

1-1-1980

Nongame Birds of the Rocky Mountain Spruce- Fir Forests and Their Management

Kimberly G. Smith

Recommended Citation

Smith, K. G. (1980). Nongame birds of the Rocky Mountain spruce- fir forests and their management, pp. 258-279. In: R. DeGraaf (Tech. Coord.) Management of western forest and grassland for nongame birds. USDA Forest Service General Technical Report INT-89.

This Contribution to Book is brought to you for free and open access by the Quinney Natural Resources Research Library, S.J. and Jessie E. at DigitalCommons@USU. It has been accepted for inclusion in T.W. "Doc" Daniel Experimental Forest by an authorized administrator of DigitalCommons@USU. For more information, please contact becky.thoms@usu.edu.



NONGAME BIRDS OF THE ROCKY MOUNTAIN SPRUCE-FIR FORESTS AND THEIR MANAGEMENT

Kimberly G. Smith

Department of Biology and Ecology Center UMC 53
Utah State University, Logan

ABSTRACT

Spruce-fir forests in the Rocky Mountains consist mainly of Engelmann spruce and subalpine fir. The breeding avifaunas in these forests show remarkable consistency in composition along a latitudinal gradient from Montana to Arizona and New Mexico, and with avian communities in the Hudsonian life zone in Washington, Oregon, and California. Woodpeckers, corvids, and seed-eating finches are the most common components. Only the Golden Eagle and a few other raptors are threatened or endangered. Few species winter in these high mountain forests.

The distribution of many species is controlled primarily by the vegetation physiognomy, a variable under the control of the forest manager. Fire control and snag management will generally benefit the avifauna, whereas most forest harvesting practices adversely affect, to differing degrees, the bird communities. It is suggested that the "life-form" approach to avian communities may be easily implemented in these forests. It is recommended that high elevation spruce-fir forests be minimally harvested and used as reservoirs for spruce-fir birds. Lower elevational stands should be managed for harvesting and bird diversity, with special attention given to relic stands.

KEYWORDS: Engelmann spruce, forest management, life-form approach, logging, spruce-fir avifauna, subalpine fir.

In the western United States, true spruce-fir forests which are found only at the high elevations in the Rocky Mountains and central Washington and Oregon are usually classified as climax forests. In the Rockies, these forests have generally changed little for many hundreds, if not thousands, of years, occurring where remoteness, rough terrain, and relatively low timber values have discouraged exploitation and where moist conditions have kept fires to a minimum (Marr 1967). The avifaunas associated with these forests are well-known and show remarkable consistency from one area to the next, but little ornithological research has been done in these forests, probably due to their remoteness.

Spruce-fir forests are some of the most extensive and most productive timber resources in the Central Rocky Mountains, as well as important watersheds, providing habitats for a wide variety of wildlife, forage for livestock, and recreational opportunities and scenic beauty (Alexander 1977). As we approach the 21st century, these forests will come under increasing pressure for all these interests, so it is imperative that guidelines be established or reevaluated for management of both the forests and the associated nongame wildlife. In this report, I review the literature concerning the avifauna of western spruce-fir forests, discuss the relationships between the avifauna and the spruce-fir forests, and suggest some management options that may benefit the nongame bird species.

THE SPRUCE-FIR FOREST

Forest Description

ROCKY MOUNTAINS

The dominant tree species of the spruce-fir forest of the Rocky Mountains are Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*). Other tree species that are often associated with spruce-fir forests in the Rockies are aspen (*Populus tremuloides*), lodgepole pine (*Pinus contorta*), and Douglas-fir (*Pseudotsuga menziesii*). Spruce-fir forests generally occur in the coldest, wettest, and highest areas of the Mogollon Plateau, White and San Francisco Mountains, and Kaibab Plateau in Arizona (Merkle 1954); the higher mountains of northern New Mexico; the Rocky Mountains through Colorado (Marr 1967), Wyoming, Idaho and western Montana; and the Uinta and Wasatch Mountains in Utah (Hayward 1945)(Fig. 1).

Typical old spruce-fir stands are homogeneous and simple, having a dominant spruce overstory with a fir understory (Whipple and Dix 1979), with few other tree species present since none can germinate in the shade of spruce and fir (Marr 1967). The shrub and herb layers are poorly developed (Merkle 1954, Marr 1967, Schimpf et al. 1980), but wind throw and fallen trees (both living and dead) are common (e.g., Rasmussen 1941, Loope and Gruell 1973), sometimes making passage through a spruce-fir forest a "tedious and tiresome activity" (Marr 1967). More specific information concerning vegetational characteristics of these spruce-fir forests may be found in Peet (1978), Whipple and Dix (1979), Schimpf et al. (1980), and references therein.

CASCADES AND SIERRA NEVADA

Engelmann spruce-subalpine fir forests occur on the east slope of the Cascades in Washington and Oregon, the Okanogan Highlands of northeastern Washington, and the Blue and Wallowa Mountains in northeastern Oregon and southeastern Washington (Fig. 1). These forests are typically found in frost pockets and other habitats characterized by draining and accumulation of cold air, such as glaciated valley bottoms (Franklin and Dyrness 1973). Franklin and Dyrness (1973) concluded that subalpine fir is the major and often sole climax species in these forests. Many tree species are associated with subalpine fir forests in this region, and the ecological associations and successional relationships of these areas are much more complex than in the spruce-fir forests of the Rockies.

In the Sierra Nevada, white fir (*Abies concolor*) and California red fir (*A. magnifica*) predominate in Merriam's Hudsonian Life Zone (Fig. 1), which is analogous to the *Abies lasiocarpa* Zone of Washington and Oregon and the spruce-fir forests of the Rockies (Franklin and Dyrness 1973). No spruce species occurs in the Sierra Nevada.

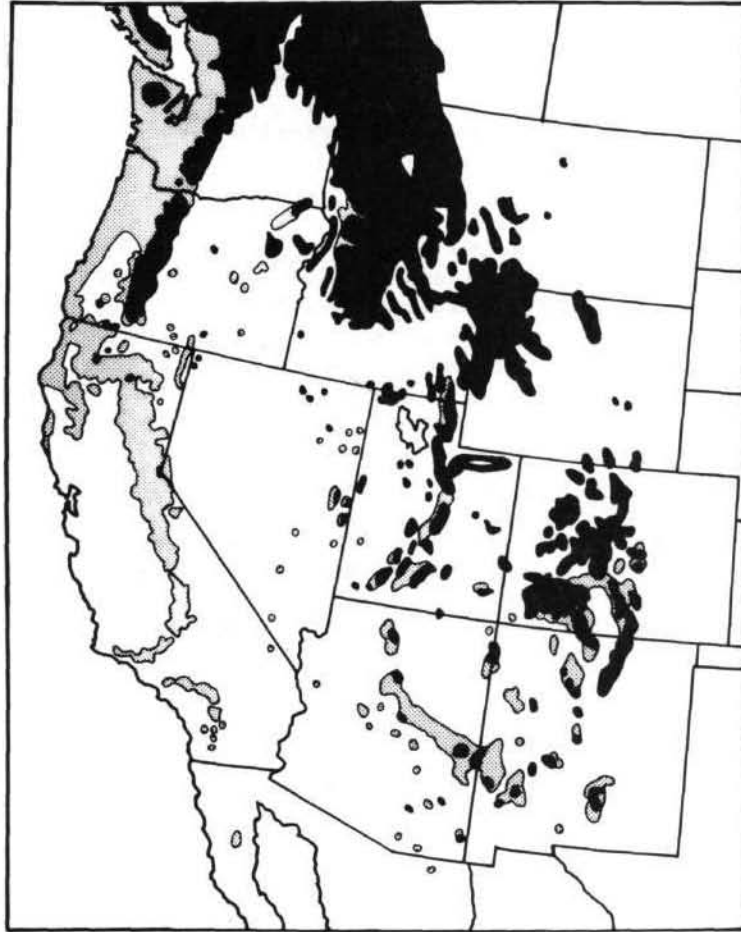


Figure 1.--Distribution of spruce and firs in the western United States. Dark areas depict the range of Engelmann spruce and subalpine fir in the Rocky Mountains (which is the emphasis of this paper) and in the *Abies lasiocarpa* Zone (Franklin and Dyrness 1973) of Washington and Oregon. Stippled areas in the Northwest show range of Sitka spruce (*Picea sitchensis*) and Pacific silver (*Abies amabilis*), grand (*A. grandis*), and noble (*A. procera*) firs where they occur outside of the Engelmann spruce-subalpine fir range. Stippled areas in the Sierra Nevada show the range of white and California red firs in the Hudsonian Life Zone. Stippled areas in the Southwest are patches of white fir. The range of blue spruce (*P. pungens*) is completely within the range of Engelmann spruce. Map adapted from Little (1971).

Forest Succession

The climax spruce-fir forests are often complex mosaics of various seral stages (Habeck and Mutch 1973) due to effects of weather, fire, infestations, etc. Whipple and Dix (1979) advise caution in using the term climax for spruce-fir forests, suggesting that a more appropriate statement would be that these forests are relatively unchanging and appear to be perpetuating themselves. Because of short growing seasons and low temperatures where these forests occur, natural processes are slow and it is possible that spruce-fir forests actually cycle every 500-1000 years, a scale too long for human perception (see, e.g., Bloomberg 1950).

Since several pathways may be possible in the same region, depending on climatic and edaphic conditions, elevation, and seed sources (see Schimpf et al. 1980), vegetation recovery following a disturbance is difficult to predict in spruce-fir forests (Habeck and Mutch 1973). Where spruce-fir forests are destroyed at lower elevations, aspen or lodgepole pine usually invade first. The shade of these trees facilitates the germination of spruce and fir and both species are usually found in lodgepole stands within 60-105 years (Whipple and Dix 1979). Subalpine fir can replace a lodgepole pine stand in 250-400 years (Loope and Gruell 1973); Billings (1969) has estimated that it takes 6-7 centuries to obtain a pure spruce-fir stand with 300-500 year old trees. Engelmann spruce tends to dominate such stands since it lives much longer than subalpine fir (Whipple and Dix 1979), although subalpine fir may, in certain situations, be the true climax (see Franklin and Dyrness 1973).

At high elevations, either subalpine fir or Engelmann spruce can replace a destroyed spruce-fir forest (if no aspen roots are present to sucker) within several centuries (Billings 1969). However, subalpine fir does not grow or reproduce as well at high elevations (Whipple and Dix 1979). Billings (1969) points out another possibility: if the removal of a spruce-fir forest changes the snow drift pattern so that late-lying snowbanks form, coniferous seedling establishment becomes impossible and no reforestation will occur.

THE SPRUCE-FIR AVIFAUNA

Species Composition

BREEDING AVIFAUNA

In the Rocky Mountains, one generally is impressed with the consistency of the spruce-fir avifauna during the breeding season as one moves south from Montana to Arizona and New Mexico (Table 1). Twenty-one of 48 species were reported in 5 or more of the 10 studies listed in Table 1. Mountain Chickadee, Ruby-crowned Kinglet, Yellow-rumped (Audubon's) Warbler, Pine Siskin, and a junco occurred in all studies, Hermit Thrush, Clark's Nutcracker in 9, and Hairy Woodpecker, Red-breasted Nuthatch, and American Robin in 8 (see Table 2). Based on this consistent pattern, Hubbard (1965) concluded that the spruce-fir avifauna of the Mogollon Mountains in New Mexico had Rocky Mountain affinities, and Carothers et al. (1973) concluded that the spruce-fir avifauna of the White Mountains in Arizona were more closely related to spruce-fir avifauna in Colorado and Wyoming than to the Chiricahua Mountains only 150 miles to the south. The similarity of the avifaunas indicated in Table 1 is undoubtedly an underestimate since most studies did not report non-passerines (except woodpeckers), and studies were conducted for various lengths of time (e.g., 1 breeding season [Snyder 1950] to 30 consecutive months, 3 breeding seasons [Smith 1980]). (Only species recorded in 2 or more studies were included in Table 1, with 14 additional species that were recorded only once deleted.)

Table 1.--Bird species observed during the breeding season in spruce-fir forests in at least 2 studies along a latitudinal gradient in the Rocky Mountains. MT=Montana, WY=Wyoming, CO=Colorado, UT=Utah, AR=Arizona, NM=New Mexico. Montane birds of the Intermountain Region (IM) and the North American boreomontane forest (BF) are included for comparison.

SPECIES	SCIENTIFIC NAME	MT ^{1/}	WY ^{2/}	CO ^{3/}	UT ^{4/}	UT ^{5/}	UT ^{6/}	AR ^{7/}	AR ^{8/}	NM ^{9/}	NM ^{10/}	IM ^{11/}	BF ^{12/}
TURKEY VULTURE	<i>Cathartes aura</i>				X				X		X		
GOSHAWK	<i>Accipiter gentilis</i>				X					X			
COOPER'S HAWK	<i>A. cooperii</i>	X			X								
SHARP-SHINNED HAWK	<i>A. striatus</i>				X				X				
GOLDEN EAGLE	<i>Aquila chrysaetos</i>	X			X								
AMERICAN KESTREL	<i>Falco sparverius</i>	X						X	X				
BAND-TAILED PIGEON	<i>Columba fasciata</i>									X	X		
GREAT HORNED OWL	<i>Bubo virginianus</i>				X		X						
BROAD-TAILED HUMMINGBIRD	<i>Selasphorus platycercus</i>				X		X		X	X	X		
COMMON FLICKER	<i>Colaptes auratus</i>	X		X	X		X	X	X		X		
WILLIAMSON'S SAPSUCKER	<i>Sphyrapicus thyroides</i>				X		X				X		
HAIRY WOODPECKER	<i>Picoides villosus</i>	X	X	X	X	X	X	X	X	X	X	X	
DOWNY WOODPECKER	<i>P. pubescens</i>									X	X		
NORTHERN 3-TOED WOODPECKER	<i>P. tridactylus</i>	X			X			X	X	X	X		
DUSKY FLYCATCHER	<i>Empidonax oberholseri</i>	X			X			X			X	X	X
WESTERN WOOD PEWEE	<i>Contopus sordidulus</i>				X						X		X
OLIVE-SIDED FLYCATCHER	<i>Nuttallornis borealis</i>	X						X					
STELLER'S JAY	<i>Cyanocitta stelleri</i>				X			X	X	X	X		
GRAY JAY	<i>Perisoreus canadensis</i>					X	X		X				
BLACK-BILLED MAGPIE	<i>Pica pica</i>	X			X								
CLARK'S NUTCRACKER	<i>Nucifraga columbiana</i>	X	X	X	X	X	X	X	X	X	X	X	
COMMON RAVEN	<i>Corvus corax</i>				X				X		X		
MOUNTAIN CHICKADEE	<i>Parus gambeli</i>	X	X	X	X	X	X	X	X	X	X	X	X
WHITE-BREASTED NUTHATCH	<i>Sitta carolinensis</i>				X			X			X	X	X
RED-BREASTED NUTHATCH	<i>S. canadensis</i>	X	X		X	X	X		X	X	X		
BROWN CREEPER	<i>Certhia familiaris</i>	X			X	X	X		X	X	X		X
HOUSE WREN	<i>Troglodytes aedon</i>							X		X	X		X
AMERICAN ROBIN	<i>Turdus migratorius</i>		X		X	X	X	X	X	X	X		X
TOWNSEND'S SOLITAIRE	<i>Myodestes townsendi</i>	X		X	X		X	X	X	X	X		X
HERMIT THRUSH	<i>Catharus guttata</i>	X	X	X	X		X	X	X	X	X	X	X
SWAINSON'S THRUSH	<i>C. ustulata</i>	X	X										X
MOUNTAIN BLUEBIRD	<i>Sialia currucoides</i>	X						X				X	
GOLDEN-CROWNED KINGLET	<i>Regulus satrapa</i>	X	X		X				X	X			X
RUBY-CROWNED KINGLET	<i>R. calendula</i>	X	X	X	X	X	X	X	X	X	X		X
WARBLING VIREO	<i>Vireo gilvus</i>							X		X	X		X
ORANGE-CROWNED WARBLER	<i>Vermivora celata</i>				X								X
YELLOW-RUMPED WARBLER	<i>Dendroica coronata</i>	X	X	X	X	X	X	X	X	X	X	X	X
WESTERN Tanager	<i>Piranga ludoviciana</i>	X			X				X	X	X		
EVENING GROSBEAK	<i>Hesperiphona vespertina</i>							X					X
CASSIN'S FINCH	<i>Carpodacus cassinii</i>		X		X		X	X				X	X
PINE GROSBEAK	<i>Pinicola enucleator</i>	X	X	X	X	X	X					X	X
PINE SISKIN	<i>Carduelis pinus</i>	X	X	X	X	X	X	X	X	X	X		X
RED CROSSBILL	<i>Loxia curvirostra</i>	X		X					X	X	X		X
GREEN-TAILED TOWHEE	<i>Pipilo chlorura</i>								X		X	X	
DARK-EYED JUNCO	<i>Junco hyemalis</i>	X	X		X								X
GRAY-HEADED JUNCO	<i>J. caniceps</i>			X		X	X	X	X	X	X		
CHIPPING SPARROW	<i>Spizella passerina</i>	X	X		X	X	X	X	X	X	X		
WHITE-CROWNED SPARROW	<i>Zonotrichia leucophrys</i>				X	X							
TOTAL SPECIES		21	19	12	37	14	19	22	26	22	30	13	19

1/ Thompson 1978; alpine forest and spruce-lodgepole. 7/ Rasmussen 1941; spruce-fir.
2/ Salt 1957; spruce-fir. 8/ Carothers et al. 1973; spruce-fir, aspen.
3/ Snyder 1950; spruce-fir. 9/ Hubbard 1965; spruce-fir.
4/ Smith 1980; spruce-fir. (also in Schimpf et al. 1980) 10/ Tatschl 1967; spruce-fir.
5/ Winn 1976; spruce-lodgepole. 11/ Johnson 1975; Intermountain boreal birds.
6/ Austin and Perry 1979; spruce-lodgepole. 12/ Udvary 1963; North American boreomontane.

For comparison, 13 species that Johnson (1975) termed the "western American boreal birds" in his study of the Great Basin mountain top "island" avifaunas, and 19 passerine species that Udvardy (1963) suggested were part of the North American boreomontane avifauna, are included in Table 1. Carbyn (1971), Theberge (1976) and Erskine (1977) present comparable data from the spruce-fir forests of western Canada.

Generally, the avifaunas in the Hudsonian Life Zone of the Sierra Nevada and the Cascade Mountains appear quite similar to those reported in Table 1 for the Rocky Mountains (see, e.g., Grinnell et al. 1930, Gabrielson and Jewett 1940, Jewett et al. 1953). The major differences between the two regional avifaunas are a replacement of the Northern 3-toed Woodpecker by the Arctic 3-toed Woodpecker (Picoides arcticus) due to the lack of spruce in the Sierra Nevada (Bock and Bock 1973), and the addition of Varied Thrush (Ixoreus naevius), Hermit (Dendroica occidentalis) and Townsend (D. townsendi) warblers to the Hudsonian Life Zone forests of the Far West.

In contrast to eastern spruce-fir forests where warblers (primarily the genus Dendroica) are the most common element of the avifauna (e.g., Sabo and Whittaker 1979, Titterton et al. 1979), western spruce-fir forests have few warblers (e.g., Wiens 1975), but many woodpeckers, corvids, and finches (Table 1). This suggests that unlike eastern forest avifaunas which primarily key on foliage insects, western spruce-fir avifaunas are adapted to old-growth stands where "infaunal" insects are more plentiful (Haapanen 1965, Nilsson 1979). Foliage insects and ground invertebrates are relatively rare in western spruce-fir forests (e.g., Hayward 1945). Also, cone crops are larger in the west; Engelmann spruce usually produces large cone crops (>200 cones/tree) at frequent intervals (Franklin 1968).

The number of breeding species reported ranged from 12 (Snyder 1950) to 27 (Smith 1980). Reported total densities ranged from 134 individuals/40ha in mature lodgepole spruce (Austin and Perry 1979) to 170-187 pairs/40ha in spruce-fir and aspen (Carothers et al. 1973) to 210 pairs/40ha in the spruce-fir of New Mexico (Tatschl 1967). As mentioned before, some of these discrepancies are due to the different ways in which the studies were conducted. Topography will influence the distribution of some species, such as Turkey Vulture, Golden Eagle, and White-throated Swift (Aeronautes saxatalis), which depend on cliffs for nesting, and, as will be discussed later, the physiognomy of the plots themselves will influence the distribution of certain species. World-wide, there are generally 20-30 species of birds present in any spruce forest (Schimpf et al. 1980).

WINTER AVIFAUNA

Few species spend the winter months in high-elevation climax coniferous forests in western North America, since these forests are located where winters are severe and food is scarce. For example, of the 250 avian species that breed in the coniferous forests of western Canada, only 45 species winter in that area (Erskine 1977). Not many species winter in the spruce forests in northern Europe (Hansson 1979) presumably for the same reasons.

Species that do spend the winter in spruce-fir forests usually travel in small, mixed-species flocks (e.g., chickadees, nuthatches, siskins), and occur in "pockets" (Wing 1950). Thus, one may walk (or ski) for several kilometers without hearing or seeing any birds, then find a small area of great bird activity.

Haapanen (1965) concluded (as have others) that winter mortality due to food supply and/or severe weather is the most decisive factor limiting permanent resident populations in spruce-fir forests. Most species are adapted to withstand the severe weather, either behaviorally (e.g., via communal roosting) or physiologically

(e.g., hypothermia [Haftorn 1972, Chaplin 1974, Andreevan 1979]). There is relatively little forest managers can do to shield the birds from severe weather.

However, managers can insure that forests contain maximum food resources. Woodpeckers are generally more dependent on dead trees in winter. Males and females of the same species may also use different tree species for obtaining food resources (e.g., Hogstad 1976, 1977). Some species, such as Mountain Chickadees (Haftorn 1974) and Red-breasted Nuthatches (personal observation), cache food (arthropods and seeds) in trees during late summer and fall for winter consumption, but most insectivores are dependent on spiders (Askenmo et al. 1977) and insect eggs. Seed-eating finches and jays search out large cone crops. All these feeding requirements suggest again the dependence of the avifauna on old-growth spruce-fir forests.

HOLE-NESTING SPECIES

The recent interest in hole-nesting species and snag management (reviewed in Raphael and White 1978) is pertinent to management of spruce-fir forests. Of all the woodpeckers found in spruce-fir forests, apparently only the Northern 3-toed Woodpecker is capable of making holes in the dense wood of living spruce trees (Haapanen 1965). Therefore, other hole-making species are dependent on either snags, aspen, or to some extent fir trees. Haapanen (1965) reported that in a stand composed of 90% spruce, only 8 of 76 nesting holes occurred in spruce trees. Likewise, in a western larch (*Larix occidentalis*)-Douglas-fir forest in Montana, McClelland et al. (1975) found only 2 of 83 active snag nests in Engelmann spruce.

Understandably, there are fewer secondary-cavity nesters (birds dependent on other species to excavate cavities) associated with spruce-fir forests than with, say, an aspen grove (see Smith 1980). Only 6 species of secondary-cavity nesters are listed in Table 1 - American Kestrel, Mountain Chickadee, White-breasted Nuthatch, Red-breasted Nuthatch, House Wren, and Mountain Bluebird. (Although not reported, I suspect that some of the western owls which are secondary-cavity nesters, e.g., Pygmy Owl [*Glaucidium gnoma*], Flammulated Owl [*Otus flammeolus*], also rarely occur in western spruce-fir forests.) Only the Mountain Chickadee and Red-breasted Nuthatch occur commonly and both are capable of excavating their own nesting cavities (Scott et al. 1977). Haapanen (1965, 1966) concluded that in old forests the number of hole-nesters decreases at the same rate as the forest changes into pure spruce.

SEED-EATING SPECIES

Seed-eating species, primarily cardueline finches and corvids, are common and wide-ranging in western spruce-fir forests. Cone crops may primarily determine the density of some of these species (Haapanen 1966). Most tend to be nomadic, appearing whenever large cone crops exist (e.g., Smith 1978). Godfrey (1966), discussing the Red Crossbill stated: "Nesting time is as erratic as its wanderings and may occur in any month of the year. The breeding range is not well known. Its presence in an area is no guarantee that it is breeding there. Its nesting in a given area is no indication that it will nest there next year or in the next decade, or that it nested there last year". The male of many of these finches defends a territory around a female, so that the abundance of females determines the breeding densities (along with cone crop), and not suitable habitat (Samson 1976, Smith 1978). Furthermore, in times of cone surfeit, species not normally associated with coniferous cones, such as Common Redpolls (*Carduelis flammea*), may feed on them (Smith 1979).

Most people associate the presence of these seed-eating species in the United States with periodic winter eruptions from the northern boreal forests of Canada. However, in analyzing the pattern of these eruptions, Bock and Lepthien (1976) cautioned that frequently populations of seed-eating birds in coniferous forests

of the western United States do not erupt in synchrony with those species occurring in the northern boreal forest. This is probably due to the several different options available to the seed-eating birds in the Rockies - they can move south, north, or elevationally in search of seed crops. Bock and Lepthien (1976) conclude that the appearance of unusual numbers of a species during winter in western areas usually does not represent an eruption, although this is not always the case^{1/}.

RARE AND ENDANGERED SPECIES

The only endangered species associated with the western spruce-fir forests is the Golden Eagle. Although most eagle nests are placed on cliffs, some do occur in conifers, and eagles frequently hunt within the spruce-fir ecosystem. Forest harvesting and eagle nesting are probably incompatible; in the mountains of New Mexico and western Texas, 85% of nest failures were due to human disturbance (Boeker and Ray 1971). However, the presence of small clear-cut openings may be beneficial for foraging since more raptors tend to be observed around clear-cuts than in the forest (Winn 1976). These clear-cut areas would possibly benefit other rare raptors, such as Merlin (Falco columbarius) (reported in Thompson 1978), Cooper's, and Sharp-shinned hawks, all of which may be declining in western United States (Arbib 1978). I suspect that Peregrines (Falco peregrinus) may also occasionally use the spruce-fir clearing for feeding.

Goshawks are rare in spruce-fir forests and their presence seems dependent on large aspen trees within the forest for nesting (personal observation) since spruce trees apparently cannot support the weight of their large nest (Haapanen 1966). As suggested earlier, several small owls may be rare in the western spruce-fir forests, but I found no abundance estimates. Proper snag management probably would be beneficial to small owls.

With the possible exception of the Mountain Bluebird (Arbib 1978), all passerines (including those deleted from Table 1) found in spruce-fir forests of western United States are relatively common, although they may of course be locally rare in certain areas due to such factors as zoogeography, elevation, and climate (see Johnson 1974, Smith^{2/}).

FORAGING TYPE STRUCTURE

Referring to the "western American boreal birds" of the Intermountain area, Johnson (1975) stated that each species within this group was fundamentally different in its place or style of feeding, and even in the simplest communities, there were fundamental foraging roles that were always performed, usually by the same species. Thompson (1978) reached the same conclusion concerning a standard set of montane species, and offered the explanation that the addition of a coniferous forest layer increases to near maximum the number of guilds (= foraging types), whereas adding more species of conifers results in expansion within these guilds. This pattern of fundamental guilds is probably characteristic of the entire western spruce-fir ecosystem. Considering the 16 most common species from Table 1, few foraging type members show a similar preferred foraging substrate (Table 2). Almost all the other species (excluding raptors) listed in Table 1 fall into the foraging types defined by these first

^{1/}Vander Wall, S. B., W. K. Potts, and S. Hoffman. Eruptive behavior of Clark's Nutcracker. Unpublished Manuscript. Utah State University

^{2/}Smith, K. G. The effects of an extreme drought on a temperate subalpine bird community. Unpublished manuscript. Utah State University.

16 species. For example, comparing the species reported in 5 studies from Table 1 with those reported in more studies (Table 2), Red Crossbill is similar in foraging type and substrate to Pine Siskin, Western Tanager to Yellow-rumped Warbler, and Golden-crowned Kinglet to Mountain Chickadee. Steller's Jay is termed an omnivore, but probably overlaps greatly with Clark's Nutcracker, Hermit Thrush, and Pine Grosbeak.

TABLE 2.--The 21 most commonly reported bird species in Rocky Mountain spruce-fir forests (from 10 field studies listed in Table 1), their foraging type, and preferred foraging substrate.

Species	Number of Studies	Foraging Type	Foraging Substrate
Mountain Chickadee	10	Foliage-Insect	Fir
Ruby-crowned Kinglet	10	Foliage-Insect	Spruce
Yellow-rumped Warbler	10	Foliage-Insect	Forest
Pine Siskin	10	Foliage-Seed	Spruce
Junco sp.	10	Ground-Insect/Seed	Openings
Clark's Nutcracker	9	Foliage-Seed	Pines
Hermit Thrush	9	Ground-Insect	Forest
American Robin	8	Ground-Insect	Openings
Red-breasted Nuthatch	8	Timber-Search	Dead Trees
Hairy Woodpecker	8	Timber-Drill	Spruce-Fir
Chipping Sparrow	7	Ground-Insect/Seed	Forest
Townsend Solitaire	7	Ground-Insect/Seed(?)	(?)
Brown Creeper	7	Timber-Search	Live Trees
Common Flicker	6	Ground-Insect	Openings
Northern 3-toed Woodpecker	6	Timber-Drill	Spruce
Pine Grosbeak	6	Ground-Insect/Seed	Forest
Red Crossbill	5	Foliage-Seed	Spruce
Steller's Jay	5	Omnivore	Forest
Western Tanager	5	Foliage-Insect	Spruce-Fir
Golden-crowned Kinglet	5	Foliage-Insect	Fir
Broad-tailed Hummingbird	5	Nectivore	Openings

An analysis of the foraging type structure (excluding raptors) of the spruce-fir avifauna on a latitudinal gradient from Montana to Arizona and New Mexico (Table 3) demonstrates again the relative consistency of these avifaunas, but reveals some interesting trends. Aerial feeders form a relatively small component of the spruce-fir avifauna, primarily because soaring species, e.g., White-throated Swift, Violet-green Swallow (*Tachycineta thalassina*), do not ordinarily nest in spruce-fir forests, and sallying flycatchers do not often hunt from perches in the closed canopy of the spruce-fir forest (personal observation). Sallying flycatchers prefer forests with open understories (e.g., Smith 1977) or forest edges. The nectivorous Broad-tailed Hummingbird is rare due to the paucity of flowers in the spruce-fir forest (Schimpf

et al. 1980), and the omnivores (jays and crows) are also a minor component. Collectively, these 3 foraging types average less than 13% of the total number of species in the spruce-fir avifaunas.

TABLE 3.--The foraging type structure (excluding raptors) observed in the 10 field studies listed in Table 1. Numbers of species in each category are listed with percent of total species in each category in parentheses. The Intermountain Region avian foraging type structure is presented for comparison.

FORAGING TYPE	MT ^{1/}	WY	CO	UT	UT	UT	AR	AR	NM	NM	IM
AIR - PERCH/SOAR	2(11)	1(5)	0(0)	2(7)	0(0)	0(0)	4(18)	1(4)	0(0)	2(8)	2(14)
FOLIAGE - INSECT	4(21)	5(26)	4(33)	6(22)	3(21)	3(17)	5(23)	5(22)	6(33)	5(20)	3(21)
FOLIAGE - SEED	4(21)	2(21)	4(33)	5(18)	3(21)	4(22)	2(9)	2(9)	3(17)	3(12)	1(7)
TIMBER - SEARCH	1(5)	2(11)	0(0)	3(11)	2(14)	2(11)	1(5)	2(9)	2(11)	3(12)	1(7)
TIMBER - DRILL	0(0)	2(11)	1(8)	3(11)	1(7)	1(6)	2(9)	2(9)	3(17)	3(12)	1(7)
GROUND - INSECT	3(16)	3(16)	1(8)	3(11)	2(14)	3(17)	4(18)	3(13)	3(17)	3(12)	3(21)
GROUND - INSECT/SEED	3(16)	2(11)	2(17)	2(7)	2(14)	3(17)	3(14)	4(17)	1(6)	4(16)	3(21)
OMNIVORE	2(11)	0(0)	0(0)	1(4)	1(7)	1(6)	1(5)	3(13)	1(6)	1(4)	0(0)
NECTIVORE	0(0)	0(0)	0(0)	1(4)	0(0)	1(6)	0(0)	1(4)	1(6)	1(4)	0(0)
TOTAL BREEDING SPECIES	19	19	12	26	14	18	22	23	20	25	14

^{1/} Order and abbreviations as in Table 1.

The other foraging types were also relatively consistent along the gradient (Table 3). A few timber-using species were found in each study area, averaging about 18% of the avifauna. Ground-feeders were common due to the open understory of spruce-fir forests. Gray-headed Juncos may be responsible for most Engelmann spruce first-year seedling mortality which had usually been attributed to rodents (Noble and Sheppard 1973). (Interestingly, the junco is also the only ground-nesting species associated with spruce-fir forests, the number of ground-nesters being low due to the lack of ground cover (Haapanen 1965).)

The foliage-seed foraging type tended to be better represented in the northern studies, with only 2 members of this foraging type present in each of the Arizona studies. Foliage insectivores consistently accounted for about 25% of the avifaunas.

Referring to coniferous forests in general, Wiens (1975) hypothesized that most foraging opportunities exist in the outer zone of the canopies, where twigs and needles will support only small individuals or where food resources may be available only to small individuals. Most members of this foliage-insect foraging type in western spruce-fir forests are small. Wiens further suggested that foliage foraging types numerically dominate coniferous forest avifaunas, with ground-foraging, timber-foraging, and aerial feeders decreasing in importance in that order. This appears to be true for western spruce-fir forests.

On theoretical grounds, Valiela (1971) argued that during the course of succession, a trend in increasing feeding specialization would be expected, primarily through addition of avian insectivores and carnivores. The climax spruce-fir forest supports this observation. A myriad of carnivores is associated with the spruce-fir forest, but not with the earlier successional stages (e. g., aspen) and most species in the spruce-fir forests belong to the insectivorous foraging type (Table 3). (A complete treatment of the avian successional relationships in a western spruce-fir

forest can be found in Smith and MacMahon^{3/})

SPRUCE-FIR PHYSIOGNOMY AND AVIAN DISTRIBUTION

The physiognomy of most spruce-fir forests is probably the most important factor determining both the number of bird species present and their density, and also is the factor that forest managers have most control over. Forests with Engelmann spruce support some of the least diverse avifaunas of all the coniferous forests in the western United States (e. g., Hayward 1945); the number of bird species and densities decrease as spruce invasion increases (e. g., Haapanen 1965, Austin and Perry 1979).

Influence of Specific Vegetational Components

TREE LAYER

In discussing the role of habitat structure in avian community organization, Willson (1974) concluded (in part) that the mere presence of a tree layer is more closely associated with species addition than is the total amount of foliage or its distribution. Many species of birds occur throughout coniferous forests in western North America regardless of the tree species that dominate the plant community (Erskine 1977). Equally important to some birds of western spruce-fir forests, however, is the species composition of the tree layer. In general, all climax forests in North America are characterized by comparatively few birds (and mammals) except where these forests come in contact with subclimax vegetation (Shelford and Olsen 1935), and the spruce-fir forests of western United States are an excellent example of this phenomenon.

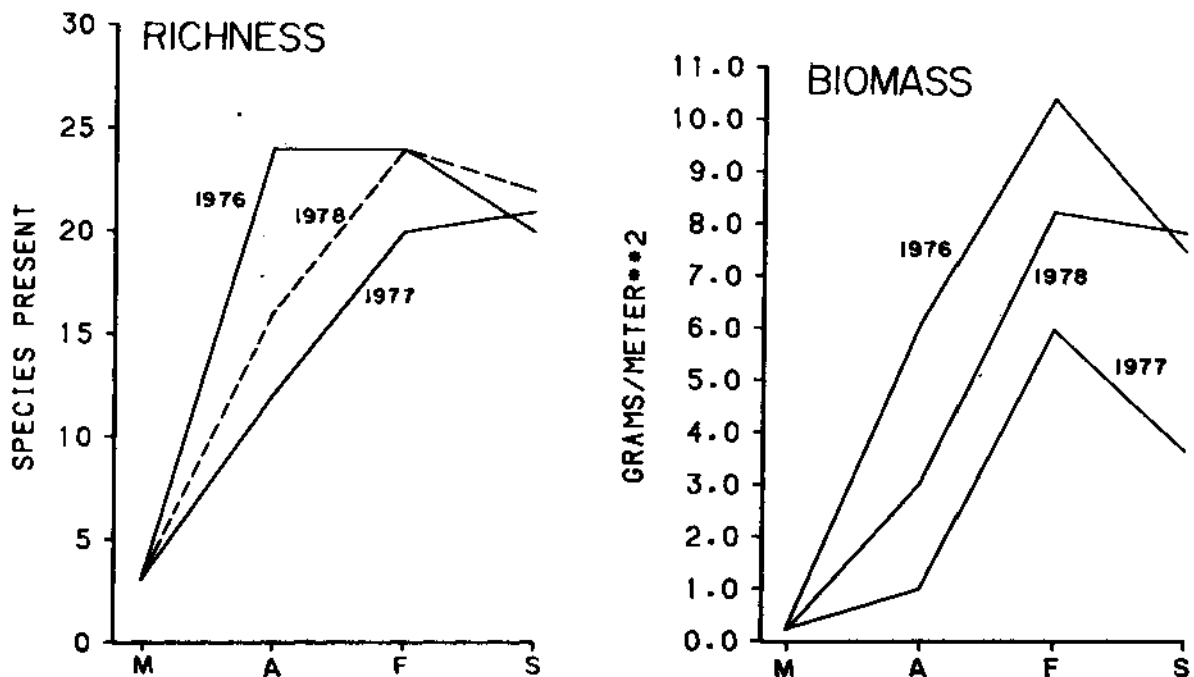
ASPEN

The amount of aspen within the spruce-fir forest will influence the distribution of species that use aspen for nesting, e. g., Goshawk, Downy Woodpecker, Mountain Bluebird, Violet-green Swallow, and feeding, e. g., Yellow-bellied Sapsucker (*Sphyrapicus varius*), Warbling Vireo, Orange-crowned Warbler. Sallying flycatchers, e. g., Western Wood Pewee, Dusky Flycatcher, tend to be associated with aspen since aspens usually grow within forest openings and have open canopies which the flycatchers can either sally in or under. In general, a patch of deciduous forest has an enriching effect on the avifauna of a coniferous forest (Winternitz 1976) and high avian species diversity is associated with an aspen-conifer overstory (Winn 1976).

SUBALPINE FIR

Subalpine fir can also have an enriching effect on a forest. Johnson (1978) found an increase in number of avian species at both the east and west side of the Great Basin correlated with the appearance of fir. When subalpine fir forests occupy the successional stage between aspen and climax spruce-fir, the number of bird species (Fig. 2) and avian biomass (Fig. 3) is usually much greater in the fir forest since the forest is a conglomeration of spruce, fir, and aspen. In this situation, the fir forest is a transition from deciduous to coniferous forest and species characteristic of both habitats are present.

^{3/}Smith, K. G., and J. A. MacMahon. Bird communities in a montane sere: Community structure and energetics. Unpublished manuscript. Utah State University.



Figures 2 and 3.--Species richness and total annual avian biomass present during the breeding season in 1976, 1977, and 1978 in the Bear River Mountains of northern Utah and southern Idaho on 4-10 ha plots, one in each seral stage. M=meadow, A=aspen, F=fir, S=spruce. Data from Smith and MacMahon^{3/}.

UNDERSTORY

A second point made by Willson (1974) was that the presence of a particular layer of vegetation may be quite important biologically. In western spruce-fir forests, the understory is usually in need of management, as is generally true of most coniferous forests (e. g., Dickson and Segelquist 1979). Winn (1976) found that on the North Slope of the Unita Mountains of Utah, the more diverse understories in coniferous forests supported the most diverse avian communities. Winternitz (1976) found bird species favored spruce mixed with aspen and suggested that it may be due to the increased understory.

WIND THROW AND FALLEN TREES

The amount of downed material in spruce-fir forests also influences the distribution of some species. Winn (1976) found a correlation between downed material and increased numbers of Yellow-rumped Warbler, Hermit Thrush, and Gray-headed Junco. The presence of House Wrens may be determined by the number of fallen logs (Hubbard 1965).

MANAGEMENT OF WESTERN SPRUCE-FIR FORESTS

Forest Management Practices

FIRE CONTROL

Engelmann spruce and subalpine fir are easily killed by fire (Loope and Gruell 1973), although in some areas the mesic nature of Engelmann spruce forests are such that they seldom burn (Weaver 1974). In the Front Range of Colorado, spruce-fir forests are entirely absent from areas where fires have occurred repeatedly over the last several hundred years (Marr 1967), and centuries old spruce-fir communities are hard to find in the northern Rockies due to fire (Habeck and Mutch 1973). Since the practice of fire suppression started at the turn of the century, Engelmann spruce and subalpine fir stands have greatly increased in area at the expense of lodgepole and aspen in the Rockies (Houston 1973, Loope and Gruell 1973), and white fir has greatly increased in the Sierra Nevada (Parsons and DeBenedetti 1979). Because biological processes are usually quite slow in spruce-fir forests, frequent fires are not needed to maintain diversity and conversely fires in spruce-fir forests can have extremely long-lasting effects (Habeck and Mutch 1973). Thus, in general, fire control is good for perpetuating old-growth spruce-fir forests. In the long run, fire control has helped cavity-nesting species that depend on rotting trees (Loope and Gruell 1973).

CUTTING

In the Rocky Mountains, spruce-fir forests are presently harvested by clear-cutting, shelterwood, and selection systems and the choice of cutting method depends largely on management objectives and on resources, social, and economic values (see review by Alexander 1977). Generally, all cutting practices are detrimental (Fig. 4) to birds that forage on or in trees (Thomas et al. 1975), and clear-cutting of large tracts of spruce-fir forest can greatly disrupt the species composition (Titterington et al. 1979), population densities (Franzreb 1977), and guild structure (Franzreb and Ohmart 1978), with aerial and ground feeders being favored by harvesting. If large areas of spruce-fir must be cut, patches of old-growth forest should be left with corridors (MacClintoch et al. 1977) connecting the patches if possible. McClelland et al. (1979) recommend 50-100 acres (20-40 ha) of old forest be left for every 1000 acres (400 ha) cut.

Smaller clear-cuts are more desirable for nongame birds since small open areas will favor certain species, such as raptors (Winn 1976), American Robin, and juncos (Hubbard 1965), and will not be as detrimental to tree-using species as would be large cuts. Austin and Perry (1979) concluded that clear-cuts of less than 100 acres (40 ha), with irregular borders (to increase edge effect), probably benefit wildlife in general. Natural regeneration of spruce-fir is possible when clear-cuts are not more than 5-8 chains (about 100-180 m) in width at any point (Noble and Ronco 1978).

Shelterwood and individual selection harvesting seem to hold promise for combining elements of both open and closed forest avian species (Fig. 4), but I can find no studies of avian response to these harvesting techniques in western spruce-fir. Overstory removal logging adversely affects the nongame bird avifauna (Franzreb 1978).

SHORT ROTATIONS

As economic pressures upon the forests of the United States increase, not only for paper and lumber, but also for energy (Pimentel et al. 1979), the outlook for old-growth spruce-fir forests may become grim. Winn (1976) stated that any management scheme that speeds up the rotation of overstories eliminates avian communities associated with the final successional stage. Forestry harvesting models are now appearing

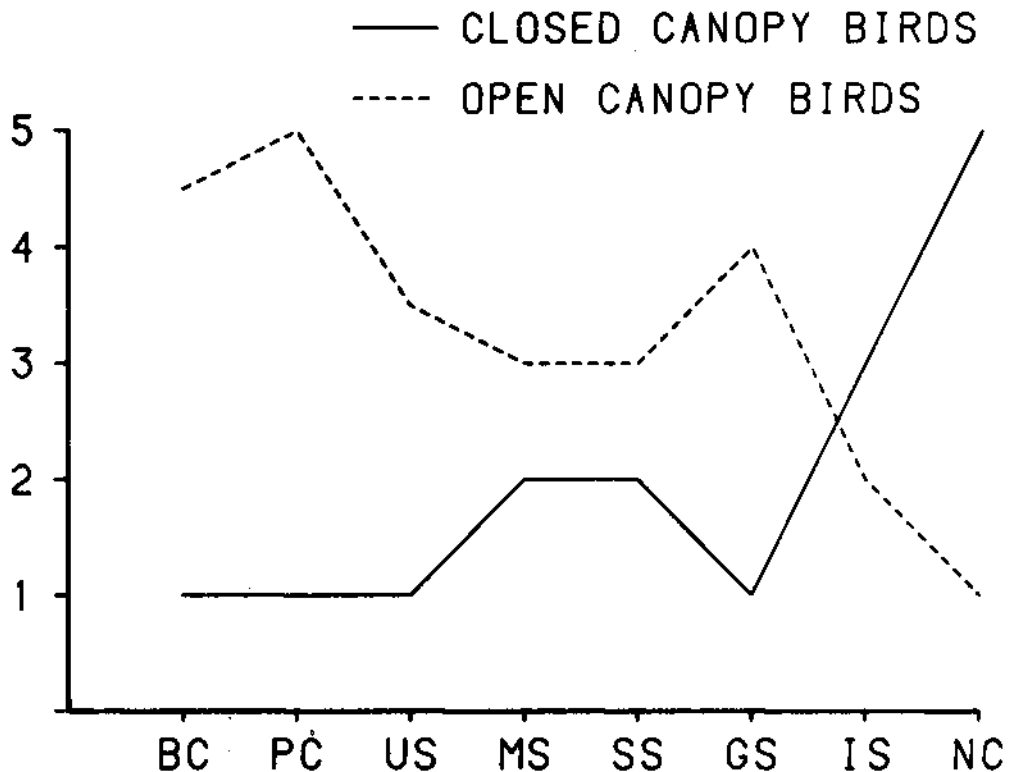


Figure 4.--Relative rankings of the effect of silvicultural systems on the open forest bird species (dotted line) and the closed forest bird species (solid line). Scale factor 1 signifies least favorable, 5 most favorable. BC=Block cutting over 10 acres, PC=Patch clear-cutting 3-5 acres, US=Uniform shelterwood, MS=Modified shelterwood, SS=Simulated shelterwood, GS=Group selection 2.0 acres, IS=Individual tree selection, NC=No cutting. Adapted from Alexander 1977.

based on the accelerated liquidation of old-growth stands, rotations of 50 years with an emphasis on monocultures, and the harvesting of much smaller, uniform trees (e.g., Gedney et al. 1975, Tedder 1979). These practices are obviously not compatible with the concept of relic, old-growth forests and maintenance of wildlife populations.

AERIAL SPRAYING

Very little research has been conducted in western coniferous forests on the effects of aerial spraying for the western budworm (*Choristoneura occidentalis*). DeWeese et al. (1979) detected a decline in bird populations after spraying of 2 insecticides in Montana coniferous forests that contained some spruce-fir. The results were not statistically significant. They found that canopy-feeding species came in contact with the insecticides more often than other guilds, and 79% of 202 birds examined showed traces of a dye that was mixed with the insecticides.

Birds consume budworms in relation to budworm abundance, consuming large quantities during outbreaks and few at other times (Mook 1963). The same is true for the relationship of birds and the spruce beetle (*Dendroctonus rufipennis* [Kirby]), especially the Northern 3-toed Woodpecker (see review by Schmid and Frye[1977]).

Spraying of herbicides to remove deciduous undergrowth would also affect bird communities in spruce-fir forests. In a spruce plantation in Norway, Slagsvold (1977) found a 30% reduction in bird density the spring following application of a herbicide and the bird communities had not fully recovered 4 years later. He attributed much of the change in bird populations not only to the lack of understory, but also to a reduction in the invertebrate fauna which many species used for food.

Wildlife Management Practices

LIFE-FORM APPROACH

The life-form approach, originally applied to spruce forest birds by Haapanen (1965,1966) and recently expanded for all vertebrates of the Blue Mountains of Oregon and Washington by Thomas and his colleagues (1975,1976,1978), would seem to hold great promise for the management of western spruce-fir forests. This approach links animals to specific vegetational communities based on where the animal reproduces and forages. Due to the consistency of both the avifaunas and the guild structure from one area to another, general management objectives may be possible for vast areas of spruce-fir forests in the western states. Also, the life-form approach might be useful in identifying those species (or types of species) most dependent on old-growth spruce forests and those that would benefit from management of spruce-fir forests.

KEY SPECIES

Graul et al. (1976) suggested another technique whereby a single species (or small group of species) that is an ecological indicator of a particular ecosystem are managed for, rather than attempting to manage for all the nongame species within that ecosystem. If the species is truly an environmental indicator, then by managing for that species, the entire ecosystem will be preserved if that species is preserved. Bird populations are excellent choices as indicator species since they are quite sensitive to environmental changes (e.g., Järvinen and Väisänen 1979a). A prime candidate for the spruce-fir ecosystem would be the Northern 3-toed Woodpecker, a species found throughout the world wherever spruce occurs (Bock and Bock 1974). The Northern 3-toed Woodpecker also uses a variety of tree resources (both dead and alive) and exhibits sexual dimorphism in its foraging behavior (Hogstad 1976,1977). Although seed-eating finches and corvids are also certainly characteristic of western spruce-fir forests, it would be hard to propose specific management plans since these species have a tendency to wander widely throughout (and sometimes beyond) the spruce-fir ecosystem.

SNAG MANAGEMENT

As noted earlier, snag management is extremely important in spruce forests, and is addressed elsewhere in this volume (paper by Eileen Miller). Thomas et al. (1976) recommend that snags should be created if they do not naturally occur, a situation which may obtain in spruce forests. They point out that species can be managed at some level below maximum population size and present guidelines for such management. In spruce forests in Finland, Haapanen (1965) found fewer hole-nesters in managed forests than in a natural forest. In southern Sweden, Nilsson (1979) found hole-nesters equally as common in managed and unmanaged spruce forests.

A practice employed in northern Europe is the placement of nest boxes in forests where availability of cavities may influence breeding distribution and densities. Competition for nest holes has been documented in western forests (e.g., Franzreb 1976), but, to my knowledge, no studies have been conducted to examine the effects of supplying supplemental nest boxes in coniferous forests of the western United States.

A NORTHERN EUROPEAN EXAMPLE

In northern Europe this century, there has been a great expansion of spruce forests for harvesting. For example, in the 1920's, spruce forests comprised 28% of the forests in southern Finland. By the early 1970's, 42% of the forests were primarily spruce (Järvinen et al. 1977). Such silvicultural practices certainly have had long-term effects on the associated avifauna (e.g., Järvinen and Väisänen 1979b) and have benefitted species dependent on spruce (Haapanen 1965). In Finland bird species associated with spruce have roughly doubled in population density in the 30 years since World War II due in part to the increase in spruce (Järvinen et al. 1977); 22 of 40 species (55%) increased within the last 50 years, in part due to the increase in spruce (Järvinen and Väisänen 1978). One might thus conclude that management for spruce forests greatly benefits nongame birds, but this is not true--many species were adversely affected by spruce forest management.

In the first place, almost all species that showed an increase were common species (Järvinen et al. 1977). Not uncommonly avian densities may be high in managed spruce stands, but the number of bird species is comparatively low (e.g., Batten 1976). Second, most species dependent on old-growth stands declined. In southern Finland, there has been a 70% decrease in the number of birds which favor old forests (>140 years) (Järvinen et al. 1977). In southern Sweden, where spruce forests are intensively managed for production and not for nongame birds, Nilsson (1979) reported that bird density and number of species were 3 times lower in managed spruce and 9 times lower in young planted spruce than in naturally occurring spruce forests. He further found that with intensive management, i.e., the elimination of all deciduous elements, 5 species disappeared from the spruce forest. Haapanen (1965) found a 15-30% decrease in managed spruce avifaunas in Finland and Nilsson (1979) attributes the greater differences in Sweden to the more intense management for production in Sweden. Moss (1978a,b) documents similar declines in spruce plantations in Scotland.

CONCLUSIONS AND RECOMMENDATIONS

Two options facing forest managers concerning nongame birds in spruce-fir forests of the western United States are: manage for increased diversity or manage for old-aged stands. Managing for avian diversity would be compatible with some harvesting techniques which create openings in the forest or that open the canopy. Johnson (1975) found that habitat variety was most important in controlling the number of bird species on mountain tops in the Great Basin and Hansson (1979) has developed a model showing that landscape heterogeneity is important for the winter survival of climax conifer birds. Since little food exists in climax coniferous forests in winter, he argues that most species have to use earlier successional stages or man-made disturbances where food may be more abundant. However, managing for harvest and diversity is probably incompatible with managing for old-stand species in the same area.

Clearly, one must attempt to manage for both diversity and conservation, with the emphasis on conserving endangered or rare species, not the common and abundant species (Järvinen and Väisänen 1978). The following might be a way in which both objectives could be accomplished.

High elevation (over 3000 m) spruce-fir forests should be harvested only after much forethought has been given to the outcome and regeneration of the forest. These high elevation areas should be allowed to drift into "silvic senility" and serve as reservoirs for the spruce-fir forests that occur at lower elevations.

Lower elevation spruce-fir forests should be managed for harvesting (e.g., small clear-cuts, selection harvest), with snag management practices implemented and some deciduous elements allowed to persist. Where large areas must be harvested, patches

of old-growth forest should be left. Winn (1976) recommends that the avoidance of relic areas which represent the final stages of succession should be planned in any overall drainage sale philosophy.

Nongame bird population densities and species composition in western spruce-fir forests should be periodically estimated (i.e., every 5-10 years), and guidelines along the life-form concept should be implemented in as many areas as possible. No species intimately associated with these forests is threatened at this time, but as pressure for use of these forests increases in the near future, we must be careful that the common birds do not become even more common at the expense of the rarer species, a situation that has apparently transpired in northern Europe.

Proper snag management is important to insure that nesting cavities are available. Fire suppression in general will benefit spruce-fir avifaunas, and caution should be used with aerial spraying until more research is done in this area.

ACKNOWLEDGMENTS

James A. MacMahon, Douglas Andersen, Peter Landres, Stephen Vander Wall, and Eric Zurcher all made helpful comments on an earlier version of this manuscript. Linda Finchum kindly typed the final copy. Robert Bayn Jr. drew the map. My spruce-fir research has been supported by a NSF grant (DEB 78-05328) to James A. MacMahon.

LITERATURE CITED

- Alexander, R. R.
1977. Cutting methods in relation to resource use in central Rocky Mountain spruce-fir forests. *J. For.* 75:395-400.
- Andreevan, A. V.
1979. Winter energy balance and hypothermia of the Siberian Jay. *Soviet J. Ecol.* 9:352-357. (English translation)
- Arbib, R.
1978. The Blue List for 1979. *Amer. Birds* 32:1106-1113.
- Askenmo, C., A. van Bromssen, J. Ekman, and C. Jansson.
1977. Impact of some wintering birds on spider abundance in spruce. *Oikos* 28:90-94.
- Austin, D. D., and M. L. Perry.
1979. Birds in six communities within a lodgepole pine forest. *J. For.* 77:584-586.
- Batten, L. A.
1976. Bird communities of some Killarney woodlands. *Proc. Royal Irish Acad. Sec. B* 76:285-313.
- Billings, W. D.
1969. Vegetational pattern near alpine timberline as affected by fire-snowdrift interactions. *Vegetatio* 19:192-207.
- Bock, C. E., and J. H. Bock.
1974. On the geographical ecology and evolution of the 3-toed woodpeckers, *Picoides tridactylus* and *P. arcticus*. *Amer. Midl. Nat.* 92:397-405.
- Bock, C. E., and L. W. Lephien.
1976. Synchronous eruptions of boreal seed-eating birds. *Amer. Nat.* 110:559-571.
- Boeker, E. L., and T. D. Ray.
1971. Golden Eagle population studies in the Southwest. *Condor* 73:463-467.
- Bloomberg, W. J.
1950. Fire and spruce. *For. Chron.* 26:157-161.
- Carbyn, L. N.
1971. Densities and biomass relationships of birds nesting in boreal forest habitats. *Arctic* 24:51-61.

- Carothers, S. W., R. P. Balda, and J. R. Haldeman.
1973. Habitat selection and density of breeding birds of a coniferous forest in the White Mountains, Arizona. In Breeding birds of the San Francisco Mountains area and the White Mountains, Arizona. S. W. Carothers, J. R. Haldeman, and R. P. Balda. p. 22-36. Mus. Northern Ariz. Tech. Ser. No. 12.
- Chaplin, S. B.
1974. Daily energetics of the Black-capped Chickadee, Parus atricapillus, in winter. J. Comp. Physiol. 89:321-330.
- DeWeese, L. R., C. J. Henry, R. L. Floyd, K. A. Bobal, and A. W. Schultz.
1979. Response of breeding birds to aerial sprays of trichlorfon (Dylox) and carbaryl (Sevin-4-Oil) in Montana forests. USDA Fish Wildl. Serv. Spec. Sci. Rep. - Wildl. No. 224, 29 p.
- Dickson, J. G., and C. A. Segelquist.
1979. Breeding bird populations in pine and pine-hardwood forests in Texas. J. Wildl. Manage. 43:549-555.
- Erskine, A. J.
1977. Birds in boreal Canada: Communities, densities and adaptations. Canadian Wildl. Ser. Rep. Ser. Num. 41, 73 p.
- Franklin, J. F.
1968. Cone production by upper-slope conifers. USDA For. Ser. Res. Pap. PNW-60, 21 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon.
- Franklin, J. F., and C. T. Dyrness.
1973. Natural vegetation of Oregon and Washington. USDA For. Ser. Gen. Tech. Rep. PNW-8, 417 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon.
- Franzreb, K. E.
1976. Nest site competition between Mountain Chickadees and Violet-green Swallows. Auk 93:836-837.
- Franzreb, K. E.
1977. Bird population changes after timber harvesting of a mixed conifer forest in Arizona. USDA For. Ser. Res. Pap. RM-184, 26 p. Rocky Mountain For. and Range Exp. Stn., Fort Collins, Colorado.
- Franzreb, K. E.
1978. Tree species used by birds in logged and unlogged mixed-coniferous forests. Wilson Bull. 90:221-238.
- Franzreb, K. E., and R. D. Ohmart.
1978. The effects of timber harvesting on breeding birds in a mixed-coniferous forest. Condor 80:431-441.
- Gabrielson, I. N., and S. G. Jewett.
1940. Birds of Oregon. Oregon State Monogr. Stud. Zool. No. 2. Oregon State College, Corvallis.
- Gedney, D. R., D. D. Oswald, and R. D. Fight.
1975. Two projections of timber supply in the Pacific Coast States. USDA For. Ser. Res. Bull. PNW-60, 40 p. Pac. Northwest For. and Range Exp. Stn., Portland, Oregon.
- Godfrey, W. E.
1966. The birds of Canada. Nat. Mus. Can. Bull. No. 203 Biol. Ser. No. 73.
- Graul, W. D., J. Torres, and R. Denny.
1976. A species-ecosystem approach for nongame programs. Wildl. Soc. Bull. 4:79-80.
- Grinnell, J., J. Dixon, and J. M. Linsdale.
1930. Vertebrate natural history of a section of northern California through the Lassen Peak region. Univ. Cal. Pub. Zool. 35.
- Haapanen, A.
1965. Bird fauna of the Finnish forests in relation to forest succession. I. Ann. Zool. Fenn. 2:154-196.

- Haapanen, A.
1966. Bird fauna of the Finnish forests in relation to forest succession. II. Ann. Zool. Fenn. 3:176-200.
- Habeck, J. R., and R. W. Mutch.
1973. Fire-dependent forests in the Northern Rocky Mountains. Quatern. Res. 3:408-424.
- Haftorn, S.
1972. Hypothermia of tits in the arctic winter. Ornis Scand. 3:153-166.
- Haftorn, S.
1974. Storage of surplus food by the Boreal Chickadee Parus hudsonicus in Alaska, with some records on the Mountain Chickadee Parus gambeli in Colorado. Ornis Scand. 5:145-161.
- Hansson, L.
1979. On the importance of landscape heterogeneity in northern regions for the breeding population densities of homeotherms: a general hypothesis. Oikos 33: 182-189.
- Hayward, C. L.
1945. Biotic communities of the southern Wasatch and Uinta Mountains, Utah. Great Basin Nat. 6:1-124.
- Hogstad, O.
1976. Sexual dimorphism and divergence in winter foraging behaviour of Three-toed Woodpeckers Picoides tridactylus. Ibis 118:41-50.
- Hogstad, O.
1977. Seasonal changes in intersexual niche differentiation of the Three-toed Woodpecker Picoides tridactylus. Ornis Scand. 8:101-111.
- Houston, D. B.
1973. Wildfires in northern Yellowstone National Park. Ecology 54:1111-1117.
- Hubbard, J. P.
1965. The summer birds of the forests of the Mogollon Mountains, New Mexico. Condor 67:404-415.
- Järvinen, O., and R. A. Väisänen.
1978. Long-term population changes of the most abundant south Finnish forest birds during the past 50 years. J. Ornithol. 119:441-449.
- Järvinen, O., and R. A. Väisänen.
1979a. Changes in bird populations as criteria of environmental changes. Holarctic Ecol. 2:75-80.
- Järvinen, O., and R. A. Väisänen.
1979b. Climatic changes, habitat changes, and competition: dynamics of geographical overlap in two pairs of congeneric bird species in Finland. Oikos 33:261-271.
- Järvinen, O., K. Kuusela, and R. A. Väisänen.
1977. Effects of modern forestry on the numbers of breeding birds in Finland in 1945-1975. Silva Fenn. 11:284-294. (in Finnish)
- Jewett, S. G., W. P. Taylor, W. T. Shaw, and J. W. Aldrich.
1953. Birds of Washington state. 767 p. University of Washington Press, Seattle.
- Johnson, N. K.
1974. Montane avifaunas of southern Nevada: Historical change in species composition. Condor 76:334-337.
- Johnson, N. K.
1975. Controls of number of bird species on montane islands in the Great Basin. Evolution 29:545-567.
- Johnson, N. K.
1978. Patterns of avian geography and speciation in the Intermountain region. In Intermountain biogeography: A symposium. p. 137-159. Great Basin Nat. Mem. 2.
- Little, E. L., Jr.
1971. Atlas of United States trees. Vol. 1, Conifers and important hardwoods. USDA For. Ser. Misc. Pub. No. 1146, unpaginated.

- Loope, L. L., and G. E. Gruell.
1973. The ecological role of fire in the Jackson Hole area, northwestern Wyoming. *Quatern. Res.* 3:425-443.
- MacClintock, L., R. F. Whitcomb, and B. L. Whitcomb.
1977. II. Evidence for the value of corridors and minimization of isolation in preservation of biotic diversity. *Amer. Birds* 31:6-12.
- Marr, J. W.
1967. Ecosystems of the east slope of the Front Range in Colorado. *Univ. Colorado Stud. Ser. Biol.* No. 8.
- McClelland, B. R., and S. S. Frissell.
1975. Identifying forest snags useful for hole-nesting birds. *J. For.* 73:414-417.
- McClelland, B. R., S. S. Frissell, W. C. Fischer, and C. H. Halverson.
1979. Habitat management for hole-nesting birds in forests of western larch and Douglas-fir. *J. For.* 77:480-483.
- Merkle, J.
1954. An analysis of the spruce-fir community on the Kaibab Plateau, Arizona. *Ecology* 35:316-322.
- Mook, L. J.
1963. Birds and the spruce budworm. *In* The dynamics of epidemic spruce budworm populations. R. F. Morris, ed. p. 268-271. *Mem. Ent. Soc. Canada* No. 31.
- Moss, D.
1978a. Diversity of woodland song-bird populations. *J. Anim. Ecol.* 47:521-527.
- Moss, D.
1978b. Song-bird populations in forestry plantations. *Quart. J. For.* 72:5-14.
- Nilsson, S. G.
1979. Effect of forest management on the breeding bird community in southern Sweden. *Biol. Conserv.* 14:135-143.
- Noble, D. L., and F. Ronco, Jr.
1978. Seedfall and establishment of Engelmann spruce and subalpine fir in clearcut openings in Colorado. *USDA For. Ser. Res. Pap. RM-200*, 12 p. Rocky Mountain For. and Range Exp. Stn., Fort Collins, Colorado.
- Noble, D. L., and W. D. Sheppard.
1973. Grey-headed Juncos. Important in first season mortality of Engelmann spruce. *J. For.* 71:763-765.
- Parsons, D. J., and S. H. DeBenedetti.
1979. Impact of fire suppression on a mixed-conifer forest. *For. Ecol. Manage.* 2:21-33.
- Peet, R. K.
1978. Latitudinal variation in southern Rocky Mountain forests. *J. Biogeogr.* 5:275-289.
- Pimentel, D., S. Chick, and W. Vergara.
1979. Energy from forests: Environmental and wildlife implications. *Trans. 44th Nor. Amer. Wildl. Nat. Res. Conf.* 44:66-79.
- Raphael, M. G., and M. White.
1978. Snags, wildlife, and forest management in the Sierra Nevada. *Cal-Neva Wildl.* 1978:23-41.
- Rasmussen, D. I.
1941. Biotic communities of Kaibab Plateau, Arizona. *Ecol. Monogr.* 11:229-275.
- Sabo, S. R., and R. H. Whittaker.
1979. Bird niches in a subalpine forest: an indirect ordination. *Proc. Nat. Acad. Sci.* 76:1338-1342.
- Salt, G. W.
1957. An analysis of avifaunas in the Teton Mountains and Jackson Hole, Wyoming. *Condor* 59:373-393.
- Samson, F. B.
1976. Territory, breeding density, and fall departure in Cassin's Finch. *Auk* 93:477-497.

- Schimpf, D. J., J. A. Henderson, and J. A. MacMahon.
1980. Some aspects of succession in the spruce-fir forest zone of northern Utah. *Great Basin Nat.* 40:(in press).
- Schmid, J. M., and R. H. Frye.
1977. Spruce Beetle in the Rockies. USDA For. Ser. Gen. Tech. Rep. RM-49, 38 p. Rocky Mountain For. and Range Exp. Stn., Fort Collins, Colorado.
- Scott, V. E., K. E. Evans, D. R. Patton, and C. P. Stone.
1977. Cavity-nesting birds of North American forests. USDA For. Ser. Agric. Handbook 511, 112 p.
- Shelford, V. E., and S. Olson.
1935. Sere, climax and influent animals with special reference to the Transcontinental coniferous forest of North America. *Ecology* 16:373-402.
- Slagsvold, T.
1977. Bird population changes after clearance of deciduous scrub. *Biol. Conserv.* 12:229-244.
- Smith, K. G.
1977. Distribution of summer birds along a forest moisture gradient in an Ozark watershed. *Ecology* 58:810-819.
- Smith, K. G.
1978. White-winged Crossbills breed in northern Utah. *West. Birds* 9:79-81.
- Smith, K. G.
1979. Common Redpolls using spruce seeds in northern Utah. *Wilson Bull.* 91:621-623
- Smith, K. G.
1980. Resource partitioning by a spruce-fir avian community within and among seral stages in northern Utah and southern Idaho. Ph.D. thesis. Dept. Biology, Utah State Univ., Logan.
- Snyder, D. P.
1950. Bird communities in the coniferous forest biome. *Condor* 52:17-27.
- Tatschl, J. L.
1967. Breeding birds of the Sandia Mountains and their ecological distribution. *Condor* 69:479-490.
- Tedder, P. L.
1979. Oregon's future timber harvest: The size of things to come. *J. For.* 77:714-716.
- Theberge, J. B.
1976. Bird populations in the Kluane Mountains, southwest Yukon, with special reference to vegetation and fire. *Can. J. Zool.* 54:1346-1356.
- Thomas, J. W., G. L. Crouch, R. S. Bumstead, and L. D. Bryant.
1975. Silviculture options and habitat values in coniferous forests. In *Proceedings of the symposium on management of forest and range habitats for nongame birds*. D. R. Smith, tech. coord. p. 272-287. USDA For. Ser. Gen. Tech. Rep. WO-1.
- Thomas, J. W., R. J. Miller, H. Black, J. E. Rodiek, and C. Maser.
1976. Guidelines for managing and enhancing wildlife habitat in forest management in the Blue Mountains of Oregon and Washington. *Trans. 41st North Amer. Wildl. Nat. Resources Conf.* 41:452-476.
- Thomas, J. W., R. Miller, C. Maser, R. Anderson, and B. Carter.
1978. The relationship of terrestrial vertebrates to plant communities and their successional stages. In *Classification, inventory, and analysis of fish and wildlife habitat*. A. Marmelstein, gen. chairman. p. 281-303. USDI Fish Wildl. Biol. Serv. Prog. FWS/OBS-78/76.
- Thompson, L. S.
1978. Species abundance and habitat relations of an insular montane avifauna. *Condor* 80:1-14.
- Titterington, R. W., H. S. Crawford, and B. N. Burgason.
1979. Songbird responses to commercial clear-cutting in Maine spruce-fir forests. *J. Wildl. Manage.* 43:602-609.

- Udvardy, M. D. F.
1963. Bird faunas of North America. Proc. XIII International Ornithol. Conf.
p. 1147-1167.
- Valiela, I.
1971. Food specificity and community succession: Preliminary ornithological evidence for a general framework. Gen. Syst. 16:77-84.
- Weaver, H.
1974. Effects of fire on temperate forests: Western United States. In Fire and ecosystems. T. T. Kozlowski and C. E. Ahlgren, eds. p. 279-319. Academic Press, New York.
- Whipple, S. A., and R. L. Dix.
1979. Age structure and successional dynamics of a Colorado subalpine forest. Amer. Midl. Nat. 101:142-158.
- Wiens, J. A.
1975. Avian communities, energetics, and functions in coniferous forest habitats. In Proceedings of the symposium on management of forest and range habitats for nongame birds. D. R. Smith, tech. coord. p. 226-265. USDA For. Ser. Gen. Tech. Rep. WO-1.
- Willson, M. F.
1974. Avian community organization and habitat structure. Ecology 55:1017-1029.
- Wing, L. W.
1950. Some counts of bird populations in coniferous forests near the limit of trees. Can. Field-Nat. 64:87-88.
- Winn, D. S.
1976. Terrestrial vertebrate fauna and selected coniferous forest habitat types on the North Slope of the Uinta Mountains. USDA For. Ser. Region 4, Wasatch National Forest, Ogden, Utah. 145 p.
- Winternitz, B. L.
1976. Temporal change and habitat preference of some montane breeding birds. Condor 78:383-393.