?	?	?		
Northern flicker	P	+	+	P	P	P	P	P	P	P	P	P	P	P	P		
Pileated woodpecker	P	P	+	P	P	+	P	P	+	P	P	+	P	+	+		
Red-breasted sapsucker	P	P	+	P	P	+	P	P	+	P	P	*	P	P	P		
Dusky/Hammond's flycatcher	/	/	/	P	+	+	/	/	/	P	P	P	/	/	/		
Hammond's flycatcher	+	+	P	?	?	?	P	P	P	?	?	?	P	P	P		
Olive-sided flycatcher	P	P	+	P	+	+	P	P	P	P	P	P	P	P	P		
Western flycatcher	P	P	+	P	P	+	P	P	+	P	P	+	P	+	*		
Western wood-pewee	P	P	P	?	?	?	P	P	P	?	?	?	P	P	P		
Common raven	P	P	P	P	+	+	P	P	P	P	P	P	P	P	P		

Continue

Birds	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Regional Analyses for Oregon and Washington			Northern California and Southern Oregon			Endemic[a]	Broadly endemic[b]
Species	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**		
Gray jay (spring)	P	P	P	P	P	P	P	P	+	P	P	P	?	?	?		
Gray jay (winter)	?	?	?	?	?	?	P	P	+	?	?	?	?	?	?		
Steller's jay	P	P	P	P	+	+	P	P	P	P	P	P	P	P	P		
Black-capped chickadee	P	P	P	?	?	?	?	?	?	?	?	?	/	/	/		
Chestnut-backed chickadee (spring)	P	P	+	P	P	+	P	P	+	P	P	+	P	+	+		×
Chestnut-backed chickadee (winter)	?	?	?	?	?	?	P	P	+	?	?	?	?	?	?		×
Red-breasted nuthatch (spring)	P	P	+	P	P	P	P	P	+	P	P	+	P	P	P		
Red-breasted nuthatch (winter)	?	?	?	?	?	?	P	P	+	?	?	?	?	?	?		
White-breasted nuthatch	P	P	P	?	?	?	?	?	?	?	?	?	?	?	?		
Brown creeper (spring)	P	P	+	P	+	+	P	+	+	P	+	+	P	+	*		
Brown creeper (winter)	?	?	?	?	?	?	P	P	P	?	?	?	?	?	?		
House wren	P	P	P	?	?	?	?	?	?	?	?	?	?	?	?		
Winter wren (spring)	P	P	P	P	+	+	P	P	+	P	P	P	+	P	+		
Winter wren (winter)	?	?	?	?	?	?	P	P	P	?	?	?	?	?	?		
Golden-crowned kinglet (spring)	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P		
Golden-crowned kinglet (winter)	?	?	?	?	?	?	P	P	P	?	?	?	?	?	?		
Ruby-crowned kinglet	P	P	P	?	?	?	?	?	?	?	?	?	?	?	?		
American robin	P	P	P	+	P	P	P	P	P	P	P	P	P	+	+		
Hermit thrush	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P		
Swainson's thrush	P	P	P	+	P	P	P	P	+	P	P	P	?	?	?		
Townsend's solitaire	P	P	P	P	P	P	P	P	P	P	P	P	+	P	P		
Varied thrush (spring)	P	+	+	P	+	+	P	P	+	P	P	P	P	P	P		×
Varied thrush (winter)	?	?	?	?	?	?	P	P	P	?	?	?	?	?	?		×

Birds	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Regional Analyses for Oregon and Washington			Northern California and Southern Oregon			Endemic[a]	Broadly endemic[b]
Species	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**		
Wrentit	P	P	P	/	/	/	/	/	/	P	P	P	P	P	+		
Black-throated gray warbler	P	P	P	+	P	P	+	P	P	+	P	P	+	+	P		
Hermit warbler	+	P	P	P	P	P	?	?	?	?	?	?	P	+	+		
Hermit/Townsend's warbler	/	/	/	/	/	/	+	P	P	+	P	P	/	/	/		
MacGillivray's warbler	P	P	P	P	P	P	P	P	P	P	P	P	?	?	?		
Nashville warbler	+	P	P	P	P	P	?	?	?	P	P	P	P	P	P		
Orange-crowned warbler	+	P	P	?	?	?	?	?	?	P	P	P	P	P	P		
Townsend's warbler	?	?	?	+	P	P	?	?	?	?	?	?	?	?	?		
Wilson's warbler	P	P	P	+	P	P	P	P	+	P	P	P	P	P	P		
Yellow-rumped warbler	P	P	P	+	+	P	P	P	P	P	P	P	P	P	P		
Hutton's vireo	+	P	P	P	P	P	+	P	P	P	P	P	P	P	P		
Solitary vireo	?	?	?	+	+	P	P	P	P	?	?	?	P	+	+		
Warbling vireo	+	P	P	?	?	?	P	P	P	?	?	?	P	P	P		
Western tanager	+	P	P	+	+	P	+	+	P	P	P	P	P	+	+		
Chipping sparrow	P	P	P	?	?	?	?	?	?	?	?	?	?	?	?		
Dark-eyed junco	+	P	P	P	P	P	P	P	P	P	P	P	P	P	P		
Rufous-sided towhee	P	P	P	?	?	?	?	?	?	?	?	?	P	P	P		
Song sparrow	P	P	P	?	?	?	P	P	P	?	?	?	?	?	?		
Black-headed grosbeak	+	P	P	+	P	P	P	P	P	P	P	P	P	+	+		
Evening grosbeak	P	+	P	+	+	P	+	+	P	P	P	P	P	P	P		
Pine siskin (spring)	P	P	P	P	P	P	P	P	P	P	P	P	P	P	P		
Pine siskin (winter)	?	?	?	?	?	?	P	P	+	?	?	?	?	?	?		
Purple finch	+	P	P	?	?	?	P	P	P	P	P	P	P	P	P		
Red crossbill (spring)	P	P	P	P	P	+	P	P	+	P	P	P	P	P	P		

Birds	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Regional Analyses for Oregon and Washington			Northern California and Southern Oregon			Endemic[a]	Broadly endemic[b]
Species	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**	**Y**	**M**	**OG**		
Red crossbill (winter)	?	?	?	?	?	?	P	P	+	?	?	?	?	?	?		
Guilds																	
Aerial foragers	?	?	?	?	?	?	?	?	?	+	P	+	?	?	?		
Bark foragers (spring)	P	P	+	P	P	+	P	P	+	P	P	*	?	?	?		
Bark foragers (winter)	?	?	?	?	?	?	P	P	+	?	?	?	?	?	?		
Canopy seedeaters (winter)	?	?	?	?	?	?	P	P	+	?	?	?	?	?	?		
Totals																	
All resident species	?	?	?	?	?	?	?	?	?	P	P	+	?	?	?		
Total abundance (spring)	?	?	?	?	?	?	P	P	+	P	P	+	?	?	?		
Total abundance (winter)	?	?	?	?	?	?	P	P	*	?	?	?	?	?	?		

Mammals	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Regional Analyses for Oregon and Washington			Northern California and Southern Oregon			Endemic[a]	Broadly endemic[b]
Species	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG		
Marsh shrew	P	+	+	P	P	P	P	P	P	P	P	P	?	?	?	×	
Montane shrew	/	/	/	+	+	P	P	P	P	P	P	P	/	/	/		
Pacific shrew	P	+	P	P	+	+	/	/	/	P	P	P	P	P	P	×	
Trowbridge's shrew	P	+	P	P	P	P	P	P	P	P	P	P	P	P	P		×
Vagrant shrew	P	P	P	+	P	P	P	P	P	P	P	P	?	?	?		
Coast mole	P	P	P	P	+	P	P	P	P	P	P	P	?	?	?		
Shrew-mole	P	+	+	P	+	+	P	P	P	P	P	*	?	?	?	×	
Big brown bat and/or Fringed myotis	P	P	*	?	?	?	?	?	?	?	?	?	?	?	?		
Long-legged myotis	P	P	*	?	?	?	P	P	*	?	?	?	?	?	?		
Myotis A bats[d]	P	P	*	?	?	?	P	P	*	?	?	?	?	?	?		
Myotis B bats[e]	P	P	*	?	?	?	P	P	*	?	?	?	?	?	?		
Silver-haired bat	P	P	*	?	?	?	P	P	+	?	?	?	?	?	?		
Douglas' squirrel (spring)	?	?	?	?	?	?	?	?	?	?	?	?	P	+	+		×
Douglas' squirrel (winter)	?	?	?	?	?	?	P	P	+	?	?	?	?	?	?		×
Northern flying squirrel	P	P	+	+	P	P	?	?	?	P	P	P	?	?	?		
Townsend's chipmunk	?	?	?	P	P	P	P	P	P	?	?	?	/	/	/	×	
Creeping vole	?	?	?	P	P	P	P	P	P	P	P	P	?	?	?	×	
Red tree vole	P	P	*	P	*	*	/	/	/	P	P	*	P	P	+	×	
Southern red-backed vole	/	/	/	/	/	/	P	P	P	?	?	?	/	/	/		
Western red-backed vole	P	+	P	P	+	P	/	/	/	P	P	P	P	+	+	×	
Deer mouse	P	P	P	P	+	+	P	P	+	P	P	+	P	P	P		
Forest deer mouse	/	/	/	/	/	/	P	+	+	?	?	?	/	/	/	×	
Piñon mouse	/	/	/	/	/	/	/	/	/	/	/	/	P	P	P		
Pacific jumping mouse	?	?	?	P	P	P	P	P	P	?	?	?	?	?	?	×	

Mammals

	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Regional Analyses for Oregon and Washington			Northern California and Southern Oregon			Endemic[a]	Broadly endemic[b]
Species	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG		
Ermine	?	?	?	P	P	P	?	?	?	P	P	P	?	?	?		
Fisher[c]	P	P	+	P	P	+	P	P	+	P	P	+	P	P	+		

Amphibians and Reptiles	Oregon Coast Range			Oregon Cascade Range			Southern Washington Cascade Range			Regional Analyses for Oregon and Washington			Northern California and Southern Oregon			Endemic[a]	Broadly endemic[b]
Species	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG	Y	M	OG		
Amphibians																	
Northwestern salamander	P	P	P	P	P	+	P	P	*	P	P	*	?	?	?	×	
Cope's giant salamander	/	/	/	?	?	?	P	P	+	/	/	/	/	/	/	×	
Olympic salamander	P	P	*	P	P	+	P	P	+	P	P	+	P	P	*		×
Pacific giant salamander	P	P	+	P	P	+	P	P	+	P	P	+	P	P	P		×
Black salamander	/	/	/	/	/	/	/	/	/	/	/	/	P	P	P		×
California slender salamander	/	/	/	/	/	/	/	/	/	/	/	/	P	+	+		×
Clouded salamander	P	P	+	P	P	+	/	/	/	/	/	/	P	P	+	×	
Del Norte salamander	/	/	/	/	/	/	/	/	/	/	/	/	P	P	*	×	
Dunn's salamander	P	P	+	P	P	P	/	/	/	/	/	/	?	?	?	×	
Ensatina	P	P	P	P	P	P	P	P	P	P	P	P	P	P	+		
Oregon slender salamander	/	/	/	P	P	+	/	/	/	/	/	/	/	/	/	×	
Western redback salamander	+	P	P	P	P	P	+	P	P	*	P	P	/	/	/	×	
Roughskin newt	P	P	+	+	P	P	P	P	*	P	P	P	P	P	P		×
Pacific treefrog	?	?	?	?	?	?	?	?	?	?	?	?	P	P	P		
Tailed frog	P	P	+	+	P	+	P	+	+	P	P	+	P	*	*		×
Foothill yellow-legged frog	?	?	?	/	/	/	/	/	/	/	/	/	P	P	P		
Red-legged frog	+	P	P	P	P	P	P	P	P	P	P	P	?	?	?		
Reptiles																	
Northern alligator lizard	?	?	?	?	?	?	?	?	?	?	?	?	P	P	P		×

[a] Geographic distribution is located primarily within the Douglas-fir/western hemlock zone of western Oregon and Washington and northwestern California.

[b] Geographic distribution is located primarily within the humid coastal zone north of San Francisco and the northern Sierra Nevada and west of the Cascade Crest in Oregon, Washington, and British Columbia.

[c] Degree of association with old-growth forests based on data from other studies.

[d] Includes the little brown and/or Yuma myotis.

[e] Includes the California, Keen's, long-eared, and/or western small-footed myotis.

Applying Results of Old-Growth Research to Management: Information Needs, Development of Technical Tools, and Future Research

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Introduction

The objectives of this paper are to describe the application of results from the Old-Growth Forest Wildlife Habitat Program to forest management in the Pacific Northwest Region of the Forest Service, and to identify needed research on old-growth Douglas-fir forests.

The analysis of vertebrate community data presented in this book was designed primarily to identify vertebrate species associated with old growth and to describe habitat features that may account for observed patterns of association. While it does not lend itself to precise predictions about the effects of management on those species, it could and should play an important and immediate role in implementing Forest Plans. Information presented here allows, for the first time, the development of a reliable and scientifically defensible list of vertebrate species associated with old-growth Douglas-fir forests. All of these species should be carefully considered when allocations for late-seral habitat on the National Forests are actually implemented. Information on the habitat associations of these species will help managers make better decisions about the types of forests to include in old-growth management areas, and how best to provide critical habitat features, such as large snags and down wood, in managed stands. Information on the effects of forest fragmentation on wildlife will enable managers to make better decisions about the sequence and spatial arrangement of management activities scheduled in Forest Plans.

During the time this information is being used to help guide the implementation of Forest Plans, it should also be evaluated to see if amendments to Plans are appropriate. Amendments will be appropriate if these results, and other new research and monitoring information, indicate that the Plans will not meet objectives for wildlife habitat, including maintaining viable populations within diverse communities. Recognizing that absolute knowledge is not attainable, managers must make reasonable judgments about the viability of species based on existing information. Amendments may also be made for other reasons, such as the identification of new issues or unexpected effects from implementing Forest Plans. Experience from other Regions of the Forest Service suggests that such amendments may be fairly common and serve to keep the Plans up to date between major revisions. Finally, this information (along with other new findings from monitoring and continued research) will be used to revise Forest Plans either after 10 years or sooner.

Goals, Objectives, and Legal Requirements for Old Growth

For old-growth research information to be applied to management, the goals, objectives, and legal requirements for old growth must be understood. Goals for old-growth management on National Forests include providing recreation, esthetic experiences, and opportunities for scientific study; maintaining water quality; producing high-quality wood products; maintaining biological diversity and long-term productivity; and providing wildlife habitat. The specific goals for wildlife habitat management are established in the National Forest Management Act of 1976 and pursuant regulations (36 CFR 219.19 and 219.27). They are:

- Manage "to maintain viable populations of existing native and desired non-native vertebrate species in the planning area;"
- "...establish objectives for the maintenance and improvement of habitat for management indicator species" selected during the planning process; and
- "...provide for diversity of plant and animal communities...in order to meet overall multiple-use objectives."

Information presented here can eventually help managers address all three of these mandates. Results of the community studies provide the initial scientific basis for determining whether viability is a concern for any of the species demonstrated to be closely associated with old growth. The results will also allow managers to do a better job of selecting management indicator species for future amendments and revisions of Forest Plans. Although using indicator species in forest planning has been controversial, we believe that all species found to be closely associated with old growth should be considered in the management process. Results from these studies will provide information on how to establish and meet objectives for such species. Finally, these results will help to answer questions about biological diversity. A fundamental aspect of managing for diversity of plant and animal communities is to provide for persistence of the full array of seral stages in all forest types. To ensure that we have identified all significant types and stages, forest (and especially, old-growth) classifications should be based on both plant and wildlife communities. Information presented here will be fundamental to developing these classifications.

Information Needed From Old-Growth Research

To develop very specific objectives for management, devise alternative actions that could meet those objectives, and evaluate the effectiveness of such alternatives, very specific information about old-growth habitats and associated species is required. Some specific questions that must be addressed include:

- What species occur in old-growth forests, and how consistent and close is their association with old growth?
- What stand attributes are associated with each species? Can species be classified according to sets of stand attributes? What is the effect on species of different amounts and patterns of these attributes in unmanaged and managed stands?
- What amounts and patterns of old-growth forests should be provided across the landscape to maintain viable and well-distributed populations of old-growth-associated species? What sizes and shapes of old-growth stands are best for providing for old-growth species? What kinds and patterns of edges adversely affect old-growth forest habitat conditions, and how can such effects be mitigated? How is dispersal affected by different forest conditions and the juxtaposition of those conditions?
- What forest management activities (for example, roads, recreation, hunting, timber production) can take place in or near old-growth stands and still be compatible with maintaining adequate habitat for old-growth-associated species? What is the effect of various rotation lengths on old-growth attributes in managed stands? How suitable are stands where elements of old growth (for example, large snags and logs) are maintained, but the surrounding stand is modified by timber harvest? Can old-growth conditions be created in areas currently lacking old-growth forest habitats?

Research information available in this book goes a long way toward answering the first set of questions and provides some information on the second. Ongoing research, especially at the landscape (multi-stand) scale, will provide additional insights into the second and third set of questions. Autecological studies will provide better information on the relationship of old-growth species to their environment, and proposed manipulative experiments will directly test the effects of habitat type, edge, size, and configuration on population and community response.

Answers to the fourth set of questions may be inferred from correlations between habitat attributes and abundances of old-growth species. We believe, however, that providing old-growth conditions or attributes in managed stands and landscapes as a means of increasing the viability of old-growth wildlife populations should be treated as a working hypothesis that needs to be tested empirically. Experimental forests may be ideal settings for testing how well we can create old-growth systems through management, and whether or not old-growth species will persist if provided with old-growth components in habitats modified by timber harvesting.

Developing Information From Research Into Needed Tools and Evaluation Procedures

Once basic information on the ecology and biology of old-growth forests is available from research, it must be assimilated by managers to guide specific management prescriptions. Ultimately, the information must be incorporated into existing administrative procedures and policies for assessing and planning old-growth forest management. This process entails developing the research information into classification and inventory systems, particularly on the abundance and distribution of old-growth forest types and associated wildlife species; summaries of habitat conditions or attributes associated with old-growth wildlife species; summaries of demographics of old growth-associated species; and models depicting the response of wildlife populations to habitat conditions at both stand and landscape scales.

Forest Service wildlife biologists at both Forests and Districts will use the information and assessment procedures in daily operational tasks. These tasks include assessing the effects of proposed forest management activities, and identifying activities consistent with conserving old-growth resources. In addition, specialists in related disciplines-specifically, fisheries biologists, silviculturists, botanists, ecologists, and landscape architects-must also play central roles. They would help bring old-growth evaluation tools and information to the forefront of multiple-resource planning. Educating specialists and managers alike should be part of the development and application of old-growth research information.

Classification Systems

Applying old-growth information to habitat management requires a system of classifying habitats and wildlife communities. Five major objectives and uses define the need for habitat and community classification systems: to reliably predict the successional development of habitats and related changes in wildlife communities; to identify forest conditions with which specific sets of old-growth-dependent wildlife species may be associated; to predict responses of habitat conditions and wildlife populations to management activities; to serve as precursors to inventories and monitoring; and to provide a basis for planning and implementing both research and management activities. In particular, predicting successional development is important for projecting future habitat conditions and response by vegetation and wildlife communities to proposed management activities.

Plant community classifications-Classifications of old-growth forest types should be based on the ecological characteristics of climax or subclimax forest stands and their successional states. The objective is to array ecological forest types along a successional gradient. Successional stages can be inferred from studies on vegetation structure across an age gradient (chronosequence) of young, mature, and old-growth forests. A classification of old-growth habitats may build on the Franklin and Spies (this volume) approach of an index of "old-growthness," much as Raphael and Barrett (1984) developed multivariate correlations of vegetation conditions with stand age in old-growth forests in northwestern California. An old-growth index would describe the degree to which a forest stand, given its dominant plant species and its age, provides various attributes associated with increasing stand age and successional development. These attributes in turn can be related to use by wildlife species. An old-growth index of this type encourages the view of late-successional forests as developmental gradients rather than as discrete types.

Forest habitat conditions associated with each wildlife species and community can be further analyzed to produce a classification of old-growth forest habitats. Several analytical techniques may prove useful. For example, a hierarchical clustering algorithm (see Gauch and Whittaker 1981, Hill and others 1975) applied to the vegetation data from each stand may help identify sets of stands with unique conditions. This approach, however, may merely serve to mirror the criteria that were used originally to select the study stands. Other techniques with which a vegetation classification could be developed include discriminant function analysis and various ordination techniques, such as principal component analysis (see Hill and Gauch 1980, Kantrud and Kologiski 1982, Whittaker 1987).

These classification techniques rely on analysis of vegetation data alone. An old-growth habitat classification could also be developed by correlating the abundance of wildlife species with various old-growth forest attributes. One useful approach is canonical correlation analysis (Gauch 1973, Goldstein and Grigal 1972, Smith 1981), in which variation in the vegetation data is explained through correlations with variation in wildlife abundance data. Conversely, canonical correlation could be used to explain variation in wildlife data, given the vegetation data (see McIntire 1978). Results of canonical correlation analysis are sometimes difficult to interpret, however, and the procedure requires many samples (study stands) relative to the number of variables (vegetation and wildlife attributes of each stand) (Pimentel 1979, Smith 1981). Also, like other ordination techniques, canonical correlation analysis does not produce a classification per se, although component scores can be ordinated along the canonical vectors and a classification of sites (or species) can be derived (see Noy-Meir 1973).

Care must be taken to avoid errors when interpreting results of multivariate analyses (Garsd 1984, Rexstad and others 1988, Wilson 1981). Errors may result from spurious correlations, inadequate sample sizes, and violations of assumptions of normality, linearity, and independence of the data.

Ideally, old-growth habitat classifications would be based on variables found in forest inventory information used by Ranger Districts and National Forests. Forest inventories currently available include Total Resource Inventory (TRI) data bases and ongoing updates to Vegetative Resource Surveys (VRS). Results of Mature and Overmature (MOM) inventories are reported elsewhere in this volume by Marcot and others. A first step will be to determine if TRI, VRS, and MOM data bases contain the necessary habitat variables for use in an old-growth habitat classification system, and if the data have acceptable precision and resolution (scale). At present, the kinds, accuracy, and precision of data bases on old-growth forest habitats vary among National Forests and Districts. Old-growth classification strategies should be flexible enough to be useful in the short term with data bases of varying resolution and accuracy. They should also help identify additional inventory needs in the longer term-that is, define new variables or refine existing variables to greater precision or resolution.

Wildlife community classifications-The objective in developing wildlife community classifications is to identify wildlife guilds and species assemblages that are associated with various forest types and successional stages. A wildlife community classification would identify sets of species associated with specific old-growth conditions and stages, which could be done by producing classifications of species occurring in various successional stages or along gradients of various habitat attributes. Analysis techniques include clustering algorithms, as discussed above. One approach might be to apply gradient analyses on the abundance of each wildlife species, guild, or assemblage for various habitat attributes. Analytical techniques may include ordinations and various multivariate methods that produce mathematical models of species distribution or abundance as functions of habitat conditions.

We anticipate that both classification and gradient approaches will prove useful. Classifications would reveal which groups of wildlife species are likely to be associated with specific sets of habitat conditions. Various species groups may overlap. Gradient analyses may provide information on how the relative abundances of species or species groups change along various environmental gradients, such as stand development, elevation, latitude, or moisture regime in old-growth forests (see Smith and MacMahon 1981).

Specifically, what is needed is a test of how well wildlife species can be classified based on various gradients associated with old-growth forests. Clustering or ordination techniques may be used to test further associations of wildlife species, guilds, or assemblages with unmanaged forest age-classes, moisture-classes, and especially old-growthness gradients and indices. For the latter, a much better understanding of the contribution to wildlife species presence and abundance from old-growth attributes in younger stands is needed, particularly in intensively managed, even-aged stands. One approach might be to use scatter diagrams, simple correlations, stepwise multiple linear regression, logistic regression, and discriminant function analysis to predict the presence or abundance of wildlife species as a function of old-growth stand attributes in young unmanaged forests. Prediction variables may include density of large snags, large logs, large-diameter live trees, and high foliage volumes. Then, the models would be applied to young managed forests, to help identify the kinds and amounts of late-successional forest conditions that might provide for old-growth wildlife species.

Inventories

Inventories are required to apply predictive models of old-growth habitats and species. Although uses of inventory data will vary, basic guidelines for inventories should be rigorously standardized among National Forests.

Habitat-The main objective of producing inventories of old-growth forest habitats is to provide reliable information on location, distribution, and amount of old-growth and younger forests that contain old-growth attributes, such as large live trees, large snags, and large logs. Appropriate sampling and inventory techniques should be applied to various forest types at stand, landscape, and National Forest scales, and under several standards of reliability.

Habitat inventories should ultimately provide vegetation class-specific and stand-specific data on vegetation structures and flora. Inventories on all National Forests must be conducted by supplementing remotely sensed data with field surveys. Identifying which old-growth habitat attributes to sample will come from analysis of both community and species-specific old-growth research data.

Ongoing VRS and MOM inventories on National Forests in Washington and Oregon (Marcot and others, this volume) are currently scheduled for completion by 1994. The MOM inventory will include data on structures of late-successional forest stands for each plant association. Once entered into a geographic information system, these data can provide information on the distribution and extent of stand conditions specified by the user. Such specifications could include, for example, the quantitative "ecological" definitions of old growth advanced by the Old-Growth Definition Task Group (1986). They may also include definitions of stands corresponding to quantitative descriptions of habitat for wildlife species or species groups associated with various forest conditions. Forest inventory data must be accessible to Ranger Districts to help in planning and executing projects in an integrated approach to resource management (Chalk and others 1984).

Wildlife species-Inventories of selected wildlife species associated with late-successional forests are also needed. Such species include those identified in this volume as "closely associated" with old-growth conditions (table 1; see also Ruggiero and others, this volume).

Other species classified as "associated" with old growth, which are expected to decline in a managed forest landscape, may also need to be inventoried. These include cavity-nesting birds (Lundquist and Mariani, this volume; Manuwal, this volume), birds associated with old-growth forests during winter (Huff and others, this volume), some amphibians (Aubry and Hall, this volume; Bury and others, this volume), and vertebrate species sensitive to edges and other landscape patterns created by forest management activities. Also of interest are species recognized by administrative or legal directives, and keystone species whose functions in late-successional forest ecosystems affect the presence and abundance of other plant and animal species (table l), such as mycophagous small mammals and prey species for spotted owls.

Developing inventories of the distribution, abundance, and trends of populations for each of these species--especially those that are wide-ranging, rare, or secretive-is a formidable and expensive task (see Franzreb 1977, Raphael and Rosenberg 1983, Ratermann and Brode 1983). Complete censuses of all of these species (table 1) will never be possible because of the huge investments of time and money required for even one species in a small area. Sample surveys, however, can determine distributions, relative abundances, and population trends. Sampling could be undertaken among physiographic provinces, National Forests, or any given land allocation. Validated models of habitat relationships could be used to identify appropriate habitats to inventory within such strata.

Table I-Categories of species that may require extensive inventories or additional study

- Species closely associated with old-growth conditions in one or more physiographic provinces
  - Northern spotted owl
  - Vaux's swift
  - Marbled murrelet
  - Hairy woodpecker
  - Red-breasted sapsucker
  - Brown creeper
  - Western flycatcher
  - Big brown bat
  - Fringed myotis
  - Long-legged myotis
  - Silver-haired bat
  - Shrew-mole
  - Red tree vole
  - Olympic salamander
  - Northwestern salamander
  - Del Norte salamander
  - Roughskin newt
  - Tailed frog

- Species associated with old-growth forests that may suffer declines in managed forest landscapes
  - Cavity-nesting birds
  - Birds and mammals closely associated with late-successional forests during winter
    - Chestnut-backed chickadee
    - Red-breasted nuthatch
    - Red crossbill
    - Gray jay
    - Douglas' squirrel
  - Species associated with interior late-successional forest conditions

- Keystone species
  - Selected prey species of the spotted owl
    - Northern flying squirrel
  - Mycophagous mammals
  - Insectivorous birds, especially those preying on forest insect pests

- Species with special administrative or legal status
  - Old-growth indicator species
    - Northern spotted owl
    - Pileated woodpecker
    - Marten
  - Rare, threatened, endangered, or sensitive species
    - Northern spotted owl
    - Northern goshawk
    - Great gray owl

In addition to sampling habitats for the presence and distribution of late-successional forest wildlife species, appropriate techniques may need to be developed for estimating the absolute abundance and reproductive attainment of certain species. Substantial progress has been made on region-wide inventories of northern spotted owls, although at high cost (O'Halloran and others, this volume). Similarly, survey protocols are being developed for determining the distribution and relative abundance of marbled murrelets at inland sites (Nelson, this volume; Paton and Ralph, this volume). No reliable methods for assessing the reproductive success or absolute abundance of marbled murrelets are currently available, however. Such intensive efforts to gather data on the absolute abundance and reproductive success of other wildlife species associated with late-successional forests may be initiated only for those species that are listed (or proposed to be listed) by the U.S. Fish and Wildlife Service as threatened or endangered.

Information on Wildlife Habitat Relationships

Understanding habitat relationships of old-growth wildlife species is crucial to predicting their responses to present and future habitat conditions in managed landscapes. Habitat relationships should be evaluated throughout the geographic range in which each species occurs, and for each habitat that may be used for various life-history functions, such as feeding, resting, reproduction, migration, or dispersal.

Habitat relationships information can be used to predict the abundance of wildlife species in various structural or successional stages of late-successional or other forest types. Information on the habitat relationships of old-growth-associated species should include specific habitat elements associated with the species' presence, variation in abundance and reproductive success, and other life-history traits. Applying such information for each species would help identify the range of occurrence of various habitat elements in the landscape-density, size, and quality of habitats-and effects on species' presence and abundance. Of particular concern are the effects on wildlife population sizes and trends of fragmenting old-growth forests. Fragmentation greatly changes spacing, size, shape, context, and amount of edge of old growth in the landscape.

Managers need to understand to what degree different vegetation structures and species assemblages (at both stand and landscape scales) provide for viability of each old-growth wildlife species. Integral to this understanding is predicting stand and landscape conditions that result from management activities by all land owners throughout each species' range. To help develop such predictions, researchers and managers need to know what stand and landscape attributes to track. The old-growth research results presented in this volume represent the first step toward developing information for such uses. To use such information, we also need to test how well variation in species presence, abundance, survival, reproductive success, and long-term population viability can be predicted by using existing habitat data or that which can be collected through typical forest inventory procedures.

One main objective is to produce area-analysis models for assessing cumulative effects on late-successional forest wildlife species from management activities at both the stand and landscape scale. Such analyses may initially be useful only for predicting the presence of various species. Ongoing studies of landscape-scale patterns (Lehmkuhl and others, this volume) will provide essential information for this purpose.

In such models, attributes would be defined along gradients rather than by discrete stand age-classes. An example would be a discriminant function equation that estimates the probability that a species is present based on habitat conditions. The equation would discriminate between stand conditions with which the species' presence is highly likely and those with which it is highly unlikely. Of course, species' presence is not simply a function of habitat: historical factors, random catastrophic events, and barriers to colonization are also important determinants.

Predictive species models developed from the old-growth research data should be validated, especially against an independent data set. Where additional data sets are lacking, predictive models can be developed with cross-validation techniques, such as bootstrap or jackknife analyses (Meyer and others 1986, Solow 1989). In such tests, the robustness of the models are assessed by developing prediction equations or correlations from multiple, randomly chosen subsets of the data base and testing how values of the model parameters vary. Cross-validation also entails testing the predictions of a model derived from a portion of a data base against a complementary portion not used to develop the model.

Demography Information

Finding through field inventories that a wildlife species is present in a particular area, or predicting its presence by a habitat capability model, does not ensure that existing habitat conditions or landscape patterns will provide for either reproductive success or long-term population viability (Van Home 1983). Empirical information on demographic parameters is critical for making such determinations. Such expensive and time-consuming studies, however, will likely be conducted on only a few species of key scientific, administrative, or social concern, such as spotted owls and their prey.

Priorities among species may need to be set for these studies. Forest species with a high priority for demographic studies may include those that are associated with late-successional forests; have restricted or disjunct ranges and small population sizes; or that are known or suspected to have suffered recent population declines, especially those resulting from management activities. Forest-scale inventories may need to be conducted to determine which species associated with late-successional forests would fall into these priority categories.

Advisor or Prescription Models

To aid resource managers, advisor or prescription models can be built to help evaluate old-growth habitat conditions at stand and landscape scales and to recommend appropriate courses of action to meet specified management objectives (Marcot and others 1988). Such models may include expert systems, in which knowledge bases of if-then rules represent expert assessments of habitat conditions (Marcot 1986). An example is the expert system developed for guiding habitat management for black-tailed deer in coastal British Columbia (McNay and others 1987).

Advisory models are used to assess habitat conditions for various species and to set priorities and guide management prescriptions. At a landscape scale, they can also be used to guide cumulative effects analysis. That such models be evaluated through peer review and validated with independent empirical data is critical, however (Marcot 1987). Also, such models should not be used to make decisions, but merely to provide information. For example, an expert systems model could be designed to advise on priorities for retention or silvicultural treatment of late-successional forest stands in a given landscape. Especially if tied to a geographic information system to visualize stand conditions and habitat patch patterns, such a decision-aiding tool would provide a consistent and reliable means of interpreting old-growth forest conditions for wildlife.

Development of these models is several years away. Key information still needs to be gathered or developed to produce prediction equations at stand and landscape scales and expert advice on habitat and species' responses to various management presciptions. Inventories of vegetative conditions at the stand scale need to be conducted or refined. Regardless of whether such an advisory system is produced in the form of a model per se, or as an evaluation process for resource managers to follow, a thorough understanding of species-habitat relationships is needed to guide such prescriptions.

Further Research Needs

We consider further research needs to fall into five basic categories: autecological studies, studies on developmental patterns in old-growth forests, landscape studies, research on inventory and monitoring techniques, and studies on the effects of management activities and natural disturbances such as fire.

The team that planned the research reported in this book has identified autecological studies as the next phase of research after the community studies (Research Work Unit Description on file at the Forestry Sciences Laboratory in Olympia, Washington). The results presented in this volume will go a long way towards identifying species for which autecological study is needed. In addition, researchers and managers can work together to identify priorities for other species that were not included in the sampling design for the community studies reported here. The species presented in table 1 should all be considered candidates for more detailed study. Autecological studies must be conducted over a wide range of stand conditions so that the effects of various stand conditions can be adequately evaluated. Such studies may sometimes require manipulation of existing stands to simulate conditions likely to exist in the managed stands of the future.

Further information on developmental patterns in old-growth forests is essential to providing full understanding of options for managing old growth. Many areas currently contain forests that have some of the characteristics of old growth but fail to meet all criteria for ecological old growth (see Franklin and Spies, this volume; Morrison 1988; Old-Growth Definition Task Group 1986). We need to fully understand developmental patterns in older forests so that we better predict their future characteristics.

Landscape ecology studies must focus on two essential questions. The first is how fragmentation affects old-growth forest conditions. How the integrity of old-growth habitats can be maintained at the landscape scale must be understood. Research is needed to determine how well adjacent stands of different ages and structures act to buffer the effects of fragmentation on old-growth stands. Some of this research is already being conducted by Forest Service scientists in the Pacific Northwest. The second essential question at the landscape scale concerns the effects of various amounts and patterns of old growth and other forest types on populations of wildlife species that are associated with old growth. Such studies must focus (to the extent possible) on long-term rather than short-term effects on species. Although these studies are likely to prove very difficult and expensive, they offer the only real means of evaluating management hypotheses about landscape conditions that will sustain species' viability over time. These studies must include demographic measures of the species being investigated. They must also be designed to look at a broad array of landscape conditions. The careful setting of priorities of species to be studied at the landscape scale, and of needed standards of reliability, will be critical because of the expense and time required for such studies.

The third category of studies needed are those directed at developing more effective inventory and monitoring techniques for both old-growth habitats and wildlife species associated with those habitats. Such inventories are time consuming and expensive, but management plans cannot be properly implemented without site-specific knowledge of habitats and species. In addition to more efficient techniques, evaluation systems that would set priorities among stands for species-specific inventories would be useful. Inventories could then be conducted in those habitats that are most likely to support species of interest.

Finally, studies are needed on the effects of management and of natural disturbance on old-growth conditions. Studies of management techniques should ask what techniques are useful to retain elements of old-growth forests in newly regenerated stands; accelerate the development of these characteristics in young, unmanaged stands; and accelerate the development of these characteristics in stands that have already come under management. Studies of natural disturbances should address questions about the frequency, size, and intensity of natural disturbances and the ways in which they may be influenced by various stand and landscape characteristics.

Conclusions

The information presented in this volume provides clear evidence about species' associations with old-growth forests. That information should be further analyzed to provide a better understanding of the stand characteristics associated with each of these species. Community-scale analyses of this data set has provided information on the diversity of old-growth forest communities and associated wildlife communities. This information will allow managers to make more-informed decisions about which stands to include in old-growth management areas. Such information can be applied directly in implementing Forest Plans. A combination of further analysis of this information and collection of additional data will elucidate how different amounts and patterns of old-growth stands will affect the species that are most closely associated with them. Such analyses will also play a role in determining if amendments to Forest Plans are needed.

It is vitally important that the research and management branches of the Forest Service work closely together to further develop this information and identify priorities for needed information. Although we acknowledge that additional information is always desirable, we urge resource managers to make the best possible use of the results presented here. A cooperative effort between researchers and managers is currently underway to make this information more readily accessible to potential users. The products of this effort should provide essential tools to managers faced with tough decisions about maintaining old-growth forest conditions in a multiple-use context. ❑

Research on Wildlife in Old-Growth Forests: An Attempt at Perspective

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This volume presents the results of research conducted under the auspices of the Forest Service's Old-Growth Forest Wildlife Habitat Program. At least another 100 papers have been prepared from research conducted by or funded by the Program; more are to come. Some of these papers are published, some in press, and some undergoing review. A vast amount of data was gathered by the Old-Growth Program. Such a comprehensive, detailed data set on animal communities related to the successional or structural stages in Douglas-fir forests of western Oregon and Washington is unlikely ever to be collected again.

New evidence and insights about the relationships (or lack thereof) of a myriad of wildlife species to Douglas-fir forests in western Oregon and Washington has been presented in this volume. And, more specifically, the degree of association between many wildlife species and old-growth forests, as compared to earlier stages of forest development, has been extensively examined.

In my introductory paper (Thomas, this volume), I suggested that the research reported here would be used to formulate an answer to an overriding question-do old-growth Douglas-fir forests represent unique wildlife habitat compared to other forested environments? In my opinion, the answer to this question is yes. The papers included here have shown that many wildlife species in Douglas-fir forests occur in greater abundances in old-growth than in young or mature forest stages, and that several wildlife species are closely associated with old growth.

The studies reported here, however, dealt with a comparison of wildlife and habitat relationships across a spectrum of unmanaged forest conditions in young, mature, and old-growth stands (and sometimes, in clearcuts). The stands examined in these studies were naturally regenerated, usually after fire, and had not been silviculturally treated during their development. Such stands are not likely to contain communities representative of those in managed stands that have been subject to site preparation, planting with spacing to selected stock of selected species, thinning to predetermined spacing, control of competing vegetation, and so on.

Intuition tells me (and I submit that for scientists to offer intuition and opinion is acceptable, provided they are identified as such) that fully managed stands are apt to be more simplified in structure than unmanaged stands. And, in turn, managed stands would be expected to support simplified plant and animal communities compared to unmanaged stands of similar age. The comparisons of animal communities across the spectrum of unmanaged successional stages reported here must not be uncritically assumed to apply to managed stands or forested landscapes of the future.

Information presented on habitat features in these successional stages typically showed a carryover of some of the ecological attributes of the preceding old-growth stand in younger stands. Such attributes include large, down woody material, large snags, and some large living trees, all of which provide important habitat for wildlife (Thomas 1979). Do these carryover attributes influence the habitat quality of the young and mature stands studied? That seems likely.

Initiating wildlife studies in intensively managed stands will be critical, regardless of the limitations on available study sites. Obviously, locating fully managed stands much older than 60 to 80 years will be impossible. In most areas, only fully managed stands of 50 years of age or less will be available for study. Stands that are studied should be as large as possible, however, to accommodate the broadest array of wildlife species that might occur there. Comparisons of wildlife densities in younger managed stands with those in unmanaged stands of the same age will be required to adequately evaluate the quality of wildlife habitat provided in managed forests. Such studies are necessary to determine if, as several authors have suggested, simplication of forest structure and tree species composition in managed stands is indeed reflected in simplication of the attendant animal community.

Any research effort usually ends with the researchers' cautioning against inappropriate use of the data presented or the conclusions drawn, and identifying additional needed research. There is no final truth in ecological research--only better and better approximations of what passes as truth; and there are no final questions-only better and more specific questions whose answers put us closer to truth. Managers will, of course, **use** the research to guide management in spite of the researchers' cautions; they have no other choice.

Today's forest planning procedures rely heavily on the use of linear mathematical models that consider the effect of several variables and their interactions to predict outcomes of various biological processes-say timber production or population sizes of a wildlife species. The data that goes into these models are seldom precise, and the interactions between the variables considered are even less perfectly understood. Such models were not intended by their developers to provide precise information. Rather, they **were** intended to provide indications of the direction of change, rough estimates of the magnitude of expected change, and the time frames surrounding such change.

Unfortunately, because the predictions of these models are numbers that have been used to guide management allocations, some have taken the results to be more precise than is justified. Political conflict over the allocation of resources results in political demands for more and more precision, whether or not more precision is possible. The models are then, sometimes, "tweaked" over and over to satisfy demands for greater accuracy and "politically correct" decisions. Such continued tweaking often only provides an illusion of precision that produces increasingly unwarranted faith in what finally appears on the computer printouts. Such events make monitoring the results of management applications (as required by law and regulations, and promised in the Forest Plans) so very critical. Only adequate monitoring can enable the necessary mid-course corrections in management activities to be made if the models have produced projections that are out of line with reality-whether too high or too low. All concerned have a vested interest in ensuring that adequate monitoring is carried out. And that means adequate design and resources to get the job done.

The biology of certain wildlife populations and wildlife habitat relationships are not conducive to precise estimates, no matter how much they are studied. The precision of such estimates can only become marginally better regardless of how politically desirable that may be. The answer will always involve a mean and be qualified with confidence intervals. Year-to-year perturbations in number will occur that are unrelated to habitat. Extremes or exceptions will always tempt those who long for a different answer than that indicated by the mean. Collecting enough data to determine long-term trends associated with habitat quality and quantity will be difficult and expensive. But good monitoring will require that.

The political process is not yet attuned to dealing with science as part of that process. When land-use decisions are to be made that have large-scale economic, social, and political impacts, individuals who stand to lose from those decisions typically demand unreasonable degrees of certainty in the information on which those decisions are based. All concerned need to recognize that the provision of a degree of certainty adequate to satisfy those whose welfare is threatened by the result is not likely to be attained. This problem is exacerbated when the decision criteria involve biological systems that are dynamic and highly variable. When is the information base adequate to support emotionally laden, economically explosive decisions so that all parties will be satisfied? The answer, likely, is never, In addition, scientists do not seem well suited by training or inclination to deal with the political process. Some biologists dwell on qualification of extant data and lean toward emphasizing uncertainty and the need for more information. Although they are quite correct, scientists also need to be cognizant that the world marches on, regardless of the state of knowledge. So the scientific community, while imparting the caution that science demands, needs to emphasize the considerable knowledge that is available, rely on extant theory, and contribute in whatever way they can to forest planning and management.

Decision-makers in land management agencies are usually not biological scientists. That may be fortunate. Some say that scientists think too much, feel too little, and have inadequate appreciation for economics and politics. Biologists should recognize that biological considerations are only part of any political land-use decision-making process-including any resulting legal proceedings. Such recognition implies some degree of sympathy, if not empathy, for those who must ultimately make land-use decisions. Those decision-makers must consider the law, policy, public desire, political pressures, economics, politics, and budgetary direction from Congress, as well as any biological considerations. To pretend otherwise is both naive and foolish.

In the United States, the management of old-growth forests in the Pacific Northwest, and the political events that surround this issue, could emerge as the most significant natural resource issue of this century. The ultimate resolution of this controversy will set the tone for natural resource management in the first half of the 21st century. What lies ahead? Intensified conflict? Total preservation? Management for old-growth habitat features? Emergence of a “new” forestry? Compromise? Changes in law? Abandonment of multiple-use concepts in favor of dedication of land to various uses? Other actions? Who knows?

Certainly there is much more to understand about the ecological aspects of this issue. Given the huge potential economic and social impacts of land-use decisions on managing old growth, support seems likely to be available for additional ecological studies. But it is critical, now, for the scientific community to step back and carefully examine our ecological knowledge of old-growth forests. At what questions should new research on old growth be directed? How much more of the limited funds available for wildlife and forest ecology research should be shifted to the old-growth arena? Perhaps the questions and approaches that would emerge from debate within the scientific community would differ markedly from the “hot issues” that may be targeted by the political and congressional appropriations processes. These issues may well be settled, one way or the other, before adequate research can be conducted and brought to bear on them. The scientific community and those in the research arena must be careful not to be used inappropriately in the fight over old-growth management. The scientific community should not take part in premature actions predicated on inadequate understanding, nor in the use of research as a means of delaying management decisions where adequate information exists to justify action.

Undoubtedly, hot-issue research on potentially threatened and endangered species will be given increased funding. But, at the same time, scientists and managers should strive to ensure that additional research on the community ecology of managed and unmanaged forests goes on simultaneously-perhaps as part of the hot-issue research. For therein lies the information of more lasting scientific and political value as the old-growth issue evolves to encompass the broader issues to be faced by forest managers over the next decades. Foremost among these will be the need to determine the size and spacing of old-growth stands within managed forest landscapes that will provide for the “maintenance of viable populations of native species...well-distributed” throughout public lands.

The results presented in this volume have moved us a bit closer to truth. The challenge, now, is to synthesize this information so that it may be incorporated into decision-making processes, political debates, and legal proceedings on the management of old-growth forests.

As a last word, I am reminded of the admonitions of several who philosophize about ecology, mixed together here in paraphrase. There is no final ecological truth. All knowledge is a current approximation, and each addition to that knowledge is but a small, incremental step toward understanding. For not only are ecosystems more complex than we think-they are more complex than we **can** think. ☐

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Part 9

References

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References

Able, K.P.; Noon, B.R. 1977. Avian community structure along elevational gradients in the northeastern United States. Oecologia. 26(3):275-294.

Adams, D.P. 1986. Quaternary pollen records from California. In: Bryant, V.M., Jr.; Holloway, R.G., eds. Pollen records of Late-Quaternary North American sediments. Austin, TX: American Association of Stratigraphic Palynologists Foundation: 125-140.

Afifi, A.A.; Clark, V. 1984. Computer-aided multivariate analysis. Belmont, CA: Lifetime Publications, Wadsworth, Inc. 458 p.

Agee, J.K. 1989. A history of fire and slash burning in westem Oregon and Washington. In: Hanley, D.P.; Kammenga, J.J.; Oliver, C.D., eds. The burning decision: a regional symposium on slash. Contribution 66. Seattle: College of Forest Resources, University of Washington, Institute of Forest Resources: 3-20.

Agee, J.K. 1990. The historical role of fire in Pacific Northwest forests. In: Walstad, J.D.; Radosevich, S.R.; Sandberg, D.V., eds. Natural and prescribed fire in Pacific Northwest forests. Corvallis, OR: Oregon State University Press: 25-38.

Agee, J.K. This volume. Fire history of Douglas-fir forests in the Pacific Northwest.

Agee, J.K.; Dunwiddie, P.W. 1984. Recent forest development on Yellow Island, Washington. Canadian Journal of Botany. 62:2074-2080.

Agee, J.K.; Flewelling, R. 1983. A fire cycle model based on climate for the Olympic Mountains, Washington. Fire and Forest Meteorology Conferences. 7:32-37.

Agee, J.K.; Huff, M.H. 1987. Fuel succession in a western hemlock/Douglas-fir forest. Canadian Journal of Forest Research. 17(7):697-704.

Alaback, P.B. 1982. Dynamics of understory biomass in Sitka spruce-western hemlock forests of southeast Alaska. Ecology. 63(6): 1932-1948.

Alaback, P.B. 1984. A comparison of old-growth and second-growth forest structure in the western hemlock-Sitka spruce forests of southeastern Alaska. In: Meehan, W.R.; Merrell, T.R. Jr.; Hartley, T.A., eds. Fish and wildlife relationships in old-growth forests. Proceedings of a symposium; 1982 April 12-15; Juneau, AK. Morehead City, NC: American Institute of Fishery Research Biologists: 219-226.

Allard, M.W.; Gunn, SJ.; Greenbaum, I.F. 1987. Mensural discrimination of chromosomally characterized *Peromyscus oreas* and *Peromyscus maniculatus.* Journal of Mammalogy. 68:402-406.

Allen, J.W. 1959. White pine in western Washington. Journal of Forestry. 57:573-576.

Altig, R.; Brodie, E.D., Jr. 1971. Foods of *Plethodon* larselli, *Plethodon dunni* and *Ensatina eschscholtzi* in the Columbia River Gorge, Multnomah County, Oregon. American Midland Naturalist. 85:226-228.

Alverson, W.S.; Waller, D.S.; Solheim, S.L. 1988. Forests too deer: edge effects in northern Wisconsin. Conservation Biology. 2:348-358.

American Ornithologists' Union. 1983. Checklist of North American birds, 6th ed. Lawrence, KS: Allen Press.

American Society of Mammalogists. 1987. Acceptable field methods in mammalogy: preliminary guidelines approved by the American Society of Mammalogists. Journal of Mammalogy. 68(suppl.):l-18.

Anderson, H.M. 1988. Old-growth forests: a conservationist's perspective. Natural Areas Journal. 8: 13-16.

Anderson, P.K. 1980. Evolutionary implications of microtine behavioral systems on the ecological stage. The Biologist. *62:70-88.*

Anderson, S.H. 1979. Changes in forest bird species composition caused by transmission-line corridor cuts. American Birds. 33:3-6.

Anderson, S.H.; Shugart, H.H. 1974. Habitat selection of breeding birds in an east Tennessee deciduous forest. Ecology. 55:828-837.

Andrus, C.; Froehlich, H.A. 1988. Riparian forest development after logging or fire in the Oregon Coast Range: wildlife habitat and timber value. In: Raedeke, K.J., ed. Streamside management: riparian wildlife and forestry interactions. Proceedings of a symposium; 1987 February 11-13; University of Washington, Seattle. Contribution 59. Seattle: Institute of Forest Resources, University of Washington: 139-152.

Anonymous. 1983a. A fire history of the Douglas-fir/mixed evergreen forests of the Northern California Coast Range Preserve. Walnut Creek, CA: Wildland Resource Management. 40 p.

Anonymous. 1983b. The great fire of 500 years ago. Quinault Natural Resources. 4(5):23.

Anonymous. 1983-1985. Annual cone crop reports. States of Washington and Oregon. Compiled by State of Washington, Department of Natural Resources; Oregon State Forestry Department; and USDA Forest Service, Pacific Northwest Region.

Anthony, E.L.P.; Kunz, T.H. 1977. Feeding strategies of the little brown bat, *Myotis lucifugus,* in southern New Hampshire. Ecology. 58:775-786.

Anthony, R.G.; Forsman, E.D.; Green, G.A. [and others]. 1987. Small mammal populations in riparian zones of coniferous forests in western Oregon. The Mm-relet. 68:94-102.

Anthony, R.G.; Morrison, M.L. 1985. Influence of glyphosate herbicide on small mammal populations in western Oregon. Northwest Science. 59: 159-168.

Antos, J.A.; Zobel, D.B. 1984. Ecological implications of belowground morphology of nine coniferous forest herbs. Botanical Gazette. 145(4):508-517.

Arnolds, E. 1981. Ecology and coenology of macrofungi in grasslands and moist heathlands in Drenthe, the Netherlands. Part 1. Introduction and synecology. Cramer, Vaduz: Bibliotheca mycologica 83.407 p.

Asher, S.C.; Thomas, V.G. 1985. Analysis of temporal variation in the diversity of a small mammal community. Canadian Journal of Zoology. 63: 1106-l109.

Askins, R.A.; Philbrick, M J. 1987. Effect of changes in regional forest abundance on the decline and recovery of a forest bird community. Wilson Bulletin. 99:7-21.

Atzet, T.; Wheeler, D. 1982. Historical and ecological perspectives on fire activity in the Klamath Geological Province of the Rogue River and Siskiyou National Forests. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 16 p.

Atzet, T.; Wheeler, D.; Gripp, R. 1988. Fire and forestry in southwest Oregon. FIR Report. 9(4):4-7.

Aubry, K.B.; Crites, M J.; West, S.D. This volume. Regional patterns of small mammal abundance and community composition in Oregon and Washington.

Aubry, K.B.; Hall, P.A. This volume. Terrestrial amphibian communities in the Southern Washington Cascade Range.

Aubry, K.B.; Jones, L.L.C.; Hall, P.A. 1988. Use of woody debris by plethodontid salamanders in Douglas-fir forests in Washington. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 32-37.

Aubry, K.B.; Putera, J.A. Personal communication. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Olympia, WA 98502.

Aubry, K.B.; Senger, C.M.; Crawford, R.L. 1987. Discovery of Larch Mountain salamanders (Plethodon *lurselli) in* the central Cascade Range of Washington. Biological Conservation. 42:147-152.

Bailey, V. 1936. The mammals and life zones of Oregon. North American Fauna. 55:1-416.

Baker, R.G. 1983. Holocene vegetational history of the Western United States. In: Wright, H.E., Jr., ed. Late-Quaternary environments of the United States. The Holocene. Minneapolis: University of Minnesota Press. 2:109-127.

Balda, R.P. 1975. The relationship of secondary cavity nesters to snag densities in western coniferous forests. Wildl. Hab. Tech. Bull. Albuquerque, NM: U.S. Department of Agriculture, Forest Service, Southwest Region. 37 p.

Baldwin, P.H.; Zaczkowski, N.K. 1963. Breeding biology of the Vaux's swift. Condor. 65:200-206.

Bangs, O. 1898. Description of a new white-footed mouse from the Mount Baker Range, British Columbia. Procecdings of the Biological Society of Washington. 12:83-84.

Barbour, R.W.; Davis, W.H. 1969. Bats of America. Lexington, KY: University Press of Kentucky. 286 p.

Barnosky, C.W. 1981. A record of Late Quaternary vegetation from Davis Lake, Southern Puget Lowland, Washington. Quaternary Research. 16:221-239.

Barnosky, C.W. 1985. Late Quaternary vegetation near Battle Ground Lake, southern Puget Trough, Washington. Geological Society of American Bulletin. 96:263-271.

Barnosky, C.W.; Anderson, P.M.; Bartlein, PJ. 1987. The northwestern U.S. during deglaciation: vegetation and climatic implications. In: Ruddiman, W.F.; Wright, H.E., Jr., eds. North America and adjacent oceans during the last deglaciation. Boulder, CO: Geological Society of America, The Geology of North America series. (K-3):289-321.

Barrett, S.W.; Arno, S.F. 1982. Indian fires as an ecological influence in the northern Rockies. Journal of Forestry. 80(10):647-651.

Bartels, R.; Dell, J.D.; Knight, R.L.; Schaefer, G. 1985. Dead and down woody material. In: Brown, E.R., tech. ed. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part 1 - Chapter narratives. Publ. R6-F&WL-192-1985. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 171-186.

Bartlein, P.J.; Prentice, I.C. 1989. Orbital variations, climate and paleoecology. Trends in Ecology and Evolution. 4(7):195-199.

Bartlett, M.S. 1947. Multivariate analysis. Journal of the Royal Statistical Society (Series B). 9:176-197.

Battacharyya, H. 1981. Theory and methods of factor analysis and principal components. In: Capen, D.E., ed. The use of multivariate statistics in studies of wildlife habitat. Gen. Tech. Rep. RM-87. Fort Collins, CO: Rocky Mountain Forest and Range Experiment Station: 72-79.

Beedy, E.C. 1982. Bird community structure in coniferous forests of Yosemite National Park, California. Davis, CA: University of California. 167 p. Ph.D. dissertation.

Bell, G.P. 1980. Habitat use and responses to patches of prey by desert insectivorous bats. Canadian Journal of Zoology. 58:1876-1883.

Belwood, JJ.; Fenton, M.B. 1976. Variation in the diet of *Myotis lucifugus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology. 54: 1674-1678.

Benkman, C.W. 1987. Food profitability and the foraging ecology of crossbills. Ecology. 57:251-267.

Bennett, S.H.; Gibbons, J.W.; Glanville, J. 1980. Terrestrial activity, abundance and diversity of amphibians in differently managed forest types. American Midland Naturalist. 103:412-416.

Bent, AC. 1964. Life histories of North American woodpeckers. New York: Dover Publications. 334 p. [first published in 1939 as U.S. National Mus. Bull. 174.]

Berntsen, C.M. 1960. Productivity of a mature Douglas-fir stand. Res. Note 188. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 4 p.

Berntsen, C.M.; Rothacher, J. 1959. A guide to the H.J. Andrews Experimental Forest. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 21 p.

Beschta, R.L.; Bilby, R.E.; Brown, G.W. [and others]. 1987. Stream temperature and aquatic habitat: fisheries and forestry interactions. In: Salo, E.O.; Cundy, T.W., eds. Streamside management: forestry and fishery interactions. Proceedings of a symposium; 1987 February 12-14; University of Washington, Seattle. Contribution 57. Seattle: Institute of Forest Resources, University of Washington: 191-232.

Best, L.B.; Stauffer, D.F. 1986. Factors confounding evaluation of bird-habitat relationships. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7- 11; Fallen Leaf Lake, California Madison, WI: University of Wisconsin Press: 209-216.

Bierlmaier, F.A. Unpublished data. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331.

Bierlmaier, F.A.; McKee, A. 1989. Climatic summaries and documentation for the primary meteorological station, H.J. Andrews Experimental Forest, 1972 to 1984. General Technical Report PNW-GTR-242. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 56 p.

Bingham, B. Personal communication. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Arcata, CA 95521.

Bingham, B.; Sawyer, J.O., Jr. This volume. Distinctive features and definitions of young, mature, and old-growth Douglas-fir/hardwood forests.

Birks, H J.B.; Birks, H.H. 1980. Quaternary paleoecology. London: Edward Arnold (Publishers) Limited. 289 p.

Biswell, B.L.; Boulanger, J.; Carey, A.B. This volume. Comparison of small mammal abundance in climax and young forests of the Olympic Peninsula, Washington (abstract). Appendix B.

Biswell, B.L.; Carey, A.B. This volume. Flying squirrel abundance in young and old-growth forests of the Pacific Northwest (abstract). Appendix B.

Blake, J.G.; Hoppes, W.G. 1986. Influence of resource abundance on use of tree-fall gaps by birds in an isolated woodIot. Auk. 103(2):328-340.

Blinn, T.; Swanson, FJ.; McKee, A., camps. 1988. Research publications of the H.J. Andrews Experimental Forest, Cascade Range, Oregon: 1988 supplement. Gen. Tech. Rep. PNW-223. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 25 p.

Bloom, S.A. 1981. Similarity indices in community studies: potential pitfalls. Marine Ecology-Progress Series. 5:125-128.

Blymer, M.J.; McGinnes, B. 1977. Observations on possible detrimental effects of clearcutting on terrestrial amphibians. Bulletin of the Maryland Herpetological Society. 13:79-83.

Bock, C.E.; Lepthien, L.W. 1976. Synchronous eruptions of boreal seed-eating birds. American Naturalist. 110:559-571.

Bogert, C.M. 1960. The influence of sound on the behavior of amphibians and reptiles. In: Lanyon, W.W; Tavolga, W.N., eds. Animal sounds and communication. American Institute of Biology. 7: 137-320.

Bond, R.R. 1957. Ecological distribution of breeding birds in the upland forests of southern Wisconsin. Ecological Monographs. 27:351-384.

Bowles, J.B. 1963. Ornithology of changing forest stands on the western slope of the Cascade Mountains. Seattle: University of Washington. 87 p. M.S. thesis.

Boyce, J.S.; Wagg, J.W.B. 1953. Conk rot of old-growth Douglas-fir in western Oregon. Bulletin 4. Oregon Forest Products Laboratory and Oregon State Forest Department. 96 p.

Boyd, RJ., Jr. 1980. Western white pine. In: Eyre, F.E., ed. Forest cover types of the United States and Canada. Washington, DC: Society of American Foresters: 94-95.

Boyd, R. 1986. Strategies of Indian burning in the Willamette Valley. Canadian Journal of Anthropology. 5(1):65-86.

Briese, L.A.; Smith, M.H. 1974. Seasonal abundance and movement of nine species of small mammals. Journal of Mammalogy. 55:615-629.

Brokaw, N. 1985. Gap-phase regeneration in tropical forest. Ecology. 66:682-687.

Brown, E.R., tech. ed. 1985. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part l-Chapter narratives, 332 p. Part 2-Appendices, 302 p. Publ. R6-F&WL-192-1985. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.

Brown, J.H. 1971. Mammals on mountaintops: nonequilibrium insular biogeography. American Naturalist. 105:467-478.

Brown, J.H. 1978. The theory of insular biogeography and the distribution of boreal birds and mammals. Great Basin Naturalist. 2:209-227.

Brown, J.H.; Kodric-Brown, A. 1977. Turnover rates in insular biogeography: effect of immigration on extinction. Ecology. 58:445-449.

Brown, R.B.; Parsons, R.B. 1973. Soils of the reference stands-Oregon IBP. Coniferous Forest Biome Internal Report 128. Seattle: University of Washington. 76 p,

Brubaker, L.B. 1986. Tree population responses to climatic change. Vegetatio. 67: 119-130.

Brubaker, L.B. This volume. Climate change and the origin of old-growth Douglas-fir forests in the Puget Sound lowland.

Bryant, M.D. 1985. Changes 30 years after logging in large woody debris and its use by salmonids. In: Johnson, R.R.; Ziebell, C.D.; Patton, D.R. [and others], tech. coords. Riparian ecosystems and their management: reconciling conflicting uses. First North American Riparian Conference; 1985 April 16-18; Tucson, AZ. Gen. Tech, Rep. RM-120. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 329-334.

Buchanan, T.S.; Englerth, G.H. 1940. Decay and other losses in windthrown timber on the Olympic Peninsula, Washington. Tech. Bull. 733. Washington, DC: U.S. Department of Agriculture, Forest Service. 30 p.

Buhlman, K.A.; Pague, C.A.; Mitchell, J.C.; Glasgow, R.B. 1988. Forestry operations and terrestrial salamanders: techniques in a study of the Cow Knob salamander, *Plethodon punctatus.* In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 38-44.

Bull, E.L. 1980. Resource partitioning among woodpeckers in northeastern Oregon. Moscow, ID: University of Idaho. 120 p. Ph.D. dissertation.

Bull, E.L.; Meslow, E.C. 1977. Habitat requirements of the pileated woodpecker in northeastern Oregon. Journal of Forestry. 75:335-337.

Bull, E.L.; Peterson, S.R.; Thomas, J.W. 1986a. Resource partitioning among woodpeckers in northeastern Oregon. Res. Note PNW-444. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 19 p.

Bull, E.L., Thomas, J.W.; Horn, K. 1986b. Snag management on National Forests in the Pacific Northwest-1984. Western Journal of Applied Forestry. 1:41-43.

Burgess, R.L.; Sharpe, D.M., eds. 1981. Forest island dynamics in man-dominated landscapes. New York: Springer-Verlag. 310 p.

Burke, R.M.; Birkeland, P.W. 1983. Holocene glaciation in the mountain ranges of the Western United States. In: Wright, H.E., Jr., ed. Late-Quaternary environments of the United States. The Holocene. Minneapolis: University of Minnesota Press. 2:3-l1.

Burnham, K.P.; Anderson, D.R.; Laake, J.L. 1980. Estimation of density from line transect sampling of biological populations. Wildlife Monographs 72. Washington, DC: The Wildlife Society. 202 p. Supplement to Journal of Wildlife Management.

Burnham, K.P.; Anderson, D.R.; Laake, J.L. 1981. Line transect estimation of bird population density using a Fourier series. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-3 1; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:466-481.

Burton, T.M.; Likens, G.E. 1975. Salamander populations and biomass in the Hubbard Brook Experimental Forest, New Hampshire. Copeia. 1975:541-546.

Bury, R.B. 1968. The distribution of *Ascaphus truei* in California. Herpetologica. 24:39-46.

Bury, R.B. 1983. Differences in amphibian populations in logged and old-growth redwood forest. Northwest Science. 57:167-178.

Bury, R.B. 1988. Habitat relationships and ecological importance of amphibians and reptiles. In: Raedeke, K.J., ed. Streamside management: riparian wildlife and forestry interactions. Contribution 59. Seattle: Institute of Forest Resources, University of Washington: 61-76.

Bury, R.B.; Corn, P.S. 1987. Evaluation of pitfall trapping in northwestern forests: trap arrays with drift fences. Journal of Wildlife Management. 51: 112-119.

Bury, R.B.; Corn, P.S. 1988a. Douglas-fir forests in the Oregon and Washington Cascades: relations of the herpetofauna to stand age and moisture. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 11-22.

Bury, R.B.; Corn, P.S. 1988b. Responses of aquatic and streamside amphibians to timber harvest: a review. In: Raedeke, K.J., ed. Streamside management: riparian wildlife and forestry interactions. Proceedings of a symposium; 1987 February 11-13; University of Washington, Seattle. Contribution 59. Seattle: Institute of Forest Resources, University of Washington: 165-181.

Bury, R.B.; Corn, P.S. In press. Sampling methods for amphibians in streams. Gen. Tech. Rep. PNW-XXX. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Bury, R.B.; Corn, P.S.; Aubry, K.B. This volume(a). Regional patterns of terrestrial amphibian communities in Oregon and Washington.

Bury, R.B.; Corn, P.S.; Aubry, K.B. [and others]. This volume(b). Aquatic amphibian communities in Oregon and Washington.

Bury, R.B.; Martin, M. 1973. Comparative studies on the distribution and foods of plethodontid salamanders in the redwood region of northern California. Journal of Herpetology. 7:331-335.

Bury, R.B.; Raphael, M.G. 1983. Inventory methods for amphibians and reptiles. In: Bell, J.F.; Atterbury, T., eds. Renewable resource inventories for monitoring changes and trends. Proceedings of an international symposium; 1983 August 15-19; Oregon State University, Corvallis. SAF 83-14. Corvallis, OR: Society of American Foresters: 416-419.

Cain, S.A.; Castro, G.M. De O. 1959. Manual of vegetation analysis. New York: Harper and Brothers. 325 p.

Cajander, A.K. 1949. Forest types and their significance. Acta Forestalia Fennica. 56: l-71.

Campbell, H.W.; Christman, S.P. 1982. Field techniques for herpetofaunal community analysis. In: Scott, N.J., Jr., ed. Herpetological communities. Wildlife Res. Rep. 13. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service: 193-200.

Capen, D.E., ed. 1981. The use of multivariate statistics in studies of wildlife habitat. Gen. Tech. Rep. RM-87. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 249 p.

Carey, A.B. Personal communication. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, 3625 93d Avenue SW, Olympia, WA 98502.

Carey, **A.B. 1983.** 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: 188-199.

Carey, A.B. 1984. A critical look at the issue of species-habitat dependency. In: New forests for a changing world. Proceedings of 1983 Convention of the Society of American Foresters; 1983 October 16-20; Bethesda, MD: 346-351.

Carey, A.B. 1985. A summary of the scientific basis for spotted owl management. In: Gutierrez, R.J.; Carey, A.B., 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: 100-l14.

Carey, A.B. 1988. The influence of small streams on the composition of upland bird communities. In: Raedeke, K., ed. Streamside management: riparian wildlife and forestry interaction. Seattle: University of Washington: 153-162.

Carey, **A.B. 1989.** Wildlife associated with old-growth forests in the Pacific Northwest. Natural Areas Journal. 9:151-162.

Carey, A.B.; Castellano, V.E.; Chappell, C. [and others]. 1990. Training guide for bird identification in Pacific Northwest Douglas-fir forests. Gen. Tech. Rep. PNW-260. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 28 p.

Carey, A.B.; Hardt, M.M.; Horton, S.P.; Biswell, B.L. This volume. Spring bird communities in the Oregon Coast Range.

Carey, A.B.; Ruggiero, L.F., tech. eds. In press. Wildlife-habitat relationships: sampling procedures for Pacific Northwest vertebrates. Series of Gen. Tech. Reps. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Carey, A.B.; Spies, T.A. This volume. Sampling design of the Old-Growth Forest Wildlife Habitat Program.

Carey, A.B.; Witt, J.W. 1991. Track counts as indices to abundances of arboreal rodents. Journal of Mammalogy. 72:192-194.

Castellano, M.A. Personal observation. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331.

Castellano, M.A.; Trappe, J.M.; Maser, Z.; Maser, C. 1989. Key to spores of the genera of hypogeous fungi of north temperate forests with reference to animal mycophagy. Eureka, CA: Mad River Press. 186 p.

Center, G.S.; Casler, B.R.; Carey, A.B. This volume. Woodrat abundance in forests of the southern Oregon Coast Range (abstract). Appendix B.

Chalk, D.E.; Miller, S.A.; Hoekstra, T.W. 1984. Multi-resource inventories: integrating information on wildlife resources. Wildlife Society Bulletin. 12:357-364.

Claussen, D.L. 1973a. The thermal relations of the tailed frog, *Ascaphus truei,* and the Pacific treefrog, *Hyla regilla.* Comparative Biochemistry and Physiology. 44A:137-153.

Claussen, D.L. 1973b. The water relations of the tailed frog, *Ascaphus truei,* and the Pacific treefrog, *Hyla regilla.* Comparative Biochemistry and Physiology. 44A: 155-171.

Clevinger, W.R. 1951. S.W. Washington’s legendary ‘Big Fire.’ Seattle Times Magazine. 10/28/51:2.

Cline, S.P.; Berg, A.B.; Wight, H.M. 1980. Snag characteristics and dynamics in Douglas-fir forests, western Oregon. Journal of Wildlife Management. 44:773-786.

Cochran, W.G.; Mosteller, F.; Tukey, J.W. 1954. Principles of sampling. Journal of the American Statistical Association. 49:13-35.

COHMAP members. 1988. Climatic changes of the last 18,000 years: observations and model simulations. Science. 241:1043-1052.

Collins, J.P. 1975. A comparative study of the life history strategies in a community of frogs. Ann Arbor, MI: University of Michigan. 148 p. M.S. thesis.

Collins, J.T. 1990. Standard common and current scientific names for North American amphibians and reptiles, 3d ed. Society for the Study of Amphibians and Reptiles, Miscellaneous Publications, Herpetological Circular. 19: l-41.

Colwell, R.K.; Futuyama, DJ. 1971. On the measurement of niche breadth and overlap. Ecology. 52:567-576.

Conner, R.N. 1979a. Minimum standards and wildlife management. Wildlife Society Bulletin. 7:293-296.

Conner, R.N. 1979b. Seasonal changes in woodpecker foraging methods: strategies for winter survival. In: Dickson, J.G.; Conner, R.N.; Fleet, R.R. [and others], eds. The role of insectivorous birds in forest systems. New York: Academic Press: 95-106.

Conner, R.N. 1980. Foraging habitats of woodpeckers in southwestern Virginia. Journal of Field Ornithology. 51(2):119-127.

Conner, R.N. 1981. Seasonal changes in woodpecker foraging patterns. Auk. 98(3):562-570.

Conner, R.N.; Adkisson, C.S. 1977. Principal component analysis of woodpecker nesting habitat. Wilson Bulletin. *89:* 122-129.

Conner, R.N.; Hooper, R.G.; Crawford, H.S.; Mosby, H.S. 1975. Woodpecker nesting habitat in cut and uncut woodlands in Virginia. Journal of Wildlife Management. 39(1):144-150.

Conner, R.N.; Miller, O.K.; Adkisson, C.S. 1976. Woodpecker dependence on trees infected by fungal heart rots. Wilson Bulletin. 88:575-581.

Connor, E.F.; McCoy, E.D. 1979. The statistics and biology of the species-area relationship. American Naturalist. 113:791-833.

Connor, E.F.; Simberloff, D. 1986. Competition, scientific method, and null models in ecology. American Scientist. 74:155-162.

Cooke, W.B. 1955. Fungi, lichens and mosses in relation to vascular plant communities in eastern Washington and adjacent Idaho. Ecological Monographs. 25: 119-180.

Cooke, W.B. 1972. The Exeter papers. Program and introduction. Mycopathologia et Mycologia Applicata. 48: l-3.

Cormack, R.M. 1971. A review of classification. Journal of the Royal Statistical Society, Series A. 134:321-367.

Corn, J.G.; Witt, J. This volume. Flying squirrel live-trapping success (abstract). Appendix B.

Corn, P.S.; Bury, R.B. 1986. Habitat use and terrestrial activity by red *tree* voles *(Arborimus longicaudus) in* Oregon. Journal of Mammalogy. 67:404-406.

Corn, P.S.; Bury, R.B. 1989. Logging in western Oregon: responses of headwater habitats and stream amphibians. Forest Ecology and Management. 29:39-57.

Corn, P.S.; Bury, R.B. 1990. Sampling methods for terrestrial amphibians and reptiles. Gen. Tech. Rep. PNW-256. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 34 p.

Corn, P.S.; Bury, R.B. This volume (a). Small mammal communities in the Oregon Coast Range.

Corn, P.S.; Bury, R.B. This volume (b). Terrestrial amphibian communities in the Oregon Coast Range.

Corn, P.S.; Bury, R.B.; Spies, T.A. 1988. Douglas-fin forests in the Cascade Mountains of Oregon and Washington: Is the abundance of small mammals related to stand age and moisture? In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 340-352.

Cowan, I.M.; Guiguet, C **J. 1965.** The mammals of British Columbia. British Columbia Provincial Museum Handbook 11. 414 p.

Crawford, H.S.; Hooper, R.G.; Titterington, R.W. 1981. Song bird response to silvicultural practices in central Appalachian hardwoods. Journal of Wildlife Management. *45(3):680-692.*

Cross, S.P. 1976. A survey of bat populations and their habitat preferences in southern Oregon. Unpublished report to the National Science Foundation by Southern Oregon State College. On file at Southern Oregon State College, Ashland, OR 97520. 89 p.

Crump, M.L. 1982. Amphibian reproductive ecology at the community level. In: Scott, N.J., Jr., ed. Herpetological communities. Wildlife Res. Rep. 13. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service: 21-36.

Cwynar, L.C. 1987. Fire and the forest history of the North Cascade Range. Ecology. 69:791-802.

Dalquest, W.W. 1941. Ecologic relationships of four small mammals in western Washington. Journal of Mammalogy. 22:170-173.

Dalquest, W.W. 1948. Mammals of Washington. Lawrence, KS: University of Kansas Publications, Museum of Natural History. 2: l-444.

Dalquest, W.W.; Orcutt, D.R. 1942. The biology of the least shrew-mole, *Neurotrichus gibbsii minor. American* Midland Naturalist. 27:387-401.

Daubenmire, R. 1968. Soil moisture in relation to vegetation distribution in the mountains of northern Idaho. Ecology. 49:431-438.

Daugherty, C.H.; Allendorf, F.W.; Dunlop, W-W.; Knudsen, K.L. 1983. Systematic implications of geographic patterns of genetic variation in the genus *Dicamptodon.* Copeia. 1983:679-691.

Daugherty, C.H.; Sheldon, A.L. 1982. Age-specific movement patterns of the frog *Ascaphus truei.* Herpetologica. *38:468-474.*

Davis, J.W.; Goodwin, G.A.; Ockenfels, R.A., tech. coords. 1983. Snag habitat management. Proceedings of a symposium; 1983 June 7-9; Flagstaff, AZ. Gen. Tech. Rep. RM-99. Ft. Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 226 p.

Davis, L.S.; Henderson, J.A. 1977. Many uses and many users: some desirable characteristics of a common land and water classification system. In: Marmelstein, A., chairman. Classification, inventory, and analysis of fish and wildlife habitat. Proceedings of a national symposium: 1977 January 24-27; Phoenix, AZ. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. FWS/OBS-78/76: 13-34.

Dawson, D.G. 1981. Counting birds for a relative measure (index) of density. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:12-16.

DeBell, D.S.; Franklin, J.F. 1987. Old-growth Douglas-fir and western hemlock: a 36-year record of growth and mortality. Western Journal of Applied Forestry. 2: 111 - 114.

DeGraaf, R.M.; Chadwick, N.L. 1987. Forest type, timber size class and New England breeding birds. Journal of Wildlife Management. 51:212-217.

DeGraaf, R.M.; Rudis, D.D. 1986. New England wildlife: habitat, natural history and distribution. Gen. Tech. Rep. NE-108. Broomall, PA: U.S. Department of Agriculture, Forest Service, Northeastern Forest Experiment Station. 491 p.

de Vlaming, V.L.; Bury, R.B. 1970. Thermal selection in tadpoles of the tailed frog, *Ascaphus truei.* Journal of Herpetology. 4:179-189.

Diamond, J.M. 1972. Biogeographic kinetics: estimation of relaxation times for avifaunas of southwest Pacific islands. Proceedings of the National Academy of Sciences (USA). 69:3199-3203.

Diamond, J.M. 1984. "Normal" extinctions of isolated populations. In: Nitecki, M.H., ed. Extinctions. Chicago: University of Chicago Press: 191-246.

Diamond, J.M.; Bishop, K.D.; Van Balen, S. 1987. Bird survival in an isolated Javan woodland: island or mirror? Conservation Biology. 1:132-133.

Dice, L.R. 1945. Measures of the amount of ecological association between species. Ecology. 26:297-302.

Dixon, J.R.; Heyer, W.R. 1968. Anuran succession in a temporary pond in Colima, Mexico. Bulletin of Southern California Academy of Science. 67:129-137.

Dixon, W.J., ed. 1985. BMDP statistical software manual. Berkeley, CA: University of California Press. 734 p.

Dodwell, A.; Rixon, T.F. 1902. Forest conditions of the Olympic Reserve, Washington. U.S. Geologic Survey Professional Paper 7. Washington, DC: U.S. Geologic Survey.

Draper, N.R.; Smith, H. 1981. Applied regression analysis, 2d ed. New York: John Wiley and Sons. 709 p.

Dueser, R.D.; Shugart, H.H., Jr. 1979. Niche pattern in a forest floor small mammal fauna. Ecology. 60:108-118.

Dumas, P.C. 1956. The ecological relations of sympatry in *Plethodon dunni* and *Plethodon vehiculum.* Ecology. 37:484-495.

Dunnett, C.W. 1980. Pairwise multiple comparisons in the unequal variance case. Journal of the American Statistical Association. 75:796-800.

Dunwiddie, P.W. 1986. A 6,000-year record of forest history on Mount Rainier, Washington. Ecology. 67:58-68.

Dyrness, C.T. 1973. Early stages of plant succession following logging and burning in the western Cascades of Oregon. Ecology. 54:57-69.

Dyrness, C.T.; Franklin, J.F.; Moir, W.H. 1974. A preliminary classification of forest communities in the central portion of the western Cascades of Oregon. Coniferous Forest Biome Bulletin 4. Seattle: US/IBP, University of Washington. 123 p.

Eberhardt, L.L. 1976. Quantitative ecology and impact assessment. Journal of Environmental Management. 4:27-70.

Edmonds, R.L., ed. 1982. Analysis of coniferous forest ecosystems in the Western United States. US/IBP Synthesis Series 14. Stroudsburg, PA: Hutchinson Ross Publishing Co. 419 p.

Efron, B. 1982. The jackknife, the bootstrap, and other resampling plans. Philadelphia: S.I.A.M. Reg. Conf. Ser. 38.

Ehrlich, P.R.; Dobkin, D.S.; Wheye, **D. 1988.** The birder's handbook. New York: Simon and Schuster, Inc. 785 p.

Emlen, J.T. 1971. Population densities of birds derived from transect counts. Auk. 88:323-342.

Emlen, J.T. 1977. Estimating breeding season bird densities from transect counts. Auk. 94:455-468.

Emlen, J.T. 1984. An observer-specific, full-season strip-map method for censusing songbird communities. Auk. 101:730-740.

Emlen, J.T.; DeJong, M.J.; Jaeger, MJ. [and others]. 1986. Density trends and range boundary constraints of forest birds along a latitudinal gradient. Auk. 103(4):791-803.

Enge, K.M.; Marion, W. 1986. Effects of clearcutting and site preparation on herpetofauna of a north Florida flatwoods. Forest Ecology and Management. 14: 177-192.

Engelhardt, N.T. 1957. Pathological deterioration of looper-killed western hemlock on southern Vancouver Island. Forest Science. 3:125-136.

Evans, K.E.; Conner, R.N. 1979. Snag management. In: DeGraaf, R.M.; Evans, K.E., eds. Management of north-central and northeastern forests for nongame birds. Gen. Tech. Rep. NC-51. St. Paul, MN: U.S. Department of Agriculture, Forest Service, North Central Forest and Range Experiment Station: 214-225.

Everest, F.H.; Armantrout, N.B.; Keller, S.M. [and others]. 1985. Salmonids. In: Brown, E.R., tech. ed. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part l-Chapter narratives. Publ. R6-F&WL- 192- 1985. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 199-230.

Faaborg, J. 1979. Qualitative patterns of avian extinction on neotropical land-bridge islands: lessons for conservation. Journal of Applied Ecology. 16:99-107.

Fahnestock, G.R.; Agee, J.K. 1983. Biomass consumption and smoke production by prehistoric and modem forest fires in western Washington. Journal of Forestry. 81:653-657.

Fenton, M.B. 1988. Detecting, recording, and analyzing vocalizations of bats. In: Kunz, T.H., ed. Ecological and behavioral methods for the study of bats. Washington, DC: Smithsonian Institution Press: 91-104.

Fenton, M.B.; van Zyll de Jong, C.G.; Bell, G.P. [and others]. 1980. Distribution, parturition, and feeding of bats in south-central British Columbia. Canadian Field-Naturalist. 94:416-420.

Findley, J.S. 1955. Speciation of the wandering shrew. Manhattan, KS: University of Kansas Publications, Museum of Natural History. 9:1-68.

Fleiss, J.L. 1973. Statistical methods for rates and proportions. New York: John Wiley and Sons, Inc. 223 p.

Flint, H.R. 1925. Fire resistance of northern Rocky Mountain conifers. Idaho Forester. 7(7):7-10,41-43.

Fogel, R.M. 1976. Ecological studies of hypogeous fungi. II. Sporocarp phenology in a western Oregon Douglas-fir stand. Canadian Journal of Botany. 54: 1152-l162.

Fogel, R.M. 1981. Quantification of sporocarps produced by hypogeous fungi. In: Wicklow, D.T.; Carroll, G.C., ed. The fungal community, its organization and role in the ecosystem. New York: Marcel Dekker: 553-568.

Fogel, R.M.; Hunt, G. 1979. Fungal and arboreal biomass in a western Oregon Douglas-fir ecosystem: distribution patterns and turnover. Canadian Journal of Forest Research. 9:245-256.

Fogel, R.; Ogawa, M.; Trappe, J.M. 1973. Terrestrial decomposition: a synopsis. Coniferous Forest Biome Internal Report 135. Seattle: College of Forest Resources, University of Washington. 12 p.

Fogel, R.M.; Trappe, J.M. 1978. Fungus consumption (mycophagy) by small animals. Northwest Science. 52: l-31.

Force, J.E. 1986. Firewood use on National Forests in the Western United States. Western Journal of Applied Forestry. l:lll-115.

Forman, R.T.T.; Galli, A.E.; Leck, C.F. 1976. Forest size and avian diversity in New Jersey woodlots with some land use implications. Oecologia. 26: l-8.

Forman, R.T.T.; Godron, M. 1986. Landscape ecology. New York: John Wiley and Sons. 619 p.

Forsman, E.D.; Meslow, E.C.; Wight, H.M. 1984. Distribution and biology of the spotted owl in Oregon. Wildlife Monographs. 87:1-64.

Fosburg, W. 1986. Wildlife issues in the National Forest system. In: Di Silvestro, R.L., ed. Audubon Wildlife Report. New York: The National Audubon Society: 159-173.

Fowells, H.A., camp. 1965. Silvics of forest trees of the United States. Agric. Handbk. 271. Washington, DC: U.S. Department of Agriculture, Forest Service. 762 p.

Frank, E.C.; Lee, R. 1966. Potential solar beam irradiation on slopes: tables for 30° to 50° latitudes. Res. Pap. RM-18. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 116 p.

Frankel, O.H.; Soul& **M.E. 1981.** Conservation and evolution. New York: Cambridge University Press. 327 p.

Franklin, J.F. 1979. Vegetation of the Douglas-fir region. In: Forest soils of the Douglas-fir region. Pullman, WA: Washington State University Cooperative Extension: 93-112.

Franklin, J.F. 1989. Toward a new forestry. American Forests. November/December:37-44.

Franklin, J.F.; Cromack, K., Jr.; Denison, W. [and others]. 1981. 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. **48** p.

Franklin, J.F.; DeBelI, D.S. 1988. Thirty-six years of tree population change in an old-growth *Pseudotsuga-Tsuga* forest. Canadian Journal of Forest Research. 18:633-639.

Franklin, J.F.; Dyrness, CT. 1971. A checklist of vascular plants on the H.J. Andrews Experimental Forest, western Oregon. Research Note PNW-138. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 37 p.

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

Franklin, J.F.; Forman, R.T.T. 1987. Creating landscape patterns by forest cutting: ecological consequences and principles. Landscape Ecology. l(l):518.

Franklin, J.F.; Hemstrom, M.A. 1981. Aspects of succession in the coniferous forests of the Pacific Northwest. In: West, D.C.; Shugart, H.H.; Botkin D.B., eds. Forest succession. New York: Springer-Verlag: 222-229.

Franklin, J.F.; Moir, W.H.; Hemstrom, M.A. [and others]. 1988. The forest communities of Mount Rainier National Park. Scientific Monograph Series 19. Washington, DC: U.S. Department of the Interior. 194 p.

Franklin, J.F.; Shugart, H.H.; Harmon, M.E. 1987. Tree death as an ecological process. Bioscience. 37550-556.

Franklin,, J.F.; Spies, T.A. 1984. Characteristics of old-growth Douglas-fir forests. In: Proceedings of the 1983 National Convention; 1983 October 16-20; Portland, OR. Washington, DC: Society of American Foresters: 328-334.

Franklin, J.F.; Spies, T.A. This volume. Ecological definitions of old-growth Douglas-fir forests.

Franklin, J.F.; Waring, R.H. 1980. Distinctive features of the northwestern coniferous forest: development, structure, and function. In: Waring, R.H., ed. Forests: fresh perspectives from ecosystem analysis. Proceedings of the 40th Annual Biological Colloquium; 1979 April 27-28; Corvallis, OR. Corvallis, OR: Oregon State University **Press: 59-86.**

Franzreb, K. 1977. Inventory techniques for sampling avian populations. Technical Note T/N 307. Denver, CO: U.S. Department of the Interior, Bureau of Land Management. 17 p.

Fredriksen, R.L. 1972. Nutrient budget of a Douglas-fir forest on an experimental watershed in western Oregon. In: Research on coniferous forest ecosystems: first year progress in the coniferous forest biome, US/IBP. Proceedings of a symposium; 1972 March 23-24; Bellingham, WA. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 115-131.

Freemark, K.E.; Merriam, H.G. 1986. Importance of area and habitat heterogeneity to bird assemblages in temperate forest fragments. Biological Conservation. 36: 115-141.

Fretwell, S.D. 1972. Populations in a seasonal environment. Princeton, NJ: Princeton University Press. 217 p.

Freund, RJ.; Littell, RX.; Spector, P.C. 1986. SAS System for linear models. Cary, NC: SAS Institute, Inc.

Gabrielson, I.N.; Jewett, S.G. 1940. Birds of Oregon. Corvallis, OR: Oregon State Monographs, Studies in Zoology **2. 650** p.

Galli, A.E.; Leck, C.F.; Forman, R.T.T. 1976. Avian distribution patterns in forest islands of different sizes in central New Jersey. Auk. 93:356-364.

Garsd, A. 1984. Spurious correlation in ecological modelling. Ecological Modelling. 23:191-201.

Gashwiler, J.S. 1959. Small mammal study in west-central Oregon. Journal of Mammalogy. 40:128-139.

Gashwiler, J.S. 1970a. Further study of conifer seed survival in a western Oregon clearcut. Ecology. 51:849-854.

Gashwiler, J.S. 1970b. Plant and mammal changes on a clearcut in west-central Oregon. Ecology. 51:1018-1026.

Gauch, H.G., Jr. 1973. A quantitative evaluation of the Bray-Curtis ordination. Ecology. 54:829-836.

Gauch, **H.G., Jr. 1982.** Multivariate analysis in community ecology. New York: Cambridge University Press. 298 p.

Gauch, H.G.; Wentworth, T.R. 1976. Canonical correlation analysis as an ordination technique. Vegetatio. 33:17-22.

Gauch, H.G.; Whittaker, R.H. 1981. Hierarchical classification of community data. Journal of Ecology. 69:537-557.

Gaud, W.S.; Balda, R.P.; Brawn, J.D. 1986. The dilemma of plots or years: the case for long-term studies. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7- 11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 223-227.

Gholz, **H.L. 1982.** Environmental limits on aboveground net primary production, leaf area, and biomass in vegetation zones of the Pacific Northwest. Ecology. 63(2):469-48 1.

Gibbons, J.W. 1988. The management of amphibians, reptiles and small mammals in North America: the need for an environmental attitude adjustment. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 4-10.

Gilbert, F.F. 1985. Old-Growth Wildlife Habitat Project (OGWHP) Oregon Cascades: April 1984-May 1985. Final report submitted to U.S. Department of Agriculture, Forest Service. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Olympia, WA 98502. 151 p.

Gilbert, F.F; Allwine, R. This volume(a). Small mammal communities in the Oregon Cascade Range.

Gilbert, F.F.; Allwine, R. This volume(b). Spring bird communities in the Oregon Cascade Range.

Gilbert, F.F.; Allwine, R. This volume(c). Terrestrial amphibian communities in the Oregon Cascade Range.

Gilbert, F.S. 1980a. The equilibrium theory of island biogeography: fact or fiction? Journal of Biogeography. 7:209-235.

Gilbert, L.E. 1980b. Food-web organization and conservation of neotropical diversity. In: Soule M.E.; Wilcox, B.A., ed. Conservation biology: an evolutionary-ecological perspective. Sunderland, MA: Sinauer Associates: 11-35.

Gill, D.E. 1978. The metapopulation ecology of the red-spotted newt, *Notophthalmus viridescens* (Rafinesque). Ecological Monographs. 48: 145-166.

Gillesberg, A.; Carey, A.B. This volume. Red tree voles in the Oregon Coast Range (abstract). Appendix B.

Gilpin, M.E.; Soule **M.E. 1986.** Minimum viable populations: processes of species extinction. In: Soule M.E. Conservation biology: the science of scarcity and diversity. Sunderland, MA: Sinauer Associates: 19-34.

Gnaedinger, L.K.; Reed, C.A. 1948. Contribution to the natural history of the plethodont salamander *Ensatina eschscholtzi.* Copeia. 1948:187-196.

Goldstein, R.A.; Grigal, D.F. 1972. Definition of vegetation structure by canonical analysis. Journal of Ecology. 60:277-284.

Good, **D.A. 1989.** Hybridization and cryptic species in *Dicamptodon* (Caudata: Dicamptodontidae). Evolution. 43:728-744.

Good, D.A.; Wurst, G.Z.; Wake, D.B. 1987. Patterns of geographic variation in allozymes of the Olympic salamander, *Rhyacotriton olympicus* (Caudata: Dicamptodontidae). Fieldiana Zoology New Series. Chicago: Field Museum of Natural History. 32(1374):1-15.

Goodman, D. 1987a. The demography of chance extinction. In: Soule M.E., ed. Viable populations for conservation. New York: Cambridge University Press: 11-34.

Goodman, D. 1987b. How do species persist? Lessons for conservation biology. Conservation Biology. 1:59-62.

Gordon, R.E.; MacMahon, J.; Wake, D.B. 1962. Relative abundance, microhabitat and behavior of some southern Appalachian salamanders. Zoologica. 47:9-14.

Gould, E. 1955. The feeding efficiencies of insectivorous bats. Journal of Mammalogy. 36:399-407.

Gould, E. 1959. Further studies on the feeding efficiency of bats. Journal of Mammalogy. 40: 149-150.

Graber, J.W.; Graber, R.R. 1976. Environmental evaluations using birds and their habitats. Biological Notes 97. Champaign, IL: Illinois Natural History Survey. 40 p.

Graber, J.W.; Graber, R.R. 1979. Severe winter weather and bird populations in southern Illinois. Wilson Bulletin. 91:88-103.

Graham, R.L.; Cromack, K., Jr. 1982. Mass, nutrient content and decay rate of dead boles in rain forests of Olympic National Park. Canadian Journal of Forest Research. 12:511-521.

Gray, A. Unpublished data. On file at: University of Washington, Seattle, WA 98195.

Green, D.M.; Campbell, R.W. 1984. The amphibians of British Columbia. Handbook 45. Victoria: British Columbia Provincial Museum. 101 p.

Green, R.H. 1979. Sampling design and statistical methods for environmental biologists, New York: John Wiley and Sons. 257 p.

Greene, S. 1988. Research Natural Areas and protecting old-growth forests on Federal lands in western Oregon and Washington. Natural Areas Journal. 8:25-30.

Gregory, S.V.; Swanson, F.J.; McKee, W.A.; Cummins, K.W. In press. An ecosystem perspective of riparian zones. Bioscience.

Grier, C.C.; Logan, R.S. 1977. Old-growth *Pseudotsuga menziesii* communities of a western Oregon watershed: biomass distribution and production budgets. Ecological Monographs. 47:373-400.

Griffin, D.R.; Webster, F.A.; Michael, E.R. 1960. The echolocation of flying insects by bats. Animal Behavior. 8:141-154.

Gruelich, G. Unpublished data. Total Resource Inventory (TRI) database. On file at: Gifford Pinchot National Forest, 6926 E. 4th Plain Blvd., Vancouver, WA 98661.

Gunn, S.J.; Greenbaum, I.F. 1986. Systematic implications of karyotypic and morphologic variation in mainland Peromyscus from the Pacific Northwest. Journal of Mammafogy. 67:294-304.

Gutierrez, R.J.; Carey, A.B., tech. eds. 1985. Ecology and management of the spotted owl in the Pacific Northwest. Proceedings of a symposium; 1984 June 19-23; Arcata, CA. Gen. Tech. Rep. PNW-185. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 119 p.

Haapanen, A. 1965. Bird fauna of the Finnish forests in relation to forest succession. I. Annales Zoologici Fennici. 2:153-196.

Haapenen, A. 1966. Bird fauna of the Finnish forests in relation to forest succession. II. Annales Zoologici Fennici. 3:176-200.

Haas, H. 1933. Die bodenbewohnenden Gropilze in den Waldformationen einiger Gebiete von Wurttemberg. Beihefte zum Botanischen Centralblatt. 50(B):35-134.

Habeck, J.R. 1961. The original vegetation of the mid-Willamette Valley, Oregon. Northwest Science. 35:65-77.

Habeck, J.R. 1968. Forest succession in the Glacier Peak cedar-hemlock forests. Ecology. 49:872-880.

Hagar, D.C. 1960. The interrelationships of logging, birds, and timber regeneration in the Douglas-fir Region of Northwestern California. Ecology. 41: 116- 125.

Hagmeier, E.M.; Stults, C.D. 1964. A numerical analysis of the distributional patterns of North American mammals, Systematic Zoology. 13:125-155.

Haila, Y. **1986.** North European land birds in forest fragments: evidence for area effects? In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Madison: University of Wisconsin Press: 315-319.

Haila, Y.; Jarvinen, O. **1981. The** under-exploited potential of bird censuses in insular ecology. In: Ralph, C.J.; Scott, J.M., eds. Estimating the numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Omithological Society. Studies in Avian Biology. 6:559-565.

Hairston, N.G., **Sr. 1987.** Community ecology and salamander guilds. New York: Cambridge University Press. 230 p,

Hall, F.C. 1988. Pacific Northwest ecoclass codes for plant associations. R6 Ecol. Tech. Pap. 289-87. Portland, OR: US. Department of Agriculture, Forest Service, Pacific Northwest Region. 164 p.

Hall, J.D.; Murphy, M.L.; Aho, R.S. 1978. An improved design for assessing impacts of watershed practices on small streams. Internationale Vereinigung fur theoretische und angewandte Limnologie, Verhandlungen. 20:1359-1365.

Halpern, C.B. 1987. Twenty-one years of secondary succession *in Pseudotsuga* forests of the western Cascade Range, Oregon. Corvallis: Oregon State University. 239 p. Ph.D. dissertation.

Halpern, C.B. 1988. Early successional pathways and the resistance and resilience of forest communities. Ecology. 69:1703-1715.

Halpern, C.B. 1989. Early successional patterns of forest species: interactions of life history traits and disturbance. Ecology. 70(3):704-720.

Hamel, P.B.; Cost, N.D.; Sheffield, R.M. 1986. The consistent characteristics of habitats: a question of scale. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 121-128.

Hansen, AJ.; Peterson, J.A. Personal communication. COPE, Hatfield Marine Science Center, 2030 S. Marine Science Dr., Newport, OR 97365.

Hansen, A.J.; Spies, T.A.; Swanson, F.J.; Ohmann, J.L. In press. Maintaining biodiversity in managed forests: lessons from natural forests. Bioscience.

Hansen, H.P. 1947. Postglacial forest succession, climate, and chronology in the Pacific Northwest. Transactions of the American Philosophical Society. Philadelphia: The American Philosophical Society. 130 p.

Hansen, J.; Lacis, A.; Rind, D. [and others]. 1984. Climate sensitivity: analysis of feedback mechanisms. In: Hansen J.H.; Takahashi, T., eds. Climate processes and climate sensitivity. Washington, DC: Maurice Ewing Service, American Geophysical Union: 130-163.

Harley, J.L.; Smith, S.E. 1983. Mycorrhizal symbiosis. New York: Academic Press. 483 p.

Harlow, W.M.; Harrar, E.S. 1969. Textbook of dendrology. 5th ed. New York: McGraw-Hill. 512 p.

Harmon, M.E.; Franklin, J.F. 1983. Age distribution of western hemlock and its relation to Roosevelt elk populations in the south fork of the Hoh Valley, Washington. Northwest Science. 57:249-255.

Harmon, M.E.; Franklin, J.F. 1989. Tree seedlings on logs in *Picea-Tsuga* forests of Oregon and Washington. Ecology. 70:48-59.

Harmon, M.E.; Franklin, J.F.; Swanson, F.J. [and others]. 1986. Ecology of coarse woody debris in temperate ecosystem. In: MacFadyen, A.; Ford, E.D., eds. Advances in ecological research. New York: Academic Press. 15:133-302.

Harn, J. 1984. Practical aspects of managing old growth forest habitats. In: Challenges for wildlife and fish-the old-growth ecosystem in managed forests. Proceedings of the 1983 Technical Session of The Wildlife and Fish Ecology Working Group, New Forests for a Changing World; 1983 October 16-20; Portland, OR. Society of American Foresters: 69.

Harr, R.D. 1982. Fog drip in the Bull Run municipal watershed, Oregon. Water Resources Research. 18:785-789.

Harr, R.D. 1986. Effects of clearcutting on rain-on-snow runoff in western Oregon: a new look at old studies. Water Resources Research. 22:1095-l100.

Harris, L.D. 1984. The fragmented forest: island biogeographic theory and the preservation of biotic diversity. Chicago: University of Chicago Press. 211 p.

Harris, L.D. 1989. Edge effects and conservation of biotic diversity. Conservation Biology. 2:330-332.

Harris, L.D.; Maser, C. 1984. Animal community characteristics. In: Harris, L.D. The fragmented forest island biogeography theory and the preservation of biotic diversity. Chicago: University of Chicago Press: 44-68.

Harris, L.D.; Maser, C.; **McKee, A. 1982.** Patterns of old growth harvest and implications for Cascades wildlife. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 47:374-392.

Harris, M.A. 1982. Habitat use among woodpeckers in forest burns. Missoula, MT: University of Montana. 63 p. M.S. thesis.

Hartigan, J.A. 1975. Clustering algorithms. New York: John Wiley and Sons, Inc. 351 p.

Hartman, *G.G.;* **Yates, T.L. 1985.** *Scapanus orarius.* Mammalian Species. 253: l-5.

Hartman, G.; Scrivener, J.C.; Holtby, L.B.; Powell, L. 1987. Some effects of different streamside treatments on physical conditions and fish population processes in Carnation Creek, a coastal rain forest stream in British Columbia. In: Salo, E.O.; Cundy, T.W., eds. Streamside management: forestry and fishery interactions. Proceedings of a symposium; 1987 February 12-14; University of Washington, Seattle. Contribution 57. Seattle: Institute of Forest Resources, University of Washington: 330-372.

Hartshorne, G.S. 1978. Treefalls and tropical forest dynamics. In: Tomlinson, P.B.; Zimmerman, M.H., eds. Tropical trees as living systems. New York: Cambridge University Press: 617-638.

Hawes, M.L. 1977. Home range, territoriality, and ecological separation in sympatric shrews, *Sorex vagrans* and *Sorex obscurus.* Journal of Mammalogy. 58:354-367.

Hawkins, C.P.; Gottschalk, LJ.; Brown, S.S. 1988. Densities and habitat of tailed frog tadpoles in small streams near Mount St. Helens following the 1980 eruption. Journal of the North American Benthological Society. *7:246-252.*

Hawkins, C.P.; Murphy, M.L.; Anderson, N.H. 1982. Effects of canopy, substrate composition, and gradient on the structure of macroinvertebrate communities in Cascade Range streams of Oregon. Ecology. 63:1840-1856.

Hawkins, C.P.; Murphy, M.L.; Anderson, N.H.; Wilzbach, M.A. 1983. Density of fish and salamanders in relation to riparian canopy and physical habitat in streams of the northwestern United States. Canadian Journal of Fisheries and Aquatic Sciences. 40:1173-l185.

Hayes, J.P.; Cross, S.P. 1987. Characteristics of logs used by western red-backed voles, *Clethrionomys californicus,* and deer mice, *Peromyscus maniculatus.* Canadian Field-Naturalist. 101:543-546.

Haynes, R.W. 1986. Inventory and value of old-growth in the Douglas-fir region. Research Note PNW-437. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 19 p.

Heatwole, H. 1982. A review of structuring in herpetofaunal assemblages. In: Scott, N.J., ed. Herpetological communities: a volume of the Society for the Study of Amphibians and Reptiles and the Herpetologists League. Wildlife Res. Rep. 13. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service: I-19.

Hebda, R.J.; Mathewes, R.W. 1984. Holocene history of cedar and native Indian cultures of the North American Pacific Coast. Science. 225:71l-7 12.

Hejl, S.J.; **Beedy, E.C. 1986.** Weather-induced variation in the abundance of birds. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 24l-244.

Hejl, S.J.; Verner, J.; Balda, R.P. 1988. Weather and bird populations in true fir forests of the Sierra Nevada, California. Condor. 90(3):561-574.

Helgerson, 0. 1988. Historic fire year for Oregon and California. FIR Report. 9(4):2-4.

Hemstrom, M.A. 1979. A recent disturbance history of forest ecosystems at Mount Rainier National Park. Corvallis: Oregon State University. Ph.D. dissertation.

Hemstrom, M.A.; Franklin, J.F. 1982. Fire and other disturbances of the forest in Mount Rainier National Park. Quaternary Research. 18:32-51.

Hemstrom, M.A.; Logan, S.E.; Pavlat, W. 1987. Plant association and management guide. Willamette National Forest. R6-Ecol257-B-86. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 312 p.

Henderson, J.A.; Peter, D. 1981. Preliminary plant associations and habitat types of the Shelton Ranger District, Olympic National Forest. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. 53 p.

Hennings, D.; Hoffman, R.S. 1977. A review of the taxonomy of the *Sorex vagrans* species complex from western North America. Occasional Paper. Manhattan, KS: University of Kansas, Museum of Natural History. 68:1-35.

Hering, T.F. 1966. The terricolous higher fungi of four Lake District woodlands. Transactions of the British Mycological Society. 49:369-383.

Herrington, R.E. 1988. Talus use by amphibians and reptiles in the Pacific Northwest. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Depart-. ment of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 216-221.

Herrington, R.E.; Larsen, J.H. 1985. Current status, habitat requirements and management of the Larch Mountain salamander *Plethodon larseffi* Burns. Biological Conservation. 34:169-179.

Hett, J.; Taber, R.; Long, J.; Schoen, J. 1978. Forest management policies and elk summer carrying capacity in the *Abies amabilis* forest, western Washington. Environmental Management. 2:561-566.

Heusser, C **J. 1977.** Quaternary palynology of the Pacific slope of Washington. Quaternary Research. 8:282-306.

Heusser, C **J. 1986.** Quaternary pollen records from the interior Pacific Northwest coast: Aleutians to the Oregon-California boundary. In: Bryant, V.M., Jr.; Holloway, R.G., eds. Pollen records of Late-Quaternary North American sediments. Austin, TX: American Association of Stratigraphic Palynologist Foundation: 141-167.

Hicks, L. 1985. Multiple-use on western private industrial timberlands. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 50:211-214.

Higgs, AJ.; Usher, M.B. 1980. Should nature reserves be large or small? Nature. 285:569.

Hill, M.O. 1973. Diversity and evenness: a unifying notation and its consequences. Ecology. 54(2):427-432.

Hill, M.O. 1979a. DECORANA: a FORTRAN program for detrended correspondence analysis and reciprocal averaging. Ithaca, NY: Ecology and Systematics, Cornell University. 52 p.

Hill, M.O. 1979b. TWINSPAN: a FORTRAN program for arranging multivariate data in an ordered 2-way table by classification of the individuals and attributes. Ithaca, NY: Ecology and Systematics, Cornell University. 90 p.

Hill, M.O.; Bunce, R.G.H.; Shaw, M.W. 1975. Indicator species analysis, a divisive polythetic method of classification, and its application to a survey of native pinewoods in Scotland. Journal of Ecology. 63:597-613.

Hill, M.O.; Gauch, H.G. 1980. Deb-ended correspondence analysis: an improved ordination technique. Vegetatio. **42:47-58.**

Hitchcock, C.L.; Cronquist, A. 1973. Flora of the Pacific Northwest. Seattle: University of Washington Press. 730 p.

Hofmann, J.V. 1917. The relation of brush fires to natural reproduction: Applegate Division of the Crater National Forest. Wind River, WA: U.S. Department of Agriculture, Forest Service. 32 p.

Holmes, R.T.; Sherry, T.W.; Sturges, F.W. 1986. Bird community dynamics in a temperate deciduous forest: long-term trends at Hubbard Brook. Ecological Monographs. 56:201-220.

Hooven, E.F. 1973. Effects of vegetation changes on small forest mammals. In: Hermann, R.K.; Black, H.C., eds. Even-aged management. Corvallis, OR: Oregon State University. 90 p.

Hooven, E.F.; Black, H.C. 1976. Effects of some clearcutting practices on small-mammal populations in western Oregon. Northwest Science. 50:189-208.

Hoover, R.L.; Wills, D.L. 1984. Managing forested lands for wildlife. Denver, CO: Colorado Division of Wildlife in cooperation with U.S. Department of Agriculture, Forest Service, Rocky Mountain Region. 459 p.

Howell, A.B. 1926. Voles of the genus *Phenacomys.* II. Life history of the red tree mouse *Phenacomys longicaudw.* North American Fauna. 48:39-64.

Hueck, H.J. 1953. Myco-sociological methods of investigation. Vegetatio. 15:84-101.

Huff, M.H. 1984. Post-fire succession in the Olympic Mountains, Washington: forest vegetation, fuels, and avifauna. Seattle: University of Washington. 240 p. Ph.D. dissertation.

Huff, M.H.; Agee, J.K.; Manuwal, D.A. 1985. Postfire succession of avifauna in the Olympia Mountains, Washington. In: Lotan, J.E.; Brown, J.K., camps. Fire's effect on wildlife habitat. Proceedings of a symposium; Missoula, MT. Gen, Tech. Rep. INT-186. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 8-15.

Huff, M.H.; Manuwal, D.A.; Putera, J.A. This volume. Winter bird communities in the Southern Washington Cascade Range.

Huff, M.H.; Raley, C.M. This volume. Regional patterns of diurnal breeding bird communities in Oregon and Washington.

Huhta, V. 1979. Evaluation of different similarity indices as measures of succession in arthropod communities of the forest floor after clear-cutting. Oecologia. 41:ll-23.

Hull, C.H.; Nie, N.H. 1981. SPSS update 7-9: new procedures and facilities for releases 7-9. New York: McGraw-Hill. 402 p.

Humphrey, S.R.; Cope, J.B. 1976. Population ecology of the little brown bat, *Myotis lucifugus,* in Indiana and north-central Kentucky. Special Publication of the American Society of Mammalogists. 4:1-79.

Hunt, G.A. Unpublished data. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331.

Hunt, G.A.; Trappe, J.M. 1987. Seasonal hypogeous sporocarp production in a western Oregon Douglas-fir stand. Canadian Journal of Botany. 65:438-445.

Huntley, 13.; Webb, T. III. 1989. Migration: species' response to climatic variations caused by changes in the Earth's orbit. Journal of Biogeography. 16:5-19.

Hutto, R.L. 1989. The effect of habitat alteration on migratory land birds in a west Mexican tropical deciduous forest: a conservation perspective, Conservation Biology. 3(2):138-148.

Hutto, R.L.; Pletschet, S.M.; Hendricks, P. 1986. A fixed-radius point count method for nonbreeding and breeding season use. Auk. 103:593-602.

Ingles, L.G. 1965. Mammals of the Pacific States. Palo Alto, CA: Stanford University Press. 506 p.

Irwin, W.P. 1960. Geologic reconnaissance of the northern Coast Ranges and Klamath Mountains, California. California Division of Mines Bulletin 179. 80 p.

Isaac, L.A. 1940. Vegetation succession following logging in the Douglas-fir region with special reference to fire. Journal of Forestry. 38:716-721.

Isaac, L.A. 1943. Reproductive habits of Douglas-fir. Washington, DC: Charles Lathrop Pack Forestry Foundation. 107 p.

Jaccard, P. 1912. The distribution of the flora in the alpine zone. New Phytology. 11:37-50.

Jackson, J.A. 1977. Red-cockaded woodpeckers and pine red-heart disease. Auk. 94:160-163.

James, F.C. 1971. Ordinations of habitat relationships among breeding birds. Wilson Bulletin. 83(3):215-236.

Janzen, D.H. 1986. The eternal external threat. In: Soule M.E. Conservation biology: the science of scarcity and diversity. Sunderland, MS: Sinauer Associates: 286-303.

Jarvinen, 0.; Vaisanen, R.A. 1978. Recent changes in forest bird populations in northern Finland. Annales Zoologici Fennica. 15:279-289.

Jewett, S.G.; Taylor, W.P.; Shaw, W.T.; Aldrich, J.W. 1953. Birds of Washington State. Seattle: University of Washington Press. 767 p.

Johnson, A.S.; Landers, J.L. 1982. Habitat relationships of summer resident birds on slash pine flatwoods. Journal of Wildlife Management. 46:416-428.

Johnson, D.H. 1981. How to measure habitat-a statistical perspective. In: Capen, D.E., ed. Use of multivariate statistics in studies of wildlife habitat. Gen. Tech. Rep. RM-87. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 53-57.

Johnson, S.G. 1979. The land-use history of the Coast Range Preserve, Mendecino County, California. San Francisco: San Francisco State University. 258 p. M.S. thesis.

Jones, J.K., Jr.; Carter, D.C.; Genoways, H.H. [and others]. 1986. Revised checklist of North American mammals north of Mexico, 1986. Lubbock, TX: Texas Tech University Press. 22 p.

Jones, K.B. 1986. Amphibians and reptiles. In: Cooperrider, A.Y.; Boyd, R.J.; Stuart, H.R., eds. Inventory and monitoring wildlife habitat. Denver, CO: U.S. Department of the Interior, Bureau of Land Management, Service Center: 267-290.

Jones, L.L.C.; Aubry, K.B. 1984. *Dicamptodon copei* (Cope's giant salamander). Geographic distribution. Herpetological Review. 15(4):114.

Jones, L.L.C.; Raphael, M.G. 1989. *Aneides ferreus* (clouded salamander). Geographic distribution. Herpetological Review. 20(1): 11.

Jones, L.L.C.; Ruggiero, L.F.; Swingie, J.K. This volume. Ecology of marten in the Pacific Northwest: technique evaluation (abstract). Appendix B.

Juday, G.P. 1976. The location, composition, and structure of old-growth forests of the Oregon Coast Range. Corvallis: Oregon State University. 206 p. Ph.D. dissertation.

Kahrl, W.L., ed. 1979. The California water atlas. Los Altos, CA: William Kaufmann, Inc. 118 p.

Kantrud, H.A.; Kologiski. 1982. Ordination and classification of North Dakota grasslands. North Dakota Academy of Sciences Proceedings. 36:35.

Karlsson, J.; Nilsson, S.G. 1977. The influence of nest-box area on clutch size in some hole-nesting passerines. Ibis. 119:207-211.

Karr, J.R.; Roth, R.R. 1971. Vegetation structure and avian diversity in several New World areas. American Naturalist. 105:423435.

Karr, J.R. 1982a. Avian extinction on Barro Colorado Island, Panama: a reassessment. American Naturalist. 119:220-239.

Karr, J.R. 1982b. Population variability and extinctions in the avifauna of a tropical land-bridge island. Ecology. 63:1975-1978.

Kendeigh, S.C. 1944. Measurement of bird populations. Ecological Monographs. 14:67-106.

Kennedy, JJ. 1983. Analyzing qualitative data. New York: Praeger Publishers. 262 p.

Kepler, C.B.; Scott, J.M. 1981. Reducing bird count variability by training. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:366-374.

Kerrick, M.A.; Johnson, K.; Pedersen, R.J. 1984. What information is necessary for planning the management of old-growth forest for wildlife? In: Proceedings of the 1983 national convention; 1983 October 16-20; Portland, OR. Washington, DC: Society of American Foresters: 383-386.

Kertis, J. 1986. Vegetation dynamics and disturbance history of Oak Patch Natural Area Preserve, Mason County, Washington. Seattle: University of Washington. 95 p. M.S. thesis.

Kessler, W.G.; Kogut, T.E. 1985. Habitat orientations of forest birds in southeastern Alaska. Northwest Science. 59:58-65.

Kilgore, B.M. 1971. The role of fire in managing red fir forests. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 36:405-416.

Kilham, L. 1971. Reproductive behavior of yellow-bellied sapsuckers I. Preference for nesting in *Fomes* infected aspens and hole interactions with flying squirrels, raccoons, and other animals. Wilson Bulletin. 83:310-321.

Kim, J.; Kohout, F.J. 1975. Multiple regression analysis: subprogram REGRESSION. In: Nie, N.H.; Hull, C.H.; Jenkins, J.G. [and others], eds. SPSS: statistical package for the social sciences. 2d ed. San Francisco: McGraw-Hill: 320-367.

Kimney, J.W.; Furniss, R.L. 1943. Deterioration of fire-killed Douglas-fir. Tech. Bull. 851. Washington, DC: U.S. Department of Agriculture, Forest Service. 61 p.

Kleinbaum, D.G.; Kupper, L.L. 1978. Applied regression analysis and other multivariate methods. Boston: Duxbury Press. *556* p.

Klockars, A.J.; Sax, G. 1986. Multiple comparisons. In: Sullivan, J.L.; Niemi, R.G., eds. Series: Quantitative applications in the social sciences. Beverly Hills, CA: Sage Publications, Inc. 87 p.

Krebs, C **J.** 1985. Ecology: the experimental analysis of distribution and abundance. 3d ed. New York: Harper and Row. 800 p.

Krebs, J.R. 1971. Territory and breeding density in the great tit, *Parus major* L. Ecology. 52:1-22.

Kunz, T.H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. Journal of Mammalogy. 54: 14-32.

Kurta, A.; Kunz, T.H. 1988. Roosting metabolic rate and body temperature of male little brown bats (Myotis *lucifugus)* in summer. Journal of Mammalogy. 69:645-651.

Kutzbach, J.T.; Guetter, T.J. 1986. The influence of changing orbital parameters and surface boundary conditions on climatic simulations for the past 18,000 years. Journal of Atmospheric Sciences. 43:1726-1759.

Lachenbruch, P.A. 1975. Discriminant analysis. New York: Hafner Press. 128 p.

Lachenbruch, P.A.; Mickey, M.R. 1968. Estimation of error rates in discriminant analysis. Technometrics. 10:1-11.

Lande, R. 1988. Genetics and demography in biological conservation. Science. 241:16-241.

Lande, R.; Barrowclough, G.F. 1987. Effective population size, genetic variation, and their use in population management. In: Soule M.E., ed. Viable populations for conservation. New York: Cambridge University Press: 87-124.

Lang, F.J. 1980. Old-growth forests of the Douglas-fir region of western Oregon and western Washington: characteristics and management. Sacramento, CA: Jones and Stokes Associates, Inc. 62 p.

Laudenslayer, W.F., Jr. 1985. Candidate old growth on National Forest System administered lands in California. San Francisco, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Region.

Laudenslayer, W.F., Jr. 1986. Summary: predicting effects of habitat patchiness and fragmentation-the manager's viewpoint. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 331-333.

Legendre, L.; Legendre, P. 1983. Numerical ecology. New York: Elsevier Scientific Publishing Co. 419 p.

Lehmkuhi, J.F. Personal communication. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Olympia, WA 98502.

Lehmkuhl, J.F. 1984. Determining the size and dispersion of minimum viable populations for land management planning and species conservation. Environmental Management. 8:167-175.

Lehmkuhl, J.F.; Ruggiero, L.F. This volume. Forest fragmentation in the Pacific Northwest and its potential effects on wildlife.

Lehmkuhl, J.F.; Ruggiero, L.F.; Hail, P.A. This volume. Landscape-scale patterns of forest fragmentation and wildlife richness and abundance in the Southern Washington Cascade Range.

Leopold, A. 1933. Game management. New York Charles Scribners. 481 p.

Leopold, E.B.; Nickman, J.I.; Hedges, J.I.; Ertel, J.R. 1982. Pollen and lignin records of Late-Quaternary vegetation, Lake Washington. Science. 218:1305-1307.

Levins, R. 1970. Extinction. In: Gerstenhaber, M. Some mathematical questions in biology. Providence, RI: American Mathematical Society. 277-107.

Lidicker, W.Z. 1975. The role of dispersal in the demography of small mammals. In: Gohey, F.B.; Petrusewicz, K.; Ryszkowski, L., eds. Small mammals: their productivity and population dynamics. New York: Cambridge University Press: 103-128.

Liu, T.T. 1954. Hybridization between *Peromyscus maniculatus oreas* and *P. m. gracilis.* Journal of Mammalogy. 35:448-449.

Long, J.N. 1977. Trends in plant species diversity associated with development *in* a series of *Pseudotsuga menziesii/Gaultheria shallon* stands. Northwest Science. 51(2):119-130.

Long, J.N.; Turner, J. 1974, Aboveground biomass of understory and overstory in an age sequence of four Douglas-fir stands. Journal of Applied Ecology. 12179-188.

Lovejoy, S. 1982. Area-perimeter relation for rain and cloud areas. Science. 216:185-187.

Lowery, D.P.; Hillstrom, W.A.; Eiert, E.E. 1977. Chipping and pulping dead trees of four Rocky Mountain timber species. Res. Paper INT-193. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 11 p.

Lumen, I.D.; Nietro, W.A. 1980. Preservation of mature forest seral stages to provide wildlife habitat diversity. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 45:271-277.

Lundquist, R.W. 1988. Habitat use by cavity-nesting birds in the southern Washington Cascades. Seattle: University of Washington. 168 p. M.S. thesis.

Lundquist, R.W.; Manuwal, D.A. 1990. Seasonal differences in foraging habitat of cavity-nesting birds in the southern Washington Cascades. In: Morrison, M.L.; Ralph, CJ.; Verner, J.; Jehl, J.R., Jr., eds. Avian foraging: theory, methodology, and applications. Proceedings of an international symposium; 1988 March 18-19; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 13:218-225.

Lundquist, R.W.; Mariani, J.M. This volume. Nesting habitat and abundance of snag-dependent birds in the Southern Washington Cascade Range.

Luoma, D.L. 1988. Biomass and community structure of sporocarps formed by hypogeous ectomycorrhizal fungi within selected forest habitats of the H.J. Andrews Experimental Forest, Oregon. Corvallis: Oregon State University. 173 p. Ph.D. dissertation.

Luoma, D.L.; Frenkel, R.E.; Trappe, J.M. In press. Fruiting of hypogeous fungi in Oregon Douglas-fir. forests: seasonal and habitat variation. Mycologia.

Lynch, J.F. 1981. Patterns of ontogenetic and geographic variation in the black salamander *Aneides flavipunctatus* (Caudata: Plethodontidae). Smithsonian Contributions to Zoology. 324:1-53.

Lynch, J.F. 1985. *The* feeding ecology of *Aneides flavipunctutus* and sympatric plethodontid salamanders in northwestern California. Journal of Herpetology. 19:328-352.

MacArthur, R.H.; MacArthur, J.W.; Preer, J. 1962. On bird species diversity. II: Prediction of bird census from habitat measurements. American Naturalist. 100:319-332.

MacArthur, R.H.; Recher, H.; Cody, M. 1966. On the relation between habitat selection and species diversity. American Naturalist. 100:310-332.

MacArthur, R.H.; Wilson, E.O. 1967. The theory of island biogeography. Princeton, NJ: Princeton University Press. *203* p.

Madsen, S.J. 1985. Habitat use by cavity-nesting birds in the Okanogan National Forest, Washington. Seattle: University of Washington. 113 p. M.S. thesis.

Magurran, A.E. 1988. Ecological diversity and its measurement. Princeton, NJ: Princeton University Press. 179 p.

Mannan, R.W. 1984a. Habitat use by Hammond's flycatchers in old-growth forests, northeastern Oregon. Mm-relet. 65:84-86.

Mannan, R.W. 1984b. Summer area requirements of pileated woodpeckers in western Oregon. Wildlife Society Bulletin. 12:265-268.

Mannan, R.W.; Meslow, E.C. 1984. Bird populations and vegetation characteristics in managed and old-growth forests, northeastern Oregon. Journal of Wildlife Management. 48(4):1219-1238.

Mannan, R.W.; Meslow, E.C.; Wight, H.M. 1980. Use of snags by birds in Douglas-fir forests, western Oregon. Journal of Wildlife Management. 44:787-797.

Mannan, R.W.; Morrison, M.L.; Meslow, E.C. 1984. Comment: the use of guilds in forest bird management. Wildlife Society Bulletin. 12:426-430.

Manuwal, D.A. Personal communication. College of Forest Resources AR-l0, University of Washington, Seattle, WA 98195.

Manuwal, D.A. This volume. Spring bird communities in the Southern Washington Cascade Range.

Manuwal, D.A.; Carey, A.B. In press. Methods for measuring populations of small, diurnal forest birds. Gen. Tech. Rep. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

Manuwal, D.A.; Huff, M. 1987. Spring and winter bird populations in a Douglas-fir forest sere. Journal of Wildlife Management. 51(3):586-595.

Manuwal, D.A.; Huff, M.; Bauer, M. [and others]. 1987. Summer birds of the upper subalpine zone of Mount Adams, Mount Rainier, and Mount St. Helens, Washington. Northwest Science. 61(2):82-92.

Manuwal, D.A.; Lundquist, R.; Mariani, J. 1986. Distribution and abundance of bird populations of different-aged Douglas-fir forests in the southern Washington Cascades. Unpublished Final Report. On file at U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Olympia, WA 98502. 96 p.

Marcot, B.C. 1983. Snag use by birds in Douglas-fir clearcuts. In: Davis, J.W.; Goodwin, G.A.; Ockenfels, R.A., tech. coords. 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: 134-139.

Marcot, B.G. 1984. Habitat relationships of birds in young-growth Douglas-fir in northwestern California. Corvallis: Oregon State University. 282 p. Ph.D. dissertation.

Marcot, B.G. 1986. Use of expert systems in wildlife-habitat modeling. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Madison, WI: University of Wisconsin Press: 145-150.

Marcot, B.G. 1987. Testing your knowledge base. AI Expert. *2:42-47.*

Marcot, B.G.; Holthausen, R.S.; Teply, J.; Carrier, W.D. This volume. Old-growth inventories: status, definitions, and visions for the future.

Marcot, B.G.; McNay, R.S.; Page, R.E. 1988. Use of microcomputers for planning and managing silviculture-habitat relationships. Gen. Tech. Rep. PNW-228. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 19 p.

Margules, C.; Higgs, A.J.; Rafe, R.W, 1982. Modem biogeographic theory: are there any lessons for nature reserve design? Biological Conservation. 24: 115-128.

Mariani, J.M. 1987. Brown creeper *(Certhia americana)* abundance patterns and habitat use in the southern Washington Cascades. Seattle: University of Washington. 72 p. M.S. thesis.

Mariani, J.M.; Manuwal, D.A. 1990. Factors influencing brown creeper *(Certhiu americana)* abundance patterns in the southern Washington Cascade Range. In: Morrison, M.L.; Ralph, C.J.; Verner, J.; Jehl, J.R., eds. Avian foraging: theory, methodology, and applications. Proceedings of an international symposium; 1988 March 18-19; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 13:53-57.

Martell, A.M.; Radvanyi, A. 1977. Changes in small mammal populations after clear-cutting of northern Ontario black spruce forest. Canadian Field-Naturalist. 91:4l-46.

Martin, T.E. 1981. Limitation in small habitat islands: chance or competition? Auk. 98(4):715-734.

Martin, T.E.; Karr, J.R. 1986. Patch utilization by migrating birds: resource oriented? Ornis Scandinavica. **17(1):165-174.**

Maser, C. 1966. Life histories and ecology of *Phenacomys albipes, Phenacomys longicaudus, Phenacomys silvicola.* Corvallis: Oregon State University. 221 p. M.S. thesis.

Maser, C.; Anderson, R.G.; Cromack, K., Jr. [and others]. 1979. Dead and down woody material. In: Thomas, J.W., tech. ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agricultural Handbook 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 78-95.

Maser, C.; Maser, Z. 1988. Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. Great Basin Naturalist. 48:358-368.

Maser, C.; Mate, B.R.; Franklin, J.F.; Dyrness C.T. 1981. Natural history of Oregon coast mammals. Gen. Tech. Rep. PNW-133. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 496 p.

Maser, C.; Tarrant, R.F.; Trappe, J.M.; Franklin, J.F., tech. eds. 1988. From the forest to the sea: a story of fallen trees. Gen. Tech. Rep. PNW-229. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 153 p.

Maser, C.; Trappe, J.M.; Nussbaum, R.A. 1978. Fungal-small mammal inter-relationships with emphasis on Oregon coniferous forests. Ecology. 59:799-809.

Mathewes, R.W.; Rouse, G.E. 1975. Palynology and paleoecology of postglacial sediments from the lower Fraser River Canyon of British Columbia. Canadian Journal of Earth Sciences. 12:745-756.

Maurer, B.A.; McArthur, L.B.; Whitmore, R.C. 1981. Effects of logging on guild structure of a forest bird community in West Virginia. American Birds. 35(1):11-13.

Mayer, K. Personal communication. California Department of Fish and Game, 1416 9th St., Sacramento, CA 95814.

Mayo, J. Personal communication. U.S. Department of Agriculture, Forest Service, Willamette National Forest Supervisor's Office, P.O. Box 10607, Eugene, OR 97440.

McClelland, B.R. 1977. Relationships between hole-nesting birds, forest snags, and decay in western larch-Douglas-fir forests of the northern Rocky Mountains. Missoula, MT: University of Montana. 438 p. Ph.D. dissertation.

McCloskey, R.T. 1975. Habitat succession and rodent distribution. Journal of Mammalogy. 56:950-955.

McCoy, E.D. 1982. The application of island-biogeographic theory to forest tracts: problems in the determination of turnover rates. Biological Conservation. 22:217-227.

McCune, B.; Allen, T.F.H. 1985. Forest dynamics in the Bitterroot Canyons, Montana. Canadian Journal of Botany. **63:377-383.**

McIntire, C.D. 1978. The distribution of estuarine diatoms along environmental gradients: a canonical correlation. Estuarine and Coastal Marine Science. 6:447-457.

McKee, A.; Stonedahl, G.M.; Franklin, J.F.; Swanson, F.J., comps. 1987. Research publications of the H.J. Andrews Experimental Forest, Cascade Range, Oregon, 1948 to 1986. Gen. Tech. Rep. PNW-201. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 74 p.

McLellan, C.H.; Dobson, A.P.; Wilcove, D.S.; Lynch, J.F. 1986. Effects of forest fragmentation on new- and old-world bird communities: empirical observations and theoretical implications. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Madison: University of Wisconsin Press: 305314.

McNay, R.S.; Page, R.E.; Campbell, A. 1987. Application of expert-based decision models to promote integrated management of forests. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 52:82-91.

McNeil, R.C.; Zobel, D.B. 1980. Vegetation and fire history of a ponderosa pine-white fir forest in Crater Lake National Park. Northwest Science. 54:30-46.

Means, J.E. 1982. Developmental history of dry coniferous forests in the western Oregon Cascades. In: Means, J.E., ed. Forest succession and stand development research in the Northwest. Corvallis, OR: Forest Research Laboratory, Oregon State. University: 142-158.

Means, J.E. Unpublished data. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331.

Meehan, W.R.; Merrell, T.R., Jr.; Hanley, T.A., eds. 1984. Fish and wildlife relationships in old-growth forests. Proceedings of a symposium; 1982 April 12-15; Juneau, AK. Morehead City, NC: American Institute of Fishery Research Biologists. 425 p.

Meehan, W.R.; Swanson, F.J.; Sedell, J.R. 1977. Influences of riparian vegetation on aquatic ecosystems with particular references to salmonid fishes and their food supply. In: Johnson, R.R.; Jones, D.A., eds. Importance, preservation and management of riparian habitat. Proceedings of a symposium; 1977 July 9; Tucson, AZ. Gen. Tech. Rep. RM-43. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 137-145.

Meents, J.K.; Rice, J.; Anderson, B.W.; Ohmart, R.D. 1983. Nonlinear relationships between birds and vegetation. Ecology. 64(4):1022-1027.

Meiselman, N.; Doyle, A.T. In press. Habitat and microhabitat selection by the red tree vole *(Arborimus longicaudus)*. American Midland Naturalist.

Mellen, T.K. 1987. Home range and habitat use by pileated woodpeckers. Corvallis: Oregon State University. 96 p. M.S. thesis.

Meslow, E.C.; Keith, L.B. 1971. A correlational analysis of weather versus snowshoe hare population parameters. Journal of Wildlife Management. 35(1):1-15.

Meslow, E.C.; Maser, C.; Verner, J. 1981. Old-growth forests as wildlife habitat. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. *46:329-335.*

Meslow, EC.; Wight, H.M. 1975. Avifauna and succession in Douglas-fir forests of the Pacific Northwest. In: Smith, D.R., tech. coord. Management of forest and range habitats for nongame birds. Proceedings of a symposium; 1975 May 6-9; Tucson, AZ. Gen. Tech. Rep. WO-1. Washington, DC: U.S. Department of Agriculture, Forest Service: 266-271.

Metter, D.E. 1964. A morphological and ecological comparison of two populations of the tailed frog, *Ascaphus truei* Stejneger. Copeia. 1964:181-195.

Metter, D.E. 1967. Variation in the ribbed frog, *Ascaphus truei.* Copeia. 1967:634-649.

Meyer, J.S.; Ingersoll, C.G.; McDonald, L.L.; Boyce, M.S. 1986. Estimating uncertainty in population growth rates: jackknife vs. bootstrap techniques. Ecology. 67: 1156-1166.

Miller, L.A.; Andersen, B.B. 1984. Studying bat echolocation signals using ultrasonic detectors. Zeitschrift fur Saugetierkunde. 49:6-13.

Miller, R.S. 1967. Pattern and process in competition. Advances in Ecological Research. 4:1-74.

Milne, K.; Hejl, S. 1989. Nest-site characteristics of white-headed woodpeckers. Journal of Wildlife Management. 53(1):50-55.

Mohler, C.L. 1987. COMPOSE: a program for formatting and editing data matrices. Ithaca, NY: Microcomputer Power. 58 p.

Moir, W.H.; Hobson, F.D.; Hemstrom, M.; Franklin, J.F. 1979. Forest ecosystems of Mount Rainier National Park. In: Linn, R.M., ed. Proceedings of the first conference on scientific research in the National Parks; New Orleans, LA. Washington, DC: U.S. Department of the Interior, National Park Service, Transactions and Proceedings Series. 1(5):201-208.

Moldenke, A.R.; Lattin, J.D. This volume. Arthropods in old growth: sensitive environmental indicators (abstract). Appendix B.

Monthey, R.W. 1984. Wildlife considerations in the management of fragmented older forests: the Coast Ranges of northwest Oregon. In: Meehan, W.R.; Merrell, T.R., Jr.; Hanley, T.A., eds. Fish and wildlife relationships in old-growth forests. Proceedings of a symposium; 1982 April 12-15; Juneau, AK. Morehead City, NC: American Institute of Fishery Research Biologists: 367-371.

Monthey, R.W.; Soutiere, E.C. 1985. Responses of small mammals to forest harvesting in northern Maine. Canadian Field-Naturalist. 99: 13-18.

Morris, D.W. 1984. Microhabitat separation and coexistence of two temperate-zone rodents. Canadian Field-Naturalist. 98:215-218.

Morris, W.G. 1932. A preliminary report, giving some of the results obtained in a study of lightning storm occurrence and behavior on the National Forests of Oregon and Washington. Forest Research Note 10. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 11 p.

Morris, W.G. 1934. Forest fires in Oregon and Washington. Oregon Historical Quarterly. 35:313-339.

Morrison, ML.; Dedon, M.F.; Raphael, M.G.; Yoder-Williams, M.P. 1986. Snag requirements of cavity-nesting birds: are U.S. Department of Agriculture Forest Service guidelines being met? Western Journal of Applied Forestry. 1:38-40.

Morrison, M.L.; Timossi, I.C.; With, K.A. 1987. Development and testing of linear regression models predicting bird-habitat relationships. Journal of Wildlife Management. 51:247-253.

Morrison, M.L.; Timossi, I.C.; With, K.A.; Manley, P.N. 1985. Use of tree species by forest birds during winter and summer. Journal of Wildlife Management. 49:1098-1102.

Morrison, P.M. 1988. Old growth in the Pacific Northwest: a status report. Washington, DC: The Wilderness Society. 46 p.

Morrison, P.H.; Swanson, F. 1990. Fire history and pattern in a Cascade Range landscape. Gen. Tech. Rep. PNW-254. Portland, Oregon: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 77 p.

Mueller-Dombois, D.; Ellenberg, H. 1974. Aims and methods of vegetation ecology. New York: John Wiley and Sons. 547 p.

Munger, T.T. 1925. Rainfall probability during the fire season in western Washington and Oregon. Monthly Weather Review. 53:394-397.

Murphy, D.D. 1989. Conservation and confusion: wrong species, wrong scale, wrong conclusions. Conservation Biology. 3:82-84.

Murphy, M.L.; Hall, J.D. 1981. Varied effects of clear-cut logging on predators and their habitat in small streams of the Cascade Mountains, Oregon. Canadian Journal of Fisheries and Aquatic Sciences. 38: 137-145.

Murphy, M.L.; Hawkins, C.P.; Anderson, N.H. 1981. Effects of canopy modification and accumulated sediment on stream communities. Transactions of the American Fisheries Society. 110:469-478.

National Atmospheric and Oceanographic Administration. 1960-1985. Monthly climatological summaries for Washington.

National Geographic Society. 1987. Field guide to the birds of North America. Washington, DC. 464 p.

Neitro, W.A.; Mannan, R.W.; Taylor, D. [and others]. 1985. Snags. In: Brown, E.R., tech. ed. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part l-Chapter Narratives. R6-F&WL-192-1985. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 129-169.

Nel, J.A.J. 1978. Habitat heterogeneity and changes in small mammal community structure and resource utilization in the southern Kalahari. Bulletin of the Carnegie Museum of Natural History. 6:118-131.

Nelson, R.D.; Black, H.; Radtke, R.E.; Mumma, J. 1983. Wildlife and fish management in the Forest Service: a goal oriented approach. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 48:87-95.

Nelson, R.D.; Salwasser, H. 1982. The Forest Service wildlife and fish habitat relationship program. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 47:174-183.

Nelson, **S.K. 1989.** Habitat use and densities of cavity-nesting birds in the Oregon Coast Ranges. Corvallis: Oregon State University. 157 p. M.S. thesis.

Nelson, S.K. This volume. The marbled murrelet in western Oregon: a summary of current knowledge (abstract). Appendix B.

Nelson, S.K.; McAllister, M.L.C.; Stern, M.A. [and others]. In press. Status of marbled murrelets in Oregon. Western Foundation for Vertebrate Zoology.

Neter, J.; Wasserman, W.; Kutner, M.H. 1989. Applied linear regression models. Homewood, IL: Richard D. Irwin, Inc. 665 p.

Newbold, J.D.; Erman, D.C.; Roby, K.B. 1980. Effects of logging on macroinvertebrates in streams with and without buffer strips. Canadian Journal of Fisheries and Aquatic Sciences. 37: 1076-1085.

Newmark, W.D. 1987. A land-bridge island perspective on mammalian extinctions in western North American parks. Nature. 325:430-432.

Nicolai, V. 1986. The bark of trees: thermal properties, microclimate and fauna. Oecologia. 69: 148-160.

Noon, B.R. Personal communication. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Arcata, CA 95521.

Noon, B.R.; Dawson, D.K.; Inkley, D.B. [and others]. 1980. Consistency in habitat preference of forest bird species. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 45:226-244.

Norse, **E.A. 1990.** Ancient forests of the Pacific Northwest. Washington, DC: Island Press. 327 p.

Norse, E.A.; Rosenbaum, K.L.; Wilcove, D.S. [and others]. 1986. Conserving biological diversity in our *National* Forests. Washington, DC: The Wilderness Society. 166 p.

Norton, H.H. 1979. The association between anthropogenic prairies and important food plants in western Washington. Northwest Anthropological Research Notes. 13(2): 175-200.

Norusis, M.J. 1988a. SPSS/PC+. Statistical package for the social sciences. Chicago, IL: SPSS Inc.

Norusis, M.J. 1988b. SPSS/PC+ V3.0 update manual. Chicago, IL: SPSS Inc.

Ness, **R.F. 1983.** A regional landscape approach to maintain diversity. BioScience. 33:700-706.

Noss, **R.F. 1987.** Corridors in real landscapes: a reply to Simberloff and Cox. Conservation Biology. 1:159-164.

Ness, R.F.; Harris, L.D. 1986. Nodes, networks, and MUMs: preserving diversity at all scales. Environmental Management. 10:299-309.

Noy-Meir, I. 1973. Divisive polythetic classification of vegetation data by optimized division on ordination components. Journal of Ecology. 61:753-760.

Nussbaum, R.A. 1970. *Dicamptodon copei,* n. sp., from the Pacific Northwest, U.S.A. (Amphibia: Caudata: Ambystomatidae). Copeia. 1970;506-514.

Nussbaum, R.A.; Brodie, E.D., Jr.; Storm, R.M. 1983. Amphibians and reptiles of the Pacific Northwest. Moscow: University Press of Idaho. 332 p.

Nussbaum, R.A.; Tait, C.K. 1977. Aspects of the life history and ecology of the Olympic salamander, *Rhyacotriton olympicus (Gaige). American* Midland Naturalist. 98: 176-199.

Nyberg, J.B.; Bunnell, L.; Harestad, A.S. 1987. Old-growth by design: managing young forest for old-growth wildlife. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 52:70-81.

O'Connor, R J. 1981. Habitat correlates of bird distribution in British census plots. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:533-537.

O'Connor, R.J. 1986. Dynamical aspects of avian habitat use. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7- 11; Fallen Leaf Lake, California. Madison: University of Wisconsin Press: 235-240.

O'Farrell, M J.; Bradley, W.G. 1970. Activity patterns of bats over a desert spring. Journal of Mammalogy. 51:18-26.

O'Halloran, K.A.; Gunderson, A.G.; Holthausen, R.S. This volume. Spotted owl monitoring in Washington and Oregon (abstract). Appendix B.

O'Neil, J.L.; Carey, A.B. 1986. Introduction: when habitats fail as predictors. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 207-208.

O'Neill, R.V.; Krummel, J.R.; Gardner, R.H. [and others]. 1988. Indices of landscape pattern. Landscape Ecology. 1:153-166.

Odum, E.P. 1969. The strategy of ecosystem development. Science. 164:262-270.

Odum, E.P. 1971. Fundamentals of ecology. 3d ed. Philadelphia: W.B. Saunders Company. 574 p.

Ohmann, J.L.; Carleson, D.; Lee, P.L.; Oakley, A.L. 1988. Status of forest- related wildlife and fish resources in Oregon. In: Lettman, G.J., ed. Assessment of Oregon's forests. Portland, OR: Oregon State Department of Forestry: 17-32.

Old-Growth Definition Task Group. 1986. Interim definitions for old-growth Douglas-fir and mixed-conifer forests in the Pacific Northwest and California. Res. Note PNW-447. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 7 p.

Oliver, C.D. 1982. Stand development-its uses and methods of study. In: Means, J.E., ed. Forest succession and stand development research in the Northwest. Corvallis: Oregon State University, Forestry Research Laboratory: 100-112.

Orians, G.H.; Willson, M.F. 1964. Interspecific territories of birds. Ecology. 45:736-745.

Osgood, W.H., 1909. Revision of the mice of the American genus *Peromyscus.* U.S. Department of Agriculture, Biological Survey of North American Fauna 28. 285 p.

Ovaska, K.; Gregory, P.T. 1989. Population structure, growth, and reproduction in a Vancouver Island population of the salamander *Plethodon vehiculum.* Herpetologica. 45:133-143.

Paine, R.T. 1969. A note on trophic complexity and community stability. American Naturalist. 103:91-93.

Paton, P.W.C.; Ralph, C J. This volume. Geographic distribution of the marbled murrelet in California at inland sites (abstract). Appendix B.

Pattie, D.L. 1973. *Sorex bendirii.* Mammalian Species. 27: l-2.

Patton, D.R. 1975. A diversity index for quantifying habitat "edge." Wildlife Society Bulletin. 3:171-173.

Patton, D.R. 1978. Run wild-a storage and retrieval system for wildlife habitat information. Gen. Tech. Rep. RM-51. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 8 p.

Perkins, J.M. 1983. Bat survey of western Coos, Lane, Douglas Counties in relation to habitat type and age class. Contract #83-0-08. Unpublished report on file at Oregon Department of Fish and Wildlife, P.O. Box 59, Portland, OR 97207. 73 p.

Perry, D.A.; Thomas, B.; Meurisse, R. [and others]. 1988. Maintaining the long-term productivity of Pacific Northwest forest ecosystems. Proceedings of a symposium; 1987 March 31 to April 2; Corvallis, OR. Portland, OR: Timber Press.

Pickett, S.T.A.; White, P.S. 1985. The ecology of natural disturbance and patch dynamics. New York: Academic Press. 472 p.

Pickford, S.P.; Fahnestock, G.R.; Ottmar, R. 1980. Weather, fuel, and lightning fires in Olympic National Park. Northwest Science. 54(2):92-105.

Pielou, E.C. 1966. Species diversity and pattern diversity in the study of ecological succession. Journal of Theoretical Biology. 10:370-383.

Pielou, EC. 1977. Mathematical ecology. New York: John Wiley and Sons. 385 p.

Pielou, E.C. 1984. The interpretation of ecological data: a primer on classification and ordination. New York: John Wiley and Sons. 263 p.

Pike, L.H.; Denison, W.C.; Tracy, D.M. [and others]. 1975. Floristic survey of epiphytic lichens and bryophytes growing on old-growth conifers in western Oregon. The Bryologist. 78:389-402.

Pike, L.H.; Rydell, R.A.; Denison, WC. 1977. A 400-year-old Douglas-fir tree and its epiphytes: biomass, surface area, and their distributions. Canadian Journal of Forest Research. 7(4):680-699.

Pimental, R.A. 1979. Morphometrics: the multivariate analysis of biological data. Dubuque, IA: Kendall/Hunt Pub. Co. 276 p.

Pimm, S.L.; Jones, H.L.; Diamond, J.M. 1988. On the risk of extinction. American Naturalist. 132:757-785.

Platts, W.S.; McHenry, M.L. 1988. Density and biomass of trout and char in western streams. Gen. Tech. Rep, INT-241. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 17 p.

Platts, W.S.; Megahan, W.F.; Minshall, G.W. 1983. Methods for evaluating stream, riparian, and biotic conditions. Gen. Tech. Rep. INT-138. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 70 p.

Porter, K.R. 1972. Herpetology. Philadelphia, PA: W.B. Saunders Co. 524 p.

Porter, S.C. Personal communication. Quaternary Research Center, University of Washington, Seattle 98195.

Porter, S.C.; Pierce, K.L.; Hamilton, T.D. 1983. Late Wisconsin mountain glaciation in the Western United States. In: Porter, S.C., ed. Late-Quaternary environments of the United States. The Late Pleistocene. Minneapolis: University of Minnesota. 1:71-111.

Pough, H.F. 1980. The advantages of ectothermy for tetrapods. American Naturalist. 115:92-112.

Pough, H.F. 1983. Amphibians and reptiles as low-energy systems. In: Aspey, W.P.; Lustick, S.I., eds. Behavioral energetics: the cost of survival in vertebrates. Columbus: Ohio State University Press: 141-188.

Pough, H.F.; Smith, E.M.; Rhodes, D.H.; Collazo, A. 1987. The abundance of salamanders in forest stands with different histories of disturbance. Forest Ecology and Management. 20:1-9.

Powell, G.V.N.; Rappole, J.H. 1986. The hooded warbler. In: Audubon Wildlife Report: 827-854.

Press, S.; Wilson, S. 1978. Choosing between logistic regression and discriminant analysis. Journal of the American Statistical Association. 73:699-705.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. American Naturalist. 132:652-669.

Pyne, S.J. 1982. Fire in America: a cultural history of wildland and rural fire. Princeton, NJ: Princeton University Press. 654 p.

Racey, P.A. 1973. Environmental factors affecting the length of gestation in heterothermic bats. Journal of Reproduction and Fertility supplement. 19: 175-189.

Racey, P.A.; Swift, S.M. 1981. Variations in gestation length in a colony of pipistrelle bats *(Pipistrellus)* from year to year. Journal of Reproduction and Fertility. 61: 123-129.

Racey, **P.A.; Swift, S.M. 1985.** Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. Journal of Animal Ecology. 54:205-215.

Raedeke, K.J., ed. 1988. Streamside management: riparian wildlife and forestry interactions. Proceedings of a symposium; 1987 February 11-13; University of Washington, Seattle. Contribution 59. Seattle: Institute of Forest Resources, University of Washington. 277 p.

Raedeke, KJ.; Lehmkuhl, J.F. 1986. A simulation procedure for modeling the relationships between wildlife and forest management. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 377-382.

Ralph, CJ.; Paton, P.W.C.; Taylor, C.A. This volume. Habitat association patterns of breeding birds and small mammals in Douglas-fir/hardwood stands in northwestern California and southwestern Oregon.

Ralph, CJ.; Scott, J.M., eds. 1981. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology 6. 630 p.

Ramotnik, C.A.; Scott, N.J., Jr. 1988. Habitat requirements of New Mexico’s endangered salamanders. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 54-63.

Ramsey, F.L.; Wildman, V.; Engbring, J. 1987. Covariate adjustment to effective area in variable-area wildlife surveys. Biometrics. 43:1-11.

Randall, J.A.; Johnson, R.E. 1979. Population densities and habitat occupancy by *Microtus longicaudus* and M. *montanus.* Journal of Mammalogy. 60:217-219.

Ranney, J.W.; Bruner, M.C; Levenson, J.B. 1981. The importance of edge in the structure and dynamics of forest islands. In: Burgess, R.L.; Sharpe, D.M., eds. Forest island dynamics in man-dominated landscapes. New York: Springer-Verlag: 67-95.

Raphael, M.G. 1980. Utilization of standing dead trees by breeding birds at Sagehen Creek, California. Berkeley: University of California. 195 p. Ph.D. dissertation.

Raphael, M.G. 1984. Wildlife diversity and abundance in relation to stand age and area in Douglas-fir forests of northwestern California. In: Meehan, W.R.; Merrell, T.R., Jr.; Hanley, T.A., eds. 1984. Fish and wildlife relationships in old-growth forests. Proceedings of a symposium; 1982 April 12-15; Juneau, AK. Morehead City, NC: The American Institute of Fishery Research Biologists: 259-274.

Raphael, M.G. 1987a. Estimating relative abundance of forest birds: simple versus adjusted counts. Wilson Bulletin. 99:125-131.

Raphael, M.G. 1987b. Wildlife-tanoak associations in Douglas-fir forests in northwestern California. In: Plumb, T.R.; Pillsbury, N.H., eds. Multiple-use management of California's hardwood resources. Proceedings of a symposium; 1986 November 12-14; San Luis Obispo, CA. Gen. Tech. Rep. PSW-100. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 183-189.

Raphael, M.G. 1988a. Douglas-fir. In: Mayer, K.E.; Laudenslayer, W.F., eds. A guide to wildlife habitats of California. California State Department of Forestry: 52-53.

Raphael, M.G. 1988b. Habitat associations of small mammals in a subalpine forest, Wyoming. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 359-367.

Raphael, M.G. 1988c. Long-term trends in abundance of amphibians, reptiles, and mammals in Douglas-fir forests of northwestern California. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 23-31.

Raphael, M.G. This volume. Vertebrate species richness within and among seral stages of Douglas-fir/hardwood forest in northwestern California.

Raphael, M.G.; Barrett, R.H. 1981. Methodologies for a comprehensive wildlife survey and habitat analysis in old-growth Douglas-fir forests. Cal-Neva Wildlife. 1981:106-121.

Raphael, M.G.; Barrett, R.H. 1984. Diversity and abundance of wildlife in late successional Douglas-fir forests. In: Proceedings of the 1983 national convention; 1983 October 16-20; Portland, OR. Washington, DC: Society of American Foresters: 352-360.

Raphael, M.G.; Marcot, B.G. 1986. Validation of a wildlife-habitat-relationships model: vertebrates in Douglas-fir sere. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 129-138.

Raphael, M.G.; Rosenberg, K.V. 1983. An integrated approach to wildlife inventories in forested habitats. In: Bell, J.F.; Atterbury, T., eds. Renewable resource inventories for monitoring changes and trends. Proceedings of an international symposium; 1983 August 15-19; Oregon State University, Corvallis. SAF 83-14. Corvallis, OR: Society of American Foresters: 219-222.

Raphael, M.G.; Rosenberg, K.V.; Marcot, B.C. 1988. Large-scale changes in bird populations of Douglas-fir forests, northwestern California. In: Jackson, J.A., ed. Bird conservation. Madison: University of Wisconsin Press.3:63-83.

Raphael, M.G.; Taylor, C.A.; Barrett, R.H. 1986. Sooted aluminum track stations record flying squirrel occurrence. Research Note PSW-384. Berkeley, CA; U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 3 p.

Raphael, M.G.; White, M. 1984. Use of snags by cavity-nesting birds in the Sierra Nevada. Wildlife Monographs. **86: l-66.**

Ratermann, M.M.; Brode, J.M. 1983. Annotated bibliography of amphibian and reptile field study methods. Sacramento, CA: State of California, The Resources Agency, Department of Fish and Game, Inland Fisheries Administrative Report 83-3.45 p.

Reese, K.P.; Ratti, J.T. 1988. Edge effect: a concept under scrutiny. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 53: 127-136.

Rexstad, E.A.; Miller, D.D.; Flather, C.H. [and others]. 1988. Questionable multivariate statistical inference in wildlife habitat and community studies. Journal of Wildlife Management. 52:794-798.

Reynolds, R.T.; Scott, J.M.; Nussbaum, R.A. 1980. A variable circular-plot method for estimating bird densities. Condor. 82:309-313.

Rice, R.M.; Tilley, F.B.; Datzman, P.A. 1979. A watershed's response to logging and roads: South Fork of Caspar Creek, California, 1967-1976. Res. Paper PSW-146. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 12 p.

Richards, D.G. 1981. Environmental acoustics and censuses of singing birds. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:297-300.

Robbins, C.S. 1980. Effects of forest fragmentation on breeding bird populations in the Piedmont of the mid-Atlantic region. Atlantic Naturalist. 33(1):31-36.

Robbins, C.S.; Dawson, D.K.; Dowell, B.A. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic States. Wildlife Monographs. 103:1-34.

Robbins, C.S.; Stallcup, R.W. 1981. Problems in separating species with similar habits and vocalizations. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:360-365.

Rosenberg, K.V.; Raphael, M.G. 1986. Effects of forest fragmentation on vertebrates in Douglas-fir forests. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 263-272.

Rosenzweig, J.L.; Winakur, J. 1969. Population ecology of desert rodent communities: habitats and environmental complexity. Ecology. 50:558-572.

Rotenberry, J.T. 1986. Habitat relationships of shrubsteppe birds: even "good" models cannot predict the future. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 217-222.

Rotenberry, J.T.; Wiens, J.A. 1981. A synthetic approach to principal components analysis of bird/habitat relationships. In: Capen, D.E., ed. The use of multivariate statistics in studies of wildlife habitat. Gen. Tech. Rep. RM-87. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experimental Station: 197-208.

Rowe, J.S. 1981. Concepts of fire effects on plant individuals and species. In: Wein, R.W.; MacLean, D.A., eds. The role of fire in northern circumpolar ecosystems. New York: John Wiley and Sons. 322 p.

Ruggiero, L.F. This volume. Wildlife habitat relationships in unmanaged Douglas-fir forests: a program of research.

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

Ruggiero, L.F.; Holthausen, R.S.; Marcot, B.G. [and others]. 1988. Ecological dependency: the concept and its implications for research and management. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 53:115-126.

Ruggiero, L.F.; Jones, L.L.C.; Aubry, K.B. This volume. Plant and animal habitat associations in Douglas-fir forests of the Pacific Northwest: an overview.

Runkle, J.R. 1981. Gap regeneration in some old-growth forests of the Eastern United States. Ecology. 62:1041-1051.

Russell, K.; Johnsey, R.; Edmonds, R. 1986. Disease and insect management for Douglas-fir. In: Oliver, CD.; Hanley, D.P.; Johnson, J.A., eds. Douglas-fir: stand management for the future. Contribution 55. Seattle: University of Washington, College of Forest Resources, Institute of Forest Resources: 189-197.

Ruth, R.H.; Yoder, R.A. 1953. Reducing wind damage in the forests of the Oregon Coast Range. Res. Pap. 7. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 30 p.

Salo, E.O.; Cundy, T.W., eds. 1987. Streamside management: forestry and fishery interactions. Proceedings of a symposium; 1987 February 12-14; University of Washington, Seattle. Contribution 57. Seattle: Institute of Forest Resources, University of Washington. 471 p.

Salwasser, H. 1987. Spotted owls: turning a battleground into a blueprint. Ecology. 68:776-779.

Salwasser, H.; Mealey, S.P.; Johnson, K. 1984. Wildlife population viability: a question of risk. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 49:421-439.

Salwasser, H.; Samson, F.B. 1985. Cumulative effects analysis: an advance in wildlife planning and management. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 50:313-321.

Salwasser,H.; Tappeiner, J.C. II. 1981. An ecosystem approach to integrated timber and wildlife habitat management. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 46:473-487.

Samson, F.B.; Knopf, F.L. 1982. In search of a diversity ethic for wildlife management. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 47:421-431.

Samson, F.B.; Marcot, B.G.; Raphael, M.G. [and others]. Unpublished manuscript. Management of old-growth forests: issues and alternatives. Presented July 1986, Habitat Futures Conference, Lake Cowichan, Vancouver Island, British Columbia, On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Portland, OR 97208.

SAS Institute, Inc. 1985. SAS user's guide: statistics. Version 5 edition. Cary, NC: SAS Institute, Inc. 956 p.

SAS Institute, Inc. 1987. SAS/STAT guide for personal computers. Version 6 edition. Cary, NC: SAS Institute, Inc. 1028 p.

Sawyer, J.O. 1980. Douglas-fir-tanoak-pacific madrone. In: Eyre, F.H., ed. Forest cover types of the United States and Canada. Society of American Foresters: 111-112.

Sawyer, J.O.; Thornburgh, D.A. 1977. Montane and subalpine vegetation of the Klamath Mountains. In: Barbour, M.G.; Major, J., eds. Terrestrial vegetation of California. New York: John Wiley and Sons: 699-732.

Sawyer, J.O.; Thornburgh, D.A.; Griffin, J.R. 1977. Mixed evergreen forest. In: Barbour, M.G.; Major, J., eds. Terrestrial vegetation of California. New York: John Wiley and Sons: 359-379.

Scharpf, R.W.; Dobler, F.C. 1985. Caves, cliffs, and talus. In: Brown, E.R., tech. ed. Management of wildlife and fish habitats in forests of western Oregon and Washington. Part l-Chapter narratives. Publ. R6-F&WL-192-1985. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region: 187-197.

Schlesinger, M.E.; Zhao, Z.C. 1988. Seasonal climatic changes induced by doubled CO_2 as simulated by the OSU atmospheric GCM/mixed layer ocean model. Climatic Research Institute, Report 70. Corvallis, OR: Oregon State University. 73 p.

Schoen, J.W.; Kirchoff, M.D.; Wallmo, O.C. 1984. Sitka black-tailed deer/old-growth relationships in southeast Alaska: implications for management. In: Meehan, W.R.; Merrell, T.R.; Hanley, T.A., eds. Fish and wildlife relationships in old-growth forests. Proceedings of a symposium; 1982 April 12-15; Juneau, AK. Morehead City, NC: American Institute of Fishery Research Biologists: 315-321.

Schoen, J.W.; Wallmo, O.C.; Kirchoff, M.D. 1981. Wildlife-forest relationships: Is a reevaluation of old growth necessary? Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 46:531-544.

Schonewald-Cox, C.M.; Chambers, S.M.; MacBryde, B.; Thomas, L., eds. 1983. Genetics and conservation: a reference for managing wild animal and plant populations. Menlo Park, CA: Benjamin/Cummings. 500 p.

Schoonmaker, P.; McKee, A. 1988. Species composition and diversity during secondary succession of coniferous forests in the western Cascade Mountains of Oregon. Forest Science. 34:960-979.

Schowalter, T.D. 1989. Canopy arthropod community structure and herbivory in old-growth and regenerating forests in western Oregon. Canadian Journal of Forest Research. 19:318-322.

Scott, D.R.M. 1980. The Pacific Northwest Region. In: Barrett, J.W., ed. Regional silviculture of the United States. New York: John Wiley and Sons. 610 p. Chapter 11.

Scott, J.M.; Csuti, B.; Jacobi, J.D.; Estes, J.E. 1987. Species richness-a geographic approach to protecting future biological diversity. Bioscience. 37:782-788.

Scott, J.M.; Csuti, B.; Smith, K. [and others]. 1988. Beyond endangered species: an integrated conservation strategy for the preservation of biological diversity. Endangered Species Update. 5:43-48.

Scott, N.J., Jr. Personal communication. U.S. Department of the Interior, Fish and Wildlife Service, National Ecology Research Center, Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87131.

Scott, NJ., **Jr., ed. 1982.** Herpetological communities. Wildlife Res. Rep. 13. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service. 239 p.

Scott, N.J., Jr. Unpublished manuscript. The effects of forest disturbance on terrestrial salamanders, family Plethodontidae. On file at: U.S. Department of the Interior, Fish and Wildlife Service, National Ecology Research Center, Museum of Southwestern Biology, University of New Mexico, Albuquerque, NM 87131.

Scott, N.J., Jr.; Campbell, H.W. 1982. A chronological bibliography, the history and status of studies of herpetological communities, and suggestions for future research. In: Scott, N.J., Jr., ed. Herpetological communities. Wildlife Res. Rep. 13. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service: 221-239.

Scrivener, J.C.; Andersen, B.C. 1984. Logging impacts and some mechanisms that determine the size of spring and summer populations of coho salmon fry *(Oncorhynchus kisutch)* in Carnation Creek, British Columbia. Canadian Journal of Fisheries and Aquatic Sciences. 41: 1097-1105.

Scrivner, J.H.; Smith, H.D. 1984. Relative abundance of small mammals in four successional stages of spruce-fir forest in Idaho. Northwest Science. 58: 171-176.

Sedell, J.R.; Swanson, F.J. 1984. Ecological characteristics of streams in old-growth forests of the Pacific Northwest. In: Meehan, W.R.; Merrell, T.R., Jr.; Hanley, T.A., eds. Fish and wildlife relationships in old-growth forests. Proceedings of a symposium; 1982 April 12-15; Juneau, AK. Morehead City, NC: American Institute of Fishery Research Biologists: 9-16.

Shaffer, M.L. 1981. Minimum population sizes for species conservation. Bioscience. 31:131-134.

Shaffer, M.L.; Samson, F.B. 1985. Population size and extinction: a note on determining critical population sizes. American Naturalist. 125: 144-152.

Sheppard, P.R.; Cook, E.R. 1988. Scientific value of trees in old-growth natural areas. Natural Areas Journal. 8:7-12.

Sheppe, W., Jr. 1961. Systematic and ecological relations of *Peromyscus oreas* and *P. maniculatus.* Proceedings of the American Philosophical Society. 105:421-446.

Shigo, A.L.; Kilham, L. 1968. Sapsuckers and *Fomes ignarius* var. *populinus.* Res. Note NE-84. Washington, DC: U.S. Department of Agriculture, Forest Service. 2 p.

Short, L.L. 1979. Burdens of the picid hole-nesting habit. Wilson Bulletin. 91:16-28.

Show, S.B.; Stuart, R.Y. 1932. Timber growing and logging practice in the coast redwood region of California. Tech. Bull. 283. Washington, DC: U.S. Department of Agriculture. 22 p.

Siderits, K.; Radke, R.E. 1977. Enhancing forest wildlife habitat through diversity. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 42:425-434.

Siegel, S. 1956. Nonparametric statistics for the behavioral sciences. New York, NY: McGraw-Hill Book Company. 312 D.

Simberloff, D. 1974. Equilibrium theory of island biogeography and ecology. Annual Review of Ecology and Systematics. 5161-182.

Simberloff, D. 1983. What a species needs to survive. Nature Conservancy News. 33:18-22.

Simberloff, D.; Abele, L.G. 1982. Refuge design and island biogeographic theory: effects of fragmentation. American Naturalist. 120:41-50.

Simberloff, D.; Cox, **J.** 1987. Consequences and costs of corridors. Conservation Biology. 1:63-71.

Simmons, J.A.; Fenton, M.B.; Ferguson, W.R. [and otbers]. 1979. Apparatus for research on animal ultrasonic signals. Toronto, ON: Life Sciences Contribution, Royal Ontario Museum. 31 p.

Simpson, G.G. 1964. Species density of North American Recent mammals. Systematic Zoology. 13:57-73.

Sirmon, J.M. 1985. A regional forester speaks out on old growth. American Forests. October: 29-30,70-71.

Slobodkin, L.B.; Sanders, W.E. 1969. On the contribution of environmental predictability to species diversity. Brookhaven Symposium of Biology. 22:88-95.

Smith, D.M. 1982a. Patterns of development of forest stands. In: Means, J.E., ed. Forest succession and stand development research in the Northwest. Proceedings of a symposium; 1981 March 26; Oregon State University, Corvallis, OR. Corvallis, OR: Forest Research Laboratory, Oregon State University. 170 p.

Smith, K.G. 1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. Ecology. 58:810-819.

Smith, K.G. 1981. Canonical correlation analysis and its use in wildlife habitat studies. In: Capen, D.E., ed. The use of multivariate statistics in studies of wildlife habitat. Gen. Tech. Rep. RM-87. Fort Collins, CO: U.S. Department of -Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 80-92.

Smith, K.G. 1982b. Drought-induced changes in avian community structure along a montane sere. Ecology. 63:952-961.

Smith, K.G.; MacMahon, J.A. 1981. Bird communities along a montane sere: community structure and energetics. Auk. 98:8-28.

Sneatb, P.H.A.; Sokal, R. 1973. Numerical taxonomy. San Francisco: W.H. Freeman Company. 573 p.

Snellgrove, T.A. 1977. White pine yields decrease as time since death increases. Forest Industry. 104(4):26-28.

Snellgrove, T.A.; Fahey, T.D. 1977. Market values and problems associated with utilization of dead timber. Forest Products Journal. 27:74-79.

Snyder, D.P., ed. 1978. Populations of small mammals under natural conditions. Pymatuning Laboratory of Ecology Special Publication Series, Vol. 5.2317 p.

Society of American Foresters Task Force. 1983. Report of the SAF task force on scheduling the harvest of old-growth timber. Bethesda, MD: Society of American Foresters. 38 p.

Society of American Foresters. 1984. Scheduling the harvest of old growth. Bethesda, MD: Society of American Foresters. 44 p.

Sokal, R.R.; Michener, C.D. 1958. A statistical method for evaluating systematic relationships. University of Kansas Scientific Bulletin. 38: 1409-1438.

Sokal, R.R.; Rohlf, F.J. 1981. Biometry. New York: W.H. Freeman Company. 859 p.

Sollins, P. 1982. Input and decay of coarse woody debris in coniferous stands in western Oregon and Washington. Canadian Journal of Forest Research. 12:18-28.

SoIlins, P.; Grier, CC.; McCorrison, F.M. [and others]. 1980. The internal element cycles of an old-growth Douglas-fir ecosystem in western Oregon. Ecological Monographs. 50:261-285.

Solow, **A.R.** 1989. Bootstrapping sparsely sampled spatial point patterns. Ecology. 70:379-382.

Soule M.E. 1980. Thresholds for survival: maintaining fitness and evolutionary potential. In: Soule M.E.; Wilcox, B.A., eds. Conservation biology: an evolutionary-ecological approach. Sunderland, MA: Sinauer Associates: 151-169.

Sonle, **M.E.** 1986. The effects of fragmentation. In: Soule ME., ed. Conservation biology: the science of scarcity and diversity. Sunderland, MA: Sinauer Associates: 233-236.

Soule, M.E.; Bolger, D.T.; Alberts, A.C. [and others]. 1988. Reconstructed dynamics of rapid extinctions of chaparral-requiring birds in urban habitat islands. Conservation Biology. 2:75-92.

Soule M.E.; Wilcox, B.A., eds. 1980. Conservation biology: an evolutionary-ecological approach. Sunderland, MA: Sinauer Associates. 395 p.

Spies, T.A. Personal communication. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331.

Spies, T.A. This volume. Plant species diversity and occurrence in young, mature, and old-growth Douglas-fir stands in western Oregon and Washington.

Spies, T.A.; Barnes, B.V. 1985. Ecological species groups of upland northern hardwood-hemlock forest ecosystems of the Sylvania Recreation Area, Upper Peninsula, Michigan. Canadian Journal of Forest Research. 15:961-972.

Spies, T.A.; Cline, S.P. 1988. Coarse woody debris in forests and plantations of coastal Oregon. In: Maser, C.; Tarrant, R.F.; Trappe, J.M.; Franklin, J.F., tech. eds. From the forest to the sea: a story of fallen trees. Gen. Tech. Rep. PNW-GTR-229. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 5-24.

Spies, T.A.; Franklin, J.F. 1988. Old growth and forest dynamics in the Douglas-fir region of western Oregon and Washington. Natural Areas Journal. 8: 190-201.

Spies, T.A.; Franklin, J.F. 1989. Gap characteristics and vegetation response in coniferous forests of the Pacific Northwest. Ecology. 70(3):543-545.

Spies, T.A.; Franklin, J.F. This volume. The structure of natural young, mature, and old-growth Douglas-fir forests in Oregon and Washington.

Spies, T.A.; Franklin, J.F.; Klopsch, M. 1990. Characteristics of canopy gaps in Douglas-fir forests. Canadian Journal of Forest Research. 20:649-658.

Spies, T.A.; Franklin, J.F.; Spycher, G. Unpublished manuscript. Biomass of Douglas-f= stands in relation to age and site conditions in western Oregon and Washington. On file at: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, CorvalIis, OR 97331.

Spies, T.A.; Franklin, J.F.; Thomas, T.B. 1988. Coarse woody debris in Douglas-fir forests of western Oregon and Washington. Ecology. 69(6):1689-1702.

Spies, T.A.; Tappener, J.; Pojar, J.; Coates, D. In press. Trends in ecosystem management at the stand level. Transactions of the 56th North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute.

SPSS, Inc. 1986. SPSSX user's guide. 2d ed. Chicago, IL: SPSS, Inc. 988 p.

Starker, T.J. 1934. Fire resistance in the forest. Journal of Forestry. 32:462-467.

States, J. 1985. Hypogeous, mycorrhizal fungi associated with ponderosa pine: sporocarp phenology. In: Molina, R., ed. Proceedings of the 6th North American conference on mycorrhizae; 1984 June 25-29; Bend, OR. Corvallis, OR: Forest Research Laboratory, Oregon State University: 271.

Stebbins, R.C. 1951. Amphibians of western North America. Berkeley, CA: University of California Press: 539 p.

Stebbins, R.C. 1954. Natural history of the salamanders of the plethodontid genus Ensatina. University of California Publications in Zoology. 54:47-123.

Stebbins, R.C. 1985. A field guide to Western reptiles and amphibians. Boston: Houghton Mifflin Company. 336 p.

Stewart, G.H. 1986a. Forest development in canopy openings in old-growth *Pseudotsuga* forests of the western Cascade Range, Oregon. Canadian Journal of Forest Research. 16(3):558-568.

Stewart, G.H. 1986b. Population dynamics of a montane conifer forest, western Cascade Range, Oregon, USA. Ecology. 67(2):534-544.

Stewart, G.H. 1988. The influence of canopy cover on understory development in forests of the western Cascade Range, Oregon, USA. Vegetatio. 76:79-88.

Stjernberg, T. 1979. Breeding biology and population dynamics of the scarlet rosefinch *Carpodacus erythrinus.* Acta Zoologici Fennici. 157:1-88.

Strahler, A.N. 1952. Hypsometric (area-altitude) analysis of erosion topography. Bulletin of the Geological Society of America. **63:1117-1142.**

Stuart, J.D. 1987. Fire history of an old-growth forest of Sequoia *sempervirens* (Taxodiaceae) in Humboldt Redwoods State Park, California. Madrono. 34: 128-141.

Stuiver, M.; Quay, P.D. 1980. Changes in atmospheric carbon- 14 attributed to a variable sun. Science. 207:11-19.

Sullivan, T.P. 1979. Demography of populations of deer mice in coastal forest and clear-cut (logged) habitats. Canadian Journal of Zoology. 57: 1636-1648.

Sullivan, T.P.; Krebs, C.J. 1980. Comparative demography of *Peromyscus maniculatus* and *Microtus oregoni* populations after logging and burning of coastal forest habitats. Canadian Journal of Zoology. 58:2252-2259.

Swanson, FJ.; Fredriksen, R.L.; McCorrison, F.M. 1982. Material transfer in a western Oregon forested watershed. In: Edmonds, R.L., ed. Analysis of coniferous forest ecosystems in the Western United States. US/IBP Synthesis Ser. 14. Stroudsburg, PA: Hutchinson Ross Publishing Co.: chapter 8.

Swanson, FJ.; Lienkaemper, G.W. 1978. Physical consequences of large organic debris in Pacific Northwest streams. Gen. Tech. Rep. PNW-69. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 12 p.

Tabachnick, B.G.; Fidell L.S. 1983. Using multivariate statistics. New York: Harper and Row. 509 p.

Takekawa, J.; Garton, E.O.; Langelier, L.A. 1982. Biological control of forest insect outbreaks:' the use of avian predators. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 47:393-410.

Taylor, C.A.; Ralph, C **J.; Doyle, A.T. 1988.** Differences in the ability of vegetation models to predict small mammal abundance in different aged Douglas-fir forests. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., eds. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 368-374,

Taylor, C.A.; Raphael, M.G. 1988. Identification of mammal tracks from sooted track stations in the Pacific Northwest. California Fish and Game. 74:4-11.

Teensma, P.D.A. 1987. Fire history and fire regimes of the central western Cascades of Oregon. Eugene, OR: University of Oregon. 188 p. Ph.D. dissertation.

Temple, S.A. 1986. Predicting impacts of habitat fragmentation on forest birds: a comparison of two models. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11, Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 301-304.

Terborgh, .J.W. 1974. Preservation of natural diversity: the problem of extinction prone species. Bioscience. 24:715-722.

Terborgh, J.W. 1988. The big things that run the world-a sequel to E.O. Wilson. Conservation Biology. 2:402-403.

Terborgh, J.W.; Winter, B. 1980. Some causes of extinction. In: Soule M.E. ed. Conservation biology: the science of scarcity and diversity. Sunderland, MS: Sinauer Associates: 119-133.

Terry, C **J. 1974.** Ecological differentiation of three species of Sorex and *Neurotrichus gibbsi* in western Washington. Seattle: University of Washington,. 101 p. M.S. thesis.

Terry, C **J. 1978.** Food habits of three sympatric species of Insectivora in western Washington. Canadian Field-Naturalist. 92:38-44.

Terry, C **J. 1981.** Habitat differentiation among three species of *Sorex* and *Neurotrichus gibbsi* in Washington. American Midland Naturalist. 106: 119-125.

Tevis, L., Jr. 1956. Responses of small mammal populations to logging of Douglas-fir. Journal of Mammalogy. 37:189-196.

Thilenius, J.F. 1968. The *Quercus garryana* forests of the Willamette Valley, Oregon. Ecology. 49: 1124-1133.

Thomas, D.W. 1988. The distribution of bats in different ages of Douglas-fir forests. Journal of Wildlife Management. 52:619-626.

Thomas, D.W.; Bell, G.P.; Fenton, M.B. 1987. Variation in echolocation call frequencies recorded from North American vespertilionid bats: a cautionary note. Journal of Mammalogy. 68:842-847.

Thomas, D.W.; LaVal, R.K. 1988. Survey and census methods. In: Kunz, T.H., ed. Ecological and behavioral methods for the study of bats. Washington, DC: Smithsonian Institution Press: 77-90.

Thomas, D.W.; West, S.D. 1989. Sampling methods for bats. Gen. Tech. Rep. PNW-243. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station. 20 p.

Thomas, J.W., ed. 1979. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agriculture Handbook 553. Washington, DC: U.S. Department of Agriculture, Forest Service.

Thomas, J.W. 1982. Needs for and approaches to wildlife habitat assessment. Transactions of the North American Wildlife and Natural Resources Conference. Washington, DC: Wildlife Management Institute. 47:35-46.

Thomas, J.W. This volume. Research on wildlife in old-growth forests: setting the stage.

Thomas, J.W.; Anderson, R.G.; Maser, C.; Bull, E.L. 1979. Snags. In: Thomas, J.W., ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agricultural Handbook 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 60-77.

Thomas, J.W.; Miller, R.J.; Black, H. [and others]. 1976. Guidelines for maintaining and enhancing wildlife habitat in forest management in the Blue Mountains of Oregon and Washington. Transactions of the North American Wildlife and Natural Resources Conference: 41:452-476.

Thomas, J.W.; Ruggiero, L.F.; Mannan, R.W. [and others]. 1988. Management and conservation of old-growth forests in the United States. Wildlife Society Bulletin. 16:252-262.

Thornburgh, D.A. 1981. Succession in the mixed evergreen forests of northwestern California. In: Forest succession and stand development research in the Northwest. Proceedings of a symposium; 1981 March 26; Oregon State University, Corvallis, OR. Corvallis: Forest Research Laboratory, Oregon State University: 87-91.

Thorson, R.M. 1980. Ice sheet glaciation of the Puget Lowland of Washington, during the Vashon Stage (Late Pleistocene), Quaternary Research. 13:303-321.

Tomoff, C.S. 1974. Avian species diversity in desert scrub. Ecology. 55:396-403.

Torrence, J.F. 1986. Statement before the Subcommittee on General Oversight, Northwest Power, and Forest Management; Committee on Interior and Insular Affairs; United States House of Representatives, concerning management of old-growth forests in the Pacific Northwest. April 28. Cited in Anderson, H.M. 1988. Old-growth forests: a conservationist's perspective. Natural Areas Journal. 8(1):13-16.

Trappe, J.M. Personal observation. U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station, Corvallis, OR 97331.

Trappe, J.M. 1962. Fungus associates of ectotrophic mycorrhizae. Botanical Review. 28:538-606.

Trappe, J.M. 1971. Mycorrhiza-forming ascomycetes. In: Hacskaylo, E., ed. Mycorrhizae. Miscellaneous Publication 1189. Washington, DC: U.S. Department of Agriculture, Forest Service: 19-37.

Trappe, J.M.; Fogel, R. 1978. Ecosystematic functions of mycorrhizae. In: Marshall, J.K., ed. The belowground symposium: a synthesis of plant-associated processes. Range Science Department Science Serial. Fort Collins: Colorado State University. 26:205-214.

Travis, J. 1977. Seasonal foraging in a downy woodpecker population. Condor. 79:371-375.

Tsukada, M. 1982. *Pseudotsuga menziesii* (Mirb.) Franco; its pollen dispersal and Late Quaternary history in the Pacific Northwest. Japanese Journal of Ecology. 32:159-187.

Tsukada, M.; Sugita, S.; Hibbert, D.M. 1981. Paleoecology in the Pacific Northwest. I. Late Quaternary vegetation and climate. Internationale Vereinegung fur theoretische and angewandte Limnologie. 21:703-737.

Twitty, V.C. 1966. Of scientists and salamanders. San Francisco: W.H. Freeman and Company. 178 p.

U.S. Department of Agriculture, Forest Service. 1976. The feasibility of utilizing forest residues for energy and chemicals. Report to the National Science Foundation and the Federal Energy Administration. Washington, DC: RANN. 193 p.

U.S. Department of Agriculture, Forest Service. 1983. The principal laws relating to Forest Service activities. Agric. Handb. 453. Washington, DC: U.S. Department of Agriculture, Forest Service. 591 p.

U.S. Department of Agriculture, Forest Service. 1985. For. Serv. Manual, R-6 Supplement 35, Title 2600-Wildlife Management, 2630.3 policy.

U.S. Department of Agriculture, Forest Service. 1986. Land areas of the National Forest System. FS-383. Washington, DC: U.S. Department of Agriculture, Forest Service.

U.S. Department of Agriculture, Forest Service. 1988a. Final supplement to the environmental impact statement for an amendment to the Pacific Northwest Regional Guide. Vol. 1: Spotted owl guidelines. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region.

U.S. Department of Agriculture, Forest Service. 1988b. Forest plan aggregate outputs and effects. Staff paper for the Regional Forester. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region. October 1, 1988, draft.

U.S. Department of Agriculture, Forest Service. 1988c. Old-growth briefing paper. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Region, Oct. 10, 1988.6 p.

U.S. Department of Commerce. 1983-84. Environmental Data Service; Climatological Data, Washington. National Climatic Center; Asheville, NC. Washington, DC: National Oceanic and Atmospheric Administration.

Udvardy, M.D.F. 1975. A classification of the biogeographical provinces of the world. Occasional Papers, International Union for Conservation of Nature and Natural Resources. 18:1-49.

Ugolini, F.C.; Schlichte, A.K. 1973. The effect of Holocene environmental changes on selected western Washington soils. Soil Science. 116(1):218-227.

Urban, D.L., O'Neill, R.V.; Shugart, H.H. 1987. Landscape ecology. Bioscience. 37: 119-127.

Ure, D.C.; Maser, C. 1982. Mycophagy of red-backed voles in Oregon and Washington. Canadian Journal of Zoology. 60:3307-3315.

Usher, M.B. 1985. Implications of species-area relationships for wildlife conservation. Journal of Environmental Management. 21:181-191.

van Dorp, D.; Opdam, P.F.M. 1987. Effects of patch size, isolation and regional abundance on forest bird communities. Landscape Ecology. 1:59-73.

Van Horn, F. Personal communication. U.S. Department of the Interior, National Park Service, Crater Lake National Park, OR 97604.

Van Horne, B. 1981. Demography of *Peromyscus maniculatus* populations in seral stages of coastal coniferous forest in southeast Alaska. Canadian Journal of Zoology. 59:1045-1061.

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

Van Horne, B. 1986. Summary: when habitats fail as predictors-the researcher's viewpoint. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 257-258.

van Zyll de Jong, C.G. 1983. Handbook of Canadian mammals. I. Marsupials and insectivores. Ottawa, ON: National Museum of Natural Sciences. 210 p.

Verner, J. 1981. Introductory remarks: sample design. In: Ralph, C.J.; Scott, J.M., eds. Estimating number of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:391.

Verner, J. 1985. Assessment of counting techniques. In: Johnson, R.F., ed. Current ornithology. New York: Plenum Press. 2:247-302.

Verner, J. 1986. Summary: predicting effects of habitat patchiness and fragmentation-a researcher's viewpoint. In: Verner, J.; Morrison, M.L.; Ralph, C.J., eds. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11; Fallen Leaf Lake, CA. Madison: University of Wisconsin Press: 327-330.

Verner, J.; Boss, A.S., tech. coords. 1980. California wildlife and their habitats: western Sierra Nevada. Gen. Tech. Rep. PSW-37. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station. 439 p.

Verner, J.; Larson, T.A. 1989. Richness of bird species in mixed-conifer forests of the Sierra Nevada, California. Auk. 106(3):447-463.

Verner, J.; Milne, K.A. 1989. Coping with sources of variability when monitoring population trends. Annales Zoologici Fennici. 26:191-199.

Verner, J.; Morrison, M.L.; Ralph, CJ., eds. 1986. Wildlife 2000: modeling habitat relationships of terrestrial vertebrates. Proceedings of an international symposium; 1984 October 7-11, Fallen Leaf Lake, CA. Madison: University of Wisconsin Press. 470 p.

Verner, J.; Ritter, L.V. 1985. A comparison of transects and point counts in oak-pine woodlands of California. Condor. 87:47-68.

Volz, **K. 1986.** Habitat requirements of northern flying squirrels in west-central Oregon. Pullman: Washington State University. 21 p. M.S. thesis.

Wainwright, T.C.; Barbour, M.G. 1984. Characteristics of mixed evergreen forests in the Sonoma mountains of California. Madrono. 31:219-230.

Waitt, R.B., Jr.; Thorson, R.M. 1983. The Cordilleran ice sheet in Washington, Idaho, and Montana. In: Porter, SC., ed. Late-Quaternary environments of the United States. The Late Pleistocene. Minneapolis: University of Minnesota Press. 1:53-70.

Wake, D.B. 1966. Comparative osteology and evolution of the lungless salamanders, family Plethodontidae. Memoirs of the Southern California Academy of Sciences. 4:1-111.

Wallmo, O.C.; **Schoen, J.W. 1980.** Response of deer to secondary forest succession in southeast Alaska. Forest Science. 26:448-462.

Weisbrod, A.R. 1976. Insularity and mammal species number in two National Parks. In: Linn, R.M., ed. Proceedings of the first conference of scientific research in National Parks. Transactions and Proceedings Series. Washington, DC: U.S. National Park *Service. 5:83-87.*

Welsh, H.H., Jr. 1985. *Ascaphus truei* (tailed frog). Geographic distribution. Herpetological Review. 16(2):59.

Welsh, H.H., Jr. 1987. Monitoring herpetofauna in woodland habitats of northwestern California and southwestern Oregon: a comprehensive strategy. In: Plumb, T.R.; Pillsbury, N.H., eds. Multiple-use management of California's hardwood resources. Proceedings of a symposium; 1986 November 12-14; San Luis Obispo, CA. Gen. Tech. Rep. PSW-100. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 203-213.

Welsh, H.H., Jr. 1990. Relictual amphibians and old-growth forests. Conservation Biology. 4(3):309-319.

Welsh, H.H., Jr.; Lind, A.J. 1988. Old growth forests and the distribution of the terrestrial herpetofauna. In: Szaro, R.C.; Severson, K.E.; Patton, D.R., tech. coords. Management of amphibians, reptiles, and small mammals in North America. Proceedings of a symposium; 1988 July 19-21; Flagstaff, AZ. Gen. Tech. Rep. RM-166. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 439-458.

Welsh, H.H., Jr.; Lind, AJ. This volume. The structure of the herpetofaunal assemblage in the Douglas-fir/hardwood forests of northwestern California and southwestern Oregon.

West, S.D. 1985. Differential capture between old and new models of the Museum Special snap trap. Journal of Mammalogy. 66:789-800.

West, S.D. In press. Sampling forest floor small mammals. Gen. Tech. Rep.. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station.

West, S.D. This volume. Small mammal communities in the Southern Washington Cascade Range.

Wetherald, R.T.; Manahe, S. 1988. An investigation of cloud cover change in response to thermal forcing. Climate Change. 8:5-23.

Wetmore, S.P.; Keller, R.A.; Smith, G.E.J. 1985. Effects of logging on bird populations in British Columbia as determined by a modified point-count method. Canadian Field-Naturalist. 99:224:233.

Whitaker, J.O., Jr.; Maser, C. 1976. Food habits of five western Oregon shrews. Northwest Science. 50:102-107.

Whitaker, J.O., Jr.; Maser, C.; Storm, R.M.; Beatty, J.J. 1986. Food habits of clouded salamanders *(Aneides ferreus)* in Curry County, Oregon (Amphibia: Caudata: Plethodontidae). Great Basin Naturalist. 46:228-240.

Whitcomb, R.F. 1977. Island biogeography and "habitat islands" of Eastern forest. American Birds. 31:3-5.

Whitcomb, R.F.; Lynch, J.F.; Klimkiewicz, M.K. [and others]. 1981. Effects of forest fragmentation on avifauna of the Eastern deciduous forest. In: Burgess, R.L.; Sharpe, D.M., eds. Forest island dynamics in man-dominated landscapes. New York: Springer-Verlag: 124-205.

White, P.S. 1979. Pattern, process, and natural disturbance in vegetation. Botanical Review. 45:229-299.

White, R. 1980. Land use, environment, and social change: the shaping of Island County, Washington. Seattle: University of Washington Press. 227 p.

Whitford, W.G. 1976. Temporal fluctuations in density and diversity of desert rodent populations. Journal of Mammalogy. 57:351-359.

Whitmore, R.C. 1977. Habitat partitioning in a community of passerine birds. Wilson Bulletin. 89(2):253-265.

Whitmore, T.C. 1978. Gaps in forest canopy. In: Tomlinson, P.B.; Zimmerman, M.H., eds. Tropical trees as living systems. New York: Cambridge University Press: 639-655.

Whittaker, R.H. 1965. Dominance and diversity in plant communities. Science. 147:250-260.

Whittaker, R.H. 1975. Communities and ecosystems. New York: MacMillan Publishing Co. 387 p.

Whittaker, R.J. 1987. An application of detrended correspondence analysis and non-metric multidimensional scaling to the identification and analysis of environmental factor complexes and vegetation structures. Journal of Ecology. 75:363-376.

Wiens, J.A. 1975. Avian communities, energetics, and functions in coniferous forest habitats. In: Smith, D.R., ed. Management of forest and range habitats for nongame birds. Proceedings of a symposium; 1975 May 6-9; Tucson, AZ. Gen. Tech. Rep. WO-1. Washington, DC: U.S. Department of Agriculture, Forest Service: 226-235.

Wiens, J.A. 1976. Population responses to patchy environments. Annual Review of Ecological Systems. 7:81-120.

Wiens, J.A. 1981a. Scale problems in avian censusing. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:513-521.

Wiens, J.A. 1981b. Single-sample surveys of communities: are the revealed patterns real? American Naturalist. 117:90-98.

Wiens, J.A.; Rotenberry, J.T. 1981a. Censusing and the evaluation of habitat occupancy. In: Ralph, C.J.; Scott, J.M., eds. Estimating numbers of terrestrial birds. Proceedings of an international symposium; 1980 October 26-31; Asilomar, CA. Lawrence, KS: Cooper Ornithological Society. Studies in Avian Biology. 6:522-532.

Wiens, J.A.; Rotenberry, J.T. 1981b. Habitat associations and community structure of birds in shrubsteppe environments. Ecological Monographs. 51:21-41.

Wiest, J.A., Jr. 1982. Anuran succession at temporary ponds in a post oak-savanna region of Texas. In: Scott, N.J., Jr., ed. Herpetological communities. Wildlife Res. Rep. 13. Washington, DC: U.S. Department of the Interior, Fish and Wildlife Service: 39-47.

Wilcove, D.S. 1987. Public lands management and the fate of the spotted owl. American Birds. 41:361-367.

Wilcove, D.S. 1988. Protecting biological diversity. In: National forests: policies for the future, Volume 2. Washington, DC: The Wilderness Society: l-50.

Wilcove, D.S.; McLeIlan, C.H.; Dobson, A.P. 1986. Habitat fragmentation in the temperate zone. In: Soule M.E., ed. Conservation biology: the science of scarcity and diversity. Sunderland, MA: Sinauer Associates: 237-256.

Wilcox, B.A. 1978. Supersaturated island faunas: a species-age relationship for lizards on post-Pleistocene land-bridge islands. Science. 199:996-998.

Wilcox, **B.A. 1980.** Insular ecology and conservation. In: Soule M.E.; Wilcox, B.A., eds. Conservation biology, an evolutionary-ecological approach. Sunderland, MA: Sinauer Associates: 95-117.

Wilcox, B.A.; Murphy, D.D. 1985. Conservation strategy: the effects of fragmentation on extinction. American Naturalist. 125:879-887.

Wilderness Society, The. 1988. End of the ancient forests. Washington, DC: The Wilderness Society. 57 p.

Wilkinson, L. 1979. Tests of significance in stepwise regression. Psychology Bulletin. 86:168-174.

Wilkinson, L. 1988. SYSTAT: the system for statistics. Evanston, IL: Systat, Inc. 822 p.

Williams, B.K. 1981. Discriminant analysis in wildlife research: theory and applications. In: Capen, D.E., ed. The use of multivariate statistics in studies of wildlife habitat. Gen. Tech. Rep. RM-87. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 59-71.

Williams, B.K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology. 64:1283-1291.

Williams, D.A. 1976. Improved likelihood ratio tests for complete contingency tables. Biometrika. 63:33-37.

Williams, D.F.; Braun, SE. 1983. Comparison of pitfall and conventional traps for sampling small mammal populations. Journal of Wildlife Management. 47:841-845.

Williamson, M. 1981. Island populations. Oxford, England: Oxford University Press. 286 p.

Williamson, R.L.; Price, F.E. 1971. Initial thinning effects in 70- to 150-year-old Douglas-fir-western Oregon and Washington. Res. Paper PNW-117. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 15 p.

Wilson, M.V.. 1981. A statistical test of the accuracy and consistency of ordinations. Ecology. 62:8-12.

Willson, M.F. 1974. Avian community organization and habitat structure. Ecology. 55:1017-1029.

Willson, M.F.; Porter, E.A.; Condit, R.S. 1982. Avian *frugivore* activity in relation to forest light gaps. Caribbean Journal of Science. 18(1):l-6.

Wolda, H. 1981. Similarity indices, sample size and diversity. Oecologia. 50:296-302.

Wright, H.A.; Bailey, A.W. 1982. Fire ecology: United States and southern Canada. New York: John Wiley and Sons. 501 p.

Wright, K.H.; Harvey, G.M. 1967. The deterioration of beetle-killed Douglas-fir in western Oregon and Washington. Res. Paper PNW-50. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station. 20 p.

Yahner, R.H. 1989. Changes in wildlife communities near edges. Conservation Biology. 2:333-339.

Yamaguchi, D.K. 1986. The development of old-growth Douglas-fir forests northeast of Mount St. Helens, Washington, following an A.D. 1480 eruption. Seattle: University of Washington. 100 p. Ph.D. dissertation.

Zar, J.H. 1984. Biostatistical analysis. 2d ed. Englewood Cliffs, NJ: Prentice-Hall. 718 p.

Zarnowitz, J.E.; Manuwal, D.A. 1985. The effects of forest management on cavity-nesting birds in northwestern Washington. Journal of Wildlife Management. 49:255-263.

Zobel, D-B.; McKee, A.; Hawk, G.M.; Dyrness, C.T. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the central western Cascades of Oregon. Ecological Monographs. 46:135-156.

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