

EFFECTS OF FIRE AND POST-FIRE SALVAGE LOGGING ON AVIAN COMMUNITIES IN CONIFER-DOMINATED FORESTS OF THE WESTERN UNITED STATES

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Abstract. Historically, fire was one of the most widespread natural disturbances in the western United States. More recently, however, significant anthropogenic activities, especially fire suppression and silvicultural practices, have altered fire regimes; as a result, landscapes and associated communities have changed as well. Herein, we review current knowledge of how fire and post-fire salvaging practices affect avian communities in conifer-dominated forests of the western United States. Specifically, we contrast avian communities in (1) burned vs. unburned forest, and (2) unsalvaged vs. salvage-logged burns. We also examine how variation in burn characteristics (e.g., severity, age, size) and salvage logging can alter avian communities in burns.

Of the 41 avian species observed in three or more studies comparing early post-fire and adjacent unburned forests, 22% are consistently more abundant in burned forests, 34% are usually more abundant in unburned forests, and 44% are equally abundant in burned and unburned forests or have varied responses. In general, woodpeckers and aerial foragers are more abundant in burned forest, whereas most foliage-gleaning species are more abundant in unburned forests. Bird species that are frequently observed in stand-replacement burns are less common in understory burns; similarly, species commonly observed in unburned forests often decrease in abundance with increasing burn severity. Granivores and species common in open-canopy forests exhibit less consistency among studies. For all species, responses to fire may be influenced by a number of factors including burn severity, fire size and shape, proximity to unburned forests, pre- and post-fire cover types, and time since fire. In addition, post-fire management can alter species' responses to burns. Most cavity-nesting species do not use severely salvaged burns, whereas some cavity-nesters persist in partially salvaged burns. Early post-fire specialists, in particular, appear to prefer unsalvaged burns. We discuss several alternatives to severe salvage-logging that will help provide habitat for cavity nesters.

We provide an overview of critical research questions and design considerations crucial for evaluating the effects of prescribed fire and other anthropogenic disturbances, such as forest fragmentation. Management of native avifaunas may be most successful if natural disturbance regimes, including fire, are permitted to occur when possible. Natural fires could be augmented with practices, such as prescribed fire (including high-severity fire), that mimic inherent disturbance regimes.

Key Words: burn severity; cavity-nesters; fire effects; fire suppression; passerine birds; prescribed fire; salvage logging; silviculture; snags; wildland fire; woodpeckers.

Understanding the consequences of anthropogenic activities that alter natural systems requires a thorough knowledge of the natural disturbance regimes that shape communities and landscapes. Often, the ecological consequences of anthropogenic activities have been evaluated in the context of relatively undisturbed, mature forest (e.g., Whitcomb et al. 1977, Mladenoff et al. 1993, King et al. 1997, Morse and Robinson 1999). However, this approach may be inadequate for systems that evolved with major and persistent disturbances, such as fire. In the West, fire has played a dominant role in shaping communities and landscapes. Thus, one of the greatest threats to the ecological integrity of western forest systems may be alteration of natural disturbance regimes and landscape structure through livestock grazing, fire suppression, logging in burned forests (hereafter "salvaging" or "salvage logging"), and other silvicultural activities.

Concern that decades of fire suppression may lead to more frequent, larger wildfires has

prompted government agencies to expand prescribed-burning programs and fire-management policies to diminish the chances of large, severe wildfires (U.S. Dept. of Interior and U.S. Dept. of Agriculture 1998). Unfortunately, our understanding of historical fire regimes remains rudimentary and may be inadequate for setting such goals (Tiedemann et al. 2000). Furthermore, the new government-sanctioned program of prescription burning focuses on reducing fuel loads, with relatively little consideration given to the effects on wildlife (Tiedemann et al. 2000). In part, this problem stems from a paucity of rigorous field studies that have evaluated the effects of fire on wildlife communities. Without a better understanding of how historical fire regimes influenced communities (Bunnell 1995) and landscapes, as well as how anthropogenic activities have altered fire regimes, programs of prescription burning and other mitigation measures could be as misguided as widespread fire suppression.

In the review and discussion that follow, we

examine avian communities in post-fire forests in conifer-dominated systems of the West, and compare them to those in unburned forests. We focus in particular on the responses of woodpeckers and passerine birds. Because avian responses to fire may vary with burn severity and size, time since fire, ecological contexts of burns, and post-fire salvage logging, these issues are also discussed. We preface our review by providing an overview of historical fire regimes of western forests and how human activities, particularly fire suppression, may have altered those regimes. This background is essential for understanding the patterns observed among avian communities using unburned and burned forests. We conclude with a discussion of compelling management implications that arise from this review, and we identify essential research questions for improving and enlarging our understanding of how fire shapes and perpetuates avian communities in western forests.

FIRE REGIMES IN CONIFEROUS FORESTS OF THE WESTERN UNITED STATES

Although current knowledge of historical fire regimes in western forests remains somewhat rudimentary, it is possible to place those systems into broad fire-regime categories. The regime that characterizes any one system is an interplay between gradients in burn severity and fire frequency (i.e., fire-return interval). Generally, burn-severity gradients are divided into three levels, based on vegetation responses to fire: (1) low-severity fires kill or temporarily remove above-ground portions of herbaceous and understory layers and sometimes scorch the lower portions of mature trees, typically without killing them; (2) moderate-severity fires may kill but usually do not consume leaves of canopy trees, although some tree mortality may result; and (3) high-severity fires usually burn the canopy, killing the majority of trees (Agee 1993). One level of burn-severity may dominate a given burn, but most burns are mosaics of various fire severities (Agee 1993, Turner et al. 1994). Furthermore, there is variation among tree species' responses to fire intensity (e.g., heat). For example, the thick, fire-retardant bark of mature ponderosa pines (*Pinus ponderosa*) generally provides them protection from understory fires, whereas subalpine firs (*Abies lasiocarpa*) are often killed by understory fires (Agee 1993). Understory fires also typically kill the above-ground biomass of quaking aspen (*Populus tremuloides*) stands, although lateral roots readily respond to fire by resprouting vigorously (Agee 1993). Thus, variations in burn severity can have profound effects on the composition and structure of plant communities.

For simplicity, most forest systems of the West can be characterized by one of three fire-regimes based on the effects of fire intensity on the dominant tree species: high frequency/low severity, moderate frequency and moderate to high severity, or low frequency/high severity (Agee 1993, 1998). High frequency/low severity fires (i.e., 1- to 40-yr fire-return intervals) are characteristic of many dry, warm forests. The combination of dry conditions and pervasive surface fuels (grasses and duff) allows fire to recur frequently. Many tree species in these systems are adapted to fire (e.g., fire-retardant bark, seedling germination requires bare substrates). Generally, fires in these systems are restricted to herbaceous and understory layers, thereby eliminating the majority of saplings and perpetuating a discontinuous forest canopy. Examples of such systems include ponderosa pine forests of foothills along the Rocky Mountains and Sierra Nevada (Arno 1980, Verner and Boss 1980, McKelvey et al. 1996).

In forests characterized by intermediate moisture and temperatures, fire regimes are generally moderate in severity and frequency, although in many cases severity can be high (Agee 1993, 1998). The mix of burn severities often results in heterogeneous burns and multiple-age structures of dominant trees (Agee 1993, 1998). Fire-return intervals tend to be longer (40–150+ yr) than those in drier sites, but can be quite variable (Agee 1993). Examples of this type of system include red fir (*Abies magnifica*) and coastal redwood (*Sequoia sempervirens*) in California (Agee 1993, 1998).

Low frequency/high severity fire regimes typically result in stand-replacement events. Because of the long fire intervals, trees in these systems often lack the ability to withstand fire (Agee 1993), although some species have reproductive adaptations to fire (e.g., serotinous cones of lodgepole pine, *Pinus contorta*; Agee 1993). Typically, climatic conditions (e.g., severe drought and strong winds) necessary for these systems to burn occur only several times per century, and fires spread only if sufficient fuels have accumulated (Romme 1982). Once started, fires in these systems often burn vast areas and may last for months (Agee 1993). Regeneration in larger burns can take decades if viable seed sources are distant (Agee 1993). Fire return intervals range from 200–300 years in lodgepole pine forests (Romme 1982, Veblen 2000) to more than 1000 years for some cedar/spruce/hemlock forests of the Pacific Northwest (Agee 1993).

Local factors, such as elevation, topography, and climate, can modify the general fire regimes described above. For example, surface fires may occur less frequently in naturally dense systems

of ponderosa pine with limited herbaceous cover; in turn, canopy fuels may become sufficiently dense to support crown fires (Shinneman and Baker 1997, Brown et al. 1999, Veblen 2000). Especially high probabilities of lightning strikes in mountainous terrain may result in small, frequent surface fires that often perpetuate open meadows in moist forests (Agee 1993, Veblen 2000). Overall, the complex mosaic of western forest systems has been shaped by an equally complex mosaic of fire regimes.

CHANGES IN FIRE REGIMES

Attempts to understand how contemporary human activities have altered natural fire regimes are fraught with difficulties. Fire regimes are inherently dynamic, largely due to variations in climate, both long-term (Clark 1988, Romme and Despain 1989, Johnson et al. 1990) and short-term (e.g., El Niño-driven events; Swetnam and Betancourt 1990, Veblen et al. 2000). In ponderosa pine systems, the degree to which severe fires result from the long-term accumulation of fuels due to fire suppression or the short-term accumulation and desiccation of fine fuels following El Niño/Southern Oscillations is poorly understood and can vary among sites (Veblen et al. 2000). Likewise, decades of fire suppression at Yellowstone National Park, which may have delayed the onset of extensive fires, were apparently overshadowed by severe drought and high winds in August 1988 (Romme and Despain 1989). Thus, the relative contributions of fire suppression and climate on extreme fire behavior remains unclear.

The relatively ephemeral nature of fire records (e.g., fire scars, stand cohorts) limits our reconstruction of fire histories for most locations (but see Agee 1998). Charcoal deposits in lake-bed sediments have revealed longer histories (Millsbaugh and Whitlock 1995), but they are influenced strongly by prevailing winds and watershed dynamics so that the overall area they represent may be quite limited. Historic accounts of fire behavior and forest conditions during Euro-American settlement can also be biased (Wagner et al. 2000). Furthermore, humans have influenced fire regimes in North America for at least 6,000–10,000 years. Native Americans used fire in warfare and for driving game (Stewart 1956), and Euro-American settlers used fire to clear land for mining, logging, and even in land disputes (Veblen and Lorenz 1991); settlers also caused many accidental fires (Johnson et al. 1990). Extensive livestock grazing after the mid-1800s coupled with effective fire suppression (particularly after World War II) led to structural changes in forest stands (Saab et al. 1995), which altered fire regimes further (Madany and

West 1983, Covington and Moore 1994; but see Swetnam et al. 1999). Thus, it is difficult to determine what constitutes “natural” or “anthropogenic” changes to fire regimes. For the purposes of this review, we focus on anthropogenic changes that began in the mid 1800s, including grazing, unprecedented fire suppression, and large-scale silvicultural activities (e.g., widespread clearcutting, salvage logging).

Effects of fire suppression

Given the complexity and limited understanding of historical fire regimes, the full ramifications of fire suppression remain unknown. Certainly, the long-term, global-scale effects of fire suppression and their potential interactions with climate changes caused by anthropogenic activities are cause for concern (Leenhouts 1998). On a continental scale, however, it is clear that fire suppression over the last six or seven decades has reduced the number of fires and the total area burned across the U.S. (Ferry et al. 1995). Using satellite imagery, maps of potential natural vegetation, and estimated fire regimes, Leenhouts (1998) concluded that only 8–14% of the area that burned annually in the conterminous United States 200–500 yr ago still burns today.

In western forest systems, effects of fire suppression vary with forest type and inherent fire regime, as well as accessibility (Romme 1982). In many systems adapted to high-frequency/low-severity fire regimes (e.g., ponderosa pine), changes in forest structure since Euro-American settlement have included increased stem densities resulting from decreased mortality of saplings and increased recruitment, and changes in species composition (Gruell 1983, Veblen and Lorenz 1991, Covington and Moore 1994, Swetnam and Baisan 1996, Belsky and Blumenthal 1997, Allen 1998). Accumulation of fuels may promote more extensive, severe fires than those that occurred prior to Euro-American settlement (Barrett 1988, Covington and Moore 1994, Lissoway 1996, Covington et al. 1997, Fule et al. 1997, Veblen et al. 2000). However, wetter climates post-settlement may also contribute to a decrease in fire frequency (Veblen et al. 2000, Wagner et al. 2000).

The consequences of fire suppression in forests characterized by infrequent fires of high severity (e.g., high-elevation spruce-fir forests of the central Rockies) are less apparent, in part because the longer fire-return intervals may delay, or reduce, the effects of fire suppression (Romme 1982, Romme and Despain 1989, Veblen 2000). Even in regions where the frequency of fires has declined, burn severity may not have changed (Romme and Despain 1989). Although the relative contribution of climate and fire suppression is debatable, clearly

the effects of both have influenced fire regimes across western landscapes.

Other human activities may amplify or confound the effects of fire suppression. Overgrazing by livestock or elevated populations of native ungulates protected from wolf predation may diminish fire frequency (Hess 1993, Belsky and Blumenthal 1997). For example, during the late 1800s to early 1900s, livestock grazing in many ponderosa pine systems led to decreased surface fuels and increased areas of exposed soil; the result was diminished fire frequencies and increased germination and survival of tree seedlings (Swetnam and Baisan 1996, Veblen 2000). In addition, the combined effects of fire suppression, grazing, and contemporary silvicultural practices in many western forests has promoted the growth of dense, monospecific, even-aged stands (Swetnam et al. 1995, Fule et al. 1997). In turn, this stand structure is believed to present opportunities for more extensive outbreaks of tree-damaging insects than would have occurred prior to the mid-1800s when stands were often more open and complex in structure (Swetnam et al. 1995, Veblen 2000, Veblen et al. 2000). Widespread tree mortality resulting from insect outbreaks can increase a given stand's susceptibility to fire. Although our current knowledge of the interactive effects of fire suppression and other factors is limited, it has become clear that these factors can alter fire regimes significantly.

EFFECTS OF FIRE AND SALVAGE LOGGING ON AVIAN COMMUNITIES

Understanding fire regimes in western forests is essential to understanding forest structure, overall landscape patterns, and the responses of bird communities to fire. Fire affects avian nesting and foraging activities by generating snags, altering insect communities, eliminating foliage, and altering the size, abundance, and distribution of tree species across the landscape (Finch et al. 1997, Huff and Smith 2000). The degree to which fire affects any of these factors depends, in part, on the severity and ecological context of a particular burn. A thorough understanding of the influence of fire and fire-management activities, such as prescribed burning and post-fire salvage logging, on avian communities is essential to both conservation biology and sound management.

Here, we summarize the best current knowledge about the influence of fire and salvage logging on avian communities in conifer-dominated forests (which often include quaking aspen) of the West. Most of the relatively few published studies were conducted in the northern Rocky Mountains. Because these studies encompassed many cover types and were usually poorly replicated, many of our conclusions are prelimi-

nary. However, some general patterns, as well as a number of questions, have emerged from four comparisons: (1) avian abundance in burned and unburned forests, (2) avian abundance among different fire severities, (3) changes in avian-community structures associated with post-fire forest succession, and (4) nesting patterns of cavity-nesting birds in salvaged and unsalvaged, burned forests.

AVIAN ABUNDANCE IN RECENTLY BURNED AND UNBURNED FORESTS

We summarized the results of 11 studies that compared the abundance of breeding bird species in early post-fire burns and adjacent mature, unburned forests (Tables 1a–1c; Fig. 1). Although "unburned" forests may have burned previously, these forests were largely mature (i.e., late-successional). All 23 burns surveyed were severe (predominantly stand-replacement) and less than 10 yr old (most were <4 yr old). All but a few burns were greater than 400 ha, and four burns were greater than 1400 ha. Conifers, including ponderosa pine/Douglas-fir (*Pseudotsuga menziesii*), Jeffrey pine (*Pinus jeffreyi*)/white fir (*Abies concolor*), lodgepole pine, spruce/fir, and mixed conifers, were the dominant cover types. The studies covered seven western states; seven studies were conducted in the northern Rocky Mountains, one was in the southern Rocky Mountains, two were in the Pacific Northwest, and one was in the Pacific Southwest (Fig. 1). Studies of post-fire bird communities that were older than 10 yr, were predominantly aspen or riparian, or sampled only burn edges were excluded from analysis.

For each species present in ≥ 3 of the 11 studies, we classified abundance patterns into three response classes by study: (1) occurred only in burns or abundance was $\geq 50\%$ higher in burns than in unburned forest; (2) occurred only in unburned forest or abundance was $\geq 50\%$ higher in unburned than in burned forest; and (3) results varied among samples or there were similar abundances in burned and unburned forest (Tables 1a–1c). Because only one study (Johnson and Wauer 1996) included both pre- and post-fire surveys, we used this comparison of abundance patterns to infer response to fire.

Many species showed remarkably consistent patterns, despite the wide geographic area and variety of cover types surveyed. Species that commonly occurred in burns, but were uncommon or absent in unburned forests (Table 1a), included Black-backed Woodpecker, Three-toed Woodpecker, Olive-sided Flycatcher, and Mountain Bluebird (see Appendix for species' scientific names). Species that used unburned forests, but rarely occurred in early post-fire forests (Table

TABLE 1. SUMMARY OF AVIAN ABUNDANCES IN BURNED AND UNBURNED FORESTS

Species	Response categories (number of studies)		
	More abundant in burns	Similar abundance or response mixed	More abundant in unburned
(A) Typically more abundant in burns			
Three-toed Woodpecker	8 ^a , b, d, e, g, h, i, j		
Black-backed Woodpecker	6 ^b , d, e, i, j, k		1 ^c
Olive-sided Flycatcher	8 ^a , c, d, f, g, h, i, k		
Mountain Bluebird	9 ^a , b, c, d, g, h, i, j, k		
Western Wood-Pewee	7 ^a , c, d, g, h, i, j		
Hairy Woodpecker	8 ^a , b, c, e, f, g, h, j	2 ^d , i	
House Wren	5 ^a , b, d, g, j	1 ^h	
Tree Swallow	4 ^b , h, i, j		1 ^c
Northern Flicker	5 ^a , c, f, i, j	3 ^b , g, h	
(B) Typically exhibited mixed or neutral response to burns			
Mourning Dove	2 ^d , h	1 ^g	
Common Nighthawk	2 ^c , h	1 ^g	
Cassin's Finch	4 ^c , h, i, j	3 ^a , d, g	
Pine Siskin	3 ^c , f, i	3 ^d , g, h	
Chipping Sparrow	2 ^a , c	4 ^g , h, i, j	1 ^d
Dark-eyed Junco	3 ^c , f, i	5 ^a , d, g, h, j	
American Robin	4 ^a , f, j, k	5 ^c , d, g, h, i	
Townsend's Solitaire	1 ^f	5 ^a , c, d, g, h	
Hammond's Flycatcher	1 ^f	3 ^d , g, h	
Clark's Nutcracker	2 ^j , h	2 ^d , g	1 ⁱ
Red-naped Sapsucker	1 ^h	1 ^g	2 ^a , b
Western Tanager	1 ^c	4 ^d , g, h, i	2 ^a , j
White-breasted Nuthatch	1 ^a	1 ^g	1 ^d
Evening Grosbeak	1 ^g	1 ^h	1 ^d
Pygmy Nuthatch	1 ^a		2 ^g , h
Yellow-rumped Warbler		5 ^a , c, g, i, k	3 ^d , h, j
Williamson's Sapsucker	1 ^a	1 ^g	2 ^h , i
Red Crossbill		2 ^g , h	1 ^d
(C) Typically more abundant in unburned forests			
Steller's Jay		1 ^g	3 ^a , f, h
Plumbeous/Cassin's Vireo		1 ^g	2 ^a , h
Warbling Vireo		1 ^g	2 ^d , h
Gray Jay		2 ^c , h	3 ^f , i, j
Ruby-crowned Kinglet		2 ^g , h	3 ^d , i, j
Brown Creeper		2 ^f , g	5 ^a , d, h, i, j
Red-breasted Nuthatch	1 ^g	2 ^h , i	6 ^a , b, d, f, j, k
Hermit Thrush		1 ^c	5 ^a , g, h, i, j
Mountain Chickadee			6 ^a , g, h, i, j, k
Golden-crowned Kinglet			6 ^a , d, f, h, j, k
Townsend's Warbler			3 ^d , f, k
Swainson's Thrush			3 ^d , j, k
Varied Thrush			3 ^d , f, k

Notes: Only species observed in three or more studies were included. More abundant in burns = only occurred in burns or abundance was $\geq 50\%$ higher in early post-fire forests than unburned forest; similar or mixed = abundance was similar in burned and unburned forest or results varied among samples; more abundant in unburned = occurred only in unburned forest or abundance was $\geq 50\%$ higher in unburned than early post-fire forests.

^a Bock and Lynch 1970.

^b Caton 1996.

^c Davis 1976.

^d Harris 1982.

^e Hoffman 1997.

^f Huff 1984, Huff et al. 1985.

^g Johnson and Wauer 1996.

^h N. Kotliar and C. Melcher, unpubl. data.

ⁱ Pfister 1980.

^j Taylor and Barmore 1980.

^k R. Sallabanks and J. McIver, unpubl. data.

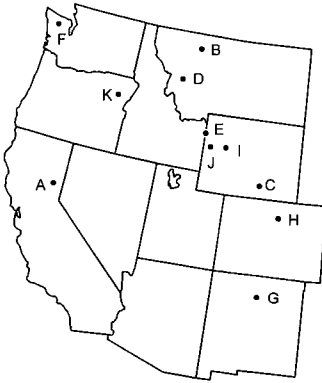


FIGURE 1. Approximate location of study sites referred to in Table 1. Center location of study area is indicated in cases where multiple burns were surveyed. References (dominant cover type; number of burns; survey years post-fire): A—Bock and Lynch 1970 (Jeffrey pine/white fir; 1 burn; 6–8 yrs); B—Caton 1996 (lodgepole pine; 1 burn; 2–4 yrs); C—Davis 1976 (lodgepole pine; 2 burns; 6 yrs, 9 yrs); D—Harris 1982 (ponderosa pine/Douglas fir; 2 burns; 2–4 yrs, 2 yrs); E—Hoffman 1997 (lodgepole pine; 2 burns; 1–2 yrs); F—Huff 1984, Huff et al. 1985 (w. hemlock/Douglas fir; 1 burn; 1–3 yrs); G—Johnson and Wauer 1996 (ponderosa pine; 1 burn; 1 yr pre-fire; 3 yrs); H—N. Kotliar and C. Melcher, unpubl. data (ponderosa pine; lodgepole; spruce/fir; mixed conifer; 8 burns; varied from 0–8 yrs); I—Pfister 1980 (lodgepole pine; 2 burns; 2 yrs, 4 yrs); J—Taylor and Barmore 1980 (lodgepole pine; spruce/fir; 2 burns; 1–3 yrs, 5/7 yrs); K—R. Sallabanks and J. McIver, unpubl. data (mixed conifers; 1 burn; 1–3 yrs).

1c), included Mountain Chickadee, Golden-crowned Kinglet, Hermit Thrush, Varied Thrush, and Townsend's Warbler. Generally, wood drillers and aerial insectivores were more abundant in early post-fire forests, whereas foliage and bark gleaners were usually more abundant in unburned forests. However, there were several exceptions to this generalization. Overall, these results suggest that species with either the strongest affinity for, or aversion to, young burns are responding primarily to the dramatic changes in structural characteristics (e.g., increased availability of snags, decrease in canopy coverage) and/or densities of insect prey brought about by burning.

Numerous species showed more varied, or apparently neutral, responses to burns (Table 1b). For example, Townsend's Solitaire, American Robin, Dark-eyed Junco, Chipping Sparrow, and Cassin's Finch were common in both burned and unburned forests, indicating that both types of forests often may provide suitable habitat for these species. Many species, including Red-breasted Nuthatch, Brown Creeper, Yellow-rumped Warbler, and Western Tanager, were fre-

quently observed in burns, but typically reached their highest abundance levels in unburned forests. Many granivores, bark gleaners, and species that prefer a mixed, open canopy had a varied responses. The mixed results may be due, in part, to the influence of site-specific characteristics (see FACTORS THAT AFFECT SPECIES' RESPONSES TO BURNS).

Several species observed in fewer than three studies exhibited higher abundances in burned compared to unburned forests, including Lewis's Woodpecker (V. Saab, unpubl. data), Rock Wren, Western Bluebird (N. Kotliar and C. Melcher, unpubl. data), Lazuli Bunting (Bock and Lynch 1970), and White-crowned Sparrow (Pfister 1980; N. Kotliar and C. Melcher, unpubl. data). Our personal observations of these species suggest that they readily use burns in certain contexts. Although the generality of these observations is unknown, the apparent suitability of burned forests for these species warrants further study.

A comparison of bird abundances in more than 30 fires that burned in the northern Rockies in 1988, with bird abundances derived from the literature for nine other major Rocky Mountain forest cover types (Table 3 in Hutto 1995), generally corresponds to the results of our review. Most of the species that exhibited higher abundances in burned forests (Table 1a) were more commonly observed in recently burned forests than in all other mature forest types (Hutto 1995). Likewise, species that exhibited higher abundances in unburned forests (Table 1c) commonly occurred in one or more mature forest types but were infrequently observed in recently burned forests (Hutto 1995); however, Mountain Chickadee and Red-breasted Nuthatch occurred in a relatively high percentage (52–74%) of the 1988 burns surveyed by Hutto (1995). Many of the species that showed a mixed or neutral response to burns (Table 1a) also had a higher frequency of occurrence in early post-fire forests compared to mature forest types (Table 3 in Hutto 1995).

Some of the species that showed mixed patterns across studies may use forest edges as well as forest interiors (e.g., Mountain Chickadee, Hermit Thrush; N. Kotliar and C. Melcher, unpubl. data), and because some are rather nomadic (e.g., Red Crossbill), the degree to which burns represent suitable habitat cannot be inferred easily from surveys that abut the edges of burns. Further research is needed to determine how various factors can alter the relative suitability of burned and unburned forests for such species (see next section).

FACTORS THAT AFFECT SPECIES' RESPONSES TO BURNS

The suitability of burns for birds often will depend on burn characteristics (e.g., severity,

time since fire, burn geometry) and landscape context (e.g., forest cover types), as well as regional variation (Finch *et al.* 1997, Huff and Smith 2000). To begin to address these issues, we summarized the results of several studies that evaluated how burn severity and time since fire influenced bird communities. To provide impetus for future studies, we also speculate (based on personal observations and a few limited studies) about the ways in which burn characteristics and context may contribute to variation in results among studies.

Burn severity

Three studies compared avian abundances across various burn severities in reference to unburned forests. Taylor and Barmore (1980) examined two burn severities (moderate, severe) for the first three yr post-fire in a 1414-ha burn in lodgepole pine and spruce/fir forests in Grand Teton and Yellowstone National Parks. Preliminary results (first three yr post-fire) are available from a study of a 9283-ha burn in Oregon in which three burn severities (low, moderate, severe) were examined in mixed coniferous forests (R. Sallabanks, unpubl. data; R. Sallabanks and J. McIver, unpubl. data). In addition, preliminary results are available for a comparison of two understory-prescribed (1 yr post-fire, 200 ha, and 1–3 yr post fire, 1200 ha) and two stand-replacement burns (1 yr post fire, 200 ha, and 3 yr post-fire, 4450 ha) in ponderosa pine/Douglas-fir forests in Colorado (N. Kotliar and C. Melcher, unpubl. data). The trends observed in the burn-severity studies generally are consistent with the patterns we found in our review of severely burned versus unburned forest, which represented the extremes of the burn-severity gradient (Tables 1a–c). The general patterns presented here should be viewed as preliminary and in need of further testing, given that two of the studies are unpublished and only six burns were studied.

Many bird species whose abundances were consistently higher in burned compared to unburned forests (Table 1a) also appeared to use stand-replacement burns more readily than low- and moderate-severity burns. These species included Black-backed Woodpecker (R. Sallabanks, unpubl. data), Three-toed Woodpecker and Cassin's Finch (Taylor and Barmore 1980; N. Kotliar and C. Melcher, unpubl. data), Olive-sided Flycatcher (R. Sallabanks and J. McIver, unpubl. data; N. Kotliar and C. Melcher, unpubl. data), Mountain Bluebird (Taylor and Barmore 1980; R. Sallabanks, unpubl. data; N. Kotliar and C. Melcher, unpubl. data), and Western Bluebird (N. Kotliar and C. Melcher, unpubl. data). Dark-eyed Juncos occurred at similar abundances across all

burn severities (Taylor and Barmore 1980; N. Kotliar and C. Melcher, unpubl. data).

Several species reached their highest abundances in moderate-severity burns. Brown Creeper and Chipping Sparrow exhibited highest abundances in moderate-severity and severe burns (Taylor and Barmore 1980). Townsend's Solitaire was fairly abundant across all severities, but was most abundant in moderately severe burns (N. Kotliar and C. Melcher, unpubl. data). Western Tanager occurred at similar abundances in moderately burned and unburned forests, but was less abundant in severely burned forests (Taylor and Barmore 1980). Cavity nesting species that usually glean the bark of live trees (e.g., nuthatches, Brown Creeper) may respond positively to moderate-severity burns that increase availability of snags for nesting, but retain live trees for foraging. Species common in open canopy forests (e.g., Townsend's Solitaire, Western Tanager, Chipping Sparrow) may use the mixed open canopy of moderate-severity burns, whereas they may avoid large areas of stand-replacement burns. Thus, the varied results observed for these species in our review of severely burned and unburned forests (Table 1b) may reflect, in part, the heterogeneity of burn severities within and across studies.

Species that were consistently more abundant in unburned than in burned forests (Table 1c) also decreased in abundance with increasing burn severity. These species include Plumbeous Vireo, Steller's Jay, and Hammond's Flycatcher (N. Kotliar and C. Melcher, unpubl. data), Gray Jay (Taylor and Barmore 1980); Mountain Chickadee (Taylor and Barmore 1980; R. Sallabanks, unpubl. data; N. Kotliar and C. Melcher, unpubl. data); Ruby-crowned and Golden-crowned kinglets (Taylor and Barmore 1980; R. Sallabanks, unpubl. data); Townsend's Warbler and Varied Thrush (R. Sallabanks, unpubl. data). Many of these species are foliage gleaners; thus their abundance patterns probably reflect the incremental loss of foliage area with increasing burn severity.

Several species showed slightly different patterns across the three studies. Red-breasted Nuthatch and Yellow-rumped Warbler were least abundant in severe burns across all three studies, but their abundances varied across other severities (Taylor and Barmore 1980; R. Sallabanks, unpubl. data; N. Kotliar and C. Melcher, unpubl. data). Western Wood-pewee increased in abundance with burn severity in a lodgepole pine burn (Taylor and Barmore 1980), but was most abundant in low-severity ponderosa pine burns (N. Kotliar and C. Melcher, unpubl. data). Again, variation in results among studies may be due to the heterogeneity of burn severities both within and among studies. Furthermore, if patches of low-

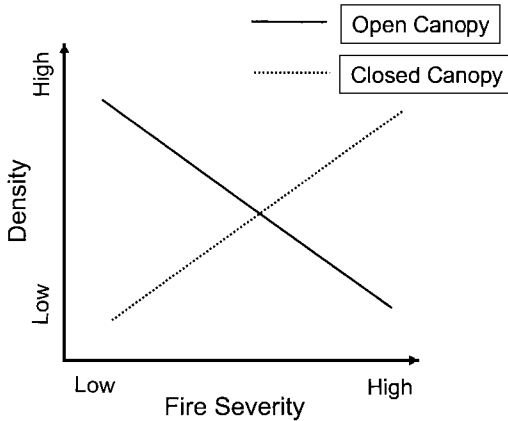


FIGURE 2. Conceptual model of the interactive effects of burn severity and forest structure on the density of avian species preferring open forest structure. In open-canopy forests (e.g., ponderosa pine) avian densities are high in unburned forests but may be low in severely burned forests. In closed-canopy forests (e.g., lodgepole pine), avian densities are low, but may increase as fire opens up the forest canopy. Thresholds responses to degree of burn severity may result in departure from linear relationships depicted here.

and moderate-severity burns occur along the burn periphery, as is often the case, it may be difficult to differentiate between the influence of burn severity and edge effects (i.e., the juxtaposition of burned and unburned forest).

Interactions between burn severity and pre-fire forest structure also may lead to mixed responses to burn severity, particularly for bird species that are sensitive to differences in canopy coverage (Fig. 2). Some species that occur in open-canopy forests (e.g., Western Wood-pewee, Western Tanager) are common in unburned ponderosa pine forests but uncommon in stand-replacement burns in this cover type (N. Kotliar and C. Melcher, unpubl. data). In contrast, these species may be uncommon in dense lodgepole pine (*Pinus contorta*) forests, but common immediately following stand-replacement fires in lodgepole pine forests (N. Kotliar, unpubl. data). Such interactions makes it difficult to predict how a species will respond to burns without a better understanding of how context (e.g., cover type, canopy closure, regional differences, previous silvicultural treatments) can alter suitability of burned forests for a particular species.

Post-fire succession and associated changes in forest structure and avian communities

No studies have followed bird communities from early through late successional stages after fire (but see Bock and Lynch 1970, Bock et al. 1978, Raphael et al. 1987, Johnson and Wauer

1996); therefore, to examine changes in bird communities from early successional to mature forests we also rely on comparisons of stands that vary in time since fire (e.g., Peterson 1982, Huff et al. 1985). In general, forest structure and avian communities change fairly rapidly after fire, although the rates of change depend, in part, on burn severity as well as pre- and post-fire cover type. Because tree mortality is low, and ground cover often rapidly resprouts, evidence of fire in understory burns may be minimal within a few years after fire. In contrast, stand-replacement burns may persist as a forest of snags for decades. The structure of burned snags typically changes within the first few years. First, needles (if remaining) and smaller branches are shed, then bark and larger branches slough away. Smaller snags typically decay faster than larger snags (Morrison and Raphael 1993, Bull et al. 1997). Factors such as topography, root depth, moisture regime, wind, and tree species can all influence how long snags remain standing, which may exceed a century.

Early post-fire forests and associated insect outbreaks attracts cavity-nesting birds due to increases in nest sites and food supplies (e.g., Blackford 1955, Koplín 1969, Lowe et al. 1978, Raphael and White 1984, Bock et al. 1978, Saab and Dudley 1998). Duration of occupancy, however, varies among bird species, presumably due to differences in preferred prey availability, as well as the size, distribution, and age of snags. Black-backed and Three-toed woodpeckers rapidly colonize stand-replacement burns within one to two years of a fire; within five years, however, they become rare, presumably due to declines in bark and wood-boring beetles (Koplín 1969, Bock and Lynch 1970, Bock et al. 1978, Bull 1980, Taylor and Barmore 1980, Apfelbaum and Haney 1985, Dixon and Saab 2000). In contrast, Lewis's Woodpecker is reported to be abundant both in recent burns (2–4 yr; Saab and Dudley 1998) and older burns (10–25 yr; Bock 1970, Linder and Anderson 1998). Hairy Woodpecker and Northern Flicker exhibit more mixed responses, but usually decline within the first 25 yr post-fire (Bock and Lynch 1970, Bock et al. 1978, Taylor and Barmore 1980, Huff et al. 1985, Raphael et al. 1987). Mountain and Western bluebirds are secondary-cavity nesters that commonly nest in recently burned forests (e.g., Hutto 1995, Saab and Dudley 1998; Table 1a), but they typically decline in mid-successional stages (Bock and Lynch 1970, Bock et al. 1978, Pfister 1980, Peterson 1982, Raphael et al. 1987).

Vegetation regrowth after fire also can lead to increases in flower, seed, and insect abundance, which attracts nectarivores, granivores, and ae-

rial and ground insectivores (Lowe et al. 1978, Apfelbaum and Haney 1981, Huff et al. 1985). Olive-sided Flycatcher may appear immediately after fires (Table 1a; Hutto 1995; N. Kotliar and C. Melcher, unpubl. data) and can persist as long as snags are available and canopy cover remains low (Huff et al. 1985; N. Kotliar and C. Melcher, pers. obs.). Seed-eating birds exhibit a mixed response to burns, but there is some evidence that several species readily use burns, Clark's Nutcracker, Pine Siskin, Cassin's Finch, and Red Crossbill in particular (Table 1b; Hutto 1995). Whether these species are responding to increased seed availability (e.g., serotinous cones), minerals in the ashes (C. W. Benkman, pers. comm.), or other factors remains unclear. Furthermore, these species are rather nomadic, or have large home ranges, and may use burned forests opportunistically.

Many species absent or uncommon immediately post-fire begin to increase in mid-successional stages as snags decay or fall, shrubs and saplings become well-developed, and canopy cover increases. Although Cordilleran and Dusky flycatchers may appear at the edges of early post-fire forests (N. Kotliar and C. Melcher, unpubl. data), they sometimes reach peak abundances at mid-successional stages (Peterson 1982, Raphael et al. 1987; N. Kotliar and C. Melcher, unpubl. data). Resprouting aspen stands can attract species commonly associated with deciduous systems (e.g., Warbling Vireo, Dusky Flycatcher; N. Kotliar and C. Melcher, pers. obs.). Red-naped Sapsucker also has been observed drilling holes in lodgepole pine and aspen saplings within 5–10 years following disturbances (N. Kotliar and C. Melcher, pers. obs.). Lewis's Woodpecker may use burned forests 10–20 yr after fires, presumably in response to improved conditions for aerial foraging following a decrease in snag density and an increase in flying arthropods associated with shrub regrowth (c.f., Bock 1970, Linder and Anderson 1998). Species such as Mountain Chickadee, Ruby-crowned Kinglet, and Swainson's and Varied thrushes reach peak abundance in late-successional forests (Bock and Lynch 1970, Bock et al. 1978, Peterson 1982, Huff et al. 1985, Raphael et al. 1987). In contrast, species that favor open canopies (e.g., American Robins) begin to decline in mid- to late-successional stages (Peterson 1982, Huff et al. 1985, Raphael et al. 1987).

Several species that occur in early post-fire forests also may occur in later successional stages. Hammond's Flycatcher occasionally has been detected in young post-fire forests (Harris 1982, Huff et al. 1985, Hutto 1995, Johnson and Wauer 1996; N. Kotliar and C. Melcher, unpubl. data), but they typically reach peak abundance in mature forests (Peterson 1982, Sedgwick

1994; N. Kotliar and C. Melcher, unpubl. data). However, its occasional occurrence immediately after fire suggests that Hammond's Flycatcher may temporarily exhibit site-fidelity. Several species, such as Olive-sided Flycatcher, Brown Creeper, and Dark-eyed Junco, initially may decline in mid-successional stages, but may increase as canopy gaps and snags are created (Huff et al. 1985, Carey et al. 1991).

Fire geometry

Although no studies have explicitly examined how birds respond to burn size or shape, one study examined whether bird abundance was affected by differing patch sizes created by the extensive fires of 1988. Of the 87 species present, only Plumbeous Vireo and Townsend's Solitaire decreased with increasing patch size (Hutto 1995). However, the relatively large minimum patch size surveyed (40 ha) may have masked important area effects at lower size ranges. Thus, the response of birds to total burn area needs additional study.

Given that area effects have been found to be important in other ecosystems, we should consider these effects as they relate to fires as well. For example, post-fire specialists may require a minimum burn size. In contrast, some species may select openings created by small burns and avoid larger burns. Increase in burn size may also lead to increased heterogeneity of burns (e.g., variation in burn severity).

The proportion of burn to edge area is also affected by burn size and shape. Thus, species that show positive responses to burns may be attracted to the juxtaposition of burned and unburned forest. For example, Olive-sided Flycatcher and Townsend's Solitaire (Table 1a) reached their highest abundances at burn edges (N. Kotliar and C. Melcher, unpubl. data). In addition, fire damaged trees (not killed outright by fire), which often occur along the periphery of crown fires, are used by several post-fire woodpecker species (Murphy and Lehnhausen 1998). Many of the species showing mixed response to burns (e.g., American Robin, Townsend's Solitaire, Western Tanager, Dark-eyed Junco, Chipping Sparrow, Pine Siskin, and Cassin's Finch; Table 1b) reached their highest abundances within 50 m of the edges of burns (N. Kotliar and C. Melcher, unpubl. data).

Many crown fires also contain "peninsulas" and "islands" of unburned forest remnants, which can increase edge habitats or retain unburned forest well inside of large burns. For example, the moist microclimate of riparian areas, which may inhibit fire or limit burn severity, can result in riparian remnants. Thus, species not typically associated with early post-fire forests

TABLE 2. NUMBER OF CAVITY-NESTING SPECIES IN UNLOGGED AND SALVAGE-LOGGED POST-FIRE FORESTS DURING THE BREEDING SEASON IN THE NORTHERN ROCKY MOUNTAINS

Forest type	Number of nesting species				Study
	Unsalvaged	Partially salvaged	Severely salvaged	Totals	
Mixed conifer/deciduous	16	12	4	17	Caton 1996 ^a
Mixed conifer/deciduous	18	—	8	18	Hitchcox 1996 ^b
Ponderosa pine/douglas-fir	9	9	—	10	Saab and Dudley 1998 ^c
Mixed conifer	8	9	—	9	S. Hejl and M. McFadzen, unpubl. data ^d

^a Salvage logging of entire 4000-ha burn included clearcuts (all trees were removed except for a few snags) and partial cuts (individual trees or small groups of trees were logged).

^b Salvage logging of entire 500-ha burn created an interspersed pattern of harvest treatments with unlogged control plots. In severely salvaged areas, all merchantable (>15 cm dbh, >4.5 m tall) fire-killed trees were harvested.

^c In salvage-logged units, about 50% of all trees >23 cm dbh, and 70% of trees >53 cm, were harvested.

^d Salvage logging varied among three burns (burns ranged from 494–3,321 ha). The salvaged portions of burns were partially logged with several areas of severe salvage logging. A portion of each burn was left unharvested.

(e.g., Wilson's Warbler, Lincoln's Sparrow; N. Kotliar and C. Melcher, pers. obs.) may be observed in remnant patches immediately post-fire.

In burns, detections of birds more typically associated with unburned forest may be artifacts of study design. Few studies explicitly control for distance from survey points in burned habitats to unburned edges and remnant patches. Yet, some species characteristic of unburned forests (e.g., Mountain Chickadee, Ruby-crowned Kinglet, Hermit Thrush) may use live trees along burn edges (N. Kotliar and C. Melcher, unpubl. data). Thus, these species, which also have highly detectable songs, may appear to use recently burned forests if survey points are too close to edges.

Conclusions: effects of fire on avian communities

Although there are relatively few studies that address the effects of fire on avian communities, the consistent presence of many woodpeckers and aerial insectivores in early post-fire forests, and the near absence of many foliage-gleaning species associated with closed-canopy forests, appear to be robust patterns. Many additional species appear to use post-fire forests in certain contexts. For most species, however, we still have a poor understanding of how fire alters habitat suitability. We clearly need more information about how species' responses to fire can be altered by burn severity (including within-burn heterogeneity), fire geometry, proximity to unburned edges and remnants, pre- and post-fire cover types (e.g., tree species, forest structure, previous silvicultural treatments), and time since fire. Finally, because most burns outside national parks are salvaged, information about the effects of post-fire salvage logging is also critical.

EFFECTS OF POST-FIRE SALVAGE LOGGING ON AVIAN COMMUNITIES

Salvage logging following stand-replacement fires has occurred since the early 1900s (D. At-

kins, pers. comm.). Initially, salvage logging was uncommon due to limited access to burned forests (K. McKelvey, pers. comm.). In the 1950s, however, the demand for lumber increased greatly, and subsequent road-building in national forests provided opportunities to harvest more burns (D. Atkins, pers. comm.). Typically, salvage logging was implemented immediately post-fire, leaving few, if any, standing snags. Only within the past two decades have forest managers begun to retain snags within salvaged areas to benefit wildlife.

The effects of salvaging on avian communities remain poorly understood. Only four studies, all of which were restricted to coniferous and mixed coniferous/deciduous (hereafter "mixed") forests of the northern Rocky Mountains (Montana and Idaho), specifically examined the effects of salvage logging on cavity-nesting bird communities (Caton 1996, Hitchcox 1996, Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data; Table 2). Two other studies evaluated salvaged burns (Blake 1982, Raphael and White 1984) but did not replicate treatments, thus they were not emphasized in this review. As a result, we focus our discussion on cavity-nesting species in the northern Rocky Mountains.

Effects of salvage logging on birds

Severely salvaged burns (Table 2) may decrease the suitability of post-fire forests for most cavity-nesting species. However, the effects of partial salvaging are more equivocal (Table 2). In general, species richness declined only in the most severely salvaged burns, although even partial salvaging altered species composition (Table 2; Raphael and White 1984).

Several cavity nesters showed consistent patterns of abundance in logged or unlogged conditions across studies. Black-backed and Three-toed woodpeckers were most abundant in unsalvaged burns and rarely nested in salvaged areas

of burns (Hitchcox 1996, Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data). In contrast, nesting Lewis's Woodpeckers were most abundant in partially salvaged burns (Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data). Mountain Bluebird and Hairy Woodpecker nested in both unsalvaged and salvaged portions of burns, but tended to nest more often in unsalvaged portions (Hitchcox 1996, Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data).

The responses of several species to salvage logging varied among studies. Red-breasted Nuthatch and Williamson's Sapsucker nested primarily in partially salvaged burns in coniferous forest (S. Hejl and M. McFadzen, unpubl. data), whereas in mixed forest they nested only in the unsalvaged portions of severely salvaged burns (Hitchcox 1996). These mixed responses to salvage logging may be due to differences in salvage severity or cover type. In general, it appears that species most closely tied to early successional post-fire forests (Table 1a) may be the most sensitive to salvage logging.

The effects of salvage logging on nesting success also varied among species and studies. In the three studies that examined nesting success (>20 nests per treatment per species), Hairy Woodpecker (Saab and Dudley 1998), Northern Flicker (Hitchcox 1996), and Mountain Bluebird (S. Hejl and M. McFadzen, unpubl. data) experienced significantly higher nesting success in unsalvaged treatments. Three-toed Woodpeckers, House Wrens, and Western Bluebirds had similar nesting success among treatments.

Variation in characteristics of snags used for nest sites and foraging

Salvage-logging practices often call for the harvest of larger, more economically valuable tree species. By altering species composition, sizes, and densities of snags, salvaging may alter resource availability for birds. Therefore, we describe characteristics of post-fire forests required for foraging and nesting cavity-nesting birds and relate those needs to management practices.

Although tree species selected for nest sites varied among bird species and studies, some general patterns were evident. In three studies of mixed forests (both salvaged and unsalvaged) dominated by conifers (95% conifers, 5% *Populus* spp.), a disproportionate percentage of nests (35–80%) were located in deciduous trees (Hutto 1995, Caton 1996, Hitchcox 1996). Most nests were located in snags. In two other studies of coniferous and mixed conifer forests, birds nested in snags of western larch (Hitchcox 1996; S. Hejl and M. McFadzen, unpubl. data) and ponderosa pine (S. Hejl and M. McFadzen, unpubl. data)

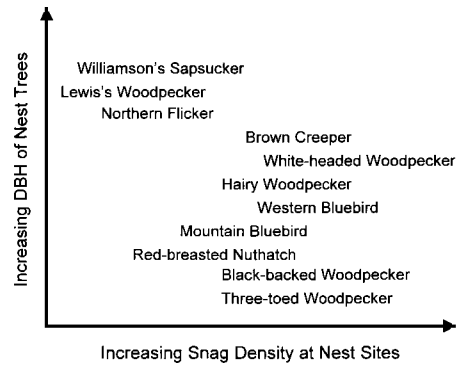


FIGURE 3. General distribution of cavity-nesting birds in burned forests (unsalvaged and salvage logged) as a function of nest-tree diameter (DBH) and snag density at nest sites (Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data).

more often than expected. In one study in Idaho and Montana, 45% of all nests were in Douglas-fir (S. Hejl and M. McFadzen, unpubl. data). Such variation in nest-tree selection among studies may result from variation in species composition and the relative availability of preferred trees (S. Hejl and M. McFadzen, unpubl. data).

The extent of snag decay influences which snags woodpeckers select for nesting. For example, strong excavators such as Black-backed, Three-toed, Hairy, and Downy woodpeckers, nested in snags with intact tops (Caton 1996, Hitchcox 1996, Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data). Weak excavators such as Lewis's Woodpecker, White-headed Woodpecker, and Northern Flicker, nested more frequently in broken-topped snags (many broken pre-fire) that were presumably more decayed than intact snags (Hitchcox 1996, Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data). Because the extent of decay influences nest-tree selection, selective salvaging of less decayed snags likely affects bird species differentially.

Cavity nesters also respond to differences in the sizes and spatial distribution of snags (Fig. 3), which, in turn, could be affected by different salvage prescriptions (Saab et al. 2002). In both coniferous and mixed burns, most cavity nesters selected large-diameter trees more often than expected (Caton 1996, Hitchcox 1996, Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data). Black-backed and Three-toed woodpeckers nested in medium-sized snags (Hitchcox 1996, Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data). This size class was among the smallest used by any woodpecker species, but is within the size-range targeted for salvaging. In general, cavity nesters selected dense patches of snags more often than dis-

persed or isolated snags (Raphael and White 1984, Saab and Dudley 1998, Saab et al. 2002).

Despite the paucity of foraging studies in post-fire forests, some general patterns regarding preferences of woodpeckers for certain tree species and sizes emerged from our review. Woodpeckers selectively foraged on large snags in both winter (Kreisel and Stein 1999) and summer (Hutto 1995, Powell 2000; S. Hejl and M. McFadzen, unpubl. data). However, use of tree species in summer varied among studies (Hutto 1995, Caton 1996, Powell 2000; S. Hejl and M. McFadzen, unpubl. data), among habitats within one study (Caton 1996, Powell 2000), and among *Picooides* woodpeckers within a study (S. Hejl and M. McFadzen, unpubl. data). In northeastern Washington during winter, Downy, Hairy, Three-toed, and Black-backed woodpeckers selectively foraged on western larch and ponderosa pine, which are also preferentially salvage logged. Thus, by altering the size, distribution, and species composition of post-fire snags, salvage logging differentially affects cavity-nesting species.

Co-occurring species of woodpeckers sometimes select different prey, which could influence avian diversity in post-fire habitats. For example, in a recent study of an unsalvaged burn in Alaska, Murphy and Lehnhausen (1998) analyzed the contents of 33 woodpecker stomachs and found that Three-toed Woodpeckers consumed bark beetle larvae (Scolytidae) almost exclusively, whereas Black-backed and Hairy woodpeckers primarily consumed wood-boring beetles (Buprestidae and Cerambycidae). In an unsalvaged burn in east-central Idaho, Black-backed Woodpeckers were observed feeding their nestlings the larvae and pupae of wood-boring beetles approximately 65% of the time (Powell 2000). Beal (1911), however, reported that 65–75% of the prey consumed by Three-toed and Black-backed woodpeckers were wood-boring beetles. Differences among studies could be due to prey availability (Powell 2000), which in turn is affected by tree species composition, burn severity, and salvage severity.

Conclusions: effects of post-fire salvage logging on cavity-nesting birds

Overall, salvage logging in burned forests can have pronounced effects on cavity-nesting species that use post-fire habitats. In conjunction with a substantial reduction in fire-killed trees due to fire suppression, salvage logging has resulted in dramatic reductions in the availability of snags in these ephemeral habitats. The effects of such reductions have serious implications for the viability of Black-backed and Three-toed woodpeckers, which rarely use even partially-logged post-fire forests. Although forest managers have begun to

retain some snags (including large snags) in salvaged areas, this is not sufficient for species that prefer high densities of snags that characterize unsalvaged burns. Some types of partial salvaging may actually benefit a few species, but historically such species may have been more closely associated with later successional stages of burns after snag densities had decreased naturally, with forests kept open by frequent, low-severity fires, or open post-fire forests. Retention of a diversity of snag species, sizes, and spatial distributions, as well as snags in various stages of decay, in burned forests is essential to the conservation of avian diversity in northern Rocky Mountain forests. The applicability of these conclusion across western forests or other avian communities (e.g., open-cup nesting species) requires further research.

MANAGEMENT IMPLICATIONS

FIRE MANAGEMENT

Given the importance of fire to many bird species, restoration of natural fire regimes may be critical to the ecological integrity of western forests. However, the problems associated with reproducing the complexity and diversity of fire processes at multiple scales pose great challenges (Baker 1993). The recent emphasis on prescribing frequent, low-intensity fires in low-elevation forests of the Rocky Mountains is a good start toward reintroducing fire in systems where frequent understory burns maintained open, old-growth stands (but see Covington and Moore 1994, Tiedemann et al. 2000), but this treatment will not be adequate for bird species that associate with stand-replacement burns. For example, prescribed fire may alter the availability of large snags, depending on fire severity (Horton and Mannan 1988, Tiedemann et al. 2000). In general, the effects of prescribed fire on avian communities are poorly understood (Finch et al. 1997, Tiedemann et al. 2000); the few studies of prescribed fire have been plagued by methodological problems, and thus the conclusions of these studies are suspect (Finch et al. 1997). Furthermore, incorrectly applied prescribed fire can alter landscape structure (Baker 1993). Fire-management practices that include allowing wildland fires of all severities to burn, when and where they are appropriate, may help re-create natural conditions (Hejl et al. 1995). Given the uncertainty about specific, local fire regimes (Baker 1994, Tiedemann et al. 2000, Veblen et al. 2000) and the variation among bird species in response to fire characteristics (Hutto 1995), managers may wish to mimic natural variation in fire regimes (e.g., size, severity, frequency, timing) that may have occurred within a given cover type and geographic area (Baker

1992, Hejl *et al.* 1995, Veblen *et al.* 2000). This approach will help to avoid overemphasis on any particular prescription.

Post-fire forests can be altered significantly by salvage logging. Although bird species will vary in their responses to different management options, few cavity-nesting species, if any, will benefit from severe salvaging (*i.e.*, clearcut, or removal of most medium and large snags). Here, we evaluate several alternatives to severe salvage logging based on our knowledge of nesting requirements for six cavity-nesting birds in the northern Rocky Mountains: (1) leave the burn unsalvaged; (2) lightly salvage throughout the burn (*e.g.*, leave many of the biggest snags); (3) salvage the burn (*e.g.*, light or partial) after a delay of several years (Murphy and Lehnhausen 1998, Kreisel and Stein 1999); (4) salvage part of the burn severely and leave the remainder unsalvaged (Hutto 1995); and (5) apply different salvage treatments across the burn (including variation in tree distributions, sizes, and species left uncut).

The species most likely to benefit from unsalvaged burns, or unsalvaged portions of burns, are those most-closely tied to early post-fire conditions. Because Black-backed and Three-toed woodpeckers appear to depend on the short-lived availability of prey resources that quickly invade post-fire habitats, a delay in salvaging may be warranted (Murphy and Lehnhausen 1998). Some species (*e.g.*, American Kestrel, Lewis's Woodpecker) may tolerate or benefit from partial or light salvage logging provided the large snags and tree species (*e.g.*, deciduous trees, Douglas-fir, ponderosa pine, western larch) they tend to select are left uncut (Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data).

Species may inhabit partially salvaged burns (Saab and Dudley 1998; S. Hejl and M. McFadzen, unpubl. data) because they resemble the later successional stages of burns (when snags begin to thin out naturally) or open forests. Given our limited understanding of the cumulative effects of fire suppression and post-fire salvage logging, and their effects on post-fire habitat availability across western landscapes, allowing succession to proceed naturally in unsalvaged burns may benefit the most species.

MIMIC NATURAL DISTURBANCE REGIME

Many bird species are adapted to, and may depend upon, natural disturbance such as fire. Over the last century, however, logging has supplanted fire as the dominant process shaping coniferous forests in many regions of the West. Yet, the consequences of this shift for avian communities is poorly understood (Hansen *et al.* 1991). It has been suggested that the disturbance created by logging may create adequate habitats for some fire-depen-

dent species in areas where severe fires are impractical (Hutto 1995). Indeed, fire and logging could have similar effects on western landscapes if logging were modified to mimic natural fires more closely (Hunter 1993, Hejl 1994). However, there are profoundly different ways in which past fire and silvicultural activities have affected western forest systems. First, they often operate on vastly different spatial and temporal scales (*e.g.*, disturbance size and frequency), which, in turn, will lead to different landscape structure (Hansen *et al.* 1991, Gluck and Rempel 1996). Second, there are many unique features produced by fire (*e.g.*, a high density of snags and consequent increases in wood-boring beetles) that may not be replicated readily by current logging practices (Hansen *et al.* 1991, Hutto 1995). Finally, selective logging often removes larger trees whereas low-severity fires typically kill smaller trees (Finch *et al.* 1997). Thus, natural disturbances may provide useful models for developing logging and salvaging techniques that would diminish the negative impacts on birds (Hunter 1993, Hejl *et al.* 1995).

Our understanding of how birds respond to silvicultural activities is based primarily on comparisons of logged versus relatively undisturbed, mature forests (Hejl *et al.* 1995). However, assessments that include comparisons of logged and naturally disturbed forests with similar disturbance severities (*e.g.*, thinned forests might be compared to moderate or understory burns) would be valuable. For example, a recent study of 16 burned and 16 logged conifer forests in Colorado found that severely logged forests (*i.e.*, logged areas contained few, if any, live or dead trees) were generally unused by most species associated with stand-replacement burns (N. Kotliar and C. Melcher, unpubl. data). Overall, avian species richness was much higher in burns than in logged forests. The pattern was especially salient when comparing clearcuts (*i.e.*, no retention trees) to unsalvaged burns. Of the species that did occur in clearcuts, most also occurred in burns, whereas the reverse was not observed. Hansen *et al.* (1995b) also found that retaining canopy trees benefits many bird species in the west Cascades of Oregon. In general, clearcut conifer forests do not function as substitutes for burned forests. In many respects, the effects of logging on avian communities in unburned forests may be similar to those of salvage logging in stand-replacement burns.

The high density of snags in burns is the most obvious distinction between burned and clearcut forests. However, the edges of these disturbances can also differ dramatically. For example, clearcut forests often have well-defined edges with few, if any standing snags. In contrast, burn edges are often a heterogeneous mix of burned

and unburned trees, except along fire breaks where burn edges are usually more abrupt. The juxtaposition of live and dead forests may be important to many species, such as Olive-sided Flycatcher, which generally sings and conducts foraging sallies from dead trees in open areas but nest in nearby live, mature trees (Altman and Sallabanks 2000). In Colorado, Olive-sided Flycatcher only occurred in cuts that contained both snags and live trees (i.e., not clearcuts; N. Kotliar and C. Melcher, unpubl. data). The complexity of burn edges may also help to diminish deleterious edge effects (e.g., increased nest predation and parasitism) in adjacent undisturbed forests that could result from high-contrast edges of clearcuts. Thus, silvicultural practices that incorporate structural elements of burns (e.g., retaining or creating high densities of snags and patches of live trees, and increasing the complexity of edges) may improve the suitability of logged forests for many post-fire bird species.

There are also important differences between natural and anthropogenic disturbances at larger spatial and temporal scales. For example, in both conifer- and aspen-dominated forests, differences in bird communities among burned and cut forests were most evident in early successional stands, but were still apparent in mid-successional forests (Hutto 1995, Hobson and Schiek 1999). We explore this idea further by comparing the fragmenting effects of severe disturbances: stand-replacement fire, silvicultural activities (e.g., post-fire salvage, clearcuts), and forest conversion. Here, we restrict the meaning of forest fragmentation to the fragmenting effects of anthropogenic disturbance relative to the natural heterogeneity of the landscape. Fragmentation can alter several landscape-scale parameters, including the number, size, and spatial distribution of forest patches, the degree of contrast between disturbed and adjacent undisturbed forests, and the persistence of the disturbed patches. By definition, natural disturbance regimes, such as stand-replacement fires, create and reinforce natural heterogeneity (e.g., spatial configuration of forest patches, variation in successional stages among patches). Because most post-fire forests eventually resemble pre-fire forests (e.g., cover type), persistence and contrast are relatively low compared to the highly persistent patches that result from forest conversion in agricultural or suburban landscapes. The fragmenting effects of silvicultural practices will generally fall somewhere between these two extremes, depending on logging severity (e.g., thinning vs. clearcutting) and frequency (e.g., cut rotation). For some species, however, the negative effects resulting from alteration of landscape structure and dynamics through fire suppression may rival the

negative consequences of forest fragmentation in some western forests. However, few studies have evaluated the consequences of fire suppression or other alterations of fire regimes on avian communities (Lyon et al. 2000).

The degree to which anthropogenic disturbance results in forest fragmentation depends on differences between the scale, intensity, and frequency of natural and anthropogenic disturbance, as well as the natural heterogeneity of the landscape. Species adapted to frequent natural disturbance may tolerate or even prefer the conditions created by disturbance over undisturbed forests. The Pygmy Nuthatch, for example, which is endemic to ponderosa pine forests (relatively short fire return intervals), had higher abundance in prescribed understorey burns than in adjacent unburned forests, and was absent in stand-replacement burns (N. Kotliar, unpubl. data). In contrast, species such as the Golden-crowned Kinglet, Varied Thrush, and Townsend's Warbler, which are most often found in association with spruce-fir and cedar-hemlock cover types (relatively long fire return intervals; Hutto 1995), consistently occurred at lower abundances in burned forests (Table 1c). Although many species may tolerate, or be adapted to, natural disturbance, we expect that most bird species (except for some generalists and introduced species) will be extremely sensitive to the high degree of persistence and contrast of forest conversion, regardless of inherent disturbance regimes. Superimposed on these factors are other landscape-scale issues such as local cowbird abundance or the composition of predator communities. Thus, local, landscape, and regional differences need to be addressed when basing silvicultural practices on natural disturbance regimes.

RESEARCH RECOMMENDATIONS

SPECIFIC RESEARCH QUESTIONS

Based on our review of past research, we have identified some general patterns regarding the responses of avian communities to fire. However, the studies have raised more questions than they have answered. Thus, applications of management prescriptions involving fire and fire-related silvicultural practices should be considered experimental and be designed to increase our knowledge about fire effects. For example, we need more information about the basic ecology of post-fire forests, including:

- how various fire characteristics (e.g., severity, size, successional stage, and season of burning), landscape contexts, and cover types (both pre- and post-fire types) affect avian communities;
- the extent to which avian use of burns is pred-

icated on the juxtaposition of burned and unburned forest;

- the effects of fire on life histories (foraging behavior, nest site selection) and demographics, particularly reproductive success, survivorship, and recruitment for both breeding and wintering populations (Finch et al. 1997, Lyon et al. 2000);
- variation in avian use of fire-generated snags for nest, foraging, or perch sites compared to use of snags generated by other process (e.g., lightning, disease, insects);
- how avian communities differ in naturally disturbed forests compared to managed forests across successional stages;
- the effects of seed-eaters, flycatchers, and other specialists on seed dispersal, forest regeneration, and overall forest health;
- the manner in which snag characteristics and distributions affect insect prey and, in turn, foraging birds; and
- whether or not there is geographic variation in avian responses to disturbances such as fire.

We also need to understand the ways in which fires differ from other natural disturbances (e.g., blowdowns, insect kills) that can be extensive and severe. In Colorado, for example, a recent windstorm uprooted or damaged trees across 10,000 ha (Flaherty 2000) and, in 1939, an outbreak of spruce beetles (*Dendrocotonus rufipennis*) killed nearly 290,000 ha of trees (Veblen et al. 1991). Information required for sound management includes:

- improved information on the range of natural variation both within, and among, historic fires;
- the effects of fire suppression on forest and landscape structure and wildlife communities;
- the ecological tradeoffs between wildland, prescribed fire, and mechanical treatments (including thinning and burning; Tiedemann et al. 2000, Wagner et al. 2000);
- appropriate management of post-fire forests, including how salvage treatments affect species that require post-fire habitats;
- how wildlife species respond to different stages of succession and whether or not those stages are similar across disturbance types;
- the responses of forests and wildlife to repeated management treatments in the same location (Andersen et al. 1998);
- the effects of severity in natural compared to anthropogenic disturbances;
- differences and similarities among fire and forest harvesting practices and how these disturbances affect avian communities; and
- which management treatments are most likely

to conserve the biological integrity of forest systems.

RESEARCH DESIGN

The inherent nature of fire limits the opportunities to conduct well-replicated, controlled experiments that evaluate the full spectrum of fire characteristics across all western forest types. Rather, we must rely on several complementary approaches, including: (1) unplanned comparisons of wildfires (e.g., Finch et al. 1997); (2) meta-analyses that combine data from numerous studies to generate larger datasets and greater statistical power (e.g., Hutto 1995); and (3) controlled experiments using prescribed (planned) burns, logged, logged and burned, and unburned controls. The collective results of all approaches should help us develop a greater overall understanding of how fire affects wildlife.

Most studies of fire effects on avian communities have been unplanned comparisons of wildfires (Finch et al. 1997). Although variation among wildfires (e.g., forest type, burn characteristics) and post-fire management strategies, plus the lack of pre- and post-fire treatments, has limited the scope of inference provided by unplanned comparisons, they nonetheless provide unique opportunities to study extensive, severe wildfires. This approach is most useful immediately after years with extensive fire, when researchers can establish numerous, similar-age replicates across regions and in many forest types. Intensive studies of single sites can provide useful information as well, especially in large burns. For example, the effects of burn severity could be studied in one large burn by stratifying survey points across severities (e.g., R. Salabanks and J. McIver, unpubl. data). In addition, single-site studies can generate data for use in meta-analyses.

Meta-analyses provide excellent opportunities for improving the results of multiple studies that have little or no replication (Brett 1997). Even non-statistical compilations of unplanned comparisons can reveal biologically meaningful trends, as we found in our review that Three-toed and Black-backed woodpeckers were either restricted to, or more abundant in, burned forests (Table 1a). In order for meta-analyses to be possible, however, researchers must publish detailed study protocols, and they must cooperate with one another to the extent possible to standardize protocols and share data.

To complement and expand the existing knowledge gained from unplanned comparisons and meta-analyses, we need more experiments that control for and test variations among fire characteristics, forest type, and landscape context (e.g., Breininger and Schmalzer 1990). Because annual variation in bird populations can be considerable,

several years of pre- and post-treatment data ideally should be collected. Whenever possible, researchers should incorporate the full range of fire characteristics provided by natural fire regimes in the systems of interest (Andersen et al. 1998). It will be difficult to find sites for conducting severe burns, but there is increasing support for conducting such studies in national parks (J. Connor, pers. comm.) and wilderness areas. In general, it will be more feasible to conduct experiments of low- to moderate-severity burns in systems that typically experience lower-severity fires.

Research programs must also take into account some important design and interpretation problems that are often ignored in fire studies. Because burn edges and burn severity may have pronounced effects on avian use of burns, survey points must be stratified across burn edges, adjacent unburned forest, and distant unburned forest, and over a range of burn severities to control for these sources of variation. In addition, to determine whether avian species use of post-fire habitats immediately after fire represents a preference for burns, or site-tenacity for breeding territories, studies need pre- and post-fire measures of abundance, as well as measures of reproductive success and recruitment over several years.

Finally, researchers need to implement long-term studies to develop a full picture of post-fire successional changes and how they affect avian communities. Although habitat loss may be the immediate effect of severe fire on species that typically inhabit mature forests (e.g., Golden-crowned Kinglet, Spotted Owl), the long-term effects (e.g., decades or centuries later) may be habitat improvement. Thus, clearing forests of fuels to prevent severe fires that could decrease Spotted Owl habitat in the short term could preclude more significant habitat improvements that would benefit Spotted Owls in the future. Overall, researchers will need to consider a wide variety of research approaches, as well as the full spectrum of fire characteristics and forest types, both unmanaged and managed, to understand how proposed management strategies may affect the future health and integrity of western-forest systems.

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APPENDIX. SCIENTIFIC NAMES OF BIRD SPECIES

Species
American Kestrel (<i>Falco sparverius</i>)
Spotted Owl (<i>Strix occidentalis</i>)
Mourning Dove (<i>Zenaidura macroura</i>)
Common Nighthawk (<i>Chordeiles minor</i>)
Northern Flicker (<i>Colaptes auratus</i>)
Lewis's Woodpecker (<i>Melanerpes lewis</i>)
White-headed Woodpecker (<i>Picoides albolarvatus</i>)
Black-backed Woodpecker (<i>Picoides arcticus</i>)
Downy Woodpecker (<i>Picoides pubescens</i>)
Three-toed Woodpecker (<i>Picoides tridactylus</i>)
Hairy Woodpecker (<i>Picoides villosus</i>)
Red-naped Sapsucker (<i>Sphyrapicus nuchalis</i>)
Williamson's Sapsucker (<i>Sphyrapicus thyroideus</i>)
Olive-sided Flycatcher (<i>Contopus cooperi</i>)
Western Wood-Pewee (<i>Contopus sordidulus</i>)
Hammond's Flycatcher (<i>Empidonax hammondi</i>)
Dusky Flycatcher (<i>Empidonax oberholseri</i>)
Plumbeous Vireo (<i>Vireo plumbeus</i>)
Cassin's Vireo (<i>Vireo cassinii</i>)
Warbling Vireo (<i>Vireo gilvus</i>)
Tree Swallow (<i>Tachycineta bicolor</i>)
Steller's Jay (<i>Cyanocitta stelleri</i>)
Clark's Nutcracker (<i>Nucifraga columbiana</i>)
Mountain Chickadee (<i>Poecile gambeli</i>)
Red-breasted Nuthatch (<i>Sitta canadensis</i>)
White-breasted Nuthatch (<i>Sitta carolinensis</i>)
Pygmy Nuthatch (<i>Sitta pygmaea</i>)
Brown Creeper (<i>Certhia americana</i>)
Rock Wren (<i>Salpinctes obsoletus</i>)
House Wren (<i>Troglodytes aedon</i>)
Ruby-crowned Kinglet (<i>Regulus calendula</i>)
Golden-crowned Kinglet (<i>Regulus satrapa</i>)
Hermit Thrush (<i>Catharus guttatus</i>)
Swainson's Thrush (<i>Catharus ustulatus</i>)
Varied Thrush (<i>Ixoreus naevius</i>)
Townsend's Solitaire (<i>Myadestes townsendi</i>)
Mountain Bluebird (<i>Sialia currucoides</i>)
Western Bluebird (<i>Sialia mexicana</i>)
American Robin (<i>Turdus migratorius</i>)
Yellow-rumped Warbler (<i>Dendroica coronata</i>)
Townsend's Warbler (<i>Dendroica townsendi</i>)
Wilson's Warbler (<i>Wilsonia pusilla</i>)
Western Tanager (<i>Piranga ludoviciana</i>)
Lazuli Bunting (<i>Passerina amoena</i>)
Dark-eyed Junco (<i>Junco hyemalis</i>)
Lincoln's Sparrow (<i>Melospiza lincolni</i>)
Chipping Sparrow (<i>Spizella passerina</i>)
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)
Pine Siskin (<i>Carduelis pinus</i>)
Cassin's Finch (<i>Carpodacus cassinii</i>)
Red Crossbill (<i>Loxia curvirostra</i>)
Pine Grosbeak (<i>Pinicola enucleator</i>)
Evening Grosbeak (<i>Coccothraustes vespertinus</i>)