

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 1985 (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 100-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 100-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 ≤ 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 pattern-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	Bird ^a	Residency ^b	Detectability ^c
Common raven		3	Understory foragers		
Northern pygmy-owl		3	American robin	R	2
Olive-sided flycatcher		3	Blue grouse	R	3
Aerial foragers			Dark-eyed junco	R	1
Dusky/Hammond's flycatcher'	M	1	Hermit thrush	M	2
Vaux's swift'	M	3	Hutton's vireo		1
Western flycatcher	M	1	MacGillivray's warbler	M	1
Bark foragers			Northern flicker ^d	R	3
Brown creeper'	R	1	Orange-crowned warbler	M	1
Hairy woodpecker ^d	R	2	Rufous hummingbird	M	1
Pileated woodpecker ^d	R	3	Rufous-sided towhee	R	4
Red-breasted nuthatch ^d	R	1	Song sparrow	R	
Red-breasted sapsucker ^d	R	3	S wainson's thrush	M	4
Canopy foragers			Townsend's solitaire	M	3
Band-tailed pigeon	M	4	Varied thrush	R	2
Black-capped chickadee ^d	R	4	Wilson's warbler	M	1
Black-headed grosbeak	M	3	Winter wren	R	1
Black-throated gray warbler	M	1	Wrentit	R	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			

^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	Variable	Transformation
Live-tree variables:			
Mean number of tree species	LOG	Bigleaf maple	
Density		Douglas-fir	ARC
Bigleaf maple		Golden chinkapin	
Douglas-fir		Grand fir	
Golden chinkapin		Incense-cedar	
Grand fir		Pacific madrone	
Incense-cedar		Pacific silver fir	
Pacific madrone		Red alder	
Pacific silver fir		Western hemlock	
Red alder		Western redcedar	
Western hemlock	SQRT	Western yew	
Western redcedar		Mean d.b.h. of live trees ^b	LOG
Western yew		Mean height of dominant trees	
Total tree density	LOG	Equitability index	
Trees 5-9 cm d.b.h.	SQRT	Tree density by diameter classes ^c	
Trees 10-24 cm d.b.h.	LOG	Tree basal area by height classes	
Trees 25-49 cm d.b.h.	LOG		
Trees 50-99 cm d.b.h.	SQRT	Stand condition variables:	
Trees 100-149 cm d.b.h.	SQRT	Density	
Trees ≥150 cm d.b.h.		Trees with fire scars	
Needle-leaved evergreen trees	LOG	Trees with excavated cavities	
Broad-leaved evergreen trees		Trees with natural cavities	LOG
Deciduous trees		Trees with root cavities	LOG
Pine trees		Trees with small amount of moss/lichen	SQRT
		Trees with moderate amount of moss/lichen	SQRT
		Trees with heavy amount of moss/lichen	LOG
Basal area		Percentage	
Bigleaf maple		Trees with fire scars	
Douglas-fir		Trees with excavated cavities	
Golden chinkapin		Trees with natural cavities	LOG
Grand fir		Trees with small amount of moss/lichen	ARC
Incense-cedar		Trees with moderate amount of moss/lichen	
Pacific madrone		Trees with heavy amount of moss/lichen	LOG
Pacific silver fir			
Red alder		Snag variables:	
Western hemlock	SQRT	Density	
Western redcedar		Decay-class-1 snags ^d	LOG
Western yew		Decay-class-2 snags	LOG
Total basal area	LOG	Decay-class-3 snags	LOG
Needle-leaved evergreen trees	LOG	Decay-class-4 snags	LOG
Broad-leaved evergreen trees		Decay-class-5 snags	SQRT
Deciduous trees		Snags 1.5-5.0 m tall	
Pine trees		Snags 10-50 cm d.b.h. and 5-15 m tall	LOG
Importance value ^a		Snags 10-50 cm d.b.h. and >15 m tall	LOG
Needle-leaved evergreen trees		Snags >50 cm d.b.h. and 5-15 m tall	SQRT
Broad-leaved evergreen trees		Snags >50 cm d.b.h. and >15 m tall	SQRT
Deciduous trees		Douglas-fir snags >1.5 m tall	LOG
Pine trees		Western hemlock snags >1.5 m tall	

Table 9—continued

Variable	Transformation	Variable	Transformation
Decay-class-1 snags	LOG	Understory variables:	
Decay-class-2 snags	LOG	Percentage cover by	
Decay-class-3 snags	LOG	Moss	
Decay-class-4 snags	LOG	Lichens	ARC
Decay-class-5 snags	LOG	Ferns	LOG
All snags	LOG	Grasses	
Volume		Herbs	LOG
Decay-class-1 snags	LOG	Evergreen shrubs	ARC
Decay-class-2 snags	LOG	Deciduous shrubs	LOG
Decay-class-3 snags	LOG	Deciduous trees ≤8 m tall	
Decay-class-4 snags	LOG	Evergreen trees ≤8 m tall	SQRT
Decay-class-5 snags	LOG	Berry (<i>Vaccinium</i> spp.) shrubs	LOG
All snags	LOG	<i>Rubus</i> species	ARC
Douglas-fir snags	LOG	Grasses, herbs, and ferns	
Western hemlock snags		Plants <0.5 m tall	
Relative frequency		Plants 0.5-2.0 m tall	SQRT
Douglas-fir snags ^e	ARC	Plants 2-4 m tall	SQRT
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		

^a Importance value = sum of relative density, basal area, and frequency.

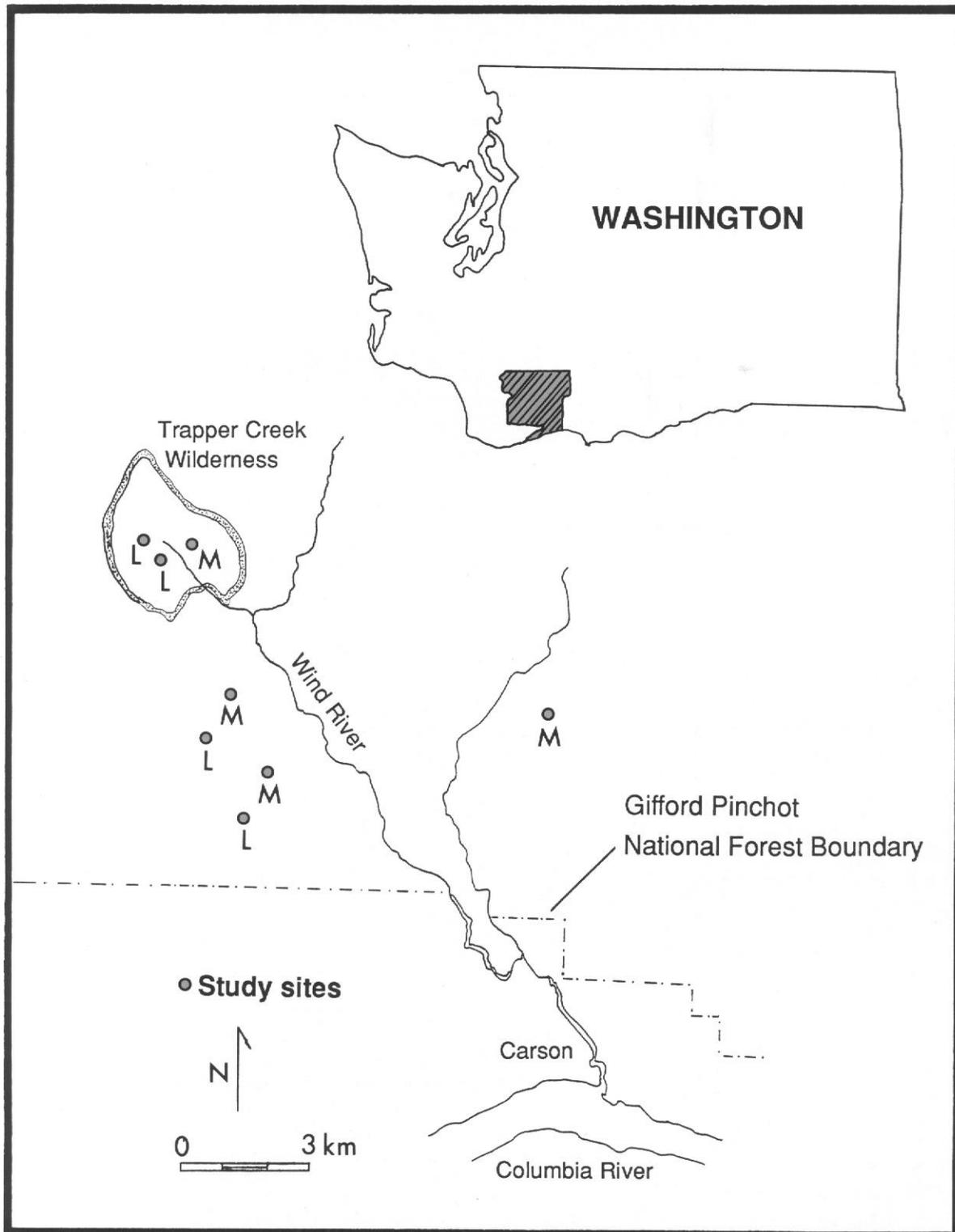
^b D.b.h. = diameter at breast height in centimeters.

^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

Mark H. Huff., David A. Manuwal, and Judy A. Putera

Authors

MARK H. HUFF is a research wildlife biologist, and JUDY A. PUTERA is a wildlife biologist, USDA Forest Service, Pacific Northwest Research Station, Olympia, Washington 98502; DAVID A. MANUWAL is a professor, Wildlife Science Group, College of Forest Resources, University of Washington, Seattle, Washington 98195.

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 examined—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.

Methods

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 (\bar{x} = 565 ha; SD = 292 ha) and mid-seral stands (\bar{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 (1981) 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 (1981). 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 insectivores; 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

<p>CANOPY SEED EATERS</p> <ul style="list-style-type: none"> Evening grosbeak Pine siskin Red crossbill White-winged crossbill 	<p>CANOPY INSECTIVORES</p> <ul style="list-style-type: none"> Chestnut-backed chickadee Golden-crowned kinglet
<p>BARK INSECTIVORES</p> <ul style="list-style-type: none"> Red-breasted nuthatch Brown creeper Hairy woodpecker Pileated woodpecker Red-breasted sapsucker 	<p>UNDERSTORY SEED EATERS AND INSECTIVORES</p> <ul style="list-style-type: none"> 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

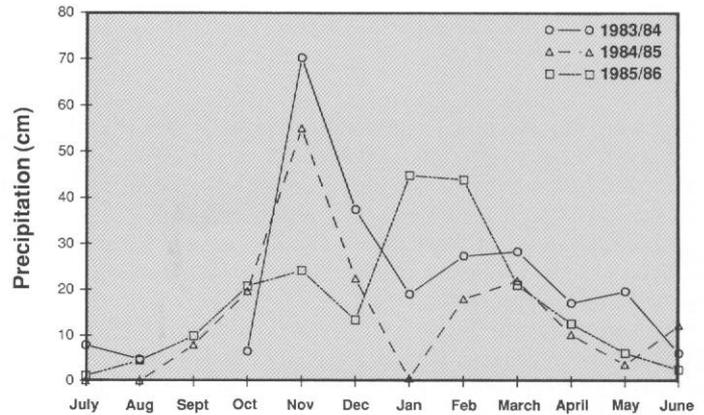


Figure 2—Monthly precipitation from July 1983 to June 1986 at the Wind River National Fish Hatchery near Carson, Washington.

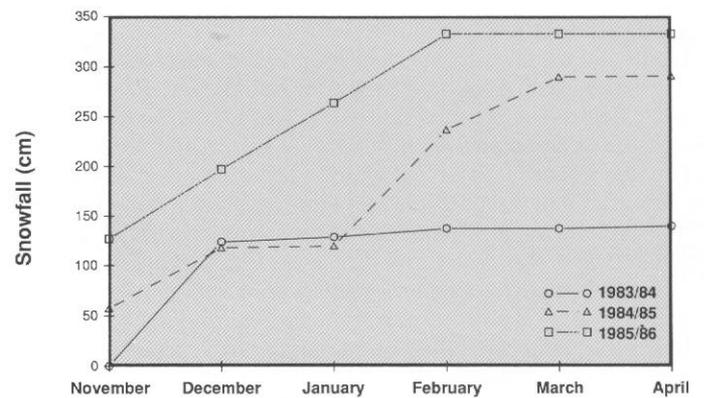


Figure 3—Cumulative snowfall over three winters at the Wind River National Fish Hatchery near Carson, Washington.

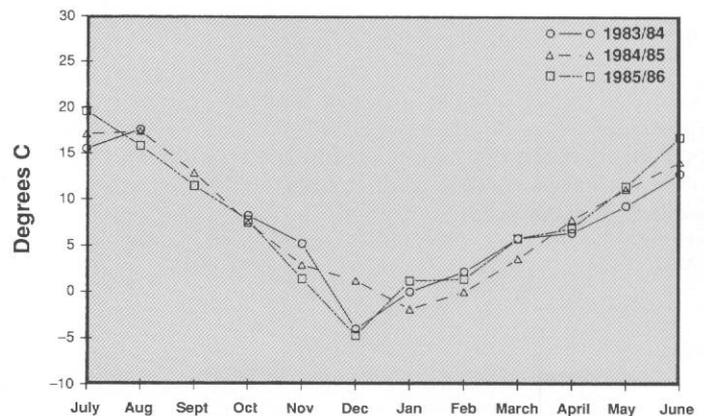


Figure 4—Monthly mean temperatures from July 1983 to June 1986 at the Wind River National Fish Hatchery near Carson, Washington.

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).

Table 1—Means and standard deviations of vegetation variables within mid- and late-seral stands in the southern Washington Cascade Range

Vegetation variable	Mid-seral		Late-seral		<i>U</i> ^a	<i>P</i> ^b
	Mean	SD	Mean	SD		
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 ^d	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.

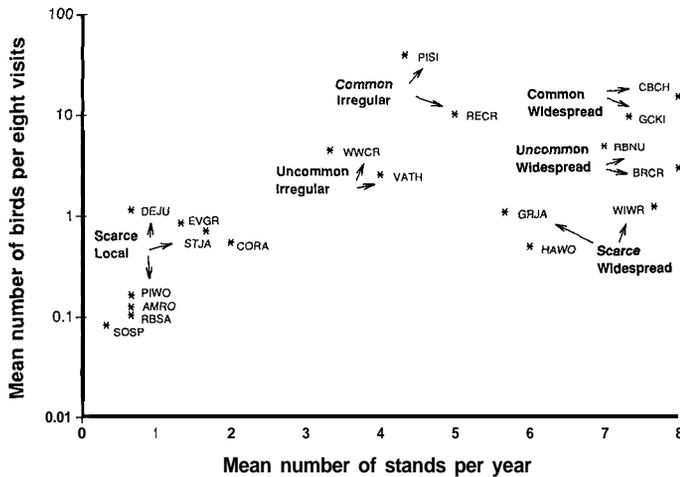


Figure 5-General distribution and abundance of the major bird species wintering in the study area, AMRO = American robin, BRGR = brown creeper, CBCH = chestnut-backed chickadee, CORA = common raven, DEJU = dark-eyed junco, EVGR = evening grosbeak, GCKI = golden-crowned kinglet, GRJA = gray jay, HAWO = hairy woodpecker. PISI = pine 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 >100-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

Location	Serai stage	Winter					
		1983-84		1984-85		1985-86	
		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

Guild	Winter			
	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

Guild	Winter					
	1983-84		1984-85		1985-86	
	<i>U</i> ^a	<i>P</i> ^b	<i>U</i>	<i>P</i>	<i>U</i>	<i>P</i>
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.

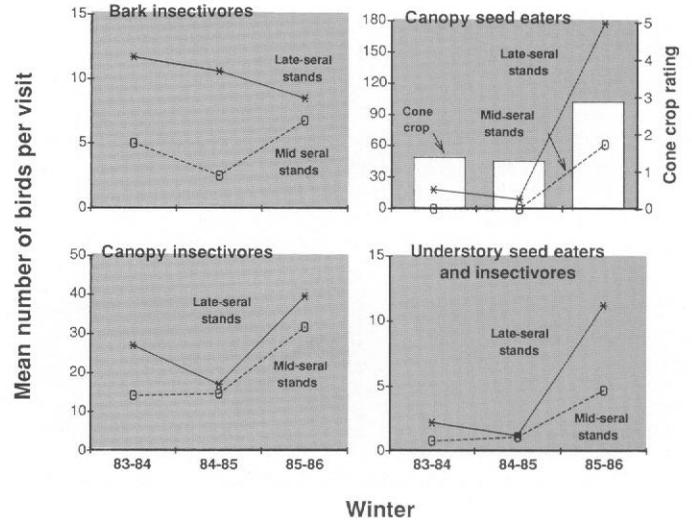


Figure 6—Abundance patterns (mean number of birds/visit) of four guilds in winter and histogram of cone-crop rating by year (absent/failure = 1, very light = 2, light = 3, medium = 4, heavy = 5).

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 -	1 ^a	1	21	6	5	2	1	6	7	U ^b	11
Mid -	-	-	4	2	3	1	1	10	U	U	-
1983-84											
Late -	1	1	5	7	3	1	U	12	7	U	1
Mid -	-	-	3	-	2	1	U	12	U	U	U
1984-85											
Late -	-	1	33	6	2	1	10	7	16	15	144
Mid -	-	-	26	4	2	2	3	6	13	8	39
1985-86											

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 -	-	1	6	-	2	4	U	9	1	U	U
Mid -	-	-	3	-	1	1	U	9	U	U	U
1984-85											
Late -	-	1	17	5	4	U	4	20	12	U	156
Mid -	-	1	10	3	4	U	2	28	6	U	49
1985-86											

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

Study area	Winter					
	1983-84		1984-85		1985-86	
	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

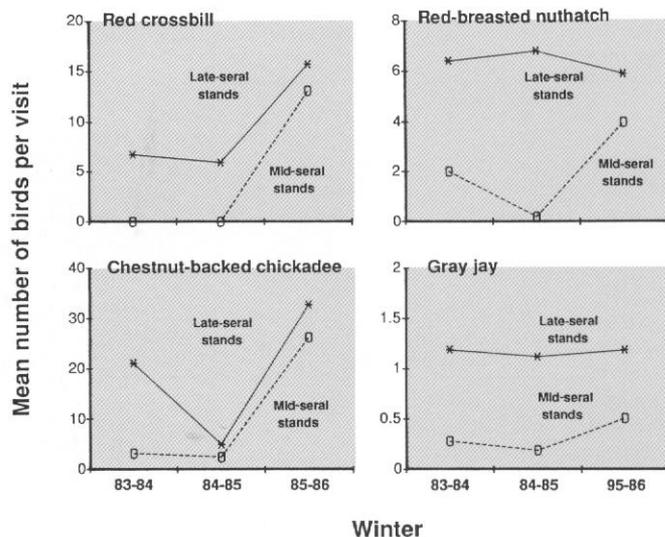


Figure 8—Abundance (mean number of birds/visit) of four species in mid- and late-seral stands over three winters.

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).

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

Species winter	Mid-seral stage				Late-seral stage			
	≤ 75 m		All distances ^a		≤ 75 m		All distances	
	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

Species and winter	Mid-seral stage		Late-seral stage	
	≤ 75 m	All distances ^a	≤ 75 m	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.

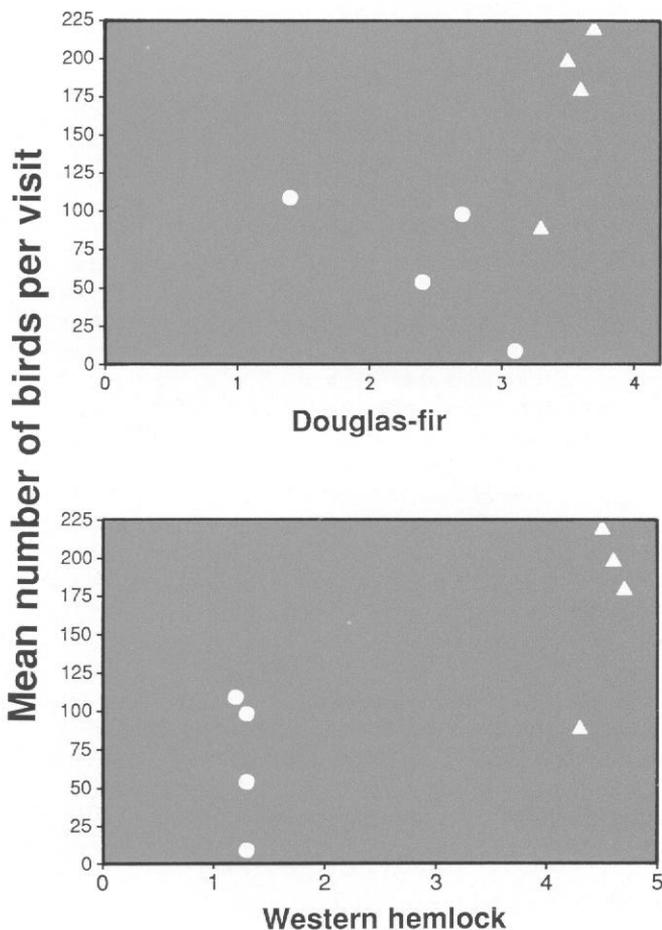


Figure 9—Abundance of seed eaters (mean number of birds/visit) in 1985-86 in mid-seral (circles) and late-seral (triangles) stands relative to cone-crop rating of Douglas-fir and western hemlock (absent/failure = 1, very light = 2, light = 3, medium = 4, heavy = 5).

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: $n_1 = 3$; $n_2 = 4$; $U = 0$; $P = 0.028$); 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.

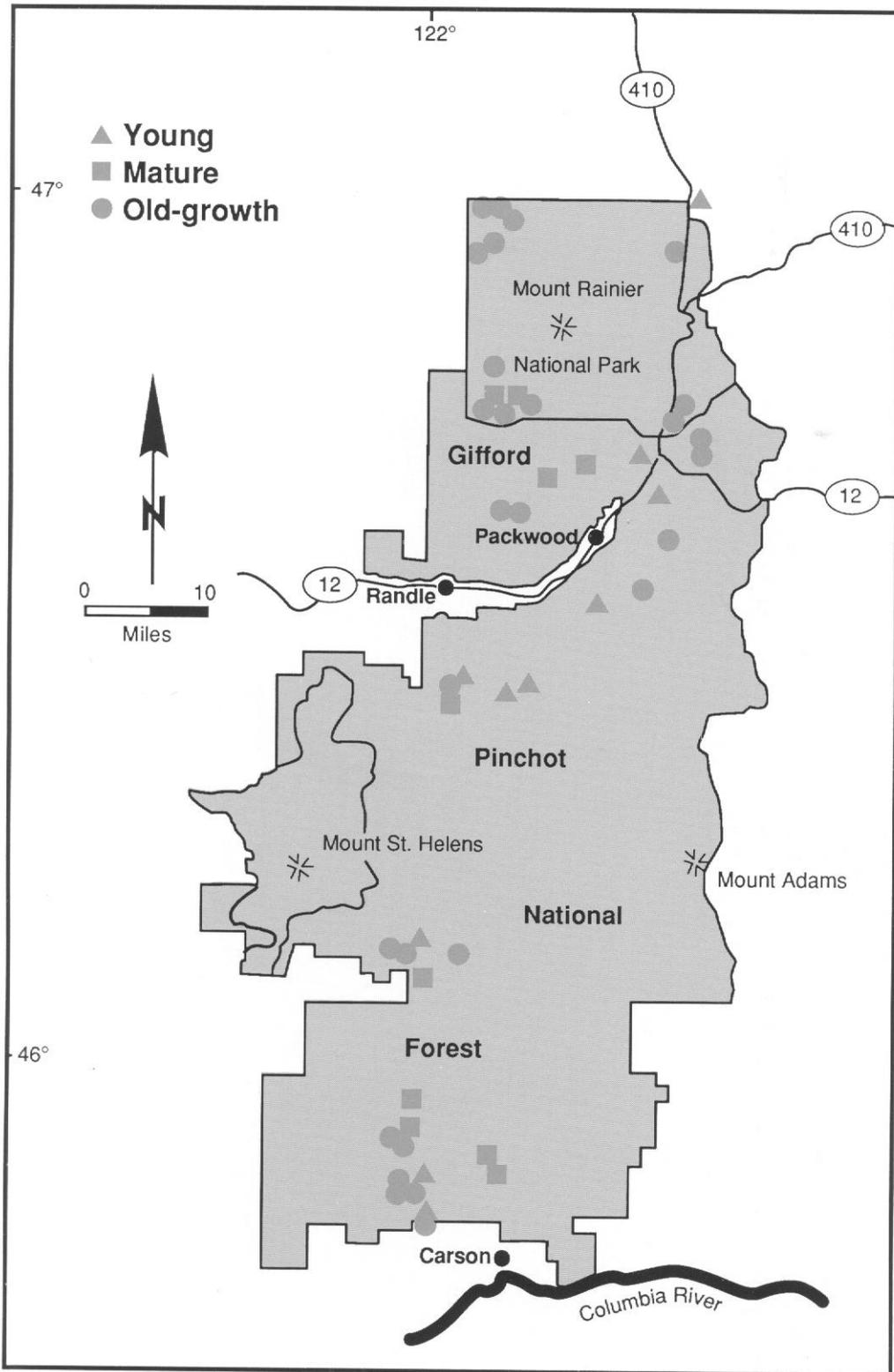
Based on the substantial differences in bird abundance between mid- and late-seral stands, we recommend that additional studies be done to substantiate the observed patterns over a wider geographic area.

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Location of study sites.