

Chapter 6

Effects and Interactions of Fire, Logging, and Grazing

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Introduction

Logging and livestock grazing are widespread management practices in Southwestern ponderosa pine forests that may act either independently or synergistically with fire management to influence habitat availability and use, reproductive success, and songbird population levels. Fire, historically an important natural process in Southwestern ponderosa pine forests, had far-reaching effects on forest structure and composition (Moir et al. this volume). Because of its influence on forest habitats, and because birds respond strongly to habitat structure and composition (MacArthur and MacArthur 1961; Rotenberry 1985), historic fires had a powerful impact on forest bird communities.

Contemporary fire suppression and prescribed burning have affected or could affect forest birds and their habitat in Southwestern ponderosa pine forests. Fire suppression has disrupted natural fire regimes by removing its influence in structuring Southwestern forests (Moir et al. this volume). This directly affects structures, stages, densities, and landscape patterns of ponderosa pine forests and influences composition and diversity of bird communities at site and landscape levels. Prescribed fire also directly alters bird habitat and may be used to create or open habitats for some bird species while eliminating or reducing habitats needed by others.

While logging may simulate some aspects of habitat alteration caused by natural fire (killing live trees and thinning tree density), current logging practices in ponderosa pine typically remove larger trees rather than saplings and poles or dead and dying trees (salvage logging). Fire does not typically select for tree size and health. Fire-killed trees are frequently left standing after a natural fire, providing nesting and foraging habitat for many bird species, whereas salvage logging deliberately culls trees killed by fire, disease, and insect infestation.

While the interactions between fire and logging complicate our understanding of forested ecosystems and forest use by birds, they are easier to interpret without the added effects of grazing. Unfortunately, the relationship between livestock grazing and bird habitat use in coniferous forests has been neglected. Consequently, our interpretation of how fire, logging, and their interactions structure forests is uncertain considering the pervasive, subtle influence that livestock management has in altering for-

est habitats. If livestock grazing causes an increased density of young ponderosa pine trees, as some studies show (Cooper 1960; Madany and West 1983), then prescribed fire and tree thinning may be important management tools to restore habitats for birds that use open forests with large, old trees or age-structure diversity.

In this chapter, we summarize current knowledge about the effects of fire, logging, and grazing on coniferous forest birds and their habitats. We critically review the results of studies evaluating how these individual factors influence bird numbers, species diversity, nesting success, and habitat use in ponderosa pine forests. Documented and potential interactions among fire, fire exclusion, logging, livestock grazing, and range management are discussed in relation to habitat structure, succession, and avian use. Finally, we outline some areas where further research is needed to better understand the effects of fire, logging, grazing, and their interactions on birds and their habitats in Southwestern ponderosa pine forests.

Fire

Effects of Fire on Forest Birds

Fire can affect forest birds directly or indirectly, positively or negatively. A number of factors determine how fire influences particular bird species including: 1) fire extent and intensity; 2) temporal scale at which effects are evaluated; 3) the particular life history of the species involved; and 4) whether salvage logging follows the fire.

Fire can affect birds directly by causing mortality or reduced reproduction (Patton and Gordon 1995; Rotenberry et al. 1995). Mortality due to fire is generally considered minor for adult birds (Rotenberry et al. 1995). However, mortality of nestlings or fledglings or reduced reproduction due to reductions in food supply is possible if fires occur during the breeding season (Patton and Gordon 1995).

Fires typically affect birds indirectly through habitat modification, changes in food supply, or changes in abundance of competitors and/or predators (Rotenberry et al. 1995). The effects of fire on habitat structure, food resources, and floristic composition may be especially important because many birds respond strongly to these habitat features (MacArthur and MacArthur 1961; Koplin 1969; Lovejoy 1974; Tomoff 1974; Power 1975; Willson

1974; James and Wamer 1982; Rotenberry 1985; Terrill 1990).

Many authors have reviewed the effects of fire on forest birds (Bendell 1974; Hutto et al. 1992; Dobkin 1994; Hejl 1994; James and Hess 1994; Hejl et al. 1995; Patton and Gordon 1995; Rotenberry et al. 1995; Ganey et al. 1996). Several recent reviewers (Hutto et al. 1992; Dobkin 1994; Hejl 1994; Ganey et al. 1996) have concluded that the literature on fire and birds suffers from serious methodological problems. Most studies on the effects of fire on birds were opportunistic rather than planned, were restricted in spatial and temporal scale, and lacked sufficient replication to show general patterns (Dobkin 1994; Hejl 1994; Hutto 1995). Many studies comparing bird communities between burned and unburned areas relied on composite statistics, such as total bird abundance or species richness, rather than examining the response patterns of individual species. These composite measures may hide rather than reveal patterns where individual species respond in an opposite manner (Mannann et al. 1984; Rotenberry 1985; Hejl et al. 1995; Hutto 1995). Most studies focused on the effects of fire on breeding bird communities, ignoring nonbreeding bird communities (but see Blake 1982). Finally, few studies examined demographic parameters (Hejl 1994). Without information on parameters, such as nest success and survival rates of birds occupying burned areas, we cannot assess how well such areas provide for the needs of the species occurring there. These problems limit our ability to draw inferences and, in some studies, the inferences drawn are unsupported by the data. Despite these problems, some generalizations are possible.

First, the effect of fire on birds and their habitat varies with the extent and intensity of the fire. Large fires generally affect more habitat and therefore more birds than do small fires, and hot fires alter forest structure more than cool fires. A stand-replacing fire may result in many or most of the species present before the fire being replaced by a new species (Hutto 1995). In contrast, cool understory burns may have little effect on species composition (Horton and Mannann 1988). How individual species respond to fire may depend on the size of the fire.

Second, fire effects also vary across temporal scales. Intense burns initially produce numerous snags for cavity-nesting birds (Hejl et al. 1995; Hutto 1995; Caton 1996; Hitchcox 1996) and abundant food resources for timber-drilling species such as woodpeckers (Koplin 1969; Wauer and Johnson 1984; Hutto 1995). However, habitat suitability for woodpeckers will decline over time as these snags fall and food resources decrease (Koplin 1969; Bock et al. 1978; Raphael and Morrison 1987; Raphael et al. 1987; Johnson and Wauer 1996). Although large, intense burns greatly alter bird habitat in the short-term, they may be necessary for long-term maintenance of natural forest succession patterns of some forest types (Hejl et al. 1995; Hutto 1995) or for habitat diversity in others.

Third, life history characteristics also influence the response of particular bird species to fire. Cavity-nesting birds, timber-drilling birds, granivores, and some flycatchers generally respond positively to burns in the short term because of increased nesting substrates and/or food supplies (Blackford 1955; Stoddard 1963; Koplin 1969; Bock and Lynch 1970; Kilgore 1971; Lowe et al. 1978; Overturf 1979; Taylor and Barmore 1980; Granholm 1982; Harris 1982; Raphael et al. 1987; Hejl 1994; Hejl et al. 1995; Hutto 1995; Sallabanks 1995; Caton 1996; Hitchcox 1996). Some species may even require intense burns for long-term population maintenance (black-backed woodpecker) (Hutto 1995). In contrast, foliage-gleaning insectivores generally respond negatively to fire due to decreased foraging substrate (Bock and Lynch 1970; Roppe and Hein 1978; Overturf 1979; Blake 1982; Granholm 1982; Sallabanks 1995). Response patterns may vary even within guilds (Skinner 1989; Hutto 1995; Mannann et al. 1984; Rotenberry 1985). For this reason, summary statistics, such as species diversity or total abundance, which are commonly reported, should be used to compare pre- and post-fire bird communities. Diversity and abundance may be similar between these communities, but species composition is often strikingly different (Hutto 1995; Sallabanks 1995).

Fourth, the response of birds or bird communities to fire may also vary depending on whether salvage logging follows the fire. As mentioned, snags created by fire can provide nest and foraging sites. Removal of some or all of these snags eliminates or reduces the benefits they provide (Moeur and Guthrie 1984; Hutto 1995; Hitchcox 1996).

Studies on the Effects of Fire on Ponderosa Pine Birds

Less is known about the effects of fire on birds in ponderosa pine forests than about the effects of fire on forest birds in general. We located only 7 studies about the effects of fire on birds in ponderosa pine forests, and only 5 of these were conducted in Southwestern ponderosa pine forests. An additional 2 studies were conducted in pine-oak forests in southeastern Arizona. Because these forests contain ponderosa pine, they have been included; however, their applicability to pure Southwestern ponderosa pine forests is unknown.

Most studies about the effect of fire on birds in ponderosa pine forest contained methodological problems (table 1). In addition, some studies (Bock and Bock 1983; Horton and Mannann 1988) focused on prescribed fire while others (Lowe et al. 1978; Overturf 1979; Blake 1982; Aulenbach and O'Shea-Stone 1983; Wauer and Johnson 1984; Johnson and Wauer 1996) focused on wildfires. This makes it difficult to compare these studies because different types of fires should have different effects on vegetation and on birds. The situation is further complicated because some

Table 1. Descriptive characteristics of studies of the effects of fire on birds in ponderosa pine and Southwestern pine-oak forests.

Reference	Forest type ^a	Location ^b	Number of plots ^c	Fire type ^d	Fire size ^e	Limitations ^f
Marshall (1963)	PO	SE AZ, Mexico	NA	NA	NA	Anecdotal; no replication; geographic effect possibly confused with fire effects
Lowe et al. (1978)	PP	N AZ	4B, 1 C (4)	W	M-L	No replication; some or all sites logged; sample areas crossed burn boundaries
Overturf (1979)	PP	N AZ	3B, 1C (3)	W	L	No replication; all burned sites logged
Blake (1982)	PP	C AZ	3B, 3U (1)	W	VL	No replication; fire effects possibly confused with logging effects
Aulenbach and O'Shea-Stone (1983)	PP	CO (1)	1B, 1C	W	S	No replication; burn very small; burn and control not independent; few observations for most bird species
Bock and Bock (1983)	PP	SD	4B, 4C (2)	P	S, M	Not in the Southwest; Bock data averaged across woodland and savannah habitats
Horton and Mannan (1988)	PO	SE AZ	3B, 3C (3)	P	S	Applicability to ponderosa pine uncertain
Johnson and Wauer (1996); Johnson (1984)	M	N NM	3B, 1C (1)	W	VL	Only 1 transect with 250% PP; data averaged Wauer and across forest types within transects

^a Forest types: PO = pine-oak; PP = ponderosa pine; M = mixture (mixed-conifer, ponderosa pine/mixed-conifer, ponderosa pine, ponderosa pine/pinyon-juniper, and pinyon-juniper).

^b Location: SE = southeast; N = northern; C = central; AZ = Arizona; NM = New Mexico; CO = Colorado; SD = South Dakota.

^c Plots: B = burned; C = unburned control. Number of separate burns studied shown in parentheses.

^d Fire type: W = wildfire; P = prescribed fire.

^e Fire size (after Heinselman 1981): S = small (<40 ha); M = medium (41-405 ha); L = large (406-4050 ha); VL = very large (> 4050 ha).

^f Aspects of study design that may limit inferences drawn about the effects of fire on birds in Southwestern ponderosa pine forest.

studies focused on small and others on large fires, and because several studies examined birds in areas that were salvage-logged following fire, confounding logging effects with fire effects. Methods differed between studies, and studies were conducted at varying times following fires.

All of the above problems limit our ability to draw inferences from these studies. Careful examination of study designs, sampling methods, and results also suggests that some of the inferences drawn by the authors are unsupported. We review these studies below in chronological order and briefly discuss methods, important results, and limitations of those results.

Marshall (1963) noted parallel variation in fire regime, habitat conditions, and bird communities between the mountains of southern Arizona and northern Mexico (Sonora and Chihuahua). Although his observations related to Madrean pine-oak forests dominated by Chihuahua and Apache pines, the natural fire regime was similar to that in ponderosa pine (Fulé and Covington 1995). Marshall's observations may be relevant to Southwestern ponderosa pine forests.

Wildfires were suppressed as quickly as possible in Arizona, but most were allowed to burn in Mexico (Marshall 1963). Consequently, forests and woodlands in Arizona were denser than similar types in Mexico. Several bird species common to brush or dense forest were more abundant in Arizona than in Mexico including the ash-throated flycatcher, blue-gray gnatcatcher, black-throated gray warbler, Scott's oriole, and spotted towhee. In contrast, several species preferring open forest conditions were either more abundant in Mexico or occurred at higher elevations. Marshall (1963) attributed this pattern to the existence of open forest conditions at higher elevations in Mexico. Examples of these species included the violet-green swallow, Cassin's kingbird, curve-billed thrasher, canyon towhee, purple martin, chipping sparrow, and both eastern and western bluebirds. Although these observations are interesting, no quantitative data were presented on differences in bird communities among areas. Further, we cannot rule out the possibility that the observed variation in bird communities was related to geographic or climatic variation or to other unknown factors rather than only to differences in fire policy.

Lowe et al. (1978) sampled birds in 1 year on 4 sites in northern Arizona ponderosa pine forests that had undergone stand-replacing fires at various times, and also on one unburned plot. Their sampling occurred either 1, 3, 7, or 20 years post-fire, depending on the particular site. They reported dramatic increases in populations of ground-foraging birds immediately after the fires, followed by a gradual decline as canopy cover increased. Timber-drilling birds also increased in burned areas, apparently in response to increased numbers of wood-boring insects. Timber-gleaning or bark-foraging birds decreased following fire, with populations remaining depressed for up to 20 years. Tree-foliage-searching birds increased immediately after fire, then declined dramatically over time. Flycatcher populations peaked approximately 7 years after fire.

Lowe et al. (1978) assumed that the observed variation in bird communities across sites was due to the length time after fire, rather than to site differences. This assumption may be unjustified (see Hejl and Woods 1991) and is impossible to test because different post-fire periods were not replicated. Also, at least some and probably all of the burned sites were salvage logged, making it difficult to distinguish fire effects from logging effects. Finally, areas on which birds were sampled crossed the boundaries between burned and unburned areas.

Overturf (1979) compared breeding bird communities on an unburned site with those on 3 sites burned by wild-fire and salvage-logged on the Coconino National Forest, northern Arizona. One of the 3 burns studied was also studied by Lowe et al. (1978). Species composition varied between burned and unburned sites. Bird communities on burned sites were dominated by ground-foraging birds (chipping sparrow, lark sparrow, dark-eyed junco, green-tailed towhee, western bluebird, northern flicker, and house wren) (Overturf 1979). Some birds using the shrub-sapling and canopy layers were lost from the burned sites (Grace's warbler, mountain chickadee, solitary vireo, Steller's jay, pygmy nuthatch, pine siskin, and mourning dove) (Overturf 1979). Large snags on burned areas were used for nesting by numerous woodpeckers, nuthatches, bluebirds, and house wrens. Woodpeckers, especially hairy and three-toed woodpeckers, foraged on large and small snags. Although the unburned site contained the greatest richness and abundance of birds, the 4 sites together housed more species than any single site. Overturf (1979) concluded that, although avian diversity might be reduced on an individual burn, the patchiness caused by burns across the landscape might enhance avian diversity. Similar to Lowe et al. (1978), Overturf (1979) studied birds on sites that were salvage-logged following fire, which makes it impossible to separate fire effects from logging effects.

Blake (1982) studied the effects of a large wildfire and logging on nonbreeding bird communities on the Prescott

National Forest, Arizona. He established 6 study plots, 3 in the burned area and 3 in unburned areas. Each burned plot was paired with an unburned plot based on 3 levels of logging activity. Plots were either unlogged, selectively-logged, or clear cut. Some species of birds were observed only on either burned or unburned sites. More of these were restricted to unburned than to burned sites. Foliage-gleaning insectivores were more abundant on unburned sites than on burned sites, whereas aerial insectivores (flycatchers and swallows) were more abundant on burned sites. Hairy woodpeckers were most abundant on burned sites, but bark-gleaning birds were most abundant on unburned sites.

Blake (1982) concluded that habitat openness was a primary determinant of nonbreeding bird community structure, and that habitat alterations caused by fire and logging had similar effects on the nonbreeding avian community. This conclusion was largely based on similarities in summary statistics such as species diversity and total bird abundance. Examination of his table 2 suggests that there were differences in community composition between burned and unburned sites within logging treatments. Blake also lacked replication within cells of his experimental design and studied birds primarily in areas that were logged (4 of 6 plots). Although inferences from this study on the effects of fire on forest birds are limited, this study is one of the best of its kind in the Southwest.

Aulenbach and O'Shea-Stone (1983) compared bird communities between a small (2 ha) area burned by wild-fire and a similar control site in ponderosa pine forest in Colorado. Pygmy and white-breasted nuthatches, downy woodpeckers, and mountain chickadees were observed only on the unburned site. Red-breasted nuthatches, chipping sparrows, yellow-rumped warblers, spotted towhees, and northern flickers were seen only on the burned site. The American robin, Steller's jay, and dark-eyed junco were seen on both plots but were most common on the burned plot. This study is particularly problematic. Study sites were not replicated and were separated by only 60 m, making their treatment as independent sampling units questionable given the high mobility of many birds. The total number of individuals observed per site in all censuses was >2 for only 4 species (Aulenbach and O'Shea-Stone 1983), suggesting that sample sizes for individual species were inadequate to support conclusions on their response to fire. For these reasons, it is impossible to draw any meaningful inference from this study.

Bock and Bock (1983) studied the response of breeding birds to cool-season prescribed burning in ponderosa pine forest in South Dakota. Populations of breeding birds were monitored for 2 years following the fires. Six species (mountain bluebird, solitary vireo, yellow-rumped warbler, western tanager, dark-eyed junco, and chipping sparrow) were more abundant on the burned areas than on unburned areas in at least 1 year (Bock and Bock 1983).

Table 2. Response patterns of selected birds to fire in ponderosa pine or Southwestern pine-oak forest. Only species with an apparent trend are listed.

Species	Location ^a	Season ^b	Response ^c	References ^d
Mourning dove	N AZ	B	More common on burned plots	1
Hairy woodpecker	N AZ	B	More common on burned plots	1
	C AZ	NB	More common on burned plots	2
Northern flicker	SE AZ	B	Declined on burned plots	3
Ash-throated Flycatcher	N NM	B	Declined on burned plots	4
Violet-green Swallow	SE AZ	B	Declined on burned plots	3
Swallow	C AZ	NB	More common on burned plots	2
Steller's jay	N AZ	B	More common on burned plots	1
Mountain chickadee	SE AZ	B	Increased on burned plots	3
	N NM	B	Declined on burned plots	4
Pygmy nuthatch	N AZ	B	More common on unburned plots	1
White-breasted Nuthatch	C AZ	NB	More common on unburned plots	2
Red-breasted Nuthatch	SD	B	Declined on burned plots in 1 of 2 yrs	5
Brown creeper	N AZ	B	More common on unburned plots	1
House wren	N NM	B	Increased on burned plots	4
American robin	SD	B	More common on burned plots in 1 yr, on unburned the other yr	5
Hermit thrush	N NM	B	Declined on burned plots	4
Mountain bluebird	SD	B	More common on burned plots in 1 yr	5
	N NM	B	Increased on burned plots	4
Western bluebird	C AZ	NB	More common on burned plots	2
	N NM	B	Increased on burned plots	4
Ruby-crowned Kinglet	C AZ	NB	More common on unburned plots	2
Solitary vireo	SD	B	More common on burned plots in 1 yr	5
Virginia's warbler	N NM	B	Declined on burned plots	4
Grace's warbler	N AZ	B	More common on unburned plots	1, 6
	N NM	B	Declined on burned plots	4
Yellow-rumped Warbler	SD	B	More common on burned plots in 1 yr	5
Western tanager	SD	B	More common on burned plots in 1 yr	5
Dark-eyed junco	SD	B	More common on burned plots in 1 yr	5
Chipping sparrow	SD	B	More common on burned plots in 1 yr	5
	N AZ	B	More common on burned plots	1
White-crowned Sparrow	C AZ	NB	More common on burned plots	2
Green-tailed Towhee	N AZ	B	More common on burned plots	1
Spotted towhee	N NM	B	Increased on burned plots	4

^a Location: SE = southeast; N = northern; C = central; AZ = Arizona; NM = New Mexico; SD = South Dakota.

^b Season: B = breeding; NB = nonbreeding.

^c Only Bock and Bock (1983) and Horton and Mannan (1988) tested for differences in abundance of individual species between treatments. Results from other studies are based on data examination or statements in text. Note that increases or decreases may vary across temporal scale.

^d References: 1 = Lowe et al. (1978); 2 = Blake (1982); 3 = Horton and Mannan (1988); 4 = Johnson and Wauer (1996); 5 = Bock and Bock (1983); 6 = Overturf (1979).

The red-breasted nuthatch was more abundant on the unburned areas in 1 year, but not in the other year. The American robin was more abundant on burned plots in the first year, and on unburned plots in the second year. This study avoided many of the pitfalls discussed previously. Results were averaged across woodland and savannah habitat. However, the applicability of results obtained in South Dakota woodlands and savannahs to Southwestern ponderosa pine forest is unknown.

Horton and Mannan (1988) studied the effects of prescribed burning on cavity-nesting birds in pine-oak forest in the Santa Catalina Mountains, southern Arizona.

They sampled birds on 6 plots in 6 separate stands; 3 were burned and 3 were unburned. The prescribed burn resulted in a moderately-intense surface fire that remained within prescription. Few differences were observed in bird populations before and after fire. Only northern flickers and violet-green swallows declined in abundance in burned stands and only mountain chickadees increased. Horton and Mannan (1988) concluded that the observed declines in northern flickers and violet-green swallows were not due to a shortage of nest sites because post-fire densities of suitable snags (snags >50 cm dbh [diameter at breast height] in particular decay classes) exceeded

densities theoretically required to support pre-fire numbers of cavity-nesting birds.

The plots studied by Horton and Mannan (1988) were dominated by ponderosa pine but also contained 2 species of evergreen oak, Mexican white pine, and Douglas-fir. They were not pure Southwestern ponderosa pine forests and the results may not be applicable to pure ponderosa pine forest.

Patton and Gordon (1995) briefly summarized the effects of fire on individual bird species, many of which inhabit ponderosa pine forest. This summary was based on evidence in the scientific literature, supplemented by personal experience ("in many cases the relationships are intuitive or self-evident from experience;" Patton and Gordon 1995). We will not repeat this summary by species, but instead refer to Appendix B in Patton and Gordon (1995). Many of the references used in evaluating the effects of fire on birds were from habitat types other than ponderosa pine forest or from geographic areas outside of the Southwestern United States. Their conclusions may not be relevant to birds in Southwestern ponderosa pine forests.

Johnson and Wauer (1996; see also Wauer and Johnson 1984) sampled birds before and after the 1977 La Mesa fire in the Jemez Mountains, northern New Mexico. Birds were sampled in 1977 (pre-fire), 1978, 1979, 1981, 1983, and 1991 on 4 transects; 3 burned and 1 unburned. Only 1 of these transects consisted of 250 percent ponderosa pine forests; the others were dominated by mixed-conifer forest, ponderosa pine/mixed-conifer forest, ponderosa pine/pinyon-juniper forest, and/or pinyon-juniper woodland (Johnson and Wauer 1996).

Many changes in community composition were noted through time. The most pronounced change was a marked increase in woodpeckers. Some flycatchers also increased following fire, but the ash-throated flycatcher declined on the transect dominated by ponderosa pine. Mountain chickadees, hermit thrush, Grace's warblers, and Virginia's warblers also declined, whereas house wrens, western bluebirds, mountain bluebirds, and spotted towhees all increased on this transect at some point in time (Johnson and Wauer 1996).

This study and Wauer and Johnson (1984) are the only ones that directly examined the composition of bird communities on particular sites over time; they therefore provide some intriguing results on succession in bird communities. However, two factors limit the strength of this data set for evaluating effects of fire on birds in Southwestern ponderosa pine forest. The first is that only 1 year of pre-fire data on bird abundance and composition is available. Consequently, it is impossible to estimate the annual variability in bird abundance before the fire on any transect. This would not be such a large problem if strong comparisons could be made between the burned transects and the unburned transect. The marked differences in vegetation types across transects weaken such comparisons.

Effects of Fire on Important Habitat Components

Because little is known about the effects of fire on birds in Southwestern ponderosa pine forest, we reviewed current knowledge regarding the effects of fire on important habitat components for forest birds. Although many habitat components may be important, we focus on snags, logs, and oaks, which are particularly relevant to evaluating the effects of fire on birds in Southwestern ponderosa pine forests. We summarize below the available information on the potential importance of these components to forest birds and discuss the results of studies on the effects of fire on these habitat components.

Snags

The importance of snags to ponderosa pine bird communities is well documented (Balda 1975; Scott 1978, 1979; Cunningham et al. 1980). Snags are preferentially used for foraging and nesting by many birds inhabiting Southwestern ponderosa pine forests (Balda 1975; Cunningham et al. 1980). Large snags are particularly important to bird communities. Nesting use is concentrated in large snags (Scott 1978; Cunningham et al. 1980; Raphael and White 1984; Horton and Mannan 1988; Caton 1996; Hitchcox 1996), and they also tend to stand longer than smaller snags (Raphael et al. 1987; Morrison and Raphael 1993). Snags appear to have a finite period during which they are heavily used for foraging and nesting. In northern Arizona, most nesting occurred in snags that were 5 to 20 years old, whereas most foraging occurred on snags that were 1 to 5 years old (Cunningham et al. 1980). This was presumably because although insects colonized these snags rapidly, their numbers declined over time (Cunningham et al. 1980). Thus, snags in this area are most useful to birds for a 20-year period following death.

Fire can create, modify, or destroy snags depending on its behavior and local conditions. Intense burns can create numerous snags that provide foraging and nesting resources for many birds (Blackford 1955; Koplin 1969; Overturf 1979; Taylor and Barmore 1980; Wauer and Johnson 1984; Raphael et al. 1987; Hutto 1995; Sallabanks 1995; Caton 1996; Hitchcox 1996; Johnson and Wauer 1996). Granholm (1982), however, noted that snags recently killed by fire in the Sierra Nevada Mountains lacked the soft heartwood required for nest excavation, whereas many suitable snags were consumed by fire. Thus, both prescribed and natural fires can negatively or positively affect availability of suitable snags for cavity-nesting birds.

Gaines et al. (1958) quantified the effects of 2 prescribed burns on snags in Southwestern ponderosa pine forest. Snags >30 cm dbh declined by 56 percent in the first burn and increased by 175 percent in a second burn. However, this large increase in snag abundance was in an area containing only 1 snag/ha before burning (Gaines et al. 1958).

Horton and Mannan (1988) studied the effects of prescribed fire on snags in a Southwestern pine-oak forest dominated by ponderosa pine. They observed a net 45 percent decrease in snags following prescribed burning. Proportional snag loss was greatest in the size (>50 cm dbh) and decay (III and IV) classes containing the most nest cavities. Horton and Mannan (1988) attributed much of the snag loss to the amount and type of woody debris at the base of the snag; snags surrounded by large amounts of loose, relatively undecayed debris were likely to burn. Many small (<15 cm dbh) snags were created in these burns, which may provide foraging opportunities but are unlikely to be used for nesting (Balda 1975; Scott 1978; Cunningham et al. 1980; Horton and Mannan 1988).

Gordon (1996) quantified the effects of 3 prescribed burns on snags in northern Arizona ponderosa pine forests. She considered all snags with dbh 220.3 cm, height 22.4 m, and <90 percent of the surface charred as suitable for use by nesting birds. Of 61 suitable snags tagged on experimental plots, 32 remained suitable for use by nesting birds following the burns and 12 could not be relocated. Thus, the proportion of snags lost or rendered unsuitable ranged from 35 to 48 percent, depending on whether or not snags that could not be relocated were actually burned. Constructing fire lines around snags influenced their fate; 50 percent of unlined snags versus 27 percent of lined snags were unsuitable after the fire. Many snags that were unsuitable for nesting were partially charred. These had fallen and broken into large pieces becoming part of the log component. Although fire can have detrimental affects on pre-burn snags, it can also cause pre-burn live trees to die and become snags.

Logs

Downed logs can also provide foraging opportunities for forest birds (Horton and Mannan 1988; Bullett al. 1995), but generally their importance to communities of forest birds is not well documented. Horton and Mannan (1988) observed signs of foraging activity before burning by cavity-nesting birds on 37 percent of ponderosa pine logs in their study area. Foraging activity was more common on logs with sapwood; 43 percent of logs with sapwood showed signs of foraging activity versus 28 percent of logs without sapwood. Following prescribed fire, log number and volume declined by 42 and 56 percent, respectively. Number and proportion of logs with sapwood declined by 62 and 16 percent, respectively (Horton and Mannan 1988). Foraging activity was not quantified in post-fire plots.

Gaines et al. (1958) also reported on effects of prescribed burning on logs. Total weight of large logs (defined as 230.5 cm maximum diameter) declined by 63 and 74 percent on the 2 burns they sampled (Gaines et al. 1958). Total weight of small logs (5 to 30 cm maximum diameter) declined by 62 percent in one burn and increased by 83 percent in another.

Gordon (1996) tagged 62 logs before prescribed burning on 3 experimental plots. Using a modification of USDA Forest Service guidelines (no citation given in Gordon 1996), she defined all logs with diameter (unspecified point of measurement) 220.3 cm, length 22.4 m, and <90 percent of the surface charred as suitable. Gordon relocated 59 of these following burning; 43 (69 to 72 percent depending on whether logs that could not be relocated actually burned) were classed as unsuitable following the fire. Of these, 77 percent suffered severe charring and reduction in diameter and 23 percent were completely consumed.

Oaks

Oaks (and possibly other hardwoods) also provide important resources for birds in Southwestern ponderosa pine forests. For example, Szaro and Balda (1979a) noted that several species of birds foraged extensively in Gambel oak in northern Arizona pine forests. Patterns of tree-species selection varied among bird species and with silviculture type, but some forest birds (yellow-rumped warbler, Grace's warbler, and white-breasted nuthatch) used oak foliage more than expected considering its contribution to the total foliage volume (Szaro and Balda 1979a).

Brawn and Balda (1988a) also commented on the importance of Gambel oak to bird communities. They noted that oaks could provide nest sites for secondary cavity nesters and important food resources, and they observed that densities of insectivorous birds were higher on plots with oaks than on similar plots containing only pines.

Both Gambel and evergreen oaks, including Emory, Arizona white, and silverleaf, also provide important resources for birds in other pine-oak forest types in the Southwestern United States (Marshall 1957; Balda 1967; Block et al. 1992). Some or all of these species resprout after fire (Babb 1992; Caprio and Zwolinski 1992; 1995; Barton 1995), and they can rapidly recolonize burned areas. Generally, however, the effects of fire on these species are not well understood, particularly in a ponderosa pine forest.

Many oak species resprout after fire and may be able to quickly recolonize sites following burns even if topkill occurs (Barton 1995; Caprio and Zwolinski 1995). Some species of oaks may need more sunlight than they would get in the shade of closed-canopy forests. Therefore, although fire may reduce the number of large oaks in the short-term, in the long-term, fire-created openings could be beneficial (or even necessary) in maintaining oak as a landscape component (but see Barton 1995).

Conclusion

The literature on the effects of fire on bird communities in Southwestern ponderosa pine forest is replete with problems. Available evidence about such results is anecdotal (Marshall 1963), without replication (Lowe et al.

1978; Overturf 1979; Blake 1982; Aulenbach and O'Shea-Stone 1983; Wauer and Johnson 1984; Johnson and Wauer 1996), has limited replication (Bock and Bock 1983; Horton and Mannan 1988), or confounds the effects of fire with those of logging (Lowe et al. 1978; Overturf 1979; Blake 1982). The picture is further clouded because some studies evaluated effects of low-intensity prescribed burns (Bock and Bock 1983; Horton and Mannan 1988), whereas others studied areas subjected to intense wildfire (Lowe et al. 1978; Overturf 1979; Blake 1982; Wauer and Johnson 1984; Johnson and Wauer 1996). Some studies were conducted in areas outside the Southwestern United States (Aulenbach and O'Shea-Stone 1983; Bock and Bock 1983) or in forest types related but not equivalent to ponderosa pine forest (Marshall 1963; Horton and Mannan 1988). Only 1 study (Johnson and Wauer 1996; see also Wauer and Johnson 1984) actually monitored bird communities over time on a burned area, and only 2 studies (Bock and Bock 1983; Horton and Mannan 1988) provided statistical comparisons of abundances of individual species of birds between burned and unburned areas. Many authors evaluated results primarily in terms of summary statistics, such as diversity or total abundance, which can mask large variation in community composition.

All of these factors limit the inferences that can be drawn about the effects of fire on birds in Southwestern ponderosa pine forests and, in some cases, cause us to question inferences drawn by the original authors. Despite these problems, however, there are some relatively consistent results when trends are evaluated about guilds or individual species. For example, large stand-replacing fires radically alter vegetation structure and bird community composition. Although the effects of cool prescribed burns are less extreme than those of intense wildfires, they follow the same trend. In general, granivores, timber-drilling birds, and some aerial insectivores increase after fires, whereas timber- and foliage-gleaning birds generally decrease (table 2). Even within these guilds, there is sometimes variation. For example, ash-throated flycatchers responded opposite of other flycatchers in the area studied by Johnson and Wauer (1996). Finally, community composition will change over time. For example, granivores such as dark-eyed junco, chipping sparrow, white-crowned sparrow, and towhees often increase significantly shortly after fire (table 2), followed by woodpeckers, which often peak in the first decade following fire, then gradually decline. Birds more closely tied to foliage availability (hermit thrush, solitary vireo; table 2) generally decline immediately after fire, then begin recovering as foliage volume increases in subsequent years. The effects of fire on birds is best understood by considering the type of fire, the amount of time that has elapsed since the fire, the response patterns of individual species, and the extent of post-fire salvage logging.

The effects of fire on important habitat components also depends on fire type. Intense burns may create different

size snags, but these may not be immediately suitable for excavation of nesting cavities (Granholt 1982) and many will not last long (Cunningham et al. 1980; Raphael et al. 1987; Morrison and Raphael 1993). Prescribed burns may also create snags. When such burns are low intensity, however, they are unlikely to kill many large trees but may destroy large snags, which results in a decrease in availability of the large snags preferentially used by forest birds (Horton and Mannan 1988). Intense wildfires and lower-intensity prescribed burns probably decrease the amount of downed logs (Gaines et al. 1958; Horton and Mannan 1988; Gordon 1996). This decrease may be alleviated in subsequent years as fire-killed snags fall, but these logs may not contain the sapwood preferred by foraging birds (Horton and Mannan 1988). Finally, the effects of fire on oaks in ponderosa pine forests is unclear.

Because fire is an important natural process in Southwestern ponderosa pine forests (Moir et al. this volume), communities of forest birds are well-adapted to cope with the natural fire regime in these forests. Disruption of that fire regime, however, along with grazing, timber harvest, and fuelwood cutting, has caused pronounced structural changes in these forests. As a result, wildfires today may burn more intensely and over larger areas than historical fires (Moir et al. this volume), which could have significant negative effects on communities of forest birds and their habitat. Currently, these effects are impossible to quantify, but they may be particularly important where past fire suppression efforts have been most successful.

Numerous authors have called for restoring fire as a natural process in ponderosa pine forests (Covington and Moore 1994a; Sackett et al. 1994; Arno et al. 1995; Fule and Covington 1995). Fire will continue to operate in these systems in spite of our attempts to exclude it (Boucher and Moody 1996). Given current forest conditions, restoring natural fire regimes will require substantial increases in prescribed burning to reduce fuel loads (Harrington and Sackett 1990; Covington and Moore 1994a; Sackett et al. 1994; Arno et al. 1995). Limited evidence on the effects of prescribed fire on forest birds and their habitat suggests that important habitat components of forest birds may be affected by prescribed fire, at least in the short term. To avoid large-scale loss of important habitat components, special techniques, including thinning dense stands and creating fire lines for snags and logs, may be required to reintroduce fire into areas where it has been excluded.

Logging

The following section evaluates the relationship of logging to habitat use by songbirds occupying Southwestern ponderosa pine forests. A review of historic and con-

temporary silviculture is provided by Raish et al. (this volume). Today's forests have been altered by fire exclusion, a decrease in the frequency of natural fires due to diminished fuel availability, and a reduction of herbaceous fuels caused by grazing and trampling by cattle and sheep in the 1880s and 1890s (Weaver 1951; Cooper 1960; Covington and Moore 1994a,b). Fire exclusion has been proposed as a primary reason for the development of overstocked forests in the Southwest (Covington and Moore 1994a,b). Covington and Moore (1994b) report that presettlement tree density was about 56 trees/ha in contrast to the current density of about 2,100 trees/ha, which is mostly small-diameter trees.

Logging contributes about 18 percent to growing stock mortality in the Southwest (Raish et al. this volume). Interpreting changes in stocking rates and volume of ponderosa pine over time is complicated by logging effects. The general rule for historic logging was to harvest the most accessible and commercially valuable trees (Scurlock and Finch this volume), which contributed to the decline of large trees. In the late 1980s, ponderosa pine accounted for about 73 percent of the lumber cut by sawmills in New Mexico and about 91 percent of the timber harvested in Arizona (Van Hooser et al. 1993). Sawtimber accounted for 90 percent of the total ponderosa pine cut in both states (Van Hooser et al. 1993). Between 1962 and 1986, sawtimber stands decreased by 10 percent in Arizona, while small trees (seedling, pole timber, sapling) increased by 3 times over the amount present in 1962 (Spencer 1966; Conner et al. 1990; Johnson 1995). While stocking volume of sawtimber with dbh < 43.2 cm increased between 1962 and 1986, volume of sawtimber with dbh 143.2 cm decreased during the same period (Raish et al. this volume).

In addition, even-aged management commonly practiced in the Southwest creates an age-class distribution of forest habitats that differs from forests without timber harvest. Depending on rotation age, natural disturbance frequency, and moisture regime, forests harvested using even-aged management could have more or less early successional forest rather than natural landscapes (Thompson et al. 1995). In the Southwest, contemporary ponderosa pine forests contain more midsuccessional growth than do unharvested forests that have a greater uniformity of habitat patch sizes and distributions (Raish et al. this volume). Given these changes in tree size, density, and seral stage distribution over time, it seems clear that logging and other types of silviculture have affected the availability, structure, age, and composition of stands at the local stand level and at the landscape and regional levels. Such changes have potentially affected the number and distribution of bird populations using ponderosa pine habitats. Unfortunately, few studies have evaluated effects of landscape-level or large-scale changes on Southwestern ponderosa pine birds (Rich and Mehlhop this volume). Further experimental research on this topic is needed (Block et al. this volume).

Bird Use of Successional Stages Created by Logging

Documented changes in the structure, density, age, and diversity of Southwestern ponderosa pine forests could potentially affect the breeding, wintering, and migration success of birds, and hence, the population status of bird species. Successional changes in habitat are produced by natural events, such as fire, or by management such as logging or prescribed burns. These effects could be positive or negative, long- or short-term, and local or regional. In this section, we review and evaluate studies that compare bird response to successional habitats created by logging. Most published studies of bird responses to logging of Southwestern ponderosa pine have been descriptive, lacking the rigor of experimental research with pretreatment periods and replicated study sites and treatments.

Southwestern ponderosa pine forests evolve through the following generalized successional stages: 1) grass-forb, shrub-seedling (0 to 10 years); 2) pole-sapling (11 to 40 years); 3) young forest (41 to 100 years); 4) mature forest (101 to 200 years); and 5) old growth (201+ years). Canopy volume, understory productivity, and plant and animal diversity varies among these successional stages. Forest management, especially silvicultural, alters the direction and pace of forest succession so that it that may be accelerated or shortened or stages may be bypassed. Several bird species inhabiting ponderosa pine forest feed and nest in mature and old-growth successional stages (Hejl 1994; Hall et al. this volume). In the past, emphasis on wood production of Southwestern ponderosa pine frequently determined silvicultural practices that favored establishment of the most economically valuable trees, emphasized rapid growth, and shortened harvest time. Ecologically, the result was a truncated successional pattern in which early and late stages were shortened or eliminated (Edgerton and Thomas 1978). Multi-storied mature and old-growth ponderosa pine forests provide feeding and nesting habitats for many bird species; several are considered specialized and adapted only to those environments. Mid-seral stages, such as pole-sapling and young forest, which are emphasized by intensive timber management, could significantly alter avian species composition and relative abundance because they lack the structural diversity qualities of older stands.

Meslow (1978) suggested that wood-production practices alter forest habitats by: 1) shortening the grass-forb and shrub stage; 2) creating an even-aged monoculture; 3) eliminating snags; and 4) eliminating old-growth. Even-aged regeneration methods almost completely remove previous stands, which can lead to a complete turnover in breeding birds. Even-aged silviculture within potential Mexican spotted owl (*Strix occidentalis lucida*) habitats in ponderosa pine forests tends to simplify stand structure and establishes stands without the key habitat char-

acteristics used by owls (USDI Fish and Wildlife Service 1995). Selection cutting maintains a specific tree-diameter distribution through periodic removal of selected trees; this results in less change to vegetation structure and bird communities within stands than even-aged management. Selectively-cut stands retain much of the mature forest-bird community and provide habitats for some species that use the ground-shrub-sapling layer (USDI Fish and Wildlife Service 1995). However, selection cutting ultimately tends to homogenize the landscape by reducing or eliminating stand differences, thereby reducing horizontal patchiness across the landscape.

Reviews of Bird Use of Logged Western Forests

Hejl (1994) summarized information on the effects of human-induced environmental change on avian populations in Western North America during the past 100 years. She reported that 13 species (three-toed woodpecker, black-capped chickadee, mountain chickadee, red-breasted nuthatch, winter wren, ruby-crowned kinglet, Swainson's thrush, varied thrush, solitary vireo, Townsend's warbler, evening grosbeak) were always less abundant in recent clearcuts than in uncut forest. In contrast, the mountain bluebird was always more abundant in recent clearcuts. Differences were less dramatic between partially-logged forests and unlogged forests. Pygmy nuthatch and pine grosbeak were always less abundant in partially-logged forests than in unlogged forests. Calliope hummingbird was always more abundant in partially-logged forests. In general, forest species were found less often in clearcuts, and species that frequent open forests or habitats were found more often in clearcuts. Resident species tended to decrease after any kind of harvesting, whereas only about half of the migrants decreased. In contrast, almost all the species that increased after partial cutting or soon after clearcutting were migrants, and most of the species using recent clearcuts were short-distance migrants.

To evaluate relationships between Southwestern bird populations and logged forests, we extracted information on ponderosa pine forests of the Southwest from a comprehensive review of bird use of logged and unlogged conifer forests of the Rocky Mountains (Hejl et al. 1995). For their analysis of widespread bird population responses, Hejl et al. (1995) compared population responses of bird species inhabiting uncut forests to those observed using 4 vegetation classes: 1) low shrub clearcuts (from grass-forb to small shrub stage; generally 0 to 10 years old); 2) tall shrub clearcuts (including tall shrubs and seedlings; generally 11 to 20 years old); 3) pole sapling clearcuts (generally 21 to 40 years old); and 4) partial cuts (any cutting treatment other than clearcutting). Their inclusion of studies from the Southwest provides an index about how bird

populations and silviculture in the Southwest compared to other geographical areas. While clearcutting is common in many forests of the Rocky Mountains, partial cuts are common in Southwestern ponderosa pine; therefore, we are cautious about interpreting abstracted results. Even so, the following analysis has merit because it compares bird population responses along a successional spectrum of stages that can be found in the Southwest.

Hejl et al. (1995) scored each bird species as less abundant (-1), similarly abundant (0), or more abundant (+1) at each logged and unlogged site cited in the literature. The potential relationship between each harvest class and each bird species was determined by calculating the average score over all such studies. An index of 1.0 indicated that every study reported more birds in treated than in untreated areas. An index of -1.0 indicated that every study reported more birds in the untreated than treated areas. An index of 0.0 indicated that either a species had similar abundances in treated and untreated areas in every study, or that no obvious trend was detected across studies. Researchers had sufficient data on 40 bird species known to use Southwestern ponderosa pine forests to evaluate responses to partial or clearcut treatments. Of these, 11 (red-breasted nuthatch, ruby-crowned kinglet, western tanager, three-toed woodpecker, white-breasted nuthatch, hermit thrush, orange-crowned warbler, western wood-pewee, and common nighthawk) were consistently less abundant (score = < 0) in all stages of clearcuts than in unlogged areas (table 3). Six species (mountain chickadee, red-breasted nuthatch, ruby-crowned kinglet, three-toed woodpecker, solitary vireo, white-breasted nuthatch) were always less abundant (score = -1) in recent, low-shrub clearcuts than in untreated sites. An additional 17 bird species were frequently less abundant (0 < score < -1) in low-shrub clearcuts (table 3). All permanent resident species were less abundant in low-shrub clearcuts. In addition, pygmy nuthatch was always less abundant (score = -1) in partially-logged areas than in untreated areas.

In contrast, 9 migrant species (chipping sparrow, broad-tailed hummingbird, dark-eyed junco, mourning dove, white-crowned sparrow, Townsend's solitaire, dusky flycatcher, mountain bluebird, and rock wren) were generally more abundant (score > 0) in low-shrub clearcuts than in unlogged areas although this trend was inconsistent among studies for some species. The rock wren was more numerous in partially logged areas than in unlogged areas in all studies (score = 1). In addition, Steller's jay, warbling vireo, black-headed grosbeak, northern flicker, red-raped sapsucker, fox sparrow, American robin, chipping sparrow, Townsend's solitaire, broad-tailed hummingbird, dark-eyed junco, dusky flycatcher, and mountain bluebird were generally more abundant (scored > 0) in either tall-shrub and/or pole-sapling clearcuts than in untreated areas.

Table 3. Abundance of bird species that occur in clearcut, partially cut, and uncut Southwestern ponderosa pine forest. A species was more abundant (+1), less abundant (-1), or similarly abundant (0) in treated versus untreated areas. Values in the table are averages of these scores over all studies on which the species was recorded. Species are ranked in ascending order from -1.00 based on low-shrub **clearcut** column. Sample sizes are in parentheses (analyses were only performed on the species with sample size ≥ 3). Table modified from Hejl et al. 1995.

Species ^a	NTMB status ^b	Clearcuts					
		Low shrub		Tall shrub		Pole sapling	Partially cut
Mountain chickadee	R	-1.00 (10)		-1.00 (5)		0.00 (3)	-0.77 (13)
Red-breasted nuthatch	R	-1.00 (10)		-1.00 (5)		-1.00 (3)	-0.70 (10)
Brown creeper	B	-1.00 (10)		-1.00 (4)			-1.00 (12)
Golden-crowned kinglet	R	-1.00 (9)		-1.00 (3)			-0.60 (10)
Ruby-crowned kinglet	B	-1.00 (9)		-1.00 (4)			-0.40 (10)
Three-toed woodpecker	R	-1.00 (6)					-0.50 (6)
Solitary vireo	A	-1.00 (5)		0.33 (3)			0.33 (9)
White-breasted nuthatch	R	-1.00 (3)					-0.14 (7)
Pygmy nuthatch	R						-1.00 (5)
Western tanager	A	-0.86 (7)		-1.00 (4)			0.09 (11)
Hermit thrush	B	-0.71 (7)					-0.80 (10)
Steller's jay	R	-0.67 (6)		0.33 (3)			-0.29 (7)
Warbling vireo	A	-0.67 (6)		1.00 (4)			0.33 (9)
Yellow-rumped warbler	B	-0.67 (12)		-0.50 (6)		1.00 (3)	-0.46 (13)
Black-headed grosbeak	A	-0.62 (8)		0.40 (5)			0.22 (9)
Orange-crowned warbler	A	-0.60 (5)					-0.50 (4)
Violet-green swallow	A						-0.60 (5)
Pine siskin	B	-0.45 (11)		0.00 (6)		0.00 (3)	-0.08 (12)
Western wood-pewee	A	-0.43 (7)					-0.50 (4)
House wren	A	-0.40 (5)		0.00 (3)			0.86 (7)
Hairy woodpecker	R	-0.36 (11)		-0.33 (6)		0.33 (3)	-0.25 (12)
Common nighthawk	A	-0.25 (4)		-0.33 (3)			-0.50 (4)
Northern flicker	B	-0.18 (11)		0.67 (6)		0.67 (3)	-0.17 (12)
Fox sparrow	B	-0.17 (6)		0.67 (3)			
Red-naped sapsucker	B	-0.14 (7)		0.00 (5)		0.67 (3)	0.17 (6)
American robin	B	-0.08 (13)		0.50 (6)		1.00 (3)	0.15 (13)
Cassin's finch	B	0.00 (5)		-0.20 (5)		0.67 (3)	0.60 (5)
Cordilleran flycatcher	A						0.00 (6)
Williamson's sapsucker	B						0.00 (5)
Chipping sparrow	A	0.18 (11)		0.67 (6)		1.00 (3)	0.60 (10)
Western bluebird	B						0.20 (5)
Olive-sided flycatcher	A	0.25 (12)		0.25 (4)			0.67 (9)
Broad-tailed hummingbird	A	0.33 (3)		1.00 (3)			0.25 (4)
Dark-eyed junco	B	0.46 (13)		1.00 (6)		1.00 (3)	0.38 (13)
Mourning dove	B	0.50 (4)					0.67 (3)
White-crowned sparrow	B	0.50 (6)					
Townsend's solitaire	B	0.57 (7)		0.25 (4)			-0.25 (8)
Dusky flycatcher	A	0.67 (3)		1.00 (3)			
Mountain bluebird	B	0.90 (10)		1.00 (5)		0.33 (3)	0.67 (6)
Rock wren	B						1.00 (3)

^a Species list is based on Szaro and Balda (1979), Franzreb and Ohmart (1978), Scott and Gottfried (1983), Blake (1982), and Franzreb (1978).

^b As designated by the Partners in Flight preliminary list: A = long-distance migrant species, those that breed in North America and spend their nonbreeding period primarily south of the United States; B = short-distance migrant species, those that breed and winter extensively in North America; C = migrants whose breeding range is primarily south of the United States/Mexican border and enter the United States along the Rio Grande Valley or where the Mexican highlands extend across the United States border (these populations largely vacate the United States during the winter months) R = permanent resident species that primarily have overlapping breeding and nonbreeding areas.

Studies in Southwestern Ponderosa Pine Forests

The most extensive series of studies about bird responses to ponderosa pine logging in the Southwest were conducted at the Beaver Creek Watershed, central Arizona (Szaro and Balda 1979a, 1979b, 1986; Gaud et al. 1986; Brawn and Balda 1988a, 1988b). Szaro and Balda (1979a) compared species diversity and relative abundance of birds among different timber management practices. These practices were: 1) clearcut (removal of all commercial woody vegetation), 2) severely thin (removal of most of the timber stock); 3) strip cut (alternate "level" strips were thinned to improve production); and 4) silviculturally cut (mature and old trees were selectively cut) (see Szaro and Balda [1979a] for more information about treatments). Because clearcuts and strip cuts are now uncommon in the Southwest, the Beaver Creek Watershed study is a historical study rather than a current standard. In addition, habitat characteristics differed among plots within treatments, making it difficult to eliminate the possibility that plot variation was due to plot differences rather than silviculture.

Compared to the control plot, bird abundance and species diversity was lower on the clearcut and severely-thinned plots but higher on strip-cut and silviculturally-cut plots (table 4). Rock wren, American robin, dark-eyed junco, spotted towhee, northern flicker, and mountain bluebird used the clearcut plot, but only rock wren and spotted towhee were favored by clearcutting. On the other hand, removal of some mature and old ponderosa pines using strip cuts and silvicultural cuts favored house wren, solitary vireo, yellow-rumped warbler, Grace's warbler, rock wren, American robin, chipping sparrow, white-breasted nuthatch, western wood-pewee, and western bluebird. The uncut control plot had higher abundances of pygmy nuthatch, red-faced warbler, hermit thrush, western flycatcher, and violet-green swallow. Four foraging guilds (pickers and gleaners, ground feeders, hammerers and tearers, and aerial feeders) were either favored or not affected by strip-cut and silvicultural-cut methods. Three nest guilds (cavity and depression nesters, foliage nesters, and ground nesters) were positively affected by the silvicultural cut.

Szaro and Balda (1986) concluded that openings generated by logging could result in major shifts in local availability of habitats for a given bird species and might be a primary factor in the selection of breeding sites. Those species that typically used more open habitats (rock wren, American robin, western wood-pewee, and western bluebird) were most abundant on either medium or heavy cuts. Those species that prefer dense foliage (western flycatcher, pygmy nuthatch, red-faced warbler, hermit thrush, and black-headed grosbeak) were less abundant in more modified habitats. Of the 15 species found on all forested plots,

33 percent (chipping sparrow, western bluebird, broad-tailed hummingbird, Grace's warbler, and dark-eyed junco) had highest population densities on treated plots, suggesting preference for a more open canopy.

Szaro and Balda (1986) predicted that inter- and intraspecific competition for food resources should be greater on heavy and medium treated sites where the foliage/bird pair was lower than on the lightly cut and untreated sites. However, an examination of the insect food base on the sites indicated that mean bird density was not correlated with either insect numbers or biomass on either relative or absolute bases. They concluded that the foliage available on these sites was not being fully used, and that other factor(s) (territoriality, lack of suitable nesting sites, non-insect food supply, lack of openings or other habitat configurations) might limit ponderosa pine bird communities on sites with dense foliage. Brawn et al. (1987) further suggested that interspecific competition for food during the breeding season was not important in structuring ponderosa pine bird communities.

Franzreb (1978) and Franzreb and Ohmart (1978) studied the effects of moderately heavy overstory removal in a mixed-conifer forest in the White Mountains of Arizona. Avian species richness was equal on the treated area and an adjacent unharvested comparison area; however, overall abundance was significantly higher on the latter. Franzreb and Ohmart (1978) also found no relationship between avian diversity and measures of vertical habitat complexity. Bird abundances on treated and untreated areas varied among species and guilds, probably reflecting differential responses to availability of foraging and nesting substrates. Thirteen species, primarily bark/foliage foragers and cup-nesters, were more abundant on the unharvested area, whereas 10 species of aerial and ground foragers were more abundant on the treated portion. Franzreb and Ohmart suggested that numerical reductions of some species on treated stands could be related to more restricted or more specialized vegetation preferences.

Scott and Gottfried (1983) examined the combined effects of several management prescriptions (individual selection, group selection, and patch cutting) on avian communities in a mixed-conifer forest of Arizona. Species richness increased by 25 percent on the harvested area but decreased by 7 percent on an adjacent, unharvested area. Post-treatment avian abundance decreased 12 and 3 percent on the 2 areas, respectively. Only 1 species showed a significant decrease in density on the treated area. These results were considerably different than those reported by Franzreb and Ohmart (1978); this was attributed by Scott and Gottfried (1983) to heavier timber harvest in their study area. However, given the absence of replicated treatment sites in both studies, we do not believe that strong inferences can be made about treatment effects for either study. In addition, results from mixed-conifer forests may differ from those in pure ponderosa pine.

Table 4. Effect of silvicultural treatment on avian abundance and diversity in Southwestern ponderosa pine forests. Numbers are average breeding pairs/40 ha. Table was modified from Szaro and Balda (1979a).

Species	Clearcut	Thinned	Strip cut	Silv cut	Control
Mountain chickadee		1	3	3.5	3.5
Pygmy nuthatch		1.3	4	13.5	14
House wren			1.8	0.8	
Solitary vireo		5.3	8	4	2.5
Yellow-rumped warbler		1	3	8	1
Grace's warbler		5.8	12	16.5	8.5
Red-faced warbler			1	2.8	
Western tanager		0.5	3	4.7	1
Hepatic tanager			1		
Mourning dove		3.5		1	2
Rock wren	5.0	4.7	6		
American robin	0.3	4.8	5.2	2	
Hermit thrush				0.3	1.5
Dark-eyed junco	1.8	7.5	9.5	16.7	13
Spotted towhee	6.4				
Chipping sparrow		5	7.5	5	1.5
Northern flicker	0.5	3	3	3	3
Acorn woodpecker		1			
Hairy woodpecker		2.3	3.8	3	3
Steller's jay		3.5	4.5	4	5
White-breasted nuthatch		6.7	8.5	8.5	5.5
Black-headed grosbeak			1	2.5	2.5
Common nighthawk		2	2	1	2
Broad-tailed hummingbird		6.5	9	2.7	4
Western flycatcher				3.8	5.3
Say's phoebe			1		
Western wood pewee		3	8.7	2.3	
Violet-green swallow			2	7.5	8.5
Western bluebird		5.8	11.2	7	4.5
Mountain bluebird	0.3	0.3			
Total	14.3	74.5	118.7	122.3	94.6
Pickers and gleaners		14.8	35.4	52	33.4
Ground feeders	13.6	25.5	28.3	25	18
Hammerers and tearers	0.5	16.5	20.8	21	19
Aerial feeders	0.3	17.3	34	24.2	24.3
Cavity and depression	0.8	20	37.3	50.5	47.3
Foliage nesters	6.8	38.8	64	52.7	28
Ground nesters	6.8	14.3	17.5	19	19.3

Mannan and Siegel (1988) and Siegel (1989) sampled avian communities in managed stands and in 3 types of old-growth (open, dense, and minimum) in northern Arizona. Managed stands were even-aged and dominated by densely-spaced, younger (80-year-old) trees. Open old-growth stands had numerous large (> 50 cm dbh) trees with an open understory and were chosen to represent presettlement conditions. Dense old-growth stands had an overstory of large trees and a well-developed understory of smaller trees; a common condition in remaining old-growth ponderosa pine in Arizona. Minimum old-growth stands had received previous

light harvest but met old-growth standards set by the USDA Forest Service. All 4 stand types differed significantly in habitat structure, although the old-growth stands often contained patches resembling other stages. Avian species richness was similar across all 3 old-growth conditions (41 to 47 species) but lower in managed stands (32 to 34 species). The highest avian abundance was in dense old-growth, whereas the lowest was in managed stands. Within the 3 old-growth types, several species varied considerably in their abundance. This was attributed to the availability of mesic microenvironments, openings, and other habitat requisites.

Keller (1992) conducted a survey of breeding birds in several ponderosa pine stand types in north central Arizona. He found that bird species diversity and density were greatest in stands containing ≥ 14 yellow pines/acre and lowest in pure stands of pole timber. Keller suggested that avian species richness and abundance might be linked to the availability of large, mature ponderosa pines.

Rosenstock (1996) studied habitat relationships of passerine breeding birds in ponderosa pine and pine-oak forests of northern Arizona from 1993-1995. He sampled 23 study sites representing a broad habitat gradient from intensively-managed stands with large openings to unmanaged stands with dense thickets of young trees under a mature pine overstory. Rosenstock found that breeding birds showed strong responses to stand structure at both the community and species levels. Species composition and bird numbers differed based on pine canopy configuration, tree size and density, and the density and physical characteristics of Gambel oaks and snags. Five species (pygmy nuthatch, violet-green swallow, Cordilleran flycatcher, house wren, and brown creeper) were positively correlated with high canopy density, low canopy patchiness, and vertical diversity. Five species (Townsend's solitaire, white-breasted nuthatch, hermit thrush, hairy woodpecker, and brown-headed cowbird) were also correlated with low horizontal patchiness and/or vertical diversity, but not with canopy density. Six species (chipping sparrow, hairy woodpecker, house wren, pine siskin, pygmy nuthatch, and violet-green swallow) were positively correlated with the coefficient of variation in pine size (dbh); given that 5 of these 7 species nest in holes or under bark, this relationship may be related to nesting preferences.

Nonbreeding Studies

Few studies have investigated the influence of logging on nonbreeding bird communities in Southwestern ponderosa pine forests. Hagar (1960) found that fall and winter densities on logged areas in California were 2 to 3 times higher than those on unlogged areas; high values were due to large numbers of granivorous birds. Blake (1982) reported that granivores in Southwestern ponderosa pine forests were more abundant than other guilds on clearcut areas in fall and winter. Most granivores left by spring, reducing overall abundance levels; following their departure, bird assemblages were dominated by insectivorous species. Blake (1982) also reported that logging produced an open canopy that was correlated with increased numbers of flycatchers and aerial and ground-feeding insectivores. He concluded that responses to logging were similar for both nonbreeding-season (spring, fall, and winter) and breeding-season bird communities and suggested that the extent of habitat modification might be more influential than the precise type of alteration. As mentioned, how-

ever, caution must be used in interpreting Blake's results because the study design was confounded by interactions with fire and by lack of replication of study plots.

Studies of Nest Site Use in Relation to Silviculture

Few demographic studies of songbird communities in Southwestern ponderosa pine forests have been conducted. Based on a study of cavity-nesting birds using a mixed ponderosa pine forest on the Mogollon Rim, central Arizona, Li and Martin (1991) reported that live and, more commonly, dead aspens (*Populus tremuloides*) were used in 88 percent of cavity nest sites, although aspens constituted only 12 percent of the trees. Preference for aspen may be related to ease of excavation of this soft wood, which is often decayed even in live trees. Aspen suckers frequently sprout in cleared mixed forests after logging or fires. The amount of large aspens in the area studied by Li and Martin (1991) may be explained by early succession of aspens after extensive conifer logging years ago.

Aspen numbers and acreage in fire-excluded forests have gradually declined in the Southwest as conifers have replaced them (USDA Forest Service 1994). According to the USDA Forest Service (1993), the acreage of aspen-dominated forests in Arizona and New Mexico has decreased from 486,000 acres in 1962 to 263,000 acres in 1986. Continued loss of aspens due to fire suppression and conifer succession may escalate competition for favored nest sites by cavity-nesting birds and may result in decreased populations of cavity-nesting birds. Logging and fire in forests mixed with aspens may improve nesting habitat for cavity-nesting birds by allowing aspen to regenerate. However, logging may also reduce the quantity of ponderosa pine snags available for nest sites by reducing the number of live mature pine trees that eventually die and become snags.

Brawn and Balda (1988b) suggested that the breeding density of cavity-nesting birds was nest-site limited for species that were locally common and relied on dead trees for nest sites in ponderosa pine forests of northern Arizona. Martin (1988) found that predation rates in Arizona ponderosa pine forests were lower at nest sites with higher foliage density at nest height and proposed that breeding birds selected habitats based in part on the availability of nest sites that minimize risk of nest predation. Because variation in foliage density in nesting layers influences the reproductive outcome of some open-cup nesting songbird species of ponderosa pine forests, for example, hermit thrush (Martin and Roper 1988), silvicultural alteration of foliage density could influence nesting success.

The above studies suggest that silviculture alters availability of desirable nest sites and may influence populations of bird species that place nests in specialized ways. Our personal observations suggest that demographic re-

sponses to silviculture are likely to differ greatly among species and treatments. Tom Martin and colleagues are studying the reproductive success of songbirds in Southwestern forests along the Mogollon Rim, and their publications should help to clarify interactions between habitat features and reproductive success. In the mean time, further speculation pertaining to the relationship between silviculture and nesting success of songbirds in ponderosa pine forest is unwarranted until specific hypotheses are tested.

Landscapes

As discussed earlier, even-aged silviculture affects the spatial distribution of different-aged stands, while uneven-aged treatments tend to reduce differences among stands. Stand size determines the size of habitat patches created by regeneration cuts and is usually in the range of 5 to 20 ha on public lands. Natural disturbances and openings are more frequent at small scales than at large scales, but these vary widely in magnitude and size. Even-aged management tends to exclude very small and very large patches, resulting in artificial uniformity of habitat patch sizes and distributions. The juxtaposition of different-aged stands may result in increased amounts of edge in the forest, which may affect the reproductive success and abundance of songbirds (see review by Thompson et al. 1995). Logging clearly modifies ponderosa pine landscapes in the Southwest. How altered landscapes ultimately affect bird populations and assemblages is discussed in more detail by Rich and Mehlhop (this volume).

Grazing and Range Management Practices

There have been many studies assessing the impact of grazing on bird populations in the West but few that focus on ponderosa pine forests (for reviews, see Bock et al. 1993; Fleischner 1994; Saab et al. 1995). Livestock grazing in Southwestern ponderosa pine forests has been common since the 19th century (Cooper 1960; Dutton 1953; Scurlock and Finch this volume), so it is likely that habitat changes due to grazing exist in most forested areas of the Southwest. These habitat changes may alter species abundances and composition in avian and other wildlife communities. While the need to study the impacts of grazing in coniferous forests on wildlife populations has long been recognized (Clary 1975), no studies have yet assessed how grazing in Western coniferous forests might affect bird populations (Bock et al. 1993; Dobkin 1994; Saab et al. 1995).

Studies in grasslands have concluded that birds do not respond to grazing *per se* but rather to habitat changes

(Bock and Webb 1984). Assuming this is true in coniferous forests as well, it is necessary to understand how grazing affects habitat structure and composition to assess the possible effects of grazing in ponderosa pine forests on songbird populations. Unfortunately, it may not be possible to assess the impact of grazing on ponderosa pine songbirds by extrapolating from studies in other habitats, as birds respond differently to grazing in different grassland habitats (Saab et al. 1995).

Grazers

Several domesticated species graze in Southwestern ponderosa pine forests. Cattle currently are the most common livestock species; sheep populations have greatly decreased since the turn of the century (Cooper 1960). Big game, such as elk (*Cervus canadensis*) and mule deer (*Odocoileus virginianus*) are also frequently present. Game species probably have similar impacts on plant growth and composition as do livestock (Barnes et al. 1991). Supporting this idea, several studies in a variety of forest ecosystems in the Western United States have indicated that there is overlap between the diets of cattle, deer, and elk (MacCracken and Hansen 1981; Skovlin et al. 1976; Thilenius and Hungerford 1967). The degree to which big game species alter the habitat depends on population sizes, but they can have measurable impacts on the quantity and composition of plant species when population sizes are large. In a Douglas-fir/ponderosa pine forest in Oregon, there was no statistical difference in herbaceous species between plots grazed and not grazed by big game; but presence of game species did lead to a statistical difference in browse species (Krueger and Winward 1974). Earlier in the century, the mule deer population on the Kaibab Plateau in northern Arizona greatly increased causing damage to the habitat by overgrazing (Mitchell and Freeman 1993; Rasmussen 1941). All grazing species, not just domestic livestock, may affect ponderosa pine habitats in ways that could influence songbird populations.

Grazing Systems

The mere presence of livestock does not mean that long-term habitat destruction is occurring (Clary 1987). Instead, the degree to which grazing affects the habitat, and hence the birds using that habitat, depends on several factors. These include the: 1) number of animals grazing in an area; 2) time of grazing; and 3) grazing system used. Greater habitat changes occur as grazing intensity increases in ponderosa pine habitats outside the Southwest (Johnson 1956; Skovlin et al. 1976), and this is likely to occur in the Southwest as well. Grazing during the spring and early summer may directly decrease the reproductive success of breeding birds through destruction or disturbance of nests on the ground or in low shrubs. Grazing during other

seasons can indirectly affect bird communities through habitat changes.

Little is known about the effects of different grazing systems in Western coniferous forests (Saab et al. 1995). In ponderosa pine forests in the Blue Mountains of Oregon and Washington, deferred rotation grazing increased vegetation cover in open grassland areas but not in forested areas, as compared with season-long grazing (Skovlin et al. 1976). Pearson et al. (1971) used a 3-pasture rest rotation system in a ponderosa pine forest in Arizona. Since cattle tended to avoid mature grasses, concentrating instead on succulent growth, the timing was adjusted so that no plant species was overgrazed. This system was effective in achieving good weight gain in cattle while maintaining a diverse balance of plant species. Some grazing systems may be less detrimental to riparian zones than others. Marlow and Pogacnik (1985) found that cattle had a lower impact on stream banks when soil moisture was high, while Clary and Webster (1989) suggested that spring grazing may have the lowest impact on riparian zones. The results of studies comparing different grazing systems in other habitats have been variable (Dwyer et al. 1984) and probably no single system will give the same results in all areas. Hence, even if more data were available from ponderosa pine forests, it may be difficult to predict what effect specific grazing practices will have on avian habitat.

Effects of Grazing on Birds

As stated, the primary effects of grazing on songbirds should be caused by habitat alterations. At least 2 species of ponderosa pine birds, the buff-breasted flycatcher and the western bluebird, have exhibited population declines that were attributed to habitat overgrazing (DeSante and George 1994). This speculative conclusion was derived from a review of historical information rather than from an analysis involving a replicated experiment. Taylor and Littlefield (1986) reported that when grazing levels were reduced in the Malheur National Wildlife Refuge in Oregon, populations of the willow flycatcher and yellow warbler increased.

Changes in the Understory

Grazing can reduce the volume of grasses and, to a lesser extent, the forbs and shrubs, which form much of the understory vegetation in ponderosa pine habitats of the Southwest (Koehler et al. 1989; Madany and West 1983) and other Western regions (Johnson 1956; Laudenslayer et al. 1989; Rummell 1951; Skovlin et al. 1976; Zimmerman and Neuenschwander 1984). Some of the more common species that may decrease in abundance are mountain muhly (*Muhlenbergia montana*), muttongrass (*Poa fendleriana*), Arizona fescue (*Festuca arizonica*), squirreltail (*Sitanion kystris*) and blue gramma (*Bouteloua gracilis*). Common

shrub species affected by grazing include serviceberry (*Amelanchier* spp.), bear-berry (*Arctostaphylos* spp.), (*Holodiscus discolor*), willow (*Salix* spp.), and spiraea (*Spiraea* spp.).

In addition to reducing the understory volume, grazing also alters the composition and structure of understory plant communities (Arnold 1950; Clary 1975; Johnson 1956; Knopf 1996; Madany and West 1983; Rummell 1951; Skovlin et al. 1976; Zimmerman and Neuenschwander 1984). This can involve changes in the abundance of different species, as plants preferred by grazers are reduced and those tolerant of grazing become dominant. Grazing also reduces the number of plant species present.

In addition to the direct reduction of understory vegetation due to grazing, grazing can also indirectly decrease understory vegetation. Growth of understory vegetation is lower in areas of high canopy cover (Arnold 1950; Moir 1966; Severson 1987). Since increases in tree density occur in response to grazing (see below), grazed areas may have greater canopy cover, leading to a further reduction in the understory vegetation.

Importance of Understory Structure to Birds — Several studies have examined the relationship between the quantity and diversity of vegetation and how this affects bird densities. In a variety of different habitats, there is a positive relationship between the volume and structural diversity of the vegetation and the density of birds in the area (Bull and Skovlin 1982; Karr 1968; Martin 1984; Mills et al. 1991; Tomoff 1974; Verner and Larson 1989; Willson 1974). While no studies have assessed these relationships in Southwestern ponderosa pine forests, understory diversity in a coniferous forest in Utah was positively related to bird community diversity (Wine 1976). Species composition of the vegetation is also important in avian community composition in grassland communities (Rotenberry 1985). This suggests that replacement of a plant species, even if the structure of the plant is the same, may affect bird species using the habitat.

Some ponderosa pine bird species are only found in areas with dense understory vegetation. These species, which include dusky flycatcher (Sedgwick 1993), Bewick's wren (DeGraaf and Rappole 1995), solitary vireo (DeGraaf and Rappole 1995), orange-crowned warbler (Sogge et al. 1994), MacGillivray's warbler (Pitocchelli 1995), Virginia's warbler (DeGraaf and Rappole 1995) and spotted towhee (DeGraaf and Rappole 1995), are likely to decrease in abundance if the volume of understory vegetation is reduced. Since grazing alters species composition, reduces the number of species in the understory, and decreases the volume of the understory, changes in the abundances, compositions, and richness of songbird species may occur in areas of Southwestern ponderosa pine forests that are heavily grazed. Such changes may involve a decrease in abundance or the disappearance of species preferring dense vegetation. However, species that prefer a more

open understory may then colonize the area or increase in abundance.

Nesting in Relation to Understory Changes — Species that nest on the ground or in shrubs may be negatively affected by changes in the understory, as sites suitable for nesting may be eliminated for some species (Knopf 1996). Spruce/ fir forests in the Rocky Mountains generally have only 1 species of ground nester (dark-eyed junco); the low number of ground-nesting species has been attributed to the lack of understory cover necessary for other avian ground nesting species (Smith 1980). Therefore, ground and shrub nesting species, such as those listed in table 5, may suffer reduced reproductive success and may decrease in abundance when the understory vegetation necessary for structural support, cover, and protection of the nest has been reduced or altered.

The avian species in table 5 are nesting generalists; multiple species of grasses and shrubs can provide suitable nesting sites. Therefore, as long as sufficient volume in the understory remains, a loss of 1 or a few understory species may not affect nesting habitat for those species. We suggest that even if all plant species are retained in grazed areas, the amount or suitability of nesting habitat will be reduced if the abundance or volume of each plant species decreases. To test this hypothesis, experiments that test the effects of shrub or grass removal on nesting success of understory-nesting birds are needed.

Foraging in Relation to Understory Changes — Structure and composition of the understory is also important for foraging. Green vegetation is relatively unimportant for ponderosa pine birds; no bird species heavily depends on greens (Ehrlich et al. 1988). However, seeds and berries, many of which are produced by understory vegetation (see list of shrubs above), are important for many bird species. When grazing changes the quantity and composition of the understory, the amount of available food for some bird species also changes.

Because most ponderosa pine birds that use understory plants are generalized feeders, they are less likely to depend on specific plant species than on plant structure and

abundance (Rotenberry 1985). The species most likely to be affected by changes in plant composition are broad-tailed and rufous hummingbirds, since these species are specialized to forage on suitably shaped flowers, such as columbine (*Aquilegia* spp.), scarlet gilia (*Ipomopsis* aggregate), and penstemon (*Penstemon* spp.). Although hummingbirds may be adapted to forage on specific flower shapes, they will also forage on a variety of other plant species (Carder and Calder 1992; Calder 1993). *Penstemon* spp. increased in a grazed ponderosa pine forest in Arizona (Arnold 1950); thus, grazing of understory plants is not necessarily correlated with reductions of hummingbird food. No studies have specifically addressed whether variation in seed and berry production or quantity and species richness of flowering or fruiting plants affects bird species that forage on understory substrates.

Insects are an important food source for songbird species, as they are the primary food for offspring. Abundance and species composition of insects may be affected by changes in the understory vegetation, as many insect species depend on specific plants to provide food and oviposition sites. Brawn et al. (1987) concluded that competition for food among breeding insectivorous birds was absent in Arizona ponderosa pine forests, even though densities of breeding birds had been increased through habitat manipulation. Further studies are needed to determine whether abundance and species composition of arthropods in Southwestern ponderosa pine forests vary in relation to grazing patterns, and whether such variation can affect species composition or bird reproduction.

The structure and density of the vegetation may be more important when foraging for insects than the number or species of insects available, as has been found in an Eastern deciduous forest (Robinson and Holmes 1984). Foliage gleaners will probably be most affected by changes in the structure of the understory, though some species are capable of adapting foraging strategies in response to changes in the vegetative structure (Robinson and Holmes 1984).

Many avian species forage, at least in part, on the ground. As more bare ground becomes available due to a

Table 5. Bird species in ponderosa pine forests that nest primarily on the ground or in low shrubs.

Species	Nest Locality	Reference
Dusky flycatcher	Shrub	Sedgwick 1993
Hermit thrush	Shrub	Martin 1993
Orange-crowned warbler	Ground	Martin 1993; Sogge et al. 1994
Virginia's warbler	Ground	Martin 1993
MacGillivray's warbler	Shrub	Martin 1993; Pitocchelli 1995
Red-faced warbler	Ground	Martin 1993; Martin and Barber 1995
Green-tailed towhee	Shrub	Martin 1993
Dark-eyed junco	Ground	Martin 1993
Song sparrow	Shrub	Kern et al. 1993

reduction in the grasses and other understory vegetation, foraging may become more efficient for some ground feeders, although conversely, there may be less to forage on. Those species that frequently forage on bare ground, such as northern flicker (Moore 1995), pinyon jay (Balda et al. 1977), chipping sparrow (Mannan and Meslow 1984), dark-eyed junco (Deborah M. Finch and Rebecca Kimball pers. obs.), and green-tailed and spotted towhees (Deborah M. Finch and Rebecca Kimball pers. obs.) may be favored by removal of patches of dense understory vegetation through grazing. Even when grass cover remains, shorter grasses may be preferred foraging habitat for some species, such as American robin (Eiserer 1980) and mountain bluebird (Power and Lambert 1996). However, ground feeders that forage among leaf litter, for example, towhees, may be negatively affected if high levels of grazing reduce all or most of the litter.

Changes in Tree Density

Grazing generally leads to an increase in the density of ponderosa pines in the Southwest (Cooper 1960; Madden and West 1983) and in other Western forests (Laudenslayer et al. 1989; Rummell 1951; Zimmerman and Neuen-schwander 1984). The reduction in grass and other understory vegetation reduces competition for pine seedlings, and hence greater establishment of seedlings occurs in areas that have been grazed (Covington and Moore 1994a,b; Doescher et al. 1987; Karl and Doescher 1993). In addition, several grass species (Arizona fescue, mountain muhly, and squirreltail) produce allelopathic compounds that inhibit germination of ponderosa pine seeds (Jameson 1968; Rietveld 1975). If these grass species are reduced through grazing, germination of pine seedlings may increase, leading to further increases in pine densities. Through this same process, pine trees may also encroach into meadows and clearings within the forest.

Many bird species of ponderosa pine prefer more open woods (table 6). As tree densities increase in relation to fire exclusion and overgrazing, populations of these bird species may begin to decrease. Supporting this hypothesis, Verner (1980) observed the greatest number of bird species in areas of lower canopy cover in coniferous forests of the Sierra Nevadas of California. In addition, several bird species associated with ponderosa pine forests primarily live in these meadows or clearings (table 6), and these species could be excluded from the area as clearings become forested.

While increases in tree density may lead to decreases in many avian species, it is less clear whether any species will increase in abundance. Several species are thought to prefer dense, old-growth forests including hairy woodpecker (Hejl 1994). However, old-growth forest is characterized by large trees, which may be more important than tree density. When tree densities increase due to grazing,

the trees are small and young. Therefore, bird species that prefer dense, old-growth forests may decrease in abundance in grazed forests dominated by young trees even though tree densities are high.

Grazing may also lead to increases in the density of tree species other than ponderosa pine. In southern Utah, comparison of a grazed and ungrazed area indicated that grazing had greatly increased the number of oak and juniper trees in ponderosa pine forests (Madany and West 1983). Grazing also increased juniper densities in a ponderosa forest in California (Laudenslayer et al. 1989). Oak (*Quercus* spp.), juniper (*Juniperus* spp.), and pinyon pine (*Pinus edulis*) provide important food resources, particularly for birds that are winter residents and whose winter diets depend heavily on access to their nuts and berries, such as Lewis' woodpecker, acorn woodpecker, Clark's nutcracker, and Townsend's solitaire. Increases in these tree species should positively affect the ability of those bird species, as well as other bird species that consume nuts and berries, to overwinter successfully in ponderosa pine forests.

Effects in Riparian Zones

Cattle forage disproportionately in and around riparian zones in forested habitats (Roath and Krueger 1982a, b; Samson 1980; Willard 1990) including Southwestern ponderosa pine forests (Glendening 1944). Clary et al. (1978) suggested that cattle preference for riparian zones in ponderosa pine forests may be minimized by careful range management practices that increase forage in surrounding areas by thinning trees to promote understory growth.

Vegetation in riparian zones of Rocky Mountain forests often differs from that in the surrounding area (Peet 1988) and may provide unique habitats for some nesting birds. Grazing, particularly since cattle selectively forage in riparian zones, can change the composition and structure of the unique riparian community. Observations in a variety of habitats have shown that herbaceous and woody vegetation may be trampled or removed, changed in plant form or habitat structure, or transformed to different seral stages or vegetation types in response to grazing (Bock et al. 1993; Fleischner 1994; Krueger 1996; Rinne 1985; Szaro 1989). Heavy grazing in combination with drought or dewatering of streams due to irrigation or flood control can reduce regeneration of deciduous native trees, altering plant species composition and age structure, and encouraging invasion of aggressive alien plants (Finchet al. 1995). These alterations in the vegetation may greatly affect bird communities in riparian areas.

Riparian zones of the Western United States have been identified as important habitats for breeding birds since more species and individuals are often found in the riparian zone than in the surrounding vegetation (reviews in

Table 6. Bird species in ponderosa pine forests that prefer an open habitat or that use meadows or clearings within the forest.

Species	Reference
Open forest species	
Rufous hummingbird	Calder 1993
Northern flicker	Moore 1995
Olive-sided flycatcher	Hejl 1994
Western wood-pewee	DeGraaf and Rappole 1995
Dusky flycatcher	Sedgwick 1993
Gray flycatcher	Cannings 1987; DeGraaf and Rappole 1995
Buff-breasted flycatcher	Bowers and Dunning 1994
Ash-throated flycatcher	DeGraaf and Rappole 1995
Cassin's kingbird	DeGraaf and Rappole 1995
Violet-green swallow	Brown et al. 1992
Pinyon jay	Balda and Bateman 1972; Marzluff (this volume)
Black-capped chickadee	Smith 1993
White-breasted nuthatch	Pravosudov and Grubb 1993
House wren	Belles-Isles and Picman 1986
Ruby-crowned kinglet	Mannan and Meslow 1984
Western bluebird	DeGraaf and Rappole 1995
Townsend's solitaire	DeGraaf and Rappole 1995
Solitary vireo	DeGraaf and Rappole 1995
Warbling vireo	DeGraaf and Rappole 1995
Yellow-rumped warbler	DeGraaf and Rappole 1995
Black-throated gray warbler	DeGraaf and Rappole 1995
Hepatic tanager	DeGraaf and Rappole 1995
Western tanager	DeGraaf and Rappole 1995
Black-headed grosbeak	DeGraaf and Rappole 1995
Chipping sparrow	Mannan and Meslow 1984
Meadow and clearing species	
Tree swallow	Robertson et al. 1992
Mountain bluebird	Power and Lombardo 1996
Yellow warbler	DeGraaf and Rappole 1995
MacGillivray's warbler	Pitocchelli 1995
Common yellowthroat	DeGraaf and Rappole 1995
Indigo bunting	DeGraaf and Rappole 1995
Spotted towhee	DeGraaf and Rappole 1995
Green-tailed towhee	DeGraaf and Rappole 1995
Lincoln's sparrow	DeGraaf and Rappole 1995
American goldfinch	Middleton 1993
Lesser goldfinch	Deborah M. Finch (personal observation)

Bock et al. 1993; Fleischner 1994; Krueper 1993,1996; Saab et al. 1995). However, this may not be true in all ponderosa pine forests. A study in Colorado found few unique breeding species in a ponderosa pine riparian zone, though riparian zones in other habitats were characterized by unique breeding species (Knopf 1985). In addition, in 1 of 2 years of the study, the density of breeding birds was not different between the riparian zone and the

Table 7. Bird species that use riparian zones adjacent to ponderosa pine for nesting and foraging.

Species	Reference
Broad-tailed hummingbird	Calder and Calder 1992
Rufous hummingbird	DeGraaf and Rappole 1995
Acorn woodpecker	Koenig et al. 1995
Northern flicker	Moore 1995
Olive-sided flycatcher	DeGraaf and Rappole 1995
Cordilleran flycatcher	DeGraaf and Rappole 1995
Buff-breasted flycatcher	Bowers and Dunning 1994
Ash-throated flycatcher	DeGraaf and Rappole 1995
Cassin's kingbird	Blancher and Robertson 1984
Gray-breasted jay	Brown 1994
Black-capped chickadee	Smith 1993
Canyon wren	Jones and Dieni 1995
Orange-crowned warbler	Sogge et al. 1994
Virginia's warbler	DeGraaf and Rappole 1995
Yellow warbler	DeGraaf and Rappole 1995
MacGillivray's warbler	Pitocchelli 1995
Red-faced warbler	Martin and Barber 1995
Common yellowthroat	DeGraaf and Rappole 1995
Black-headed grosbeak	Hill 1995
Spotted towhee	DeGraaf and Rappole 1995
Lincoln's sparrow	DeGraaf and Rappole 1995

surrounding vegetation. Therefore, riparian zones in some ponderosa pine forests and in some years may be less important for bird communities than are riparian zones in most other habitats.

Cattle grazing in riparian zones has negatively affected bird communities in a variety of Western habitats (Bock et al. 1993; Fleischner 1994; Krueper 1993,1996; Saab et al. 1995). Although there may be few or no species that breed exclusively in riparian zones of ponderosa pine forests (Knopf 1985), many species do use riparian habitats (table 7) and may be affected by grazing or trampling of riparian vegetation. Studies of a montane river in New Mexico showed that grazed areas had fewer bird species and fewer individuals, as compared with an ungrazed portion of the same river (Szaro and Rinne 1988). However, studies of montane riparian zones in Idaho and Nevada found no decrease in species numbers in a grazed as compared to an ungrazed area (Medin and Clary 1990,1991). In addition, northern flicker and American robin increased in abundance in a grazed riparian habitat (Mosconi and Hutto 1982; Schulz and Leininger 1991), probably due to an increase in open ground on which to forage (Knopf 1996). Therefore, grazing does not always reduce bird abundance and species richness in riparian habitats. Indeed, population responses to changes in riparian habitat resulting from grazing appear to be species dependent (Saab et al. 1995). Populations of individual bird species

may increase, decrease, or remain constant in relation to grazing, contributing to changes in avian community structure. Since riparian zones in ponderosa pine forests are likely to vary in structure and vegetative composition, grazing may negatively affect some bird populations in some areas but probably not all species in all areas. High grazing intensity (high stocking rate), continuous year-round grazing, and grazing during the critical breeding season are perhaps the most significant management practices that alter avian habitats in riparian zones.

Cattle can also affect other aspects of the stream, which may indirectly affect birds in the area. Studies in Southwestern forests have shown that cattle can damage stream banks (Rinne 1985), which leads to stream widening. Grazing also reduces vegetation around and overhanging streams in the Southwest and elsewhere (Platte and Raleigh 1984; Rinne 1985), leading to an increase in stream temperature and a reduction in the amount of detritus in the stream. Silt loads in the streams may also increase, reducing the size or presence of interstitial spaces that are used by aquatic invertebrates (Rinne 1985). While these changes might negatively affect aquatic insects, an important food for birds, comparison of a grazed and ungrazed region of a montane stream in New Mexico found that the grazed region had increased numbers and biomass of aquatic insects (Rinne 1988). Thus, grazing may make some streams more hospitable for aquatic insect larvae that emerge as flying insects and become food for birds. Assuming that many bird species in ponderosa pine forests are insect generalists (Brawn et al. 1987), increases in insect abundances, even if the species composition of the insects has changed, may benefit some bird species.

Other Effects of Livestock Management on Birds

Added Water Sources

While cattle grazing may affect ponderosa pine bird communities by altering the habitat, birds may also be affected by other range management practices. Areas where cattle are grazed are often supplied with stock tanks or other artificially created water supplies. These water sources can benefit bird communities because they provide water for drinking and bathing and emergent insects to feed upon. However, additional water sources may have some negative affects on bird communities. Livestock traffic may greatly reduce the vegetation around the water source, possibly damaging nesting and foraging sites (Buttery and Shields 1975). In addition, the water source may attract predatory mammals and snakes, which may increase avian nest predation in the area (Buttery and Shields 1975). Other bird species or individuals may colonize the site, increasing site activity and competing for local resources. Stagnant water also provides prime breeding habitat for mosquitoes. While mosquitoes provide food for

many avian species, they also carry malaria (*Plasmodium* spp.), which can infect avian populations. Avian malaria is common in most bird communities and can be detrimental to an individual's health or survival, particularly for birds that may be under stress (Hayworth and Weathers 1987).

Brown-Headed Cowbirds

In addition to grazing in forested areas, cattle may be moved to feedlots outside forest boundaries. Although, few forest birds are likely to travel far from forests to forage at open feedlots, brown-headed cowbirds in many regions of the United States are attracted to areas with supplemental food such as feedlots and pack stations (Lowther 1993; Rothstein et al. 1980; Thompson 1994; Trail and Baptista 1993; Verner and Ritter 1983). Radio-telemetry studies in the Sierra Nevada Mountains and the Midwest have shown that cowbirds will travel long distances (up to 10 km) between feeding and nesting areas (Rothstein et al. 1984; Thompson 1994). Therefore, even when feedlots are placed outside forested areas, they may increase the presence of cowbirds in local ponderosa pine forests.

The range expansion of the brown-headed cowbird into the Western United States has been well documented (Rothstein 1994). In addition to foraging for insects in feedlots, dairy farms, pastures, and other artificial habitats, cowbirds also follow cattle to scavenge insects and seeds from dung (Terborgh 1992). Therefore, the expansion of cowbirds into new habitats and geographic areas may be facilitated by the presence of agriculture and cattle (Hanka 1985; Rothstein 1994; Sharp 1995). Cowbird populations in New Mexico, but not Arizona, are increasing (Mehlman 1995) and further studies may help clarify whether cowbird densities are related to numbers of feedlots and cattle.

Some habitat changes associated with grazing may actually decrease the presence of brown-headed cowbirds in ponderosa pine forests. Cowbirds typically prefer open habitats, and they travel into forested areas primarily to lay eggs in host nests (Verner and Ritter 1983). Verner and Ritter (1983) suggest that differences in the cowbird distribution in the Sierra Nevada Mountains may be due to differences in forest density, with cowbirds avoiding dense coniferous forests. If this is true for Southwestern ponderosa pine forests, increases in tree density due to grazing and fire exclusion may make these forests less hospitable to cowbird invasions.

Since brown-headed cowbirds lay their eggs in the nests of other species, the reproductive output for parasitized individuals is greatly reduced because the nest is either abandoned or the host young do not survive to fledgling (Robinson et al. 1995a). Female cowbirds can lay up to 30 or 40 eggs a year (Scott and Ankney 1980); 1 female can affect the reproductive success of many different breeding pairs. However, while they affect host species, they may not be the primary cause of population declines of most host species. Instead, cowbirds may cause additional

stress to populations already stressed from other factors such as habitat loss (Rothstein 1994).

Brown-headed cowbirds occur at least occasionally in ponderosa pine forests of the Southwest especially along edges, riparian zones, campgrounds, and clearings. Cowbirds are generalist brood parasites, and many songbird species in ponderosa pine forests have been observed to raise cowbird young (Friedmann and Kiff 1985; Martin and Barber 1995), although other species reject cowbird eggs by ejecting them from the nest. Most ponderosa pine birds suffer only low levels of parasitism, but vireos, warblers, sparrows, gnatcatchers, tanagers, and towhees are commonly parasitized in at least some habitats (riparian zones) (Friedmann and Kiff 1985; Goguen 1994; Schweitzer and Leslie 1996). It is unknown whether levels of parasitism would increase for all species if cowbirds became more abundant or whether the few commonly parasitized species would be the primary targets, with other species remaining occasional hosts.

Little information is available on cowbird populations, parasitism rates, host selection, and host nesting success for Southwestern ponderosa pine forests. In pinyon-juniper woodlands near Raton, north central New Mexico, Goguen (1994) reported cowbird parasitism rates of 80 to 100 percent for solitary vireo; 78 to 92 percent for western tanager; 63 to 75 percent for blue-gray gnatcatcher; 0 to 13 percent for chipping sparrow; 0 to 25 percent for spotted towhee; and 0 to 14 percent for western wood-pewee. According to Goguen (1994), cowbird parasitism rates were usually greater in areas where cattle were present. In addition, the nesting success of parasitized nests varied greatly by host species (Goguen 1994). These same host species also occupy Southwestern ponderosa pine forests and may be parasitized in these forests.

Southwestern studies focusing on cowbird abundances and effects on hosts are limited to riparian zones at elevations lower than the ponderosa pine zone. According to Schweitzer and Leslie (1996), cowbird densities and parasitism rates vary greatly by locality. We suggest that cowbird parasitism may pose a problem for some ponderosa pine hosts in areas where forests are within 4 to 6 miles of open pastures, stockyards, corrals, stock tanks, and agricultural fields (Rothstein et al. 1984, 1987). More research is needed to determine whether and where cowbird densities and parasitism rates are high or low in ponderosa pine compared to other habitats, and whether rates of parasitism are associated with characteristics such as proximity to and extent of edge, habitat fragmentation and isolation, density of ponderosa pines, forest successional stage, dispersed or concentrated grazing, host species presence or absence, and host densities.

Vulnerable species may include small, open-nest, neotropical migrants that produce only 1 brood a year (flycatchers, vireos, warblers) (Mayfield 1977), and hosts occupying isolated, patchy habitats (Rothstein et al. 1987;

Rothstein and Robinson 1994). Small, disjunct host populations are more at risk of extirpation from cowbird parasitism than abundant hosts because cowbirds do not reduce parasitism rates as preferred hosts become rare (Mayfield 1978; May and Robinson 1985). Birds nesting in Southwestern riparian habitats are considered especially vulnerable to cowbird parasitism because this habitat is typically patchy, linear, and ecotonal; often near or within cattle pastures or agricultural fields; and preferred as congregation grounds by cows (Harris 1991; Schweitzer and Leslie 1996; Schweitzer et al. 1996).

Subdivision of Private Ranches

Increases in grazing fees may lead ranchers to subdivide their land. While subdivisions replace wildlife habitat, developments are generally concentrated and use a relatively small proportion of the land (Wuerthner 1994). As such, subdivision may benefit avian communities, as grazing would cease while much land would still remain undeveloped. However, development requires water and this will damage or destroy riparian habitats (Brown and McDonald 1995), which will negatively affect many bird species. Subdivision also fragments the habitat, increasing edges and establishing possible barriers to dispersal. Additional problems associated with subdividing land into developed properties are described by Marzluff (this volume). Fragmentation and the associated increase in edges increases nest predation and nest parasitism by cowbirds (Gates and Giffen 1991; Paton 1994; Robinson et al. 1995b), although not all studies have found that edge nests were more heavily parasitized than were interior nests (Hahn and Hatfield 1995). Subdivisions also reduce patch size of suitable habitat. Large patches of forest habitat are preferred by species, such as the hermit thrush (Keller and Anderson 1992), and these may decrease in abundance if fragmentation occurs. While these species may decrease, other species, such as the pine siskin and the Cassin's finch, may increase in abundance (Keller and Anderson 1992). Both grazing and subdivision of ranch land will, on average, negatively affect some bird species. Given existing data, it is difficult to determine which factor, grazing or subdivision, will have the lowest negative impact on avian communities.

Interactions of Fire, Grazing, and Logging

Fire, Salvage Logging, and Forest Health

Salvage logging primarily occurs in response to 3 causes of tree mortality: 1) insect attack; 2) tree diseases; and 3) fire. Salvage operations can help control insect pests and

pathogens by removing dead, dying, or high risk trees, and by helping to make a stand less susceptible to future catastrophic fire and insect outbreaks. Wood fiber that would deteriorate is salvaged. However, salvage logging in response to forest disease treats only the effect and not the cause of the problem. Following intense fire, salvage logging is implemented to help recover the economic value of fire-killed trees. Whether or not dead and dying trees should be removed from a site is possibly the most controversial aspect of forest health management today (O'Laughlin et al. 1993; Filip et al. 1996).

Regardless of the reason for a salvage operation, the result is the removal of dead and dying trees from a forest stand. Bird species that depend on dead and dying trees (snags) are most impacted by any type of salvage logging, whether it be selective harvest of individual trees or complete stand removal. Cavity nesters in ponderosa pine forests of the Southwest, such as the acorn woodpecker, hairy woodpecker, northern flicker, pygmy nuthatch, white-breasted nuthatch, western bluebird, mountain chickadee, house wren, Cordilleran flycatcher, and violet-green swallow (Szaro and Balda 1979a), will potentially be affected the most. Snags also provide important habitat features for other species (Glinski et al. 1983; Hutto 1995; Sallabanks 1995).

Empirical data on the response of ponderosa pine bird communities to salvage logging is limited and currently restricted to fire-related snag removal (Overturf 1979; Moeur and Guthrie 1984). Other studies offer insights into the response of general forest bird communities to snag harvest following fire, which can be cautiously extrapolated to ponderosa pine bird communities.

Raphael and White (1984) found 77 percent fewer pairs of cavity-nesting birds 5 years after complete snag removal on a burned plot in the Sierra Nevada Mountains. This decline was largely due to the disappearance of mountain bluebirds. Pairs of noncavity-nesters declined by only 6 percent during the 5 years after harvest. Of 3 cavity-nesting species reported before snag removal, only the northern flicker still bred on the plot post-harvest.

Raphael (1983) explored the bird response to reduced snag densities by simulating various snag-harvest levels immediately following fire. The 19 snag-harvest treatments simulated varied from leaving 1 to 10 percent of the pretreatment snag density (in 1 percent increments) to leaving 20 to 100 percent (in 10 percent increments). Total bird numbers rose dramatically from the 1 to 10 percent treatment level (corresponding to 0 to 4.5 snags >38 cm dbh per hectare). Beyond the 30 percent treatment level (15 snags/ha), bird response rose relatively slowly. The model predicted that optimum snag densities under the constraints tested would be 7 to 15 snags/ha.

Hutto (1995) reported on ongoing studies of bird communities in burned forests in the northern Rocky Mountains. These studies suggested that some bird species re-

quire burned forests to maintain viable populations. Further, bird species differed in the microhabitats that they occupy within a burn. Therefore, salvage prescriptions that tend to homogenize forest structure (selective removal of all trees of a certain size) are unlikely to maintain the necessary variety of microhabitats within a burned forest. Consequently, Hutto (1995) suggested that where salvage logging is necessary, it may be better to take trees from one part of a burn and leave another part completely untouched rather than selectively remove trees from the entire burn area. Noting that up to 60 percent of all timber sales on some forests in the northern Rocky Mountains involve salvaged timber, Hutto (1995) also argued that post-fire salvage cutting may be conducted more frequently than justified on the basis of sound ecosystem management.

In addition to these studies, 3 studies in progress will offer much-needed data on the effects of salvage logging on songbird communities. Because these are not occurring in ponderosa pine forests of the Southwest, their relevance is unknown. The first is a study of subalpine fir (*Abies lasiocarpa*) forests in the Blue Mountains of northeastern Oregon where fire-killed trees will be salvage logged (Sallabanks 1995). The second study examines how fire and salvage logging in ponderosa pine forests of west central Idaho influence the nest success of 10 cavity-nesting bird species (V. A. Saab pers. comm.). Salvage logging is underway in the third study in lodgepole pine (*Pinus contorta*) forests in south central Oregon (Arnett et al. 1996). This study is important because it will examine salvage of trees killed by the mountain pine beetle (*Dendroctonus ponderosae*) rather than wildfire. All 3 studies have collected presalvage data on breeding bird community composition so that pre- and post-salvage data may be compared.

Although little empirical data exists on the effects of snag harvest on wildlife populations following fire, even less is known about the effects of salvaging diseased and insect-infested trees on bird communities. Because bird communities differ between burned and unburned sites, the effects of salvage operations on birds may also differ between these sites. Therefore, extrapolating results from studies of salvage logging in burned sites to unburned sites may be unjustified. This area needs further research.

Relationships between bird communities and general forest health are also poorly defined for ponderosa pine forests. When forests are overstocked due to a recent history of fire suppression, trees are susceptible to a variety of insects and diseases and severe wildfires, especially during drought conditions. In some Western states, ponderosa pine forests are dying faster than they are growing (O'Laughlin et al. 1993). Insectivorous bird species would presumably benefit from insect outbreaks such as those by the Douglas-fir tussock moth. Similarly, cavity-nesters should benefit in the short term from tree mortality that occurs as a result of insect attack, disease, or wildfire. In the long term, however, processes that result in

tree mortality exceeding tree recruitment are problems for forest birds.

Bird regulation of insects that cause tree mortality is pertinent to forest health conditions. Birds consume large numbers of defoliating insects (Crawford et al. 1983). Without bird predation, it is estimated that spruce budworm populations would reach epidemic densities every 3 years in the Pacific Northwest (Takekawa and Garton 1984); actual epidemics occur about every 28 years (Dolph 1980). When insects are at endemic levels, avian predation is most effective. Crawford et al. (1983) report that in northern New England, the percentage of spruce budworm larvae and pupae eaten by birds declined from 87 percent to 2 percent of the budworm population at endemic and epidemic levels, respectively.

The relationship between forest health, salvage logging, and bird communities in Southwestern ponderosa pine forests is complex and poorly understood. The apparent decline in some species of forest-breeding neotropical migrant songbirds (Finch 1991) may profoundly affect forest health if the insects normally eaten by these bird species are frequently allowed to reach epidemic levels. Increases in insect attack may lead to weaker trees that are more susceptible to disease. This, combined with drought and management to suppress fires, could increase fuel loads and the chance of large, catastrophic, stand-replacing wild-fires. Such fires could lead to more salvage logging and further changes in the ponderosa pine bird communities. Given the complex nature of these interactions among components of the ponderosa pine ecosystem, more research is needed on the effects of salvage logging on bird communities, the role of songbirds in maintaining forest health, and the relationship between insects, disease, fire, and birds.

Cumulative Effects of Fire, Grazing, and Logging

Pre-European forests of the Southwest tended toward a wider range and diversity of tree sizes and ages, health states, patch ages, structural stages, inter- and intra-patch diversity, and landscape designs than do contemporary ponderosa pine forests. Historically, bird species with specialized needs were found at varying abundances at different, but overlapping, intervals along this temporal and spatial continuum of forest age, health, and diversity. Based on the analyses and studies described above, bird species that historically preferred open, park-like ponderosa pine forests are likely to be negatively affected by contemporary forest management that emphasizes continuous or long-term grazing in combination with fire exclusion because these practices produce a closed forest of dense, young to mid-aged trees with few grasses, forbs, or shrubs. Such vegetation changes result in poor grazing conditions for cattle, too. In addition, modern-day culling and salvage logging of snags, diseased trees, and old trees,

and clearing of old growth patches reduces the diversity and heterogeneity of stand ages and structures, intensifying the trend toward younger, more uniform, even-aged forests.

When the influences of fire exclusion, long-term grazing, and old-growth logging (heaviest in the first half of the 20th century) are fused into one management package, the resulting forests of the Southwest tend to be more mid-aged than young or old, more dense than open, and more plantation-like than variable in tree size, spacing, and understory structure. Midsuccessional stages dominate contemporary Southwestern ponderosa pine forests and are probably used to the greatest extent by bird species generalists adapted to a broad range of forest and structural types (American robin, dark-eyed junco). They may be avoided by bird species that require special habitat elements only found in open forests, old growth, burns, snags, heterogeneous landscapes, or a combination of these conditions. However, Brawn and Balda (1988a) reported that no bird species of Southwestern ponderosa pine forests has gone extinct since early turn-of-the-century surveys (Scurlock and Finch this volume), which suggests that habitat changes caused by forest management have not been so extreme as to eliminate any species, at least at the broadest spatial scales.

Species of concern that are likely to be negatively affected by forest management that emphasizes continuous grazing, fire exclusion, and post-fire salvage logging include those that nest in or forage on or from standing dead trees or large, old trees in open forests; for example, the three-toed woodpecker, pygmy nuthatch, white-breasted nuthatch, and mountain and western bluebirds. Additional open-forest species that may benefit from prescribed fire or thinning of young trees include Grace's warbler, rock wren, western wood-pewee, and chipping sparrow. Shrub-using species of open or heterogeneous forests that may benefit from livestock pasture rotation in combination with burning or clearing to increase amounts of early successional shrubs are broad-tailed hummingbird, dusky flycatcher, MacGillivray's warbler, orange-crowned warbler, Virginia's warbler, Bewick's wren, solitary vireo, white-crowned sparrow, Lincoln's sparrow, and spotted towhee.

Species whose abundances in Southwestern ponderosa pine are known or suspected to decline in relation to burns, clearcuts, natural clearings, or partial-logging, for example, the pygmy nuthatch, mountain chickadee, red-faced warbler, hermit thrush, violet-green swallow, Cordilleran flycatcher, pine grosbeak, and black-headed grosbeak, may respond negatively to local management implemented for economic gain or to benefit open-forest species. Such immediate reactions are short-lived for species that can occupy subsequent successional stages, but are longer-lasting for those that reach peak abundance in the oldest forests. While old-growth species may avoid open patches created by intense burns or clearcutting,

fewer of them avoid larger, more diverse landscapes, which can include small and large patches of dense old trees, open young forest, and open old-growth forest. For example, the pygmy nuthatch, a species that uses snags created by fires, old age, and disease to nest and roost in, avoids local bums that may increase snag density. The solution to maintaining populations of all songbird species in Southwestern ponderosa pine may be to ensure that suitable habitat resources are available at the landscape and physiographic levels, while acknowledging that local resources may not always be sufficient to satisfy the needs of all species.

Research Needs

The effects of fire, logging, and grazing on bird communities in ponderosa pine forest need further study. We describe some specific areas where further research is needed for each management practice. Probably the most critical research need is to understand the interactive effects of fire, logging, and grazing. For example, what bird species can be expected in ponderosa pine forests when managing along a gradient ranging from wilderness and research natural areas to areas combining fire exclusion, prescribed fire, continuous and rotational grazing, even-aged and uneven-aged silviculture, and salvage logging? Evaluating interactive effects will require complex study designs, high amounts of funding, close working relationships between management and research organizations, and a large team of scientists, land managers, and technical support staff. Research goals can most realistically be met if fewer interactions and objectives are addressed in each individual study. Research needs specific to each management practice are discussed below.

Research in Relation to Fire

Bird communities should be monitored through time on areas burned by large, intense wildfires to evaluate the effects of such fires on bird communities and how these communities change through time following fire. This will require opportunistic rather than planned studies. Studies should focus on fires that differ in size and intensity, so that changes in bird communities can be documented over a wide range of fire behavior. Long-term studies are needed to document changes in bird communities through various phases of post-fire succession. Studies should focus on response patterns of individual species and should evaluate demographic patterns and patterns of resource use. Studies should consider breeding and nonbreeding birds and year-round residents and migratory birds, as all of these groups are important parts of the overall bird community.

Bird communities should be studied experimentally in conjunction with prescribed burning. Studies should consider the above factors and the effects of a wide range of fire prescriptions on important habitat components. Because current forest conditions may result in an unacceptably high loss of some important habitat components even with applications of cool fire, it may be necessary to take special steps to protect these components in the short term. Therefore, techniques to mitigate the negative effects of fire on important habitat components, such as snags, should be tested and evaluated. As more natural fire regimes are restored, this problem should be alleviated and special protective measures may no longer be required.

The effects of salvage logging on post-fire bird communities and on recovery of forest structure should be studied experimentally, keeping in mind the factors listed above. Studies should include a wide range of logging prescriptions, as different prescriptions have different effects on birds and their habitat.

Efforts should be made to identify any species that are dependent on or sensitive to fire, and to evaluate the positive and negative effects of fire on those species. The three-toed woodpecker may be the species most closely linked to fire in the Southwest. This woodpecker is generally rare, but is capable of colonizing burned areas rapidly and in relatively high numbers (Koplin 1969; Wauer and Johnson 1984), suggesting that recruitment may occur over large distances (Wauer and Johnson 1984). Other species may also be partially dependent on fire to create and maintain suitable habitat.

To the extent possible, the range of variation in patch sizes of natural (pre-European settlement) bums should be evaluated so that managers can attempt to mimic natural disturbance patterns through prescribed burning (DesGranges and Rondeau 1993). In addition, the natural (pre-European settlement) range of fuel loadings should be determined so that fire managers can bring current conditions in line with historical conditions. Studies comparing the effects of fire to those of timber harvest are also needed. Studies should evaluate whether or not timber harvest can simulate the effect of fire on forest birds and, if so, under what prescriptions.

Studies exploring the relationship between grazing, fire suppression, forest structure, and bird communities are also required. Many areas now contain dense forest stands as a result of heavy grazing pressure in the past, coupled with fire suppression (Rummel 1951; Madany and West 1983). Restoring fire to these areas may require special considerations such as those described in the second paragraph of this section.

Research Pertaining to Silviculture

Conclusions based on our literature review are hampered by the rarity of studies addressing bird responses to different kinds of logging and by inconsistencies in re-

search designs. Most reports have considered only the effects of timber harvesting and were limited to relatively small spatial and temporal scales. In addition, most of these studies used secondary variables such as presence, absence, or relative abundance of species rather than demographic attributes such as reproductive output, mortality, and recruitment and return rates to indicate population trends and habitat suitability (Martin 1992). More importantly, past studies have lacked pretreatment monitoring, controls, and/or replicates, and relied on correlative evidence instead of direct experimental manipulations to assess avian habitat relationships. Present ponderosa pine forests, although relatively simple in species composition, are nevertheless a complex spatial mosaic that vary in age, health (related to disease and insects), germination history, fire history, elevation, slope exposure, microclimate, soil conditions, composition of flora and fauna, livestock management, and silviculture (Brawn and Balda 1988). Although most researchers attempt to standardize study plots by selecting "similar" stands and site characteristics for different treatments, stand vegetation may be perceived differently by avian species. In addition, logging treatments vary in size, selection criteria, treatment type, and time of treatment.

We recommend that long-term research and monitoring of bird populations, bird demographics, habitat use, and habitat structure be implemented in relation to different types of silviculture, successional stages, and landscape patterns. Studies should be designed to address local and landscape levels simultaneously to determine if patterns in bird habitat use shift with scale of resolution. Whereas changes in densities and diversities of birds may be relatively small within each treatment plot, they may be significant when summed across a landscape. Improved techniques and increased applications for inventorying, mapping, and monitoring stages and types of ponderosa pine at large geographic and temporal scales are needed to understand where and how ponderosa pine forests and associated avifaunas have changed at any given time and to enable adjustments in forest management when undesirable trends are identified.

Further research on songbirds is needed to determine population size and age structure, rate and direction of population changes, age-specific fecundity and survival, adult and juvenile dispersal, breeding success, mortality, predation rates, and return rates in relation to timber harvesting, stand age and regeneration time, intermediate treatments, and logging rotation schedules, and size, heterogeneity, and isolation of managed forests. Whitcomb et al. (1981) reported that species sensitive to fragmentation in Eastern deciduous forests were neotropical migrants that inhabited forest interiors, nested on or near the ground in open nests, and had relatively low reproductive potential. Such information is critical for understanding why, where, and which bird species are positively or negatively affected by logging directly and/or by associated seral fragmentation of forested landscapes.

Whether similar or different population and demographic associations exist among avian species using ponderosa pine forests in the Southwest has yet to be discovered; however, based on exploratory studies of bird habitat relationships, more resident bird species in Western coniferous forests seem to respond negatively to reductions in densities and amounts of mature and old growth forests than do nontropical migrants (Hejl et al. 1995).

Many avian species that use Southwestern ponderosa pine forests are transients or wintering residents. While past research has mostly focused on breeding birds, responses of nonbreeding populations to habitat alterations should be studied. During migration and winter, most bird species use a wider range of habitats, indicating greater habitat plasticity (James 1971; Anderson and Shugart 1974; Moore et al. 1995). Research is needed to investigate the degree or scale at which different bird species discriminate among habitats of different ages, structures, spatial patterns, and treatments. Given that over one-third of ponderosa pine forests in the United States are privately owned (Raish et al. this volume), research partnerships between public agencies and private entities are strongly recommended.

Research in Relation to Grazing

Grazing in ponderosa pine forests is likely to affect the abundance and species composition of bird communities breeding and living in Southwestern forests. Changes in the density and composition of the understory will greatly affect birds that nest on or near the ground.

Understory changes will also affect foraging behavior, potentially reducing the foraging efficiency of foliage gleaners, but increasing the foraging efficiency of at least some ground foragers. Many ponderosa pine bird species prefer more open forest habitats and may decrease in response to increasing tree density. Grazing also affects riparian zones in ponderosa pine forests, although this may not reduce avian diversity and abundances. Bird populations may also be affected by other range management practices such as the presence of stock tanks or feedlots. However, these practices are likely to have less of an impact on bird communities in ponderosa pine forests than the influence of habitat changes.

There are several areas of research that need to be addressed before the effects of grazing on ponderosa pine bird communities can be understood. Many prior studies have suffered from poor experimental design (Brown and McDonald 1995), and it is critical to conduct carefully controlled experiments involving replication and either the exclusion or addition of cattle. These studies should address such questions as whether breeding and wintering bird communities differ between grazed and ungrazed forests, whether trampling reduces resting success, whether increases in tree density negatively affect many species, and whether cowbird populations increase in grazed areas. In addition, studies addressing the impact

of different grazing systems and cattle densities will provide the information necessary to make management decisions that will minimize the impact of grazing on avian communities. Although riparian zones are more difficult to study due to the many confounding physical factors involved (Brussard et al. 1994), it is important to determine whether grazing negatively affects bird communities in these areas as well. Finally, other practices associated with range management should be investigated to determine if and how these might affect songbird populations.

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