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.

Acknowledgments

Wildlife Habitat Relationships and Viable Populations

Leonard F. Ruggiero

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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.
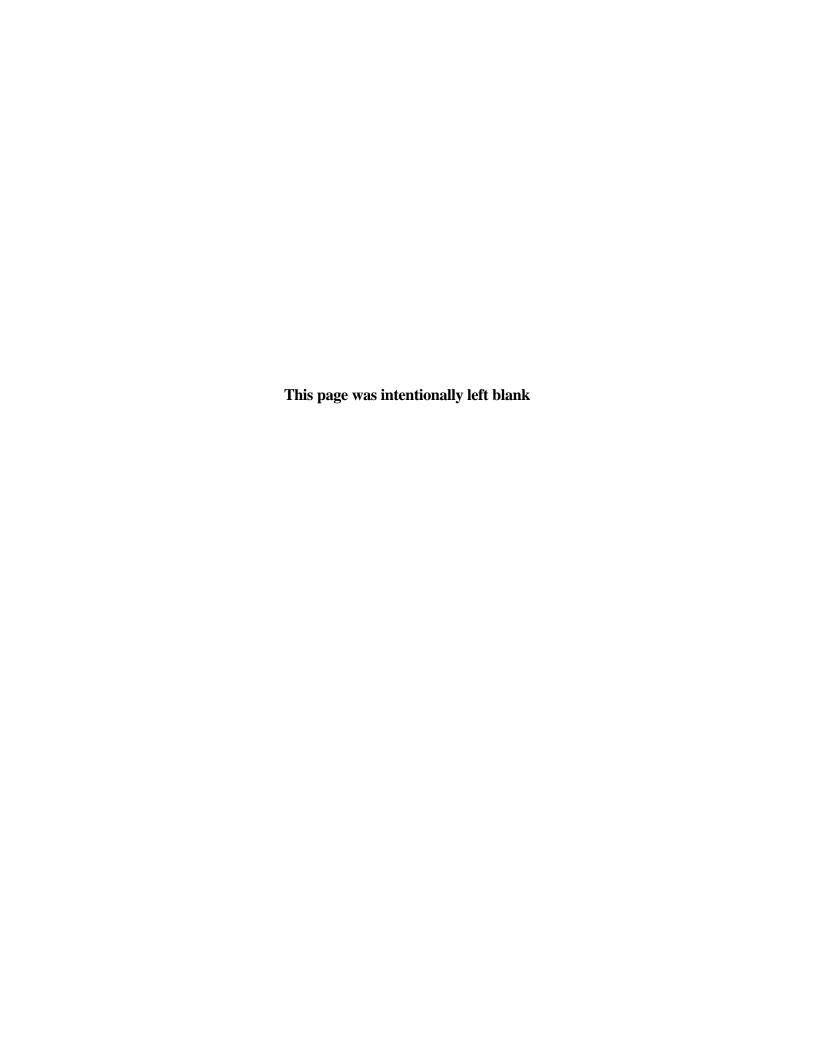
How will wildlife respond as the predominant forest type shifts toward these younger, generally less complex forests? Will short-rotation landscapes containing islands of dedicated old growth be better for late-successional wildlife than landscapes managed on a 250-year rotation, but largely devoid of 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. ☐

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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

Authors

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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 unman-aged, 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 con-sidered 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 oper-ational 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 sig-nificantly more abundant (based on statistical signifi-cance 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 charac-teristic 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.

Acknowledgments

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

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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	*	?	?	?

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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		