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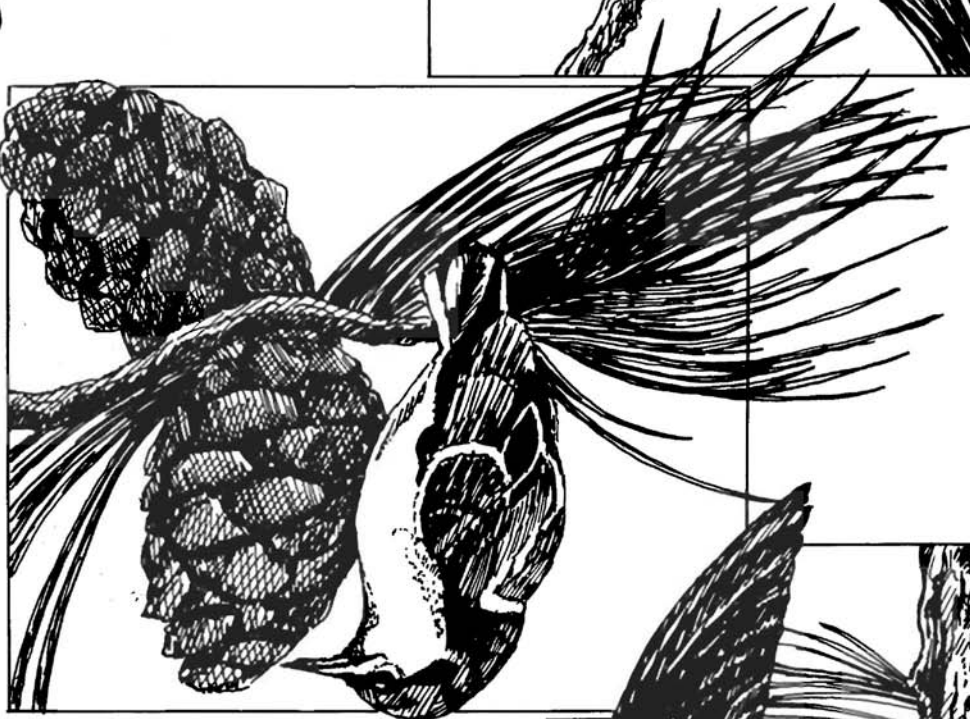
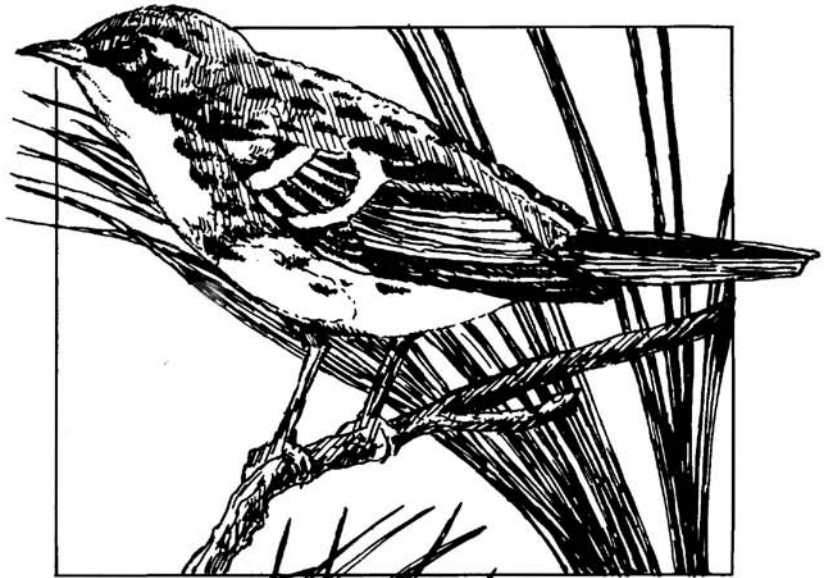
Rocky Mountain
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General Technical
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Songbird Ecology in Southwestern Ponderosa Pine Forests: *A Literature Review*



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This publication reviews and synthesizes the literature about ponderosa pine forests of the Southwest, with emphasis on the biology, ecology, and conservation of songbirds. Critical bird-habitat management issues related to succession, snags, old growth, fire, logging, grazing, recreation, and landscape scale are addressed. Overviews of the ecology, current use, and history of Southwestern ponderosa pine forests are also provided. This report is one of the outcomes of the *Silver vs Thomas* court-settlement agreement of 1996. It is intended for planners, scientists, and conservationists in solving some of the controversies over managing forests and birds in the Southwest.

Keywords: ponderosa pine, Southwest, songbirds

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*Front Cover: Grace's warbler, pygmy nuthatch, and violet-green swallow.
Artwork by Joyce Patterson.*

Songbird Ecology in Southwestern Ponderosa Pine Forests: A Literature Review

William M. Block and Deborah M. Finch
Technical Editors

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Preface

Denver P. Burns

As part of a settlement agreement related to the *Silver vs. Thomas* (1996) litigation, the Rocky Mountain Forest and Range Experiment Station agreed to summarize the current knowledge on songbirds inhabiting ponderosa pine forests in the Southwest. This review represents the state-of-knowledge of songbird ecology in Southwestern ponderosa pine forests.

Ponderosa pine is the major forest type in the Southwest, encompassing over 3 million hectares. The forest belt extending above the Mogollon Rim is the largest contiguous ponderosa pine forest in the world. These forests have been occupied by humans for thousands of years, during which time humans derived multiple benefits from a variety of resources. Not only have these forests provided human needs, but they also provide for the needs of numerous plants and animals.

A group of animals of particular interest are the songbirds, which occupy numerous habitats and stages. Each species uses a unique combination of habitat conditions, and changes to the forest may influence that species' population status. To a certain extent, birds can act as indicators of environmental conditions. By examining trends in bird populations, one might hope to index forest health, and vice versa.

Thus, understanding the ecology of birds in ponderosa pine forest, including their habitat requirements and population trends, is key to gauging health of this forested ecosystem. The chapters presented in this document summarize what we know about ponderosa pine forest ecology as well as about the birds that inhabit those forests. They represent a compilation of numerous independent studies and provide a springboard for the development of new studies. The information presented herein may also be used to assess current management direction for these forests and to fine-tune management to more effectively provide conditions to sustain populations of the native ponderosa pine avifauna well into the future.

The information provided in this document represents independent contributions by biologists, ecologists, and social scientists that summarize and synthesize current knowledge about ponderosa pine songbirds, including the ecology and use of these forests. Because topics presented in these chapters were broadly overlapping, some redundancy in materials present was unavoidable. I must also acknowledge the valuable contribution of reviewers to improving this document. Peer reviews were solicited for each chapter, and the entire document underwent rigorous blind review from three professional societies: American Ornithologists' Union, Cooper Ornithological Society, and The Wildlife Society. Collectively, these reviews provided a quality check, and response to review comments resulted in a quality document.

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William M. Block (chapters 4 and 8) is project leader and research wildlife biologist of the Southwestern Terrestrial Ecosystem research work unit in Flagstaff, Arizona, and leader of the Mexican Spotted Owl Recovery Team. He has been with the USDA Forest Service's Rocky Mountain Forest and Range Experiment Station since 1990. He received his Ph.D. from the University of California, Berkeley in wildland resource sciences; his M.S. in wildlife from Humboldt State University; a B.A. in economics from California State University, San Diego; and a B.S. in wildlife from Michigan State University. His current research interests include, and he has published widely on, avian ecology, vertebrate-habitat relationships, community ecology, threatened and endangered species, and the development of conservation plans.

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Dan Scurlock (chapters 1 and 3) is a consulting environmental historian and naturalist. He has worked for universities, public schools, government agencies, private organizations, and businesses as a researcher, instructor, planner, writer, photographer, and trip leader for 30 years in the American Southwest, Mexico, and Canada. His more than 70 academic and popular publications in history, archaeology, architectural history, and natural history range from articles to book-length reports. He holds an A.B.S. in science and B.A. and M.A. degrees in anthropology.

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Introduction

Deborah M. Finch and William M. Block

This book reviews and synthesizes the diverse literature about ponderosa pine forests of the Southwest, emphasizing the biology and ecology of songbirds in relation to habitat changes resulting from natural events such as succession and fire, and management activities such as logging, grazing, and recreation. This product is one of the outcomes of a 1996 court-ordered settlement agreement pertaining to protection of the Mexican spotted owl (*Strix occidentalis lucida*) that included a section requiring a report on the habitat requirements of and threats to songbirds inhabiting Southwestern ponderosa pine. This book fulfills those objectives by emphasizing critical habitat issues and identifying bird species that may be sensitive to changes in availability of habitat types, structures, seral stages, and special features such as snags, aspen and oak, and old trees.

To write the chapters, we assembled a team of experts from a cross-section of disciplines representing forestry, plant ecology, avian biology and ecology, endangered species conservation, environmental history, and social sciences. Biographical sketches of authors are included at the beginning of the book. Authors were instructed to address all passerines as well as doves, hummingbirds, and woodpeckers; that is, birds with sizes and behavioral responses to habitats and spatial scales that were deemed relatively similar to passerines. A comprehensive list of common and scientific names of birds known to occupy Southwestern ponderosa pine forests is in Appendix A.

Blind reviews for the entire book were obtained from three professional societies: The Wildlife Society, the American Ornithologists' Union, and the Cooper Ornithological Society. Blind reviews were sought to strengthen manuscripts and establish the book's authority.

The book starts with a chapter that summarizes the state of knowledge of the geography, ecology and diversity of Southwestern ponderosa pine forests. Chapter 1 highlights the complexity and range of variation of contemporary Southwestern forests and sets the stage for more specialized chapters. Current human uses of Southwestern ponderosa pine forests are described in Chapter 2. An understanding of how current forests are managed and how such management may alter environmental conditions is important to identify the principal causes of changes in

songbird habitats and songbird populations. Chapter 3, an environmental history of Southwestern ponderosa pine, establishes reference conditions and an understanding of past human activities that may have influenced what we think and see today. This chapter also includes a discussion of prehistoric and historic human uses of birds, avian archaeological findings, and avifaunal accounts and checklists by early ornithologists. Such information is a useful reminder of how our knowledge of Southwestern ponderosa pine and its avifauna has evolved.

Chapter 4 launches the ornithological expedition to the heart of the book by summarizing the general biology and habitat use of songbirds found in Southwestern ponderosa pine forests. This chapter clarifies the basic patterns of habitat use by different species and groups of birds and identifies habitat elements of high management priority. Chapter 5 is a thought-provoking review and analysis of the effects of urbanization and recreation on birds of ponderosa pine. This chapter is an example of the emerging body of literature that seeks to evaluate direct and indirect impacts of human population growth on wildlife. The subject of land management effects on songbirds, with a focus on fire, logging, and grazing, is tackled in Chapter 6. Because different kinds of land management are frequently practiced simultaneously, their interactions and effects are difficult to interpret. However, the authors rise to the occasion with an exhaustive discussion and interpretation of issues. Chapter 7 is a landscape overview of issues identified in previous chapters and ends with a plea for more studies at the landscape level. The book ends with a summary of key issues and a call for more research, especially research of an experimental nature.

In conclusion, the editors and authors of this book have compiled a comprehensive review of the literature on the topic of Southwestern ponderosa pine forests and its songbird inhabitants. We hope that this publication will be a useful source of information for natural resource managers, scientists, and environmentalists and will supply the basis for new standards in research and management. In addition, we hope that this review will help to solve some of the controversies pertaining to management of forests and birds in the Southwest.

Acknowledgments

We thank the Publications Office of the Rocky Mountain Forest and Range Experiment Station, especially Madelyn Dillon and Lane Eskew, for their patience in handling the time-sensitive editorial work on this book. We thank Bob Dana for conducting electronic literature searches for various chapters and Mike Means and Brenda Strohmeyer for tracking down references. We are grateful

to Nora Altamirano for formatting the manuscripts according to Station guidelines. The Southwestern Region (Region 3) of the USDA Forest Service supplied financial support for the writing and publication of this product. We thank all authors for their contributions and patience, and finally we thank Denver Burns, Station Director, for suggesting that we coordinate this project.

■

Chapter 1

Ecology of Southwestern Ponderosa Pine Forests

William H. Moir, Brian Geils, Mary Ann Benoit, and Dan Scurlock

What Is Ponderosa Pine Forest and Why Is It Important?

Forests dominated by ponderosa pine (*Pinus ponderosa* var. *scopulorum*) are a major forest type of western North America (figure 1; Steele 1988; Daubenmire 1978; Oliver and Ryker 1990). In this publication, a ponderosa pine forest has an overstory, regardless of successional stage, dominated by ponderosa pine. This definition corresponds to the interior ponderosa pine cover type of the Society of American Foresters (Eyre 1980). At lower elevations in the mountainous West, ponderosa pine forests are generally bordered by grasslands, pinyon-juniper woodlands, or chaparral (shrublands). The ecotone may be wide or narrow, and a ponderosa pine forest is recognized when the overstory contains at least 5 percent ponderosa pine (USFS 1986). At upper elevations ponderosa pine forests usually adjoin or grade into mixed conifer forests. A mixed conifer stand where ponderosa pine has more overstory canopy than any other tree species or there is a plurality of tree stocking, is an interior ponderosa pine forest (Eyre 1980).

Two distinct ponderosa pine forests occur in the Southwest. The xerophytic (drier) forests have ponderosa pine as a climax tree (reproducing successfully in mid- to late succession) and comprise the ponderosa pine life zone (transition or lower montane forest) (USFS 1991; Dick-Peddie 1993). The mesophytic (wetter) forests have ponderosa pine as a seral tree (regeneration occurs only in early- to mid-succession although older trees may persist into late succession) and are part of the mixed conifer life zone or upper montane forest (USFS 1991; Dick-Peddie 1993).

Ponderosa pine forests are important because of their wide distribution (figure 1), commercial value, and because they provide habitat for many plants and animals. Ponderosa pine forests are noted for their variety of passerine birds resulting from variation in forest composition and structure modified by past and present human use. Subsequent chapters discuss how ponderosa pine forests are associated with different types and number of passerine birds and how humans have modified these forests and affected its occupancy and use by passerine birds. This chapter discusses the ecology and dynamics of ponderosa pine forests and wildlife use in general and

describes natural and human induced changes in the composition and structure of these forests.

Paleoecology

The oldest remains of ponderosa pine in the Western United States are 600,000 year old fossils found in west central Nevada. Examination of pack rat middens in New Mexico and Texas, shows that ponderosa pine was absent during the Wisconsin period (about 10,400 to 43,000 years ago), although pinyon-juniper woodlands and mixed conifer forests were extensive (Betancourt 1990). From the late Pleistocene epoch (24,000 years ago) to the end of the last ice age (about 10,400 years ago), the vegetation of the Colorado Plateau moved southward or northward with glacial advance or retreat. Regional temperatures over the Southwest during the glacial advances may have been 6 °C lower and annual precipitation 220 mm higher in the lowlands than today. Ponderosa pine in the mountains of New Mexico occurred about 400 m lower than where it is found today (Dick-Peddie 1993; Murphy 1994).

With the beginning of warming in the early Holocene, ponderosa pine began colonization of the Colorado Plateau. Pinyon-juniper woodlands shifted upward and northward from a low elevation of just over 450 m to 1,500 m. Pinyon pine (*P. edulis*) reached its present upper limit (about 2,100 m) between 4,000 and 6,000 years ago. The present distribution of ponderosa pine forests in the interior West and Southwest was apparently the result of this rapid Holocene expansion, but the exact cause and manner of this expansion is unknown (Anderson 1989; Betancourt 1987).

Climate and Soils

Climates in ponderosa pine forests are similar throughout the interior Western United States. For example, a comparison of climates at Spokane, Washington and Flagstaff, Arizona where ponderosa pine forests occur with a grassy understory, shows that levels of mean annual precipitation (MAP) at Spokane is 41 cm and at Flagstaff is 57 cm.

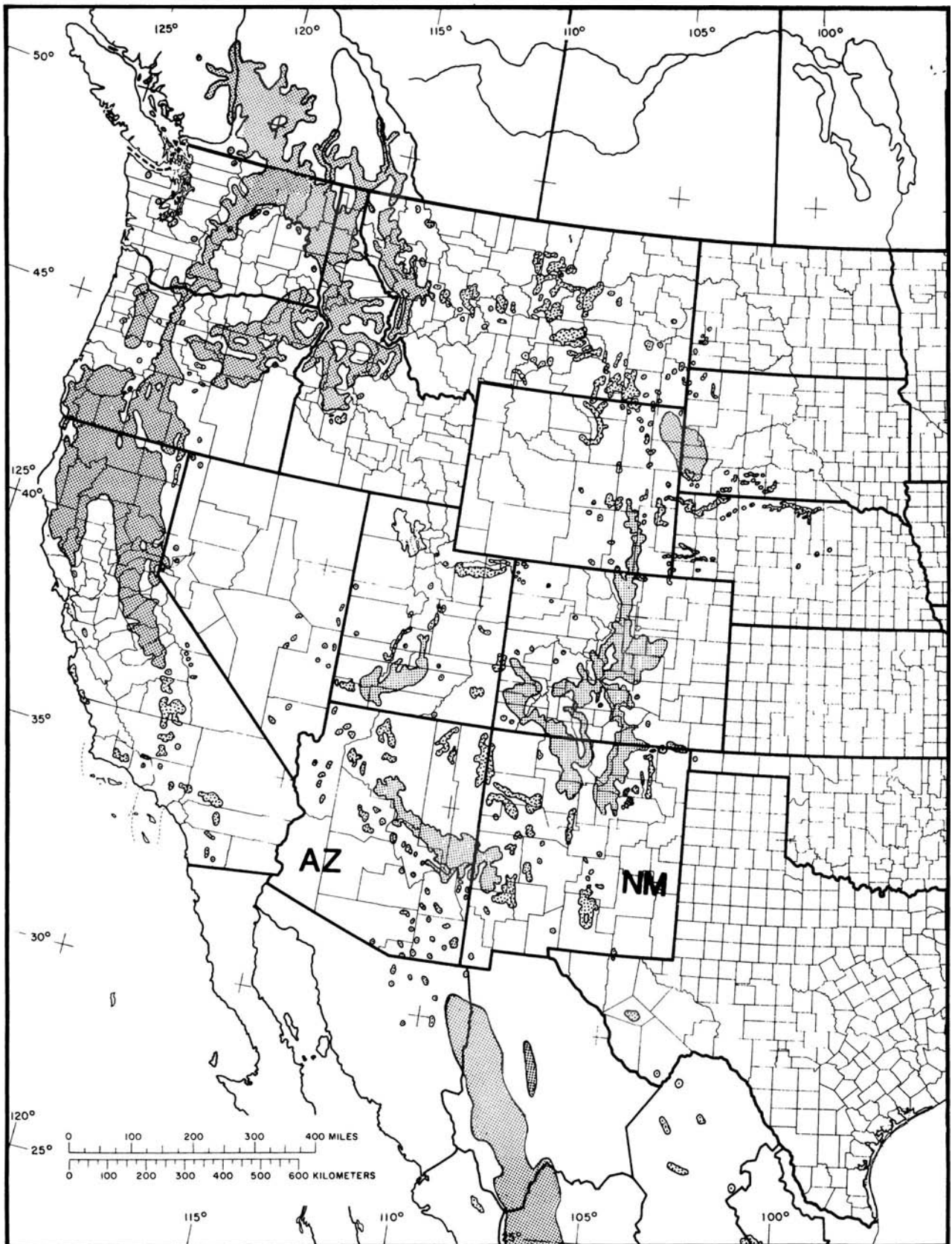


Figure 1. *Distribution of ponderosa pine in North America. Arizona and New Mexico comprise the Southwest area discussed in this chapter (Little 1971).*

Both locations have a pronounced dry season during several warm months when precipitation is insufficient to maintain plant growth. This drought is in July and August at Spokane and May and June at Flagstaff.

Climates of Arizona and New Mexico are described in the General Ecosystem Survey (USFS 1991; table 1). Ponderosa pine forests mostly occur within the High Sun Cold (HSC) and High Sun Mild (HSM) climate zones (table 1). Mean annual air temperatures (MAAT) for xerophytic and mesophytic forests are 9 °C and 6 °C in the HSM zone, and 5 to 7 °C and 4 °C the HSC zone, respectively (table 1). For these climate zones, mean annual precipitation (MAP) is 520 to 560 mm and 660 mm, respectively (table 1). The climate (figure 2a) for xerophytic forests of ponderosa pine/Arizona fescue (PIPO/FEAR) is near the mid-range of MAAT and MAP at Flagstaff (FLA), Pinetop (PIN), and Ruidoso (RUI). In contrast, ponderosa pine/blue grama (PIPO/BOGR) forests at Los Alamos (LOS) are near the lower limit of MAP, and forests of ponderosa pine/silverleaf oak (PIPO/QUHY) at Mt. Lemmon (MTL) are near the upper limit of MAP. Ponderosa pine/Arizona white oak (PIPO/QUAR) forests at Payson (PAY) have the warmest MAAT and ponderosa pine/mountain muhly (PIPO/MUMO) forests around Jacob Lake (JAC) have the coldest MAAT.

The soil moisture regime (SMR) of xerophytic forests is ustic (dry) (USFS 1991). At the stations examined (figures 2b–f), seasonal drought is most severe in May and June and understory vegetation, mostly grasses, becomes dry and flammable. Relationships between fire and climate in the Southwest have been studied by Swetnam and colleagues (Swetnam 1990; Swetnam and Baisan 1996; Swetnam and Betancourt 1990). The SMR of mesophytic forests is udic (wet) (USFS 1991); in these forests there is no drought in upper soil horizons during the average growing season. Therefore, at higher elevations where ponderosa pine is a seral tree of mixed conifer forests, the growing season precipitation is usually sufficient to maintain plant growth.

The soil temperature regime (STR) of ponderosa pine forests in Arizona and New Mexico is generally frigid; in

the southern portions of these states at lower elevations it is mesic (USFS 1991). This shift to warmer soils, coincident with May through June droughts, is indicated by an understory vegetation of broadleafed, evergreen species such as Emory, gray, wavyleaf and silverleaf oaks (*Quercus emoryi*, *Q. grisea*, *Q. undulata*, *Q. hypoleucoides*), manzanita (*Arctostaphylos pungens*), madrones (*Arbutus xalapensis*, *A. arizonica*), yuccas (*Yucca* spp.), and other shrubs and trees (table 1). Although Arizona pine (*Pinus arizonica*) replaces *P. ponderosa* on some mesic soils in southeastern Arizona, forest dynamics and structure are similar.

The distinction between xerophytic and mesophytic zones is essential to understand plant succession in ponderosa pine forests in the Southwest. Beschta (1976) described the climate of a single ponderosa pine type in central Arizona without differentiating the ustic zone, where the pine is climax, from the udic zone, where it is seral. Similarly, both zones were combined in early forest inventories in Arizona and New Mexico (Eyre 1980; Choate 1966; Spencer 1966) and showed considerably more ponderosa pine cover type than there is today (Johnson 1994).

Winter snow storms do occur in Southwestern ponderosa pine forests. In central Arizona annual snowfall ranges from 130 to 250 mm for the ponderosa pine zone to about 250 to 320 mm in the mixed conifer zone (Beschta 1976). South of the Mogollon Rim, the average annual snowfall is estimated at 90 to 165 mm, but reliable snow measurements are unavailable.

Vegetation

Xerophytic Forests

In the lower montane zone at elevations 2,150 to 2,600 m (elevations vary according to latitude and local conditions), there are 37 ponderosa pine forest types based on associated understory vegetation (Dick-Peddie 1993; Moir

Table 1. Summary of climates of Southwestern ponderosa pine forests (USFS 1991).

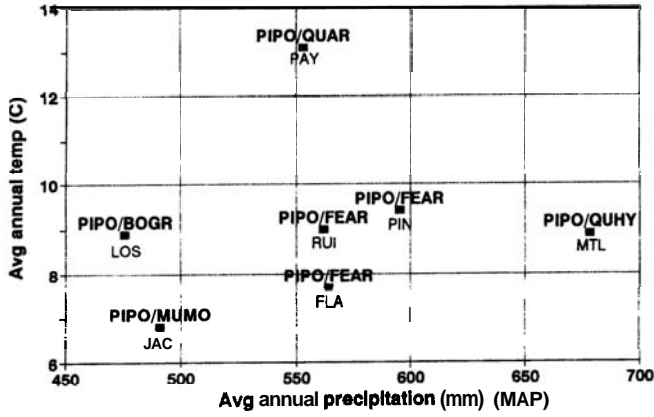
Six-month season with more than 1/2 annual precip.	Winter temp.	Climate category	Vegetation indicators	MAAT (°C)		MAP (mm)	
				XERO	MESO	XERO	MESO
High sun (HS) Apr 1 to Sep 30	Mild (M)	HSM	QUGR, QUEM	9	6	600	700
High sun (HS) Apr 1 to Sep 30	Cold (C)	HSC	PIED, QUGA	5-7	4	520-560	660
Low sun (LS) Oct 1 to Mar 30	Mild (M)	LSM	PICA, QUUN	9	7	600	700
Low sun (LS) Oct 1 to Mar 30	Cold (C)	LSC	ARTR	5-7	4	480-560	660

ARTR = *Artemisia tridentata*
 PIED = *Pinus edulis*
 QUGR = *Quercus grisea*
 QUEM = *Quercus emoryi*

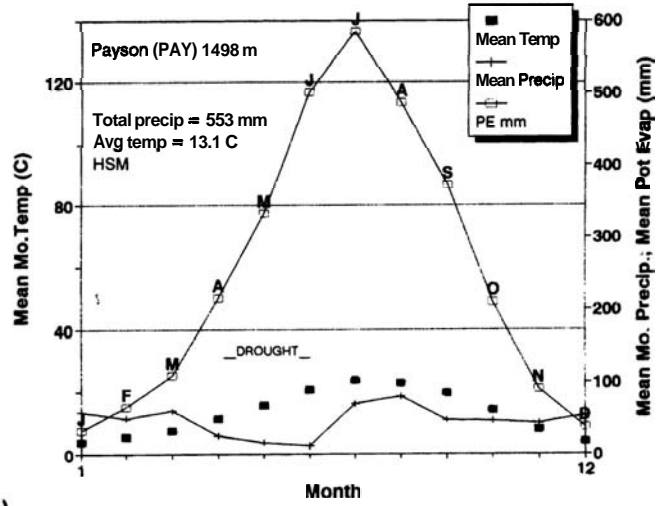
PICA = *Pinus californiarum*
 QUGA = *Quercus gambelii*
 QUUN = *Quercus undulata*

MAAT = mean annual air temp
 MAP = mean annual precipitation
 XERO = xerophytic forests
 MESO = mesophytic forest

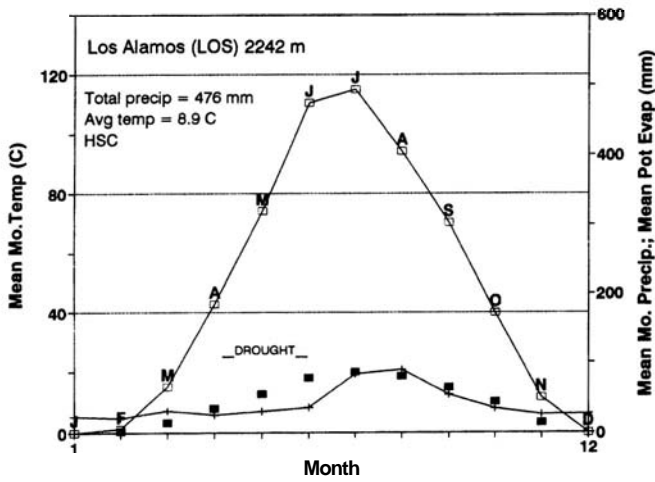
Xerophytic ponderosa pine climate
Precipitation/temperature summary



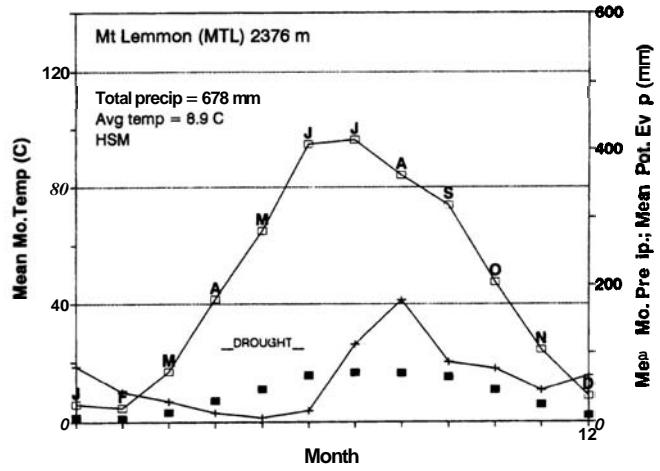
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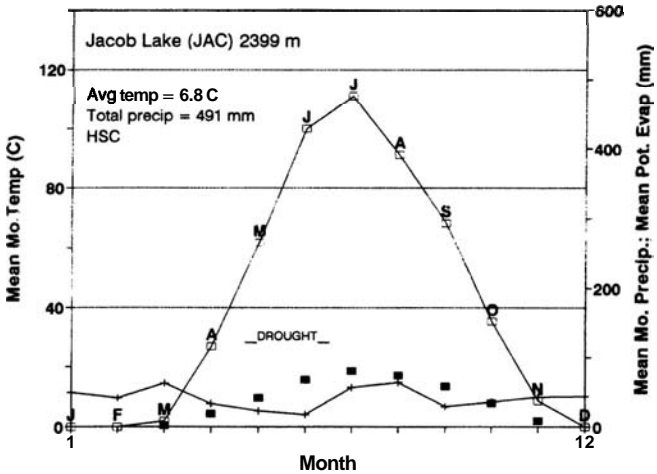
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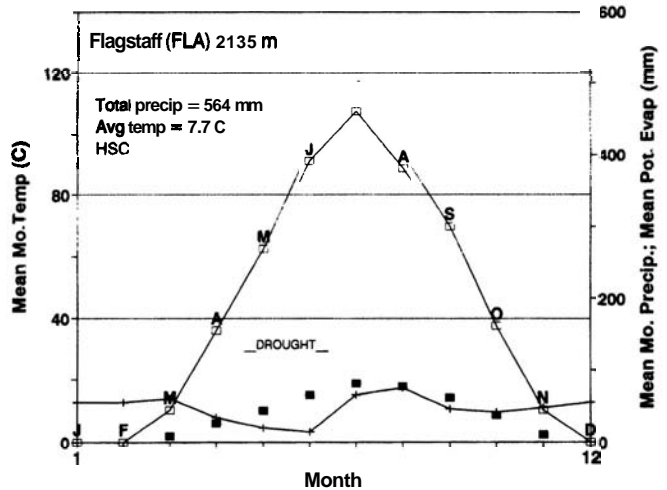
c)



d)



e)



f)

Figure 2. Climate summaries for xerophytic ponderosa pine in North America. PIPO, ponderosa pine; QUAR, Arizona white oak; BOGR, blue grama; FEAR, Arizona fescue; QUHL: silverleaf oak; MUMO, mountain muhly; PAL: Payson; LOS, Los Alamos; RUI, Ruidoso; PIN, Pinetop; MTL, Mt. Lemmon; FLA, Flagstaff; JAC, Jacob Lake.

and Fletcher 1996; USFS 1986, 1987a, 1987b). These types can be combined into 3 major groups, based on similarities in structure, composition, and fire response.

The fringe pine forest types are at dry, warm, lower elevations where ponderosa pine occurs with woody species that are common in the adjoining pinyon/juniper and pinyon/oak/juniper woodlands. Depending on geographic location, typical associated species are *P. edulis*, *P. discolor*, *P. californiarum*, *Juniperus* spp., *Quercus grisea*, *Q. arizonica*, *Q. emoryi*, *Arctostaphylos pungens*, *Artemisia tridentata*, and *Chrysothamnus nauseosus*. Associated trees form a mid-level canopy layer below the ponderosa pine overstory (Marshall 1957). These additional species provide resources for a wide variety of animals; discussed in the wildlife section of this chapter. Blue grama (*Bouteloua gracilis*) is a diagnostic species, and ponderosa pine/blue grama has widespread forest association throughout the Southwest (USFS 1986).

Where precipitation is greater than about 480 mm, blue grama is absent or minor and ponderosa pine occurs with understory bunchgrass species, mainly *Festuca arizonica*, *Muhlenbergia montana*, and/or *M. virescens*. There may be a mid-level canopy of shrubs, copses of oaks, or even an occasional oak tree (Kruse 1992), but these are minor vegetation components. Fires, either lightning- or human-caused, are frequent in these dry forests. Southwestern pine forests can be grouped with ponderosa pine forests in other areas of in the Western United States that share a similar fire ecology. Southwestern ponderosa pine/bunchgrass forests are similar to warm, dry forests in Idaho, Montana, and Utah (Davis et al. 1980; Crane and Fischer 1986; Fischer and Bradley 1987; Bradley et al. 1992). Numerous descriptions of presettlement forests in the Southwest (Woolsey 1911; reviews Cooper 1960; Covington and Moore 1994; Moir and Dieterich 1988) apply to this group of forests.

The third group of xerophytic ponderosa pine forests are those with understories dominated by shrubs and mid-level trees. Bunchgrasses may still be abundant, especially as patches in open areas. Common woody associates include *Quercus gambelii*, *Q. undulata*, *Robinia neomexicana*, *Cercocarpus montana*, and *Symphoricarpos oreophilus*. These forests are similar in structure and fire responses to the warm, moist ponderosa forests of central Idaho and Utah (Crane and Fischer 1986; Bradley et al. 1992).

Mesophytic Forests

In mesophytic forests at elevations 2,400 to 3,000 m (elevations vary according to latitude and local conditions), ponderosa pine is a major seral tree in 11 forest associations (USFS 1986, 1987a). These forests are identified by increasing importance of *Pseudotsuga menziesii* (Douglas-fir), *Abies concolor* (white fir), *Picea pungens* (blue spruce), and *Pinus strobiformis* (Southwestern white pine) as cli-

max trees (Dick-Peddie 1993; USFS 1986, 1987a, 1987b; figure 3). Thousands of hectares of ponderosa pine-dominated mixed conifer forest existed in the Southwest in the early- to mid-20th century and were inventoried as part of the ponderosa pine cover type (Johnson 1993, 1994; Eyre 1980). Ponderosa pine and the other conifers were often associated with aspen (*Populus tremuloides*), which occurs where previous fires favored its regeneration (Jones 1974; Abolt et al. 1995). Without recurring fires, however, conifers eventually replace aspen (Moir and Ludwig 1979; Dick-Peddie 1993). The aspen and coniferous mesophytic forests of the Southwest have structures and fire responses similar to those of mesic forests in the central and northern Rocky Mountains (Crane and Fischer 1986; Fischer and Bradley 1987, Bradley et al. 1992).

A number of mesophytic forest types in the Southwest include a bunchgrass understory of *Festuca arizonica*, *Muhlenbergia montana*, and/or *M. virescens*. In these types, ponderosa pine, Douglas-fir, and sometimes Southwestern white pine are the most important trees. The occasional white fir or blue spruce in these forests are evidence of the udic soil depicted in figure 3. Counterparts in western Montana and central Idaho are the warm, dry Douglas-fir forest types (Fischer and Bradley 1987; Crane and Fischer 1986).

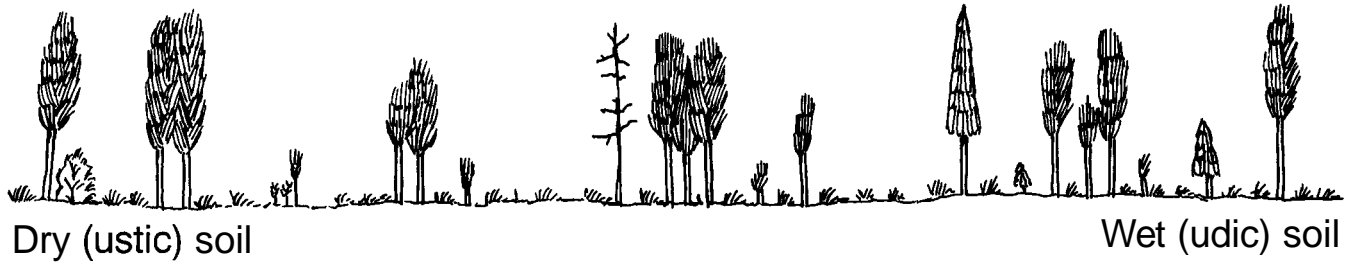
Ponderosa pine and other conifers also occur with an understory of shrubs or mid-level trees such as *Quercus gambelii*, *Robinia neomexicana*, *Symphoricarpos oreophila*, *Holodiscus dumosus*, or *Salix scouleriana* (for more complete lists of associated species see Moir and Ludwig 1979). Rather than bunchgrasses, the herbaceous layer is composed of mesic species such as *Bromus richardsonii*, *Artemisia franserioides*, *Osmorhiza chilensis*, *Geranium richardsonii*, and *Viola canadensis*. Similar forests of moist Douglas-fir occur in Idaho (Crane and Fischer 1986), western Montana (Fischer and Clayton 1983), and Utah (Fischer and Bradley 1987; Bradley et al. 1992).

Finally, there are mixed conifer forests in the Southwest where ponderosa pine is minor or absent. These are the cold coniferous forests (Dick-Peddie 1993; USFS 1986, 1987a, 1987b) where stand-replacing fires favor regeneration to aspen or tall shrubs such as *Acer glabrum*, *Salix scouleriana*, or *Holodiscus dumosus*. The coniferous species of these forests are Douglas-fir, white fir, blue spruce, Southwestern white pine, and sometimes bristlecone pine (*Pinus aristata*).

Fire

In the last decade forest fires have increased in Arizona and New Mexico (figure 4). Fire, the most important natural abiotic disturbance in ponderosa pine forests (Moir and

a)



b)



c)

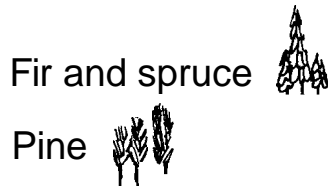


Figure 3. Generalized climate-differentiated ponderosa pine forests in Arizona and New Mexico. Diagram a) depicts the open, grassy pine forests described around the turn of the century (1890 to 1925). The open forest has a grassy understory, sparse ponderosa pine regeneration in the dry end, and, as precipitation increases, poor regeneration of ponderosa pine, Douglas-fir, blue spruce, or white fir. Diagram b) illustrates the same forest under average conditions in the 1990s (Johnson 1993, 1994). Diagram c) depicts the same forest 10 to 15 years after a fire holocaust. Natural or managed reforestation is occurring, although understory grasses may not be the same composition or density as that in diagram a) (Foxy 1996). Artwork by Joyce Patterson.

Dieterich 1988; Moody et al. 1992; Covington and Moore 1994), determines plant composition, succession, and forest structure. Fire ecology, especially since the 1930s and in the xerophytic ponderosa pine/bunchgrass forests, is well studied (Weaver 1943 and 1967; Biswell 1972; Cooper 1960; Ahlgren and Ahlgren 1960; Biswell et al. 1973; Habeck and Mutch 1973; Wright 1978; Moir and Dieterich 1988; Morgan 1994; Pyne 1996; Allen 1996). Forest succession under different fire regimes is generalized in the papers cited above and should be considered as hypotheses. Although they present sequences of species replacement and stand structure, these models generally do not specify the time between stages.

Frequent, low-intensity fires were part of the ecology and evolutionary history of ponderosa pine forests. Crown fires seldom occurred or were confined to small thickets (Woolsey 1911; Pyne 1996). Fires in the xerophytic pine forests occurred every 2 to 12 years and maintained an open canopy structure and a variable, patchy tree distribution (White 1985; Cooper 1961; Covington and Moore 1994; figure 3). The open, patchy tree distribution from fires and other disturbances, such as bark beetles and mistletoe, reduced the risk of fire holocausts. Downed woody material was sparse, and fires before about 1890 were fueled mostly by herbaceous material that accumulated at the end of the annual drought period. These low-intensity, surface fires reduced ground fuel, thinned smaller trees, and invigorated the understory maintaining the open forest structure (Ahlgren and Ahlgren 1960; Ffolliott et al. 1977).

Understory burns occurring over millennia helped forest vegetation adapt to fire (Habeck and Mutch 1973; Rapport and Yazvenko 1996). For example, the thick, corky bark of mature (15 to 20 cm diameter at breast height [dbh]) ponderosa pine and Douglas-fir insulates the cambium

from killing temperatures. Another adaptation to fire, as well as drought, is the longevity of seed trees. Successful tree reproduction occurs only when heavy seed crops and germination coincide with moist springs and summers and a long fire-free period (Pearson 1950). Because these factors only occasionally occur simultaneously, tree reproduction is episodic. Decades may pass before conditions for reproduction and seedling survival are favorable (White 1985). However, ponderosa pine and Douglas-fir are long-lived (4 to 5 centuries) and over that time numerous opportunities for reproduction and establishment exist (Pearson 1950). Although ponderosa pine and Douglas-fir have high genetic diversity over broad areas, human impacts, primarily by harvest and fire suppression, may have modified their fitness for future environments and human uses (Ledig 1992).

Many other plants of ponderosa pine forests are either fire resistant or fire dependent. For example, since most fires begin near the end of a warm season drought, understory species whose seeds have long dormancy and whose germination is stimulated by high soil temperatures (*Arctostaphylos pungens* and *Ceanothus fendleri*), are unaffected or benefitted by fire. Another fire adaptation is rapid sprouting after fire. Examples include oaks (*Quercus* spp.), alligator juniper (*Juniperus deppeana*), aspen, maples (*Acer* spp.), Scouler willow (*Salix scouleriana*), and serviceberry (*Amelanchier alnifolia*).

The length of fire-free intervals is an important attribute of an area's fire regime. Long fire-free periods allow trees to grow adequately thick bark to protect the cambial cells of the lower stem and root crown from the lethal temperatures of the next surface fire. But during a long interval between fires, woody fuels and mistletoe brooms (dense, woody structures that develop in tree crowns parasitized by dwarf mistletoe) accumulate, increasing the probability that the crown will be scorched and/or the roots killed (Harrington and Sackett 1992). To prevent destructive, high-intensity fires, tree thinning and manual fuel removal (especially around the base of large trees) is performed as part of fuel-reduction burn prescriptions (Kurmes 1989; Brown et al. 1994; Covington and Moore 1992; Harrington and Sackett 1992).

Much current research is dedicated to estimating fire frequencies in the xerophytic and mesophytic ponderosa pine forests of the Southwest (Swetnam and Baisan 1996). Working in a ponderosa pine/Arizona white oak stand surrounded by chaparral in Arizona, Dieterich and Hibbert (1990) reported that low-intensity, surface fires occurred somewhere within the 87 hectare (ha) study site in 67 of the years between 1770 and 1870. In similar open pine forests of the Rincon Mountains, Baisan and Swetnam (1990) reported a mean fire interval (MFI) of 7 years in the century before 1890; these were low-intensity, surface fires. In the earliest study of a mixed conifer forest containing ponderosa pine, Dieterich (1983) reported a 22-year MFI

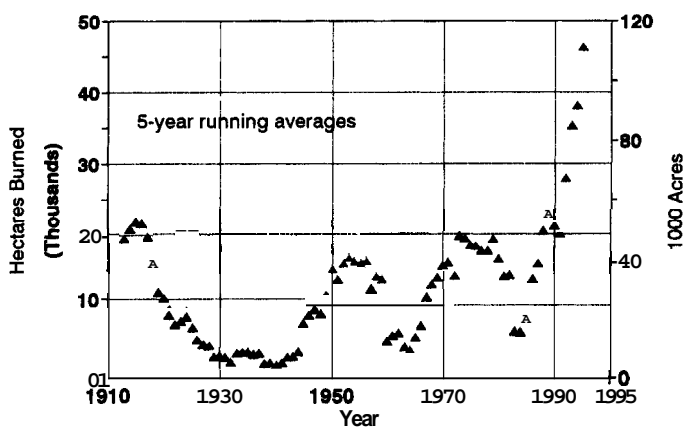


Figure 4. Forest fires in Arizona and New Mexico, 1910–1995 (U.S. Department of Agriculture, Forest Service, Southwest Region).

(combining fires in several forest communities) in the Thomas Creek drainages in Arizona before 1890. The lack of fire since then allowed shade tolerant trees, such as white fir and Engelmann spruce, to establish and increase overall tree density in the study area.

There is evidence that ponderosa pine forests with grassy understories in the xerophytic or mesophytic zones have similar fire regimes. Unpublished data from the Sacramento and White Mountains, New Mexico (Huckaby and Brown 1996) reveal high fire frequencies in Douglas-fir and white fir forests where grasses were a major component of the forest understory. Between 1712 and 1876, a Douglas-fir climax site on James Ridge had 25 fires (MFI = 7 years). Between 1790 and 1890, the MFI was 4.5 years for a white fir climax site (white fir/Arizona fescue association) on Buck Mountain. Fires at each of these sites were low-intensity, surface fires that maintained an open forest structure. High fire frequencies (low MFIs) were also found in a wide variety of other ponderosa pine and mixed conifer forest types, with or without present-day grassy understories.

Data indicating frequent ground fires before the 20th century have been collected for the Pinaleno Mountains, Arizona (Grissino-Meyer et al. 1995), the Jemez Mountains, New Mexico (Allen et al. 1995; Touchan et al. 1996), the Mogollon Mountains, New Mexico (Abolt et al. 1995), and the Sandia and Manzano Mountains, New Mexico (Baisan and Swetnam 1995b). In all cases, the MFI before 1890 was 12 years or less. Savage and Swetnam (1990), Abolt et al. (1995), and Touchan et al. (1995) suggest that continuity of understory fuels, especially the grass layer, maintained high frequencies of low-intensity, surface fires along the entire gradient from woodlands to the spruce-fir forests. This hypothesis is supported by evidence that forests with grassy understories were once extensive and continuous over a large elevational range. Descriptions of forests around the turn of the century noted open, large areas not confined to xerophytic pine forests. Most ecologists agree that hot, crown fires were not extensive in these open ponderosa pine forests, although small thickets would have been destroyed by spot crown fires. Because fires have been suppressed in the last 100 years, much of the area classified as ponderosa pine cover type was previously within the mesophytic mixed conifer climate (Beschta 1976; Johnson 1994; Covington and Moore 1994).

Other Natural Disturbances

Although only a few species of forest insects and pathogens described are the principal natural agents of change in Southwestern ponderosa pine forests, they interact with each other and with other abiotic factors to generate for-

ests with varying species composition and landscape patterns (Lundquist 1995a). Some of these organisms have coevolved with host trees, while others, such as white pine blister rust, were recently introduced (Wilson and Tkacz 1996). Each insect or pathogen attacks only certain host species and parts (foliage, stems, roots) and is controlled by various host and environmental conditions. Tree competition, drought, lightning strike, wind damage, site conditions, and fire can stress a tree and increase its vulnerability to opportunistic insects and fungi. The initial attack can lead to invasion by other insects and pathogens, tree death, and deterioration. Many insect and pathogen species do not require the host tree to be stressed before attack, instead they proceed rapidly as host resistance is overcome (Franklin et al. 1987). Injury from biotic agents can also increase damage from abiotic factors. For example, decay increases the likelihood of stem failure, and mistletoe brooms provide fuel continuity from the ground to the crown.

In addition to fire, important abiotic factors affecting ponderosa pine in the Southwest are drought, lightning, winter drying, and hail (Rogers and Hessburg 1985). Droughts several years long occur periodically across the region and are frequently severe. Pine mortality is usually associated with secondary bark beetles at the end of the drought (Lightle 1967). Lightning is a common cause of mortality for large ponderosa pine, especially in certain geographic areas with high lightning frequency such as the Mogollon Rim, Arizona (Pearson 1950). Winter drying is the result of foliage desiccation when soil and roots are frozen (Schmid et al. 1991). The affect on ponderosa pine can be devastating but most trees recover, as in 1985 in northern New Mexico (Owen 1986). Violent summer thunderstorms can produce severe hail, stripping trees of much of their foliage. Such a storm occurred on the Mescalero Apache Indian Reservation in the 1950s (Shaw et al. 1994).

Insects

Although many insect species feed on nearly every part of ponderosa pine (Furness and Carolin 1977), ecologically the most severe are the defoliators and bark beetles. Conifer sawflies (Diprionidae) and various moths, especially the pandora moth (*Coloradia pandora*), occasionally reach outbreak status; however, although foliage is removed, trees usually recover. In the mesophytic ponderosa pine zone, the western spruce budworm (*Choristoneura occidentalis*) can induce a temporary increase in ponderosa pine growth while depressing the growth of competing Douglas-fir and white fir, which are the principal budworm hosts (Swetnam and Lynch 1993). Pine bark beetles (*Dendroctonus* and *Ips*) feed on the cortex and cambium and introduce fungi that promote rapid tree death and decay.

The roundheaded pine beetle (*D. adjunctus*) is the most common bark beetle that attacks pines in the Southwest (Chansler 1967; Furness and Carolin 1977). This beetle infests ponderosa and related pines from Colorado and Utah south to Guatemala (Massey et al. 1977). Outbreaks have occurred periodically and killed large numbers of pole- and sawtimber-sized ponderosa pine (trees larger than 23 cm dbh), especially in the White and Sacramento Mountains in 1950, 1960s, 1970s, and 1990s (Lucht et al. 1974; Chansler 1967; Flake et al. 1972). Eruptions of roundheaded pine beetle are often accompanied by the western pine beetle, Mexican pine beetle, and Ips beetles, which establish on poor sites or in mistletoe infested areas. Trees are attacked in groups of 3 to over 100; smaller trees and those in dense thickets are most likely to be attacked. Killed trees rapidly develop a brown cubical decay and break near the groundline.

The western pine beetle (*D. brevicornis*) is most damaging in the far western United States and British Columbia, but its range extends into the Southwest and Mexico (DeMars and Roettgering 1982). This beetle usually occurs in one or a few widely scattered trees already weakened by drought, lightning, stagnation, root disease, or other disturbances. Although it usually creates small canopy gaps, the western pine beetle can cause significant mortality and increased fire hazard in drought and competition-stressed stands; an outbreak occurred near Flagstaff, Arizona from 1980 to 1982 (Telfer 1982).

The mountain pine beetle (*D. ponderosae*) is the most extensive bark beetle to attack ponderosa pine in western North America. In the Southwest, however, outbreaks have been restricted to the north Kaibab Plateau (Parker 1980). Like the roundheaded pine beetle, the mountain pine beetle can develop large populations in dense stands and then disperse to kill large numbers of otherwise vigorous trees.

The Arizona five-spined engraver beetle (*Ips lecontei*) is the most common bark beetle in central and southern Arizona. Although this beetle usually occurs in slash and small, weakened trees, it has multiple generations per year that allow populations to build quickly (Parker 1991).

Dwarf Mistletoe

Southwestern dwarf mistletoe (*Arceuthobium vaginatum* subsp. *cryptopodum*) is a widely distributed parasitic plant that causes severe damage and mortality to its principal host, ponderosa pine (Hawksworth and Wiens 1995). Southwestern dwarf mistletoe occurs throughout the range of ponderosa pine in New Mexico and Arizona and extends into neighboring states. Other infected pines include Arizona pine, Apache pine (*Pinus engelmannii*), and Colorado bristlecone pine (*P. aristata*). Region-wide, 40 percent of the commercial pine forest is infested. Infection is more common in some forests; 70 percent of the stands in the Lincoln National Forest are infested (Maffei

and Beatty 1988). Growth loss and mortality from this mistletoe in the Southwest is estimated at 150 to 200 million board feet per year (Walters 1978). The severity of growth loss for infected trees is related to disease intensity (Hawksworth 1977). Radial growth increment is reduced by 9 percent, 23 percent, or 53 percent for trees moderately infected (class 4), heavily infected (class 5), or very heavily infected (class 6), respectively (Hawksworth 1961). Survival of infected trees is also reduced; 10-year mortality rates of 9 percent, 12 percent, and 38 percent for trees rated class 4, 5, and 6, respectively, have been observed (Hawksworth and Lusher 1956). Other effects of mistletoe infestation include reduced reproductive output (Koristan and Long 1922) and increased likelihood of attack and mortality from bark beetles and pandora moth.

In mesophytic forests, selective loss of ponderosa pine from dwarf mistletoe can accelerate conversion to Douglas-fir or white fir. However, Douglas-fir in ponderosa pine stands is a principal host for the Douglas-fir dwarf mistletoe (*Arceuthobium douglasii*), which is very damaging to that species. The dense swollen and branching structures resulting from mistletoe infection, known as witches' brooms, often form near the ground. Broomed trees are more readily killed by even a low-intensity fire, and these brooms provide a fuel ladder into the crown (Alexander and Hawksworth 1974; Harrington and Hawksworth 1990). Mistletoe spread and intensification is greatest in stands with a multiple story structure.

Although there is evidence that mistletoe abundance has increased in the last century (Maffei and Beatty 1988), it has long been an important natural disturbance (figure 5). In addition to mistletoe shoots and associated insects providing wildlife forage, infections and brooms are especially suitable for roosting and nesting birds. Dead tops and snags created by mistletoe also enhance wildlife habitat (Bennett et al. 1996; Hall et al. this volume; Rich and Mehlhop this volume). Although mistletoe infestation can increase canopy and wildlife diversity (Mathiasen 1996), the desired amounts or tolerable levels for resource objectives other than timber production are unknown.

Plant Pathogens

Root disease fungi, including *Armillaria ostoyae* and *Heterobasidion annosum*, are a major cause of tree mortality and growth loss in the Western United States. In the Southwest, 446 thousand ha are seriously affected by root diseases (DeNitto 1985), which reduce growth by 10 percent region-wide or by 25 percent in severely damaged stands (Rogers and Hessburg 1985). Complexes of root disease with insects and pathogens were associated with 34 percent of the mortality in all stands (Wood 1983). Root disease is more common in the mesophytic than xerophytic ponderosa pine zone. *Armillaria* is generally found in stands 10 to 25 years old, but in the Jemez Mountains,

New Mexico, 50 years of selective logging intensified disease severity and lead to extensive mortality in all ages of ponderosa pine (Marsden et al. 1993). *Annosus* root disease also infects ponderosa pine throughout the Southwest but is less common than other diseases. Like the mortality patches caused by dwarf mistletoe, centers of root disease reduce

high canopy densities and increase patchiness. As discussed in the wildlife section of this chapter, these changes to forest structure are important to wildlife. Many of the organisms described here contribute to gap dynamics, forest structural diversity, and wildlife use in ponderosa pine forests (Lundquist 1995a, 1995b).



Figure 5. Stand of ponderosa pine June 4, 1990, Tonto Basin, Arizona. The multistory structure and high incidence of dwarf mistletoe disturbance is evidenced by the many large brooms in lower crowns and progressive dieback of upper crowns. Giffort Pinchot, the photographer, noted the sparsity of understory vegetation, consisting of only a little lupine.

The white pine blister rust caused by the fungus *Cronartium ribicola*, was discovered in the Sacramento Mountains of New Mexico in 1990. This fungus infects Southwestern white pine but has an indirect impact on ponderosa pine because as these tree species compete in mixed conifer forests, southwestern white pine is less susceptible to insects and diseases than ponderosa pine. Rust mortality of Southwestern white pine could possibly decrease its buffering effect on various other disturbances and will have a major impact as the disease progresses (Wilson and Tkacz 1996); at present the ecological consequences are speculation.

Wood Decay Fungi

Although there are many wood decay fungi (Basidiomycetes) of ponderosa pine (Gilbertson 1974), a few species commonly cause trunk rot. Red rot (*Dichomitus squalens*) is a major stem decay fungus of live ponderosa pine in the Southwest (Andrews 1955). An estimated 15 to 25 percent of the gross volume in old-growth ponderosa pine was decayed by red rot (Andrews 1955; Lightle and Andrews 1968). Common decay fungi that cause brown cubical rots of ponderosa pine include *Phellinus pini* (red ring rot), *Fomitopsis officinalis*, *Phaeolus schweinitzii* (more common on Douglas-fir), *Veluticeps berkeleyi*, and *Lentinus lepideus* (usually associated with fire scars). In addition to their important roles in nutrient recycling and organic decomposition, decay fungi provide the soft wood habitat in snags that is required by numerous cavity-dependent species as discussed in later chapters.

Overstory-Understory Relationships

General

Rather than directly affecting passerine birds, land managers manipulate forest composition and structure. To understand why and how the environment of passerine birds in ponderosa pine forests is always changing, it is necessary to comprehend the interactions that determine forest composition and structure. Plant succession in ponderosa pine forests is a complex of overstory-understory (O-U) dynamics responding to disturbances. **Overstory-understory** refers to the effects of tree canopies (overstory) and ground-layer plants (understory) including shrubs, herbaceous vegetation, cryptogams (mostly mosses and lichens) on the soil surface, and tree seedlings. The heights

that species display canopies is a continuum, so there is no precise definition the O and U classes. Trees, shrubs, herbs, and nonvascular plants (such as mosses and lichens) are usually easily distinguished, and their canopy levels can be assigned to local condition classes. Competition also occurs in the soil; for example, as root competition for soil water or the mycorrhizal differences between herbaceous and coniferous vegetation (Kendrick 1992; Kloptek 1995). Figure 6a, a generalized model, shows O and U competing, but their effects cannot be separated from other abiotic and biotic factors such as prescribed or wild fires, forest insects and pathogens, and soil microorganisms. At any location, both climate and soil influence the reactions shown in figure 6b. This climate, soil, vegetation influence is the basis of ecosystem classification, mapping, and interpretation used by the USDA Forest Service Southwest Region (USFS 1991). Plant succession, which after a fire holocaust killed virtually all of the above-ground vegetation, has been studied quantitatively, most notably after the La Mesa fire near Los Alamos, New Mexico (Foxx 1996).

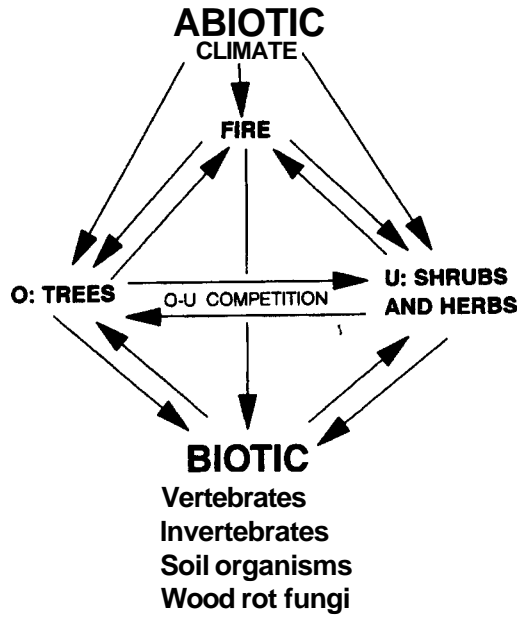
A large class of O-U relationships are associated with tree death and falls (Denslow and Spies 1990). Canopy gaps operate on individual trees, especially the larger dominant or codominant trees. In open, low density pine forests before European settlement, gap processes may have been unimportant because recurrent fires determined tree and understory spatial patterns. However, in this century as tree densities greatly increased, new spatial patterns were created by expanding root rot pockets (Wood 1983) and other diseases, increased abundance of dwarf mistletoe, insect outbreaks, and rapid filling of former open areas by tree regeneration (Allen 1989). Today, especially in xerophytic forests, canopy gap processes may be dominant in O-U dynamics (Lundquist 1995b, 1995c).

In mesophytic pine forests, the death of large trees may be important to maintain shade intolerant trees such as ponderosa pine, aspen, and gambel oak. Forest pattern is determined by combinations of patchy, natural fires (Jones 1974) and other gap-creating factors that stress trees and expose them to numerous mortality agents (Franklin et al. 1987; Lundquist 1995c). In both xerophytic and mesophytic pine forests, silvicultural (Schubert 1974; Oliver and Ryker 1990) or disturbance management (Geilset al. 1995) are used to create or maintain gaps in the absence of fire. In mesophytic forests, however, small canopy gaps are usually filled by shade tolerant trees (Dieterich 1983; Ffolliott and Gottfried 1991). Small gaps do not ensure that shade intolerant trees, such as ponderosa pine, gambel oak, or aspen, or herbs, will be maintained (Moir 1966).

Understory Influence on Trees

Research has focused on competition between the herbaceous layer, particularly grasses and tree seedlings

a)



b)

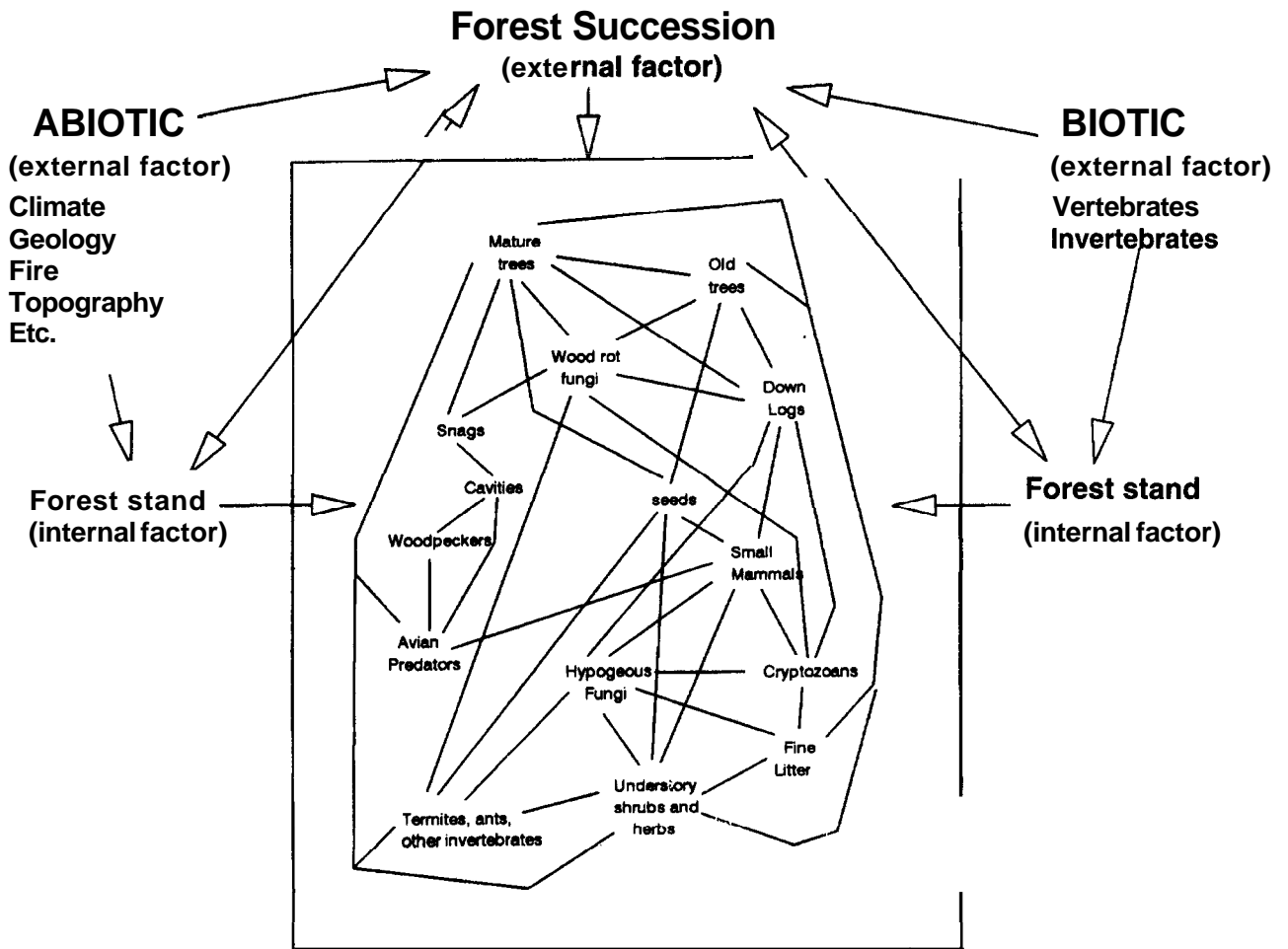


Figure 6. a) Simplified, schematic representation of overstory–understory relationships and ecological associations (Verner et al. 1992). b) A forest stand (internal factors) and the surrounding environment (external factors) that influence the nature and intensity of stand dynamics.

(figure 6a). Competition can be for light (Moir 1966), nutrients (Elliott and White 1987; Moir 1966), water (Larson and Schubert 1969; Embry 1971; Miller 1988), and combinations of these (Moir 1966). Sometimes, shrubs can lessen tree seedling survival or diameter growth (White 1987; Rejmanek and Messina 1989). In the Southwest, *Festuca arizonica* is particularly competitive because it consumes soil moisture during the drought season of April and May (Pearson 1931, 1942, 1950). Allelopathy (compounds produced by one plant species that inhibit the establishment or growth of another species) has also been suggested as a means of tree control (Rietveld 1975; Stewart 1965); however, this subject has received little recent attention. The detrimental effects of understory vegetation on tree establishment can be mitigated by grazing and burrowing animals. Browsing, grazing, or burrowing animals create microsites where reduced herb or shrub competition and exposed mineral seedbeds enhance pine seed germination, seedling survival, and growth (Rummell 1951; Doescher 1987).

Fire also has direct effects on small trees and ground cover (figure 6a). Generally, fire stimulates the understory while killing tree seedlings, saplings, or entire thickets. Fire is the principal means of restoring cover and grass vigor and maintaining or invigorating shrubs (Martin 1983; Harper and Buchanan 1983; Biswell 1972; Bunting et al. 1985; Pearson et al. 1972; Harris and Covington 1983; Andariese and Covington 1986; Ffolliott et al. 1977; Moir 1966). Fire favors understory vegetation by reducing tree competition for sunlight, moisture, and nutrients, accelerates the nutrient cycle, and, by killing trees, changes the soil-water relationship usually to the benefit of ground vegetation. In the past, fire was often carried by extensive and continuous understory vegetation, resulting in small-tree mortality over large areas (Abolt et al. 1995). Before European settlement, recurrent fire was the principal agent maintaining the relationship between overstory trees and understory vegetation. When the herbaceous or herb-shrub vegetation became depleted by overgrazing (Touchan et al. 1995; Savage and Swetnam 1990), heavy tree seedling occurred in the Southwest and elsewhere. The effects of grazing are discussed in Chapters 2, 3 and 6. Fuel reduction and reduced competition between trees and the understory have resulted in increasing tree densities during this century (Pearson 1950; Allen 1989; Savage and Swetnam 1990; Brown et al. 1994; Touchan et al. 1996; Moir and Fletcher 1996).

Tree Influence on Understory

Once past their seedling stage, continued growth of pines or other trees reduces cover, vigor, density, and biomass of many understory species. Particularly affected are species that grow best in open meadows or full sunlight (Ffolliott and Clary 1982). However, O-U dynamics vary greatly among sites and forest types, so generalized sta-

tistical models are unsatisfactory (Mitchell and Bartling 1991). Gap processes may be important, depending on fire history, gap size, and gap microclimate. Dense thickets of conifers in their sapling or pole stages of succession can extinguish understory vegetation. In livestock grazing allotments, the adverse influence of trees on ground vegetation is well-known in ponderosa pine/bunchgrass and ponderosa pine/blue grama rangelands (Arnold 1950; Reid 1965; Clary and Ffolliott 1966; Currie 1975; Johnson 1953; Smith 1967; Brown et al. 1974). Biswell (1972), citing data from research in the Black Hills, reported declines in herbage biomass from 1,860 kg/ha in openings to 39 kg/ha under closed ponderosa pine canopies. In northern Arizona pine/bunchgrass ranges, Jameson (1967), using negative exponential equations to fit tree basal areas to herbage harvest data, showed declines from 784 kg/ha in areas without trees to less than 56 kg/ha where pine basal areas exceeded 23 m²/ha. Working in ponderosa pine stands with a grassy understory in eastern Washington, Moir (1966) reported that low supplies of nitrogen and reduced light acted additively and interactively under developing pine thickets to suppress *Festuca idahoensis*. Moir found reduced inflorescence production in stressed grasses followed by reduced foliar cover.

Oaks are a valuable resource used by numerous birds and mammals. The adverse relationships between pines and oaks can be severe. Neither deciduous nor evergreen oaks tolerate shade. They grow best in full sunlight and are often quickly started by hot, stand-replacing fires that induce sprouting. Sprouts grow rapidly, soon dominate burned sites, and often suppress pine regeneration and growth (Hanks and Dick-Peddie 1974; Harper et al. 1985). However, oaks are suppressed and die back once conifers overtop them. In open stands where oaks and junipers form a distinctive mid-layer canopy, such as the pine-oak woodlands of Marshall 1957 and ponderosa pine/gambel oak forests, oaks persist as mid-level trees or as groups of clustered stems if the density or basal area of taller, emergent pines is low. But as pine canopies close during advanced stages of forest succession, oaks die back and are maintained as suckers from below-ground rootstock. Suckering can take place for decades until the next crown fire occurs (USFS 1986, 1987a, 1987b). Oaks growing in full sunlight will coppice from basal portions of the stem and grow rapidly if fire or cutting kills the overstory trees. Both coppicing and suckering are adaptations to fire. If large oak trees, those greater than a specified diameter and taller than a specified height, are part of the desired landscape, then overtopping by conifers must be prevented until the desired heights and diameters of oak are attained. Before about 1890, recurrent surface fires helped maintain oak and pine codominance (Dieterich and Hibbert 1990; Moir 1982; Swetnam et al. 1992). Marshall (1963) claimed that the grassy pine-oak savannas in northern Mexico were maintained by natural fires, whereas

comparable, densely stocked and grass deficient pine-oak forests in the United States were due to aggressive fire suppression programs.

Plant-Animal Relationships

Overstory-understory relationships are directly and indirectly linked by numerous food webs. Some of the more well-known relationships are mentioned in this chapter. Nearly all ponderosa pine forests in the Southwest contain livestock grazing allotments (Raish et al. this volume; Finch et al. this volume) and many areas contain elk and deer. Mitchell and Freeman (1993) discuss the complex interactions of fire, deer, livestock, predators (especially mountain lions), and understory vegetation on the North Kaibab Plateau, which contains extensive ponderosa pine forests (Madany and West 1983). Herbivores directly affect tree structures by trampling or browsing on tree seedlings and saplings (Cassidy 1937; Currie et al. 1978; Eissenstat et al. 1982; Pearson 1950; Crouch 1979).

Browsing on small trees may affect both conifers and deciduous trees. Aspen regeneration is a preferred food by domestic livestock, elk, and deer; severe browsing prevents regeneration where small aspen patches are part of a larger landscape (Crouch 1986). By contrast, aspen regenerates well in mesophytic forests after extensive stand-replacing fires as, for example, the Escudilla Mountain burn in Arizona. Browsing can also affect other important understory species such as gambel oak (*Quercus gambelii*), antelope bitterbrush (*Purshia tridentata*), junipers, snowberry (*Symphoricarpos* spp.), and deerbrush (*Ceanothus fendleri*) (Harper et al. 1985; Harper and Buchanan 1983; Kruse 1992).

Bark damage by bears, porcupines (whose principal food in winter includes pine phloem), antlered animals, and humans affects individual trees. Feeding impacts on selected ponderosa pines by porcupines and Abert's squirrels may have substantial affect on tree genetics (Linhart et al. 1989). The Abert's squirrel was described by Pearson (1950) as "one of the most destructive of all animals" because of twig cutting, seed and cone herbivory, and defoliation of terminal twigs of ponderosa pine. As mentioned, animals feeding on understory shrubs and herbs increase tree densities and dominance by reducing understory competition. Doescher (1987) and others suggested livestock grazing practices that create a favorable balance between livestock numbers and season of grazing, forest or plantation pine growth, and maintenance of understory productivity.

Animals have an important role through mycophagy (fungus eating) in forest regeneration and tree growth. Hypogeous fungi (fruiting below ground) are a major source food of small rodents, deer, and javelinas (Kotter and Farentinos 1984a, 1984b; Hunt and Z. Maser 1985; Fogel and Trappe 1978). Nitrogen fixing bacteria and ger-

minating spores of mycorrhizal fungi in the fecal pellets of these animals can enhance pine seedling survival and growth. Given the important but complex roles of mycorrhizal fungi, trees, and understory vegetation (Brundrett 1993; Klopatek 1995; States 1985), animals that disperse fungal spores, including small mammals, grasshoppers, worms, ants, wasps, and some birds, play an indirect but significant role in O-U relationships.

As tree strata develop they modify the composition, cover, and density of understory shrubs and herbs. As the understory changes, so does the composition of prey species dependent on it. Examples are the predator-prey relationships of the Mexican spotted owl and northern goshawk during various stages of forest succession (figure 6b). Both of these raptors are found in ponderosa pine forests of the Southwest. Their persistence may involve treatment of tree structure and density to ensure that understory shrubs and herbs have cover characteristic needed by prey populations (Ward and Block 1995; Reynolds et al. 1992, 1996). The complexity of these ecological interactions (figure 6b) was described for the California spotted owl by Verner et al. in 1992 but also applies to the Mexican spotted owl in the Southwest.

Hidden Diversity Organisms

Hidden diversity organisms (soil and litter invertebrates, plant pollinators, cone and seed predators, wood decay organisms, vertebrate parasites, mycorrhizal fungi, and other seldom studied organisms) are important in nutrient cycling and plant-water relationships in ponderosa pine forests (Castellano 1994; Mason 1995; Gilbertson 1974; Maser and Trappe 1984; States 1985). Some of these organisms are related to decay processes in litter and coarse woody debris. However, their role in ecosystem dynamics of litter and coarse woody debris has changed from what it was before European settlement. Recurrent ground fires in pine forests before about 1890 kept pine-derived fuels to a minimum. Ponderosa pine snags may have persisted for a time, but downed fuels were mostly burned off by frequent surface fires. Early settlers described grassy pine savannas, not woody ground debris, although some old photos do show some logs (Woolsey 1911; figure 5). Wood decay organisms and their associated food webs were present in pre-1900 forests, but their abundance and their roles in fire-adapted forests is unknown. The stand replacing fire holocausts experienced in the past 10 years burned the aboveground vegetation and destroyed mycorrhizae in scorched soils (Klopatek 1995; Klopatek and Klopatek 1993; Vilarino and Arines 1991). However, plant succession after these stand replacing fires has hardly been studied (see Foxx 1996).

There is concern that diversity in forest ecosystems is decreasing. Wilson (1992) discusses this situation for tropical forests, and it is also relevant to ponderosa pine for-

ests. Among functions, such as in carbon and nutrient cycles, hidden diversity organisms possibly contribute to ecosystem resilience, which is the ability of ecosystems to recover or adjust to disturbances. Management should maintain hidden and other kinds of diversity of native organisms to restore or sustain pine ecosystems (Kauffman et al. 1994; Opler 1995; Maser and Trappe 1984; Reynolds et al. 1992; Rapport and Yazenko 1996).

Wildlife

Ponderosa forests provide habitat for birds, mammals, reptiles, and amphibians including threatened or endangered species, neotropical migratory birds, and game species. Detailed information about ponderosa pine forest habitat use by passerine birds is in Chapters 3 and 6. The following section reviews the importance and use of successional stages in ponderosa pine forests by vertebrates.

Overstory Tree Influence on Wildlife

The overstory structure and plant diversity of ponderosa pine forests affect their use by wildlife. Important forest features include age, size class, and of canopy cover trees, patch size of tree groups, multiple or single canopy layers, and presence of other vegetation such as gambel oak and juniper. Review of the literature and analysis of R3HARE, which is a computerized wildlife relational database for Southwestern forests (Patton 1995), document wildlife use patterns of these ponderosa pine forest structures (Benoit 1996). The following descriptions of forest structural stages mention a few of the vertebrates associated with the stages.

Structural Stages

Six vegetative structural stages, VSS1 to VSS6 (Thomas 1979; Moir and Dieterich 1988), occur within ponderosa pine forests through timber harvest, wild or prescribed fires, diseases, insects, or windfall, which all affect the dynamics of overstory and understory of forest succession. The VSS stages apply to forest stands during succession or stand development; each stage is important to different species of wildlife for feeding, cover, or reproduction. Canopy cover classes of trees (A=0 to 40 percent, B=40 to 60 percent, C=60 percent and over) within each stage also influence how the area is used. Cover includes thermal, hiding, and reproductive cover. Many habitat generalists, such as bear, turkey, elk, mule deer, bobcat, coyote, and northern goshawks, use all structural stages.

Openings (VSS1) occur after significant disturbance, such as fire or timber harvest (Hoover and Wills 1984), or gap processes (Lundquist 1995b). Openings may be main-

tained as meadows or parks in pine savannas where recurrent surface fires occur and may include a snag stage after a stand replacing fire (Moir and Dieterich 1988). Deer and elk rely heavily on openings for forage (Hoover and Wills 1984). Openings provide primary habitat for numerous other vertebrates that use grasses for shelter or feed on grasses, seeds, or insects.

Seedlings and saplings (VSS2, trees <12.7 cm dbh) provide some hiding cover but may have little forage value depending on tree density (Hoover and Wills 1984). Small tree seedlings of low density often grow in an herbaceous or shrubby environment, which can provide some forage and cover and are used primarily by habitat generalists, some of the VSS1 species, and shrub nesting birds. As seedlings grow to saplings the tree canopies close and forage declines.

Young stands (VSS3, trees 12.7 to 30.2 cm dbh) are usually dense and clumped in unmanaged stands. Tree canopy cover often exceeds 70 percent. Stands have sparse herbaceous understory, few snags, and single-storied structure (Hoover and Wills 1984). Denser stands provide thermal cover for habitat generalists and some raptors, but their value for forage and hiding cover is minimal. With sparse understories there is little use by other vertebrates, except possibly animals feeding on fungi.

Mid-aged stands (VSS4, trees 30.5 to 45.5 cm dbh) begin cone production, tend to be multi-storied, and provide small snags suitable for some cavity nesters (Hoover and Wills 1984). Species other than generalists in this stage include squirrels, pygmy nuthatches, and various raptors.

Mature stands (VSS5, trees < 45.5 cm dbh) may be single or multi-storied, with more litter and dead and downed debris in stands without fire for a long period. Mature stands may contain larger snags than in the VSS4 stage. These stands provide a good seed crop and are used for thermal cover by big game (Hoover and Wills 1984). Species found in the VSS4 stage also use mature stands. In addition, mature stands have high value for feeding and/or cover for flickers and some owls, hawks, eagles and passerine birds.

Old growth forests (VSS6) provide single and multiple stories with many mature trees and dense canopies (>40 percent) in stands not experiencing ground fires in their VSS1 and VSS2 stages. Old, yellow-pine forests, which were extensive before European settlement, are open and relatively devoid of coarse woody debris. In ponderosa pine/ bunchgrass environments before about 1890 in Arizona and New Mexico, ponderosa pine required at least 300 years beyond the herbaceous or burned snag stages to develop old growth characteristics (Moir and Dieterich 1988). Today old growth stands are heavily stocked, have much dead and downed material and numerous large snags, and contain trees that are >61 cm dbh (Moir 1992). Without restoration, most of these decaying, old growth stands are at risk of fire holocaust similar to the La Mesa

and other large burns in the last few decades (figure 4; Allen 1996; Moir and Dieterich 1988). Large trees and snags provide the best source of cavities for vertebrates. The primary users of this stage are passerine birds (Hall et al. this volume; Rich and Mehlhop this volume) and raptors.

Understory Tree Influence on Wildlife

All plants contribute to the ecology of ponderosa pine forests and influence the number of vertebrates and invertebrates. Gambel oak (*Quercus gambelii*) and alligator juniper (*Juniperus deppeana*) are often associated with ponderosa pine and provide additional structural diversity, food, thermal and hiding cover, and nest sites for numerous species. The numbers of species below are from R3HARE (Patton 1995) and Nagiller et al. (1991).

Gambel oak provides a key habitat component for birds in pine-oak forests and offers valuable alternate cavity nesting sites when pine snags are limited (Rosenstock 1996). All stages of oak, but especially large trees, are important to wildlife (Kruse 1992). Mature trees benefit the most species with regard to food and nesting sites. Shrubby oaks result from suckering and coppicing, as discussed above. The sprouts and trunks provide food, hiding and thermal cover for deer, elk, and numerous birds (Nagiller et al. 1991). Areas of brush and sprouts may provide important fawning grounds for deer, and cover and foraging habitat for rabbits and rodents (Kruse 1992).

Taller clonal oak groups provide habitat for foliage nesting birds (Szaro and Balda 1979). Foliage and buds provide food for deer, elk, and birds (mourning dove, band-tailed pigeon, turkey, rufous-crowned and chipping sparrows, and spotted towhee). Arthropods living in the foliage and on twigs provide food for birds such as the screech owl, pygmy and white-breasted nuthatches, and brown creeper (Patton 1995).

Some clonal oak and mature trees produce acorns that feed 21 species of mammals and 20 species of birds such as corvids and woodpeckers (Patton 1995). Acorns are the preferred food of Abert squirrels, band-tailed pigeons, turkeys, deer, elk, and acorn woodpeckers. Acorn crops may influence the numbers of these species. Large trunks provide hiding and thermal cover for deer, elk, rabbits, and birds (Nagiller et al. 1991). As the trees age and become less vigorous, acorn production drops, but hollow boles and limbs offer cavities sheltering 10 species of mammals and 19 species of birds such as bats, squirrels, racoons, owls, woodpeckers, and passerine birds (Nagiller et al. 1991).

Young alligator junipers provide hiding cover for elk, deer, rabbits, turkey, small mammals, and birds (Nagiller et al. 1991). Large trees provide nesting cover for birds such as pinyon jays, scrub jays, and blue-gray gnatcatchers (Degraff et al. 1991); thermal cover for deer, elk, and

small mammals (Abbott 1991); and juniper berries as food for several species of birds and small and large mammals. Alligator juniper provides food and cover for wildlife all year long and is critically important when deep snows make other food sources unavailable.

Wildlife Communities

Although overstory and understory tree structure and diversity provide important habitat components for wildlife, no particular structure or species can satisfy the needs of the entire wildlife community. Wildlife community use of Southwestern ponderosa pine forests is illustrated using the R3HARE database (Patton 1995) and the Coconino National Forest. This forest has xerophytic and mesophytic ponderosa pine stands and numerous other habitats such as desert scrub, pinyon-juniper, riparian, mixed conifer, and grasslands (Benoit 1996). Of the 435 species that occur in the Coconino National Forest, 50 percent use ponderosa pine forests to meet some or all of their habitat needs. This includes 56 percent of the mammals, 46 percent of the birds, 61 percent of the reptiles, and 54 percent of the amphibians. Eighteen percent of Coconino species (mainly mammals, reptiles, and amphibians) use the ponderosa pine habitat year round. Thirteen percent use it in summer only, 2 percent in winter only, and 17 percent as fringe habitat or transient habitat. The majority of birds (75 percent) use it as fringe, transient or summer habitat (Benoit 1996).

Overall vegetative structural stage use by wildlife (Patton 1995; Benoit 1996) is fairly evenly distributed with slightly higher use in mature and old growth forests and B (40 to 60 percent) and C (60 percent and over) canopies. Young stands and A (0 to 40 percent) canopies are used the least. The distribution is also somewhat uniform across all stages for species for which certain vegetative structural stages have high value. Use by threatened, endangered, sensitive, or dependent species (those that depend on certain structures in ponderosa pine for survival), and birds is also fairly uniform across all stages. Mammals follow an opposing pattern, with higher use occurring in openings, seedlings, and saplings than in mature or old growth areas. Forest indicator species occur predominantly in mid-aged and mature stands, and do not indicate overall use patterns in the community or those of species of special concern. Information on structural stages use by amphibians and reptiles is limited, but they appear to prefer VSS1 and 2 and probably respond primarily on the microsite level.

Sixty-one percent of birds using ponderosa pine in the Coconino National Forest are passerines (Patton 1995; Benoit 1996). Use is primarily in summer (44 percent) or as fringe habitat (23 percent). Passerine use is highest in mature and especially old growth stands. Eight of the 12 dependent species are passerine birds associated with old

growth. Use by canopy density is evenly distributed with a slight preference for B canopies.

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Chapter 2

Contemporary Human Use of Southwestern Ponderosa Pine Forests

Carol Raish, Wang Yong, and John Marzluff

Introduction

The ponderosa pine forests of the Southwest provide land, resources, products, and recreational opportunities for both urban and rural communities of the region and the nation. These human uses and activities affect resident and migratory bird populations in both negative and positive ways. This brief review focuses on three major kinds of human use that have the greatest potential to affect bird populations of the area: 1) commercial and personal-use wood harvest; 2) livestock grazing; and 3) recreation (USDI Fish and Wildlife Service 1995). In addition, growing urbanization, which also has the potential to affect bird populations, is briefly reviewed. The geographic focus is the USDA Forest Service land within the Southwestern Region (Region 3), located in Arizona and New Mexico, with a special emphasis on New Mexico and some of the long-standing, traditional use patterns of the state. Since another portion of this overview presents a history of human use of the ponderosa pine forest, this review is concentrated upon present-day uses and issues.

Commercial and Personal-Use Wood Harvest

Southwestern ponderosa pine forests provide wood and wood products for both commercial and personal purposes. Large-scale and small-scale commercial activities include the harvest of sawtimber, poles, posts, and fuelwood. Personal-use fuelwood and Christmas trees constitute the major noncommercial products. Data from Region 3 indicate that there were 58,733 wood and wood product sales of all types during fiscal year 1995. Timber of all types cut on Forest Service lands in Arizona and New Mexico during the same period had a value approaching \$9 million.¹

¹ All figures on timber and wood product sales and volume throughout this chapter were obtained from the USDA Forest Service Southwestern Region 3, Regional Office, Albuquerque, New Mexico, with the help of Milo Larson, Marlin Johnson, and Paul Fink.

Ponderosa Pine as a Timber Resource

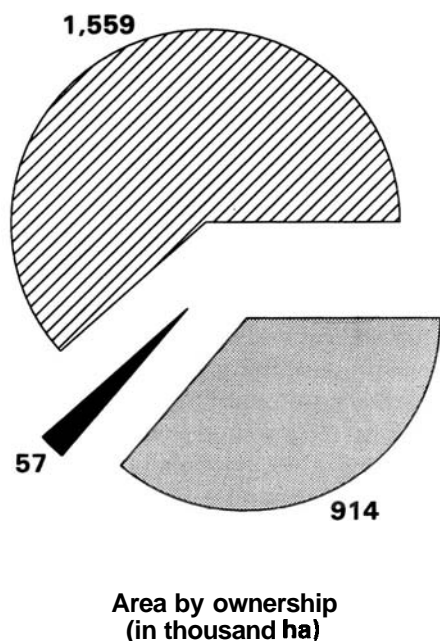
To understand the effect of the various human uses on the ponderosa pine forest, it is helpful to review background information concerning these lands and their timber resources.

Forest land falls into two major categories—timberland or woodland—based on levels of tree stocking. Timberland is forest land on which tree species, such as industrial roundwood products like ponderosa pine and Douglas-fir, make up at least 10 percent of the stocking level. Woodland areas are other forest lands on which timber species are not present at the minimum stocking level. Woodland tree species, such as pinyon and juniper, are typically not used for roundwood products other than fence posts but are an important source of fuelwood and, in some cases, Christmas trees (Conner et al. 1990).

In 1986, of the 61 million hectares (ha) in Arizona and New Mexico, about 17 million ha or 28 percent were forest lands (Conner et al. 1990; Van Hooser et al. 1993). One-fourth of the forest land is reserved or withdrawn from timber harvest through statutes or administrative designations. More than 3.5 million ha are designated as nonreserved, commercial timberland. The ponderosa pine forest is the most extensive nonreserved timberland, accounting for more than 2.5 million ha, or over 72 percent of the timberland available for harvesting roundwood products in the Southwest. Nearly two-thirds (64 percent) of the ponderosa pine timberland is administered by public agencies (figure 1). The National Forest Service, with over 1.56 million ha, manages the largest area of ponderosa pine forest in the Southwest. Other public agencies such as the Bureau of Land Management and various state, county, and municipal governments administer just over 57,000 ha. Ponderosa pine timberland in private ownership equals over 914,000 ha. Owners vary from individuals to large corporations, including Indian tribes, farmers, and ranchers (Connor et al. 1990; Van Hooser et al. 1993).

Silvicultural Systems

Silviculture has been defined as: 1) the art of producing and tending a forest; 2) the application of the knowledge of silvics in forest culture; and 3) the theory and practices of controlling forest establishment, composition, and growth (Smith 1962). In essence, silvicultural practices can be used to mold the forest in desired directions, forms, or



□ National Forest ■ Other public ▨ Private and tribal

Figure 1. Ownership and administration of ponderosa pine timberland in Arizona and New Mexico (data summarized from Conner et al. 1990; Van Hooser et al. 1993).

conditions. Economical wood production is commonly the primary objective.

A silvicultural system that includes harvest cutting, regeneration, and intermediate treatments manages a stand of trees for an entire rotation. Regeneration cuts usually harvest timber and establish tree reproduction simultaneously. Silvicultural techniques used to manage ponderosa pine forests in the Southwest produce stands with two types of age structure: even-aged and uneven-aged (Schubert 1974; Alexander and Edminster 1980). Regeneration techniques that mimic natural disturbance regimes lead to forests that are similar to "natural (unmanaged) forests," which are generally uneven-aged.

Even-Aged Management

Under even-aged management, harvest and regeneration are planned by area and are a function of rotation age, which is the age at which a stand is considered to be regenerated on the basis of management objectives. Trees of a given stand are of one or two age classes. Sustained yield is maintained at the forest, not the stand, level (Alexander 1987). Historically, techniques leading to even-aged stand management have been favored for timber harvest on public lands in the Southwest for reasons of economy and efficiency (USDI Fish and Wildlife Service 1995). Cutting methods traditionally used to harvest or regenerate stands under even-aged systems include: 1) the

shelterwood method, which consists of the gradual removal of most or all trees in a series of partial cuttings extending over a portion of the rotation; 2) the seed tree method, which consists of removing all trees in a stand except a small number (left singly or in groups) to reseed the harvested area; and 3) the clearcutting method, which consists of harvesting the timber crop in one step to establish a new stand (USDA Forest Service 1983).

Uneven-Aged Management

Under uneven-aged management, individual trees or small groups of trees are selectively removed throughout the stand on the basis of age, diameter, vigor, form, and species to maintain a relatively consistent stand structure. The individual tree selection cutting method is used to produce uneven-aged stands, which regenerate continuously. The objective is to produce a stand with trees of different sizes and age classes intermingled on the same site (USDA Forest Service 1983). The group selection cutting method is also used to selectively harvest trees in groups from geographic areas ranging from a fraction of a hectare up to about 5 ha (USDA Forest Service 1983). The area cut is generally smaller than the minimum feasible for a single stand under even-aged management.

Regeneration and Intermediate Treatments

Following or during harvest, a ponderosa pine stand is treated to create conditions favorable for regeneration of desired species. Site preparation may involve removal of slash, preparation of a loose seedbed, and removal of the competing ground vegetation by mechanical, chemical, or burning treatments (Johnsen et al. 1973; Thompson et al. 1995). Slash may be removed to reduce the fuel load for wildfires or because it physically impedes stand regeneration or causes too much shade. Slash is commonly removed in combination with planting by means of broadcast burning, piling and burning, lopping and scattering, windrowing, or chopping on site. Seedbed preparation involves removing organic matter to expose mineral soil. Predominant methods of seedbed preparation include prescribed burning and scarification, which is the mechanical removal or mixing of the organic matter and the mineral soil. Competing vegetation is usually controlled by prescribed burning, mechanical treatment, or herbicides. Prescribed burning can also be used to encourage the growth of desired fire-adapted or dependent species (Thompson et al. 1995).

Natural regeneration of ponderosa pine depends on moisture conditions. Since the seed of ponderosa pine often does not germinate until the coming of the summer rains, its vitality is impaired by the usual period of drought between April and June. The seedlings that do come up are subjected to another drought from the latter part of September to November (Woolsey 1911). Artificial regeneration is accomplished by planting young trees or by

seeding before or after removing the old stand. This technique is often used with conifers because of low natural regeneration, high probability of successful artificial regeneration, and high financial yield (Thompson et al. 1995).

Intermediate cuts include all the cutting treatments made from establishment of the new stand until replacement. Cuts are made when needed, but normally at specific intervals, to increase the quantity and quality of timber produced and to salvage material that would be lost. Common intermediate cuts in the Southwestern ponderosa pine forests include: 1) thinning, in which the smallest trees and rough dominants are removed; 2) release cutting, to release young trees from the competition of grass, brush, or trees to provide adequate growing space, light, and moisture for early rapid development; 3) improvement cutting, which resembles a sanitation-salvage cutting to improve the quality of the residual stand and reduce mortality; 4) sanitation cutting, which eliminates trees that have been attacked or are likely candidates for attack by insects or disease to prevent spread to other trees; and 5) salvage-cutting dead, dying, damaged, or deteriorating trees to derive economic benefits before decay processes reduce such values. Salvage cutting is a widespread practice often employed after insect outbreaks, fire, windstorms, and other natural disturbances (Schubert 1974; Thompson et al. 1995).

History of Management of Ponderosa Pine Forests

Prior to European settlement and management, the ponderosa pine forests in the Southwest were uneven-aged, with the trees usually arranged by even-aged groups (Myers and Martin 1963). Since forest management began in the area, both even-aged and, to a lesser extent, uneven-aged systems have been used. In the early 1900s unmanaged ponderosa pine forests were converted to managed stands to maintain higher growing stock levels and timber production (Woolsey 1911; Pearson 1950; Myers and Martin 1963).

The primitive application of the shelterwood method was the major harvest and regeneration practice used on ponderosa pine forest on Forest Service land in the Southwest. Two-thirds of an original stand was cut and the remainder was removed when the new crop was established (Woolsey 1911), which usually took 15 to 20 years. On many of the federal forests, selective cuttings were made in a series of light cuts, which generally amounted to the shelterwood method (Clapp 1912; Pearson 1910). These light cuts eventually removed 60 to 70 percent of the volume, and the rest was cut 10 to 20 years later after reproduction was established (Schubert 1974).

"Loggers' selection" (high-grading), sanitation salvage, and improvement selection cutting, which removed trees in a series of cuts on an individual or group basis, were

widely adopted in the early and mid-1900s. Cutover areas were allowed to restock naturally regardless of the time required or the stocking achieved. Management intensity was increased by the 1970s. Managers were increasingly concerned with prompt restocking of cutover areas and with increasing the growth rate of the new stand by control of stand density. They sought to improve quantity and quality of yields by periodic thinning (Alexander and Edminster 1980).

Silvicultural practices create edges and alter landscape structure, forest age, and structure that affect bird populations. Concern over these effects is often greater when timber is harvested on public forest lands since they are some of the least fragmented forests remaining in North America (Wilcove 1988; Thompson et al. 1995). The problems of meeting avian habitat needs while managing other forest resources on public lands became an important issue in selecting silvicultural practices in the late 1970s and early 1980s. A series of workshops and symposia were organized to bring together avian ecologists and forest resource managers to discuss common problems (see Smith 1975; DeGraff 1978, 1980; McComb 1984). In the late 1980s and early 1990s concern mounted over the effects of timber harvest on bird and other wildlife habitat, leading to court actions and legislatively mandated studies of habitat and wildlife populations on public land (USDI Fish and Wildlife Service 1995). A review of the status of current knowledge derived from these and other research projects and a discussion of critical future issues are presented in Martin and Finch (1995).

To manage forests for habitat requirements of bird populations (as well as other species and resources), biologists now recommend a shift away from an over-emphasis on even-aged management strategies (Szaro and Balda 1979; Thompson et al. 1995; USDI Fish and Wildlife Service 1995). They recommend a mix of silvicultural practices, including both even-aged and uneven-aged management strategies, that maximize landscape and regional diversity. A review of information gathered from bird community studies in Rocky Mountain habitats suggests that species respond individually to different silvicultural treatments. The authors (Hejl et al. 1995:236) state:

... many forest birds were less abundant in clearcuts than in uncut forests, and species that frequent open forests or open habitats were more abundant in clearcuts than in uncut forests. Most permanent residents were less abundant after either kind of harvesting treatment (clearcut or partial logging), whereas about half the migrants were less abundant and half more abundant in harvested areas.

Thus, emphasizing any one silvicultural technique or management strategy would favor some birds at the expense of others. Broad-scale management strategies and

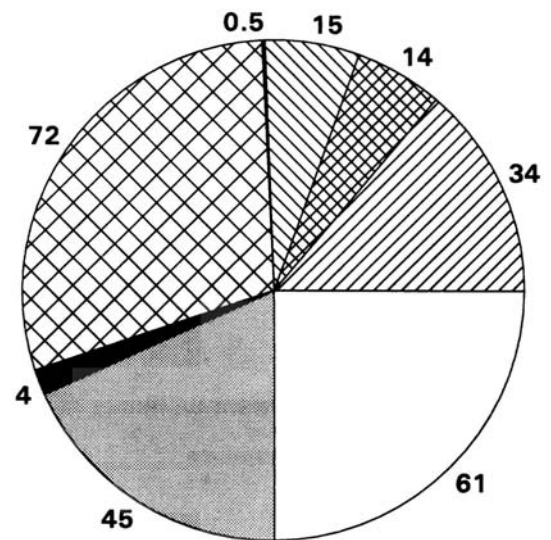
those that use many different techniques to mimic natural patterns and processes are recommended (Hejl et al. 1995). Researchers urge that stand-level management should occur with knowledge of the regional status of the species and the ecosystem and that local-level management should complement regional goals (Hejl et al. 1995; Thompson et al. 1995). The goal, admittedly difficult and unattainable if too much is asked of the land, should be to manage the forest system for simultaneous production of goods and services in an optimal manner, while maintaining a healthy and balanced environment.

Forest Changes and Silvicultural Practices

Silvicultural practices have changed the availability, structure, and conformation of the ponderosa pine timberland in the Southwest. Silvicultural prescriptions have changed as our knowledge of forest ecologies has increased. Public opinion, political expediency, and individual personalities have also affected how the land has been managed, often irrespective of silvicultural requirements, site conditions, and conflicting objectives (Hejl et al. 1995). In-depth discussions of historical human activities and pre-European settlement conditions in ponderosa pine forests of the Southwest are presented in Scurlock (this volume) and Moir et al. (this volume). Thus, we focus here on presenting some of the more detailed information on changing forest condition and composition.

In the following review, we use information gathered by the Forest Service since most ponderosa pine is under Forest Service management. Growth, mortality, and removals through harvest are the principal elements of change of ponderosa pine timberland in the Southwest today. Based on surveys conducted by the Forest Service in 1962 and 1986, it is estimated that the annual growth of ponderosa pine forests is about 4.62 million m³ in the Southwest. About 6 percent of the growing stock dies, leaving a net increase of 4.34 million m³. If one subtracts an annual logging harvest (from those years) of 2.24 million m³, the net annual addition is about 2.10 million m³. The causes of mortality in ponderosa pine that could be determined include insect infestation, disease, fire, animal damage, logging, suppression of growth by weather, and suppression by thinning and other silvicultural techniques (figure 2). In 1986, weather killed 72,000 m³ and disease accounted for another 14,000 m³.

Ponderosa pine forests have always been the mainstay of the timber industry in the Southwest (Clapp 1912; Pearson 1910; Pearson and Marsh 1935). In New Mexico, about 73 percent of the lumber cut by sawmills has been ponderosa pine (Van Hooser 1993). Although other species have gradually become more important, ponderosa pine still accounted for 54 percent of the total lumber output for New Mexico in 1962. It increased to 69 percent in 1986 (Choate 1966; Van Hooser et al. 1993). In 1986, 91



Mortality of growing stock (in thousand cubic meters)

- ▨ Insect □ Disease □ Fire ■ Animal
- ▨ Weather ■ Suppression □ Logging □ Unknown

Figure 2. Distribution of annual mortality of growing stock on ponderosa pine timberland by cause of death in Arizona and New Mexico (data summarized from Conner et al. 1990; Van Hooser et al. 1993).

percent of the 1.8 million m³ harvested in Arizona was ponderosa pine. In the two states combined, a total of 2.24 million m³ of ponderosa pine was logged in 1986, and sawtimber trees accounted for 90 percent of the total cut.

Based on surveys by Choate (1966), Spencer (1966), Conner et al. (1990), and Van Hooser et al. (1993), we found that in New Mexico and Arizona ponderosa pine accounted for 3.2 million ha of timber lands (78 percent of all the commercial forest types) in 1962 and 2.5 million ha in 1986 for a 22 percent decrease. This trend toward decrease is not consistent among stand classes. While the area of small tree stands (poletimber, sapling, and seedling) increased 238,000 ha or more than 2.5 times between 1962 and 1986, sawtimber stands decreased 892,000 ha. The sawtimber stands accounted for 92 percent of 3.2 million ha of timberland in 1962 with a 10 percent reduction in the intervening 24 years (figure 3). Within the sawtimber stands, the volume of trees of dbh 243.2 cm (17 inches) decreased 992 million board feet, while the volume of trees of dbh below 43.2 cm increased 708 million board feet (figure 4). This resulted in a net decrease of 284 million board feet of sawtimber volume. The volume of growing stock showed similar trends between 1962 and 1986. The average growing stock volume of ponderosa pine timberland was 79 m³/ha in 1962 and 72 m³/ha in 1986 (figure 5).

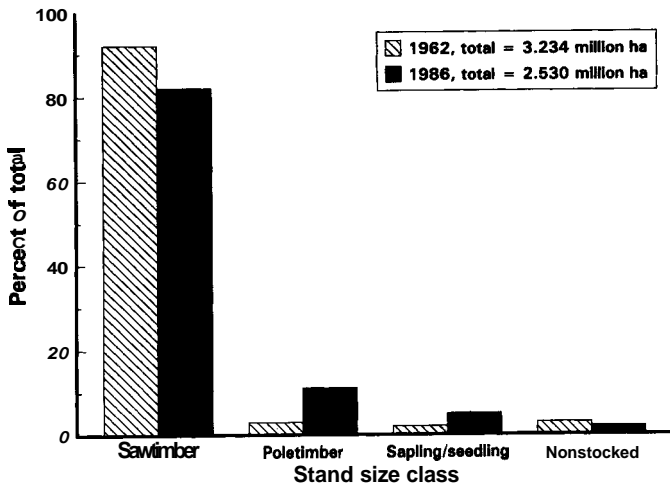


Figure 3. Change of stand size of ponderosa pine timberland in Arizona and New Mexico between 1962 and 1986 (data summarized from Choate 1966; Spencer 1966; Conner et al. 1990; Van Hooser et al. 1993).

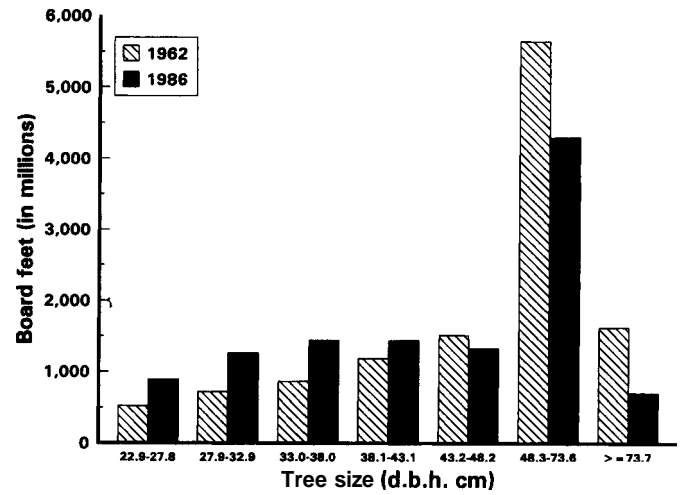


Figure 4. Change of sawtimber volume of ponderosa pine timberland in Arizona and New Mexico between 1962 and 1986 (data summarized from Choate 1966; Spencer 1966; Conner et al. 1990; Van Hooser et al. 1993).

Because the general rule of historic logging was that the most accessible and commercially valuable trees were logged before less accessible and less valuable trees, logging and other silvicultural practices affected availability, structure, and species composition not only at the stand level, but also at the landscape level. For example, even-aged management creates a specific age-class distribution of forest habitats that usually differs from forests with no timber harvest. A common trend among forests managed under even-aged systems is that the oldest age classes are often absent because rotation ages are generally shorter than tree longevity. Depending on rotation age and frequency of natural disturbances, forests managed by even-aged management could have more or less early successional forest than natural landscapes (Thompson et al. 1995). Even-aged management can result in an unnatural uniformity of habitat patch size and distribution, excluding small and very large patches. Our analysis suggests that current ponderosa pine forests in the Southwest contained more early successional forest in 1986 than in 1962.

Contemporary Sawtimber Harvest

In 1995, 27 million board feet of ponderosa pine were cut on Forest Service lands in Arizona, while 3.7 million board feet were cut in New Mexico for a Region 3 total of over 30.8 million board feet. Ponderosa pine still is the largest component of the sawtimber cut from Forest Service lands in both states, though there have been changes in the size and number of commercial sawtimber sales. A comparison of the figures from 1979, the first year for maintaining the regional data base in the current format, with 1995 figures is instructive in this regard. In 1979, 227

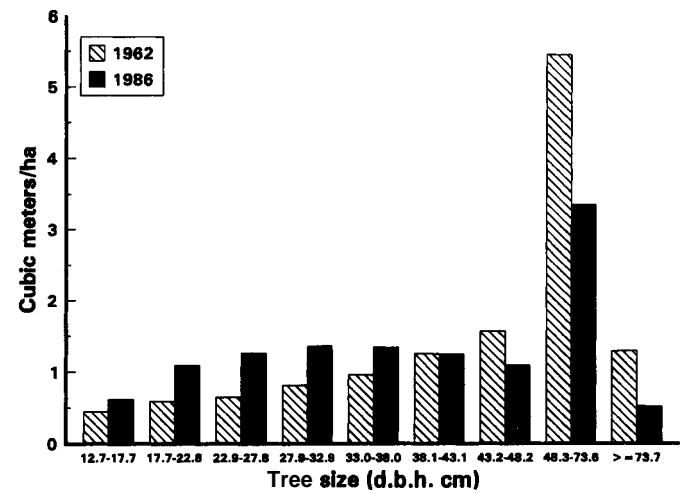


Figure 5. Change of growing stock volume of ponderosa pine timber stands in Arizona and New Mexico between 1962 and 1986 (data summarized from Choate 1966; Spencer 1966; Conner et al. 1990; Van Hooser et al. 1993).

million board feet of ponderosa pine were cut on the forests of Region 3. In 1995, that figure was about 30.8 million board feet. The number of large sales over 2 million board feet has also dropped substantially over the years from 34 in 1979 to 5 in 1995. These declines have affected the commercial timber-related industries of Arizona and New Mexico.

A Southwestern Region Forest Service white paper presents figures from 1984–1993 describing conditions and trends in the timber industry (USDA Forest Service Region 3 1994). During that period, the volume of all species cut declined from a high of 434 million board feet in 1989 to a low of 159 million board feet in 1993. In 1995, the figure had declined further to 99.6 million board feet. Volume under contract also showed a steady decline throughout the period. In 1989, most of the major mills of the region were operating two shifts but were becoming concerned about the supply problem and were considering reducing to one shift. Toward the end of that year, several mills shut down for a short period and several reduced from two shifts to one owing to low volume under contract and market conditions. During this period, 520 mill workers and 355 forestry workers were affected in New Mexico and Arizona (USDA Forest Service Region 3 1994). In the period from 1991 to 1993, all operating mills in New Mexico and Arizona reduced to one shift and eight shut down leaving about half the mill capacity that existed in 1984 (USDA Forest Service Region 3 1994). In 1984, 24 large and small mills were listed by the Forest Service in the two states, excluding mills on Indian lands. By mid-1996, 10 were operating (Buddy Stewart, USFS Regional Economist, personal communication, 1996).

Timber Industry in Rural Northern New Mexico

Information from New Mexico provides an example of the role of the timber industry in local communities. Though the timber industry in the state is modest when viewed on a national scale, lumbering is a substantial business in New Mexico (Baker et al. 1988 cited in Van Hooser et al. 1993). In 1963, 2,200 people—one of every seven manufacturing workers—were employed in logging, milling, or some other wood products-related industry (Choate 1966). The number of jobs in the lumber and wood products sector peaked between 1972 and 1977 at 3,200 per year, or approximately 10 percent of the manufacturing jobs. By 1989, the number had declined to 2,500, or 6 percent of the manufacturing workforce (Van Hooser et al. 1993).

Historically, almost two-thirds of the wood processing plants were located in the northern and central portions of the state (Van Hooser et al. 1993). Especially in the small, rural communities of the north, industries based on forest products have been major sources of employment. Six small mills that processed products from the Carson and Santa Fe National Forests have closed in the 1980s and 1990s in places such as Chama, Alamosa (Colorado), Taos, Costilla, Española, and Las Vegas (New Mexico). A larger mill operated by Duke City Lumber Company at Cuba was also shut down in 1992. Lack of supply was given as the reason for the closures (USDA Forest Service Region 3 1994). In a pattern seen commonly across the state, timber industry officials often blame closings on the lack of Forest Service timber sales resulting from environmental

legislation and litigation. Local environmental groups, on the other hand, stress the role of competition with timber coming in from Canada and the southeastern U.S. and alleged Forest Service mismanagement in the closings (Eichstaedt 1995; McClellan 1995; Toppo 1995; Korte 1996; Ragan 1996).

Small-Scale Commercial and Personal-Use Wood Harvest

The smaller scale harvest of both commercial and personal-use wood products is also important, even though these types of industries do not have the overall economic impact of large-scale, sawtimber harvests. Across the region in 1995, fuelwood formed the largest component of the non-sawtimber harvest from Forest Service lands followed by poles and posts. Christmas trees also comprise a substantial component. They are not discussed further here since ponderosa pine does not make up a large portion of this cut, ranking fourth well after pinyon, other softwoods, and true fir.

The fuelwood cut for 1995 in Region 3 was 42.5 million board feet for both personal and commercial use. Poles accounted for 7.8 million board feet, while posts comprised 455,000 board feet. Of these cuts, ponderosa pine forms the largest component of the pole harvest at over 4.5 million board feet with aspen forming the second largest component. With respect to both fuelwood and posts, ponderosa ranks second to pinyon and juniper. Of the large fuelwood harvest, ponderosa comprises only 3.3 million board feet, while it makes up 61,500 board feet of the posts. As discussed by Van Hooser et al. (1993) for New Mexico, the pinyon-juniper woodlands provide the majority of the fuelwood and fenceposts for the state. Pinyon is the favored fuelwood for both heating and cooking because it burns hot and is long-lasting. Green pinyon is especially favored for these reasons. "Dead and down" ponderosa is also used, however, because of its availability as a byproduct of timber sales (Van Hooser et al. 1993).

Fuelwood and small products harvests have the greatest potential to disturb bird habitat when they occur as unregulated activities. Habitat destruction and damage can occur through removal of snags, large downed logs (230 cm midpoint diameter), and particularly critical species (Brawn and Balda 1988; USDI Fish and Wildlife Service 1995). Poaching live trees, as well as snags and large downed logs, from undesignated areas are common occurrences in some locales that can threaten the integrity of bird habitat. In order to minimize negative impacts to habitat, fuelwood harvest should be regulated to control access and the kinds of materials that are taken. Designated harvest areas can be useful but may be difficult to enforce, especially in areas with a long tradition of ready access to forest resources and scant personnel for patrol (USDI Fish and Wildlife Service 1995).

In many rural portions of the Southwest, fuelwood gathering is a necessity, not a luxury. Homes are often heated solely with wood and cooking is done on wood stoves. This is especially true of many rural areas of northern and central New Mexico. To complicate matters, much of the Forest Service land where the wood is gathered is former Spanish land grant land lost by the original owners in the aftermath of the Mexican War of 1846–1848 (Harper et al. 1943; Eastman et al. 1971). Harvesting wood is considered to be a traditional "right" in these areas that ties the people of the villages back to their ancestral lands. Thus, many villagers often resent federal restrictions on land they consider to be rightfully theirs.

A case in point is the local response to the federal injunction issued in August 1995 placing restrictions on logging and fuelwood harvesting on Forest Service land in Arizona and New Mexico to protect Mexican Spotted Owl habitat. The court ruling stemmed from a lawsuit filed by several environmental groups against the Forest Service, charging that the agency failed to consider adequately the cumulative impacts on the owl in planning its timber program. The resulting injunction restricting wood cutting and gathering hit the rural, primarily Hispanic, communities of northern New Mexico especially hard. Most of their heating and cooking wood comes from the Carson and Santa Fe National Forests. For example, since the early 1700s people from the villages of Truchas, Las Trampas, and Peñasco have cut and gathered their fuelwood from the surrounding area—first from the Truchas Land Grant, and after portions of the grant became National Forest, from the Carson Forest (Eichstaedt 1995). Under Carson Forest policy, residents could obtain a permit to gather "dead and down" wood anywhere on the Forest and could even cut some snags. Part of the reason for allowing Forest-wide fuelwood harvesting, rare among Forests of Region 3, was that many of the wood gathering areas were part of the old land grant lost under U.S. takeover (Eichstaedt 1995).

After the injunction, gathering "dead and down" wood was limited to specific marked areas, and the species of standing dead trees that could be cut were also limited (Eichstaedt 1995). No live or green trees could be cut, and sales of these types of trees were barred. Residents feared inadequate fuelwood supplies from the designated harvest areas, many of which were also farther away than local people normally travel to obtain wood (Ragan 1996). They were also concerned about job losses from the previously discussed mill closures (Ragan 1996).

The villagers, as well as the loggers, lumber company officials, and sawmill owners and operators, blamed the environmentalists and the Forest Service for their plight. The environmentalists responded by blaming the Forest Service for inefficiency and mismanagement, and the big timber companies for greed. There were angry words and confrontations with charges of racism and "new-

comerism" reported in both the local and national press (Eichstaedt 1995; McClellan 1995; Toppo 1995; Korte 1996). A new activist group, La Herencia de Norteños Unidos, was formed to represent ranching, land, and logging interests in northern New Mexico. In late November 1995, the Herencia group staged a protest rally and hanged two Santa Fe environmental group leaders in effigy. Some lumber company officials and others with extractive interests on forest lands were also on hand to lend their support (McClellan 1995).

After the rally the situation calmed somewhat. Discussions began between the opposing groups, and community drives and donations of wood (some from the "hanged" environmentalists) allayed most residents' fears about having sufficient wood to make it through the winter. Community leaders have urged compromise and understanding that would allow both protection of wildlife species and maintenance of traditional lifeways (de Buys 1995). Whether or not compromises will be made remains to be seen, as does local community response to what are perceived as growing restrictions on forest use. These types of challenges are not unique to northern New Mexico but seem to occur with regularity throughout the West, as the economic orientation and values of local and newly arrived populations come into conflict.

Livestock Grazing

Livestock grazing in the ponderosa pine forest has a long history in Arizona and New Mexico and has been examined by various researchers. Range management in the ponderosa pine type of Arizona and prior range studies were discussed in detail by Clary (1975) and formed a portion of the symposium on Multiresource Management of Ponderosa Pine Forests, held in Flagstaff in 1989 (Teclé et al. 1989). Recently, several studies have reviewed the status of range research in varying geographic areas and vegetation types in terms of needed future direction (Evans 1990; Everett 1992; Kennedy et al. 1995; Vavra 1995). Understanding both the needs of wildlife and the needs of society concerning rangelands is mentioned as a key issue requiring study in the coming years (Kennedy et al. 1995; Vavra 1995).

Effect of Grazing on Bird Populations and Habitat

Saab et al. (1995) reviewed research on the effect of cattle grazing on bird populations and habitat in western North America. Finch et al. (this volume) present a more specific review pertaining to the effects of livestock grazing on bird species in ponderosa pine. They state that the de-

gree to which grazing affects habitat, and the birds using that habitat, relates to the number of animals grazing in an area (intensity), the timing of grazing, and the grazing system used. Not surprisingly, greater habitat changes occur as grazing intensity increases (Johnson 1956; Skovlin et al. 1976 cited in Finch et al. this volume). Grazing during the spring and early summer can directly affect reproductive success of breeding birds through destruction or disturbance of nests of ground or shrub nesting species (Finch et al. this volume). Heavy grazing during the growing season can also negatively affect regeneration of favored plant species. Vegetation in riparian areas may be especially susceptible since these zones are often over-used by cattle in forested habitats (Samson 1980; Roath and Krueger 1982 a, b; Willard 1990 cited in Finch et al. this volume).

Cattle compact soil by hoof action, remove plant materials, and indirectly reduce water infiltration, all of which can result in decreased vegetation density (Holecheck et al 1989; Saab et al. 1995). Intense grazing pressure in coniferous forests, in conjunction with fire suppression, sometimes leads to enhanced establishment of conifer seedlings and consequent conversion of montane shrub, meadow, and grassland areas to forested habitat (Saab et al. 1995). As with varying responses to silvicultural treatments, some bird species respond positively to the effects of cattle grazing while others respond negatively (Saab et al. 1995).

From their literature reviews, both Saab et al. (1995) and Finch et al. (this volume) conclude that little is known about the effects of different grazing systems on bird habitat in western coniferous forests. Saab et al. (1995) speculate that birds most likely to be negatively affected by grazing are those that are dependent upon herbaceous and shrubby ground cover for nesting and/or foraging and those requiring open savannahs as opposed to closed-canopy forests. They also suggest that as a result of foraging, the diminished fine fuels reduce fire frequency which results in a decrease in fire-caused snags. This decrease would negatively affect primary and secondary cavity nesters (Saab et al. 1995). Research is needed, however, to confirm these suggestions. Species that have increased or decreased with grazing are reviewed in Finch et al. (this volume).

Saab et al. (1995) recommend a concerted study effort to provide information where little currently exists concerning the impacts of grazing on neotropical migrants in western coniferous forests. They suggest monitoring, with attention to matched forest habitats differing in grazing regimes or grazing histories, as a means of supplying this much-needed data. In addition, studies which examine the status of bird habitat and populations in areas that have been both grazed and logged are much needed. We were unable to find reported studies from these types of areas.

Grazing on National Forest Lands in Region 3

Livestock grazing is a major, long-standing use of National Forest lands throughout the Southwest.² Table 1 gives figures on the numbers of permittees, animals, and animal unit months (AUMs) in Region 3 in 1995. An AUM is the amount of forage required to support a mature 1000 lb cow or its equivalent for one month (USDA Forest Service 1996).

Nationally, Region 2 (Colorado, Nebraska, South Dakota, and eastern Wyoming) and Region 3 rank second only to Region 4 (southern Idaho, Nevada, Utah, and western Wyoming) in amount of grazing use based on permitted head months (the time in months livestock spend on Forest Service land). Table 2 presents figures on the Region 3 allotments with a vegetation type composed of 50 percent or greater ponderosa pine and mixed conifer in 1995.

Of the 253 ponderosa pine-mixed conifer allotments in Region 3, we have information on the grazing system in use on 232 of them. Seven allotments have combination systems which are not discussed here, and the remainder do not have information on the grazing system. The systems in use are seasonal, rest rotation, deferred, and year-long. Under a seasonal system, the allotment is grazed

² All range figures were obtained from the USDA Forest Service Southwestern Region 3, Regional Office, Albuquerque, New Mexico, with the help of Dave Stewart and George Martinez. George Martinez also obtained information from Region 3 Forests on the number of allotments in ponderosa pine and mixed conifer and the types of grazing systems used on those allotments.

Table 1. Livestock grazing by permittees on National Forests in Region 3, 1995^a.

State	No. of permittees	No. of animals	AUMs
Arizona	469	137,830	1,113,230
New Mexico	1066	90,585	791,953
Total	1535	228,415	1,905,183

^a Figures obtained from the USDA Forest Service Southwestern Region 3, Regional Office.

Table 2. Grazing allotments on National Forests in Region 3 with a vegetation type consisting of $\geq 50\%$ ponderosa pine and mixed conifer, 1995^a.

State	No. of allotments	Ha of allotments	AUMs
Arizona	100	1,139,813	249,472
New Mexico	153	1,248,185	195,041
Total	253	2,387,998	444,513

^a Figures obtained from the USDA Forest Service Southwestern Region 3, Regional Office.

continuously throughout the growing season on an annual basis, while under a year-long system the allotment is grazed continuously throughout the year (Saab et al. 1995). Under rest rotation, the allotment is divided into pastures or segments with one being rested (usually for 12 months) while the others are grazed. The period of non-use is rotated among the pastures. Under deferred rotation, at least one pasture is rested during part of the grazing season and the deferment is rotated among pastures in succeeding years. This system is often used to graze one pasture during the early part of the growing season and the remaining pastures later in the season (discussed in Saab et al. 1995).

Region 3 has the following breakdown of systems in use on the ponderosa pine-mixed conifer allotments: year-long—2 allotments, seasonal—54, rest rotation—69, and deferred—107. The year-long systems are in the southern part of New Mexico on the Lincoln and Gila National Forests, while the seasonal systems are concentrated in the northern part of New Mexico on the Carson and Santa Fe National Forests (43 of the seasonal systems). The remainder are scattered throughout the Region. In future studies, this type of information will be valuable for the kinds of research that are needed to assess the effect of different types of grazing systems on bird populations and habitat as discussed by Finch et al. (this volume). In addition to different grazing systems, the types of Southwestern ranching operations themselves also have a significant impact on wildlife habitat and management, as discussed in the following section.

Commercial and Traditional Ranching Operations

Throughout the West, the rural ranching lifestyle is a deeply rooted tradition. Ranching on public lands is a strong, though not universally appreciated, aspect of this tradition, as demonstrated by the recent congressional debates and public controversy over range and grazing fee reform (Richardson 1995; Varela 1996). Scurlock (this volume) describes the history and development of range resource use in Arizona and New Mexico, from its beginnings in 1598 with Spanish colonization and the introduction of domesticated herbivores. Range statistics from Region 3 show a fluctuating but generally downward trend in numbers of permittees, animals authorized to graze, and AUMs from 1982–1995. Numbers of permittees in both states have dropped by about 25 percent, while animals authorized to graze have dropped by roughly 25 percent in Arizona and 20 percent in New Mexico. These declines relate to climatic and market fluctuations, consolidation of permits, and growing urbanization in the region. The larger commercial operations generally fare better than smaller ones in terms of profit and maximizing the opportunities of technological advances and ad-

ditional land acquisitions (Clary 1975; Harris et al. 1995). Smaller commercial operations tend to be hit more heavily by environmental and market fluctuations.

There are many small operations in the region, and many that can be considered non-commercial (or traditional) on the basis of herd size (Eastman and Gray 1987). According to a recent statement by Congressman Bill Richardson in the discussions over grazing fee and range reform, 70 percent of federal permittees (on lands from all agencies) in New Mexico have fewer than 100 head (Richardson 1995), which is about the minimum size of a small commercially viable operation as discussed by Eastman and Gray (1987). The willingness of these ranchers to implement grazing system practices and range improvements that benefit wildlife habitat will definitely be a factor in the success of habitat management strategies.

Small, traditional operations occur throughout the region but tend to be concentrated in the more mountainous, ponderosa pine zones, with a special clustering in the small Hispanic villages of northern and central New Mexico. Owning animals is a very important aspect of these operations. The animals provide the villagers with a means of reaffirming ties to their ancestral lands and heritage. In many cases, the extra buffer that the animals provide allows the family to remain in the ancestral, rural community and continue at least a part of the traditional lifestyle (Eastman et al. 1971; Eastman and Gray 1987; William de Buys [personal communication] 1995; Raish 1996; Varela 1996).

Herd sizes, goals, and methods of operation differ significantly between the small-scale, traditional ventures and even small, commercial cattle ranches. Average herd sizes for the traditional enterprises are around 19, while small commercial ranches have about 100 head. Making a profit is the number one goal of commercial ranchers (even small-scale ones), followed by maintaining a good quality of life. These producers tailor their methods to maximize profit by increasing production. They tend to seek out and adopt new practices and range improvements that increase production and the quality of the herds. They are willing to invest cash, borrow, and take risks in the hope of eventual profit (Eastman and Gray 1987).

The small-scale, traditional operators, on the other hand, rank quality of life first, followed by avoidance of being forced out of ranching, with making a profit last on the list. These goals condition their behavior and methods of operation. They are less willing to invest cash in what they perceive to be risky improvements or new techniques that may not work out. New technology often requires considerable time and effort to learn, while the benefits to the very small operation may be limited. Any increases in operational costs hit this group harder than the commercial stock raisers who sell many more animals and realize greater profits with which to fund rising costs (Eastman and Gray 1987; Richardson 1995). Thus, the small-scale operators may oppose actions that increase the cost of their

operations, such as increases in grazing fees or range improvements mandated to improve environmental conditions. Since small operators are prevalent in the region, their education and cooperation on issues of wildlife improvements may be critical to the success of habitat management programs.

Urbanization and Recreation

The ponderosa pine forests of the Southwestern United States, although currently sparsely inhabited, are disproportionately affected by increasing human population. Many small towns have grown exponentially in the last three decades as tourism and retirement industries boomed. Moreover, cool temperatures and scenic beauty attract many recreationists to the forests, especially during the summer months when desert dwellers try to escape extreme temperatures. The importance of ponderosa pine forests as recreation sites indicates that the potential impacts of humans on the forest are likely to be far greater than resident population censuses alone might suggest. Human pressures on the ponderosa pine forest will certainly continue to increase. Urban populations are projected to increase (e.g., Anderson 1995), and recreation demands throughout the United States are projected to accelerate (Boyle and Samson 1985; Flather and Cordel 1995).

Urban Growth in Ponderosa Pine Forests

The ponderosa pine forests of Arizona and New Mexico are sparsely populated by full-time residents. Flagstaff, Arizona, is the largest city situated wholly in ponderosa pine. It occupied 164 km² and held 50,000 residents in 1990 (U.S. Census Bureau). However, from 1960 to the present, Flagstaff has grown tremendously and is currently increasing at a rate of 15 percent per year (figure 6). The Arizona Department of Economic Security projects its population will exceed 100,000 in the year 2040.³

Flagstaff's growth is not unique among cities in ponderosa pine forests or adjacent pinyon-juniper woodlands. Other important urban centers in or adjacent to ponderosa pine are Santa Fe, New Mexico (primarily in pinyon-juniper), and Prescott, Arizona, both of which are increasing rapidly (Fig. 6). Five smaller cities (Payson, Pinetop,

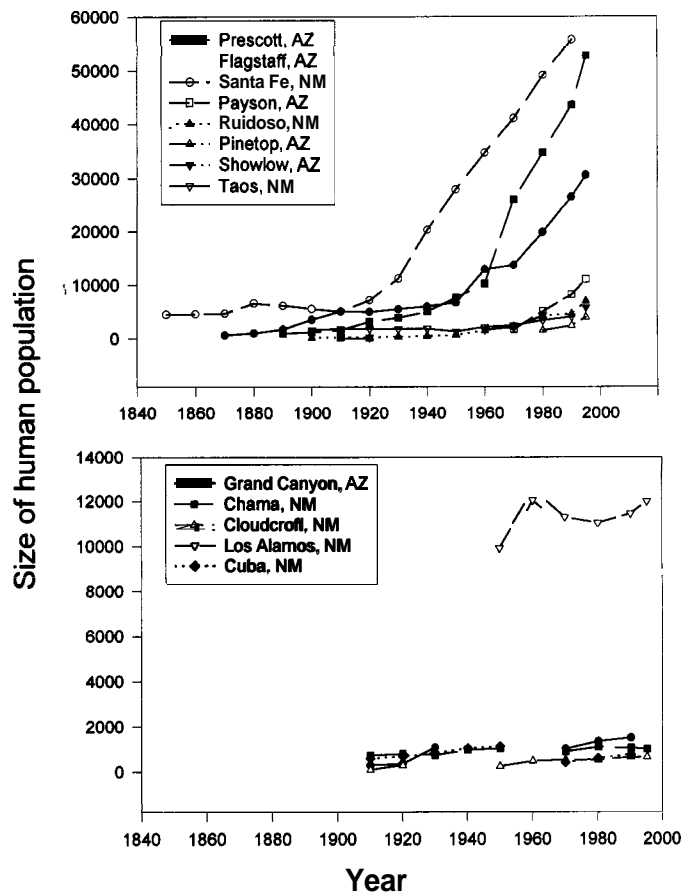


Figure 6. Human population changes in towns in and adjacent to ponderosa pine forests in Arizona and New Mexico. Towns experiencing growth are plotted in the top panel. Towns of relatively stable size are plotted in the lower panel. Data from the time records were kept until 1990 and were provided by the U.S. Census Bureau Library. Data for 1995 were obtained from local chambers of commerce or city clerks.

and Showlow in Arizona; and Ruidoso and Taos in New Mexico) are showing the first stages of rapid growth (figure 6). Payson and Ruidoso will likely follow Flagstaff's steep trajectory in the next few decades. The economic fuel for much of this rapid growth in ponderosa pine forest cities is provided by retirees, tourists, and recreationists.

Not all towns in ponderosa pine forest are increasing in size. In contrast to those in the top panel of figure 6, five towns appear relatively stable in size (lower panel of figure 6). They apparently have not grown because of their isolation and proximity to federal or private land that is unavailable for subdivision. In the interesting case of Los Alamos, New Mexico, which was built in 1942 to house those developing the atom bomb, the lack of growth has resulted because the U.S. Department of Energy has not expanded operations.

³ Judy Burding (Flagstaff Chamber of Commerce), Joyce Wachter (U.S. Census Bureau), Colleen Marzluff (S.E.I.), and Al Sanford (NM Institute of Mining and Technology) provided information on economic growth and population size in Southwestern cities. Britta Morner, Tah Yang, Bill Larsen, Lorie Long, and Buddy Stewart of the USDA Forest Service Southwestern Region 3 provided recreation use and occupancy data.

Recreation in Ponderosa Pine Forests

The national trend toward increased recreation (Boyle and Samson 1985; Flather and Cordel 1995) is evident within the ponderosa pine forests of Arizona and New Mexico. Most significant in this respect is Grand Canyon National Park, which includes campgrounds, lodges, roads, and scenic viewpoints in the ponderosa pine forest of northern Arizona. Visitation to the Park has grown tremendously since its opening in 1915 (figure 7). Nearly 5 million people visited the Park in 1995. Even if each person only stayed one day, and visitation was evenly spread throughout the year, over 13,500 visitors would have been present each day of 1995. In reality, most visitation is during the summer when numbers of visitors per day can reach a total half as large as Flagstaff's population.

Recreational use of National Forests in Arizona and New Mexico is also on the rise. Specific figures have been recorded only recently and are unavailable by forest type. However, recreation in the region is primarily in ponderosa pine and is useful for defining trends and activities. Recreation use increased from 1992 to 1995 in Region 3; over 40 million visitor-days of recreation were recorded in 1995 (figure 8). Most visitors were viewing scenery or camping, picnicking, and swimming (figure 8). Non-motorized travel (hiking, horseback riding, and river raft-

ing) has increased most rapidly, as also noted for the nation as a whole (Flather and Cordel 1995). Hunting, fishing, winter sports, and resort camping have remained fairly stable and include many fewer people than travel and camping (figure 8). Nonconsumptive wildlife recreation (bird watching, nature study/viewing/photography) has increased each year, but involves relatively few people.³ However, nonconsumptive activities can have significant impacts on species of great interest if individuals of these species are disturbed repeatedly.

Marzluff presents a detailed discussion of the effects of the various different types of recreational activities on bird populations and habitat in another section of this volume. He reviews motorized travel and viewing scenery; camping and picnicking; hiking, nature study, and wildlife photography; resorts and recreation residences; and winter sports and mechanized off-road travel in his discussion. This section also describes the types of research required to address the effects of both urbanization and recreation on songbirds in Southwestern ponderosa pine forests (Marzluff this volume).

Increased recreational use of the National Forests has led to an expansion of public facilities. Current (1995) facilities have the capacity to hold over 130,000 visitors per day, up from 98,000 in 1990 (U.S. Forest Service Annual

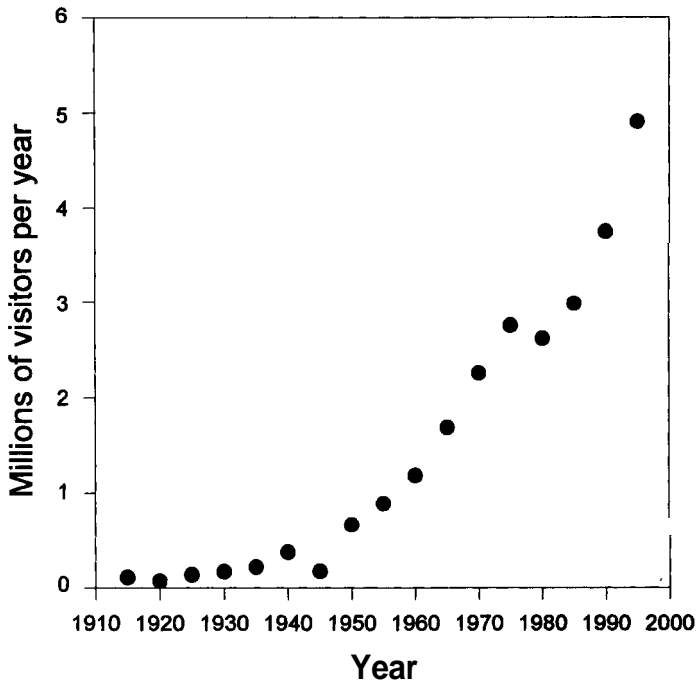


Figure 7. Visitation to Grand Canyon National Park from 1915 to 1995. Data were collected by the U.S. National Park Service. The visitor-per-day vehicle multipliers were updated during 1992. Visitation in 1995 was estimated to be reduced by 50,000 people due to a government shutdown.

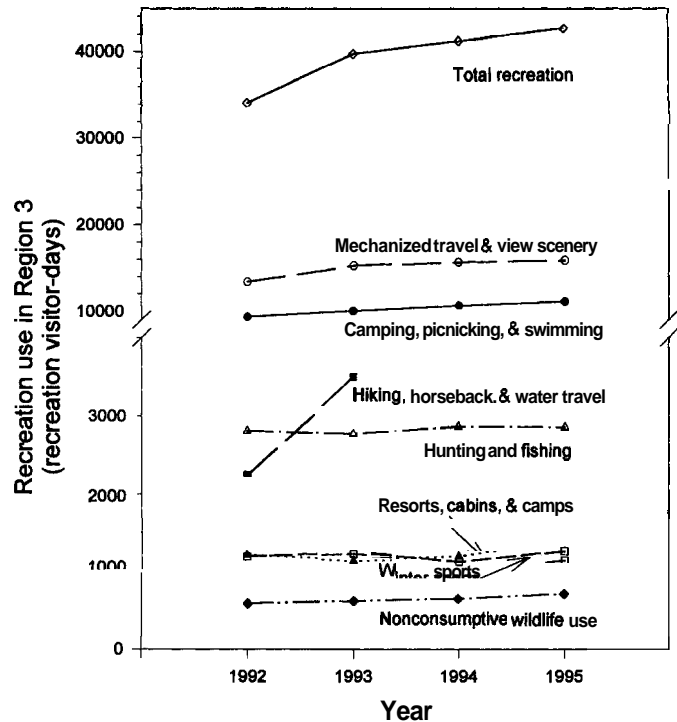


Figure 8. Recreation use in Region 3 of the USDA Forest Service (Arizona, New Mexico, and a small portion of Texas and Oklahoma). Data were collected by surveying visitors to local facilities. Data before 1992 were obtained with varying methods and are not directly comparable to those presented.

Recreation Site and Area Information). The number of campgrounds and picnic areas increased slightly from 1990 to 1995 (figure 9). The number of recreational residences in and adjacent to a National Forest has declined recently. Since Forest Service Region 3 recreation information is not maintained by vegetation type, it is difficult to determine the nature and extent of activities focusing in the ponderosa pine type. More research is needed on this topic, just as more research is needed concerning the effects of the various different types of recreational activities on bird species and habitat.

Conclusion

The issue of land use and its effects is a complex one. The environmental effects of a particular land use can be singular, synergistic, or cumulative with long- and short-term consequences. Both synergistic and cumulative land use effects require considerably more research. An especially important area that should be targeted for future studies concerns the combined effects of logging and grazing on birds and bird habitat.

Although we have focused primarily on human land uses and their negative effects to wildlife species, results of land use activities can also be positive or neutral for

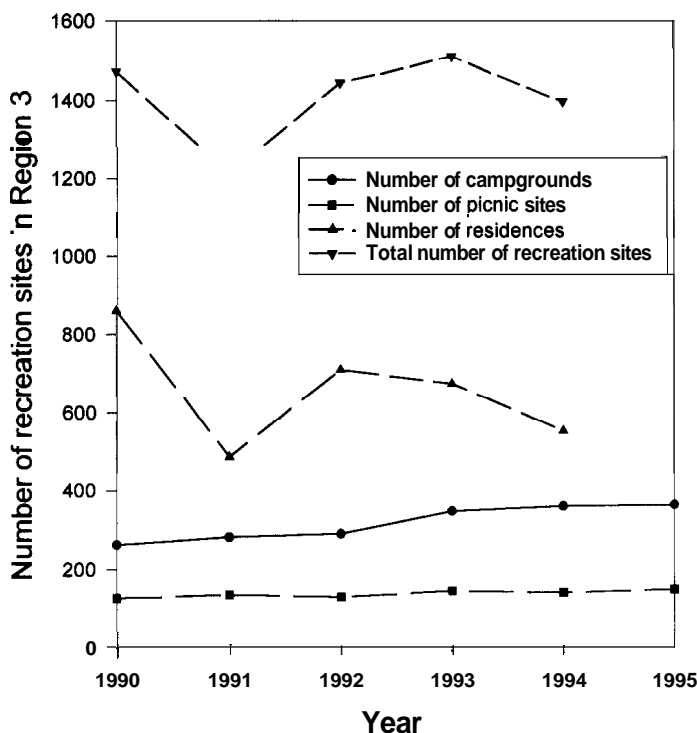


Figure 9. Number of developed recreation sites in Region 3 of the USDA Forest Service.

these species. Both Thompson et al. (1995) and Hejl et al. (1995) review positive, negative, and neutral effects of varying silvicultural treatments on selected species. Saab et al. (1995) provide a similar discussion with respect to grazing in western habitats.

Since the 1960s and 1970s, the precedence of human resource consumption and use over other considerations has been under increasing scrutiny as demonstrated by environmental protection legislation and court actions. The National Environmental Policy Act, the Endangered Species Act, the National Forest Management Act, and the Migratory Bird Treaty Act are examples of legislation designed to help protect the environment, as well as wildlife species and habitat. This legislation indicates the strength of the environmental movement and the general importance of wildlife protection to at least a certain segment of the American public.

Despite the increase in environmental protection legislation, ponderosa pine habitat declined in geographic extent and tree volume in the period from 1962 through 1986 in Arizona and New Mexico. Though the geographic extent and volume of small trees (poletimber, saplings, seedlings, and trees with a dbh below 43.2 cm) increased, these measures decreased for large trees, yielding an overall decrease. As discussed previously, logging is generally the prime cause of changes in stand geographic extent and volume (Choate 1966; Spencer 1966; Conner et al. 1990; Van Hooser et al. 1993). Historically, ponderosa pine has been a main, heavily cut component of the Southwestern timber harvest (Schubert 1974), and this pattern continued into the 1980s. Since the beginning of the 1990s, both timber sales and cut volume of all species have declined on Forest Service land. Many factors contributed to these declines, including implementation of the Mexican Spotted Owl and Goshawk Habitat Protection Guidelines (USDA Forest Service Region 3 1994). The effect of these declines on the health and extent of ponderosa pine habitat remains to be seen.

In addition to wood harvest, cattle grazing (as well as the grazing of wild herbivores such as elk) can alter ponderosa pine habitat. There is less information on the effects of grazing (Finch et al. this volume) than on the effects of timber cutting and even less on the combined effects of timber harvest and grazing. Grazing on public lands is now coming under increasing scrutiny and discussion. Recent congressional debates and public controversy over range and grazing fee reform show a changing, more negative public perception of ranching on federal lands (Kennedy et al. 1995; Richardson 1995; Mitchell and Fletcher 1996; Varela 1996). Judging the extent to which perceptions and attitudes of the general public differ from those of non-governmental organizations and advocacy groups is difficult and is becoming an area of concern to federal land managers (Mitchell and Fletcher 1996). In any event, there is growing awareness of the potentially harmful effects of grazing on birds and

other wildlife species and recognition that future range studies must consider both the needs of wildlife and the needs of society if they are to be effective (Kennedy et al. 1995; Vavra 1995).

Since the 1920s and 1930s, there has been a downward trend in the number of animals grazing on public lands in the Southwest (discussed in Raish 1996). As discussed previously, in the years from 1982 through 1995 the numbers of Forest Service permittees dropped by about 25 percent in Arizona and New Mexico, while the number of animals authorized to graze dropped by 25 percent in Arizona and 20 percent in New Mexico. However, the ways in which these figures relate to the various different grazing systems in use and the effects of these systems on wildlife and wildlife habitat are not well known. The effect of wild herbivore grazing in conjunction with cattle grazing is also a topic that requires additional research. Answering these questions requires a concerted program of study focusing on the effects of different grazing systems on wildlife in matched habitat types (Saabet al. 1995).

In addition to studies focusing on the effects of cattle grazing, more information is needed on the effects of urbanization and recreation on wildlife species and habitat. With urban populations projected to increase and recreation demands projected to accelerate throughout the United States (Boyle and Samson 1985; Anderson 1995; Flather and Cordel 1995), the potential for considerable negative effects from these activities is high. Studies designed to assess the impacts of these types of activities can assist planners to prepare growth models and recreation development strategies that are the least harmful to species and habitat.

Though there are indeed many human activities occurring in the ponderosa pine forests of the Southwest, this review has examined those that have the greatest potential to affect bird species and their habitat. Thus, commercial and personal-use wood harvest, livestock grazing, recreation, and urbanization have been considered. Of these, we have the greatest amount of research information on the effects of large-scale timber harvesting on habitat. Considerably more research is needed concerning the effects of different types of grazing systems and the effects of combined grazing and logging. Different types of recreational activities and growing urbanization in the region also require additional research. Studies of the effects of these activities are crucial for planning future developments that consider both human and wildlife needs.

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Chapter 3

A Historical Review

Dan Scurlock and Deborah M. Finch

Introduction

Many groups of people in the Southwest have been closely associated with ponderosa pine forests for at least 12,000 years. In the last 150 years, activities, such as logging, fire suppression, and grazing, have caused extensive modifications to ponderosa pine forests including changes in distribution, species composition, stand age, and a general decline in forest health. Climatic changes have also contributed to forest modification. Forest habitat alterations have affected the distribution and abundance of bird populations, resulting in population decreases or increases of some species.

This chapter reviews the historical: 1) occupancy, use of and impacts on ponderosa pine forests by early American Indians and European settlers; and 2) the human use of and impacts on birds in ponderosa pine forests. Contemporary ecology and human use of ponderosa pine forests are described in this publication by Moir et al. and Raish et al. Recent human impacts on ponderosa pine birds are discussed by Marzluff and Finch, also in this volume.

Historical Observations of Ponderosa Pine Forests

Perhaps the first European to see a ponderosa pine forest in the Southwest United States was Alvar Nunez Cabeza de Vaca, who traveled across southeastern New Mexico in 1536. Although Vaca did not specifically refer to ponderosa pine, he did describe pinyon and another pine growing in the region's mountains (Covey 1983). Fray Marcos de Niza led a small expedition from western Mexico into present southeastern Arizona and then north in search of Pueblo Indians. Niza probably observed ponderosa pine in eastern Arizona near the New Mexico border (Simmons 1977).

In late 1540, Francisco Vasquez de Coronado traveled north to the upper Rio Grande to reach Zuni Indian villages. From there he marched east to present Socorro, New Mexico before joining a second contingent at a Pueblo village near present Bernalillo, New Mexico. Coronado and

his army eventually reached present Taos and Pecos, New Mexico. The term "pino" was used by the chronicler of the expedition when describing the trees observed. Reference was made to "pillars of pine," which may have been ponderosa pine, that were used by the Pueblo Indians to construct footbridges (Strout 1971). Extensive montane pine forests in the region were mentioned by Coronado, as they were by several subsequent Spanish explorers in the late 1500s. The earliest description of ponderosa pines in the region was by Don Pedro Baptista Pino in 1812, who remarked that the trees he observed were more than 110 ft tall and 14 to 19 ft thick (Bustamante and Simmons 1995).

Descriptions of ponderosa pine forests in New Mexico and Arizona were made by early United States military personnel and scientists. Lt. James H. Simpson, on an 1849 expedition at the present border of New Mexico and Arizona, referred to "yellow pine" describing them as "about eighty feet high and twelve feet in circumference at the trunk" (McNitt 1964). In 1853, Lt. A. W. Whipple described extensive pine forests on the flanks of the San Francisco Peaks. To the west of the range he observed, "groves of magnificent pines, intermingled with cedars and dwarf oaks" (Foreman 1946). Later, C. E. Dutton wrote about the ponderosa pine forests of the Kaibab Plateau in northern Arizona:

"The trees are large and noble in aspect and stand widely apart Instead of dense forests, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade" (quoted in Mitchell and Freeman 1993).

C. Hart Merriam (1890) described the ponderosa pine forest on the Coconino Plateau.

"The pine forest is thoroughly mature, nearly all of the trees being of large size, and rarely crowded. It is a noteworthy forest, not alone on account of the size and beauty of the single species of tree of which it is composed (*Pinus ponderosa*), but also because of its openness, freedom from undergrowth, and its grassy carpet. . . ."

This openness was also noted by Leiberg et al. (1904); however, by 1904, logging was fragmenting the extensive, open stands of ponderosa pine. Cooper (1960) has published other similar historical descriptions of ponderosa pine forests.

Prehistoric and Historic Use of Ponderosa Pine Forests

American Indian

The first human contact with ponderosa pine forest occurred approximately 12,000 years ago when the earliest Paleo-Indians migrated south from Alaska and Canada into present Western United States. Although the groups that settled in this area over the next 5 millennia probably used ponderosa pine, its specific use in the Southwest was not archeologically documented until about 100 A.D. Initially, poles and small logs of ponderosa pine were used to construct the roofs of pithouses (semi-subterranean dome-shaped wooden structure with a roof of grass, sticks, and mud). Ponderosa pine was used as village architecture evolved into multiple-room surface structures and eventually into multi-storied, apartment-styled complexes after 950 A.D. (Cordell 1984; Nabokov and Easton 1989).

Many Anasazi village sites were located in pinyon-juniper woodlands where residents used nearby ponderosa pine stands for construction material. Ponderosa pine remains have been recorded at Arroyo Hondo Pueblo south of Santa Fe and at the Pajarito Plateau to the west. Chaco Canyon is the most extensive and best known prehistoric (12,000 B.P. to 1540) archeological site where ponderosa pine house beams have been found. The use of ponderosa pine by the prehistoric Pueblo for roof and other construction material continued into the historic period (1540 to 1945). The Hohokam and Mogollon of southern Arizona used ponderosa pine to build roofs (Kelley 1980; Mindeleff 1891; Nabokov and Easton 1989).

Although dead trees were generally used for fuelwood (Hughes 1983) and wood from older, abandoned rooms or villages was recycled into new construction (Ford 1987), living trees were harvested in certain locations. Packrat midden and pollen analyses at Chaco Canyon and Anasazi sites in Southwestern Colorado indicate that use of forest resources could be relatively intense, leading to soil erosion and other associated impacts that eventually caused village abandonment. Besides harvesting for construction timbers and fuelwood, the Anasazi also cleared relatively extensive acreage to farm (Betancourt and Van Devender 1981; Petersen and Matthews 1987; Wyckoff 1977).

At some large villages or village clusters, such as Chaco Canyon, ponderosa pine logs were widely used, especially as vigas (supporting rafters) in roof construction. Between 1050 and 1125, approximately 100,000 ponderosa pine logs were cut in mountain ranges 45 to 60 miles away and hauled to Chaco villages where they were used in constructing the roofs of residential rooms and kivas (round, partly underground ceremonial structures). Area pinyon-juniper woodlands and sparse ponderosa pine forests

were extensively harvested between 900 and 1125 for construction and fuelwood use (Betancourt and Van Devender 1981; Hall 1977; Murphy 1994; Toll 1985).

During the historic period, Pueblo uses of ponderosa pine included chewing the needles as a cold sore remedy, drinking a concentrate made from the roots to treat urinary problems, and making cradle boards. Ponderosa pine continued to be commonly used in construction and as fuelwood (Dunmire and Tierney 1995). The Hopi of northeastern Arizona used ponderosa pine from the San Francisco Peaks for prayer sticks and kiva roof beams (Houk 1993; Whiting 1966).

The Navajo, Southern Ute, and various Apache tribes in the Southwest used the inner bark of the ponderosa pine (Castetter 1935), which was collected by removing a rectangular or oval patch of the scaly outer bark. The stringy layer of phloem and cambium cells was removed and eaten raw, made into a flour for bread making, and used to make a tea. Sap in the spring made the inner bark more palatable than at other times of the year when it was used only as an emergency food (Cassells 1983; Swetnam 1984). The Utes placed those who were ill next to peeled ponderosa pine trees believing that doing so would help them recover (Cassells 1983). Trees scarred in the 18th, 19th, or early 20th centuries by this collecting activity are still visible on National Forest System (NFS) land in the Southwest.

The Navajo, from their late prehistoric arrival in the Southwest until recently, have also used ponderosa pine as construction material in the hogan (a building made of logs and mud and used as a dwelling). Trees that were wind-felled or lightning-struck were preferred, as was timber from prehistoric ruins or abandoned hogans; hogan sites were usually located in or close to ponderosa pine stands. Ponderosa pine was and is used by the Navajo for fencing. The Navajo used ponderosa pine for fuelwood (Jett and Spencer 1981) and obtained a reddish dye and pigment from the bark, which they used in sand paintings (Houk 1993).

European Settlers

Spanish settlers used ponderosa pine wood for building material, furniture, and tool handles. They extracted yellow dye from ponderosa pine to use in leather tanning and resin to treat scaly skin, smallpox, and liver spots (Boyd 1974; Curtin 1965). Although not as important as juniper and pinyon, ponderosa pine wood has and is used as a fuel. Ponderosa pine was used to make retablos (religious images painted on a piece of wood or metal) that were used as either part of an altar screen or as a decorative hanging in a home or business (Dickey 1970).

Anglo-American settlers in northern New Mexico began to harvest ponderosa pine for construction and fuelwood in the late 1840s. Logging operations and sawmills were established across the region from the 1850s to the 1930s to meet the demand for timber at military posts, mine and railroad construction sites, and settlements. Pon-

derosa pine has been cultivated in the West since 1827 and used as ornamental, shade, or shelter-belt plantings (Vines 1960).

Grazing

New Mexico

Livestock grazing and settlement began in the Southwest in 1598, when Juan de Oñate led the first Spanish settlers and 4,000 sheep, 1,000 cattle, 1,000 goats, and 150 mares with colts to the upper Rio Grande Basin in present New Mexico. Some of the wealthier individuals brought their own livestock (Baxter 1987; table 1). As these early herds grew, livestock grazing operations began at a number of missions and land grant (a grant of land made by the government) settlements in northern and central New Mexico. As early as 1630, overgrazing at these locations was documented (Baxter 1987; Ford 1987; Simmons 1991).

Following the appearance of spring grasses and shrubs from the pinyon-juniper to the mixed conifer zones, sheep, goats, and cattle were moved from their lower, protected winter pastures and herded into the uplands. By early summer the stock was herded as high as subalpine meadows or to the tundra above 12,000 ft. These uplands, including pinyon-juniper woodlands and/or ponderosa pine forests, were ejidos (common lands) shared by the villagers (Bailey 1890; Briggs and Ness 1987).

The development of livestock raising in New Mexico was interrupted for 13 years during the Pueblo Revolt of 1680. In 1693, the Spaniards began raising livestock again with more than 4,000 sheep, cattle, and goats. By the middle of the next century, livestock numbers had increased to more than 135,000 animals, which were grazing from Taos to Belen, New Mexico (Baxter 1987; table 1).

Montane woodlands and/or forests, part of every Spanish land grant in north central New Mexico, were intensively grazed from the 18th century until the mid-1800s. In the 18th century, some land grants in northern New

Mexico were awarded exclusively for grazing livestock (Bailey 1980; Briggs and Ness 1987). Meadows and springs were camping areas for herders and bedding grounds for goats and sheep (Scurlock 1983, 1997).

By the early 1700s, Navajos in northwestern New Mexico and northeastern Arizona had adopted Spanish sheep and herding techniques. Animal numbers ranged from 8,000 head in 1721 to 64,000 by 1742. A century later, the total number of Navajo sheep was estimated at 500,000. These numbers dropped dramatically to 30,000 in 1870 following the reduction of American Indian land holdings and placement of many tribes in the reservation system. Through land allotment, American Indians resettled most of their former territory and again raised livestock. By 1930, Navajo flocks had increased to over 1 million sheep and goats. Horse and cattle numbers had also increased significantly to 80,000 and 27,000, respectively (Bailey 1980).

Escaped horses and burros across the Southwest led to the increase of wild herds in the middle to late colonial period (1750–1821). Raids by nomadic American Indians also spread and increased the number of wild horses who ranged, in unknown numbers, into the ponderosa pine forests to graze. By the late 1700s, wild herds were locally abundant. The decline of wild horses, burros, and goats began in the 1860s with the arrival of Anglo-American ranchers who shot or captured wild horses that were competing with their cattle for grass and water (Bustamante and Simmons 1995; Wyman 1945).

In the early 1800s, some 30,000 Spanish New Mexican sheep were exported annually to Mexico. By the 1820s, the number of sheep in New Mexico, excluding the Navajo herds, had increased to between 1 and 3 million head. Cattle numbered 5,000 head, horses 850, and mules 2,150. Apache and Navajo raids on sheep flocks reduced the sheep numbers to 377,000 by 1850 (table 2). Losses due to droughts, blizzards, and predators also contributed to the decline (Baxter 1987; Denevan 1967).

Table 1. Livestock numbers in the Southwest, 1598–1820s.^a

Year	Sheep	Cattle	Goats	Horses	Mules	Total
1598	4,000	1,000	1,000	150	^d	6,150
1694	2,100	^d	^d	^d	^d	3,000
1697	4,000	650	170	^d	^d	4,820
1757	112,18 ^b	16,157	^c	7,356	^d	135,695
1777	69,000	^d	^d	^d	^d	69,000
1820s	1,000,000	5,000	^d	850	2,150	1,008,000
	to					to
	3,000,000					3,008,000

^a Does not include Navajo flocks.

^b Includes Hopi flocks.

^c Includes sheep.

^d Data not recorded.

Source: Baxter 1987; Denevan 1967; Simmons 1988.

Table 2. Livestock numbers in New Mexico, 1850–1900.^a

Year	Sheep	Cattle	Total
1850	377,000	^b	377,000
1860	830,000	^b	830,000
1870	619,000	137,314	756,314
1880s	2,000,000	500,000	2,500,000
	to		to
	5,400,000		5,000,000
1890	4,000,000	210,000	1,517,000
1900	3,500,000	843,000	4,343,000
1935	669,000	212,000	881,000

^a Does not include Navajo flocks.

^b Data not recorded.

Source: Baxter 1987; Carlson 1969; Denevan 1967; Miller 1989; Simmons 1988.

The first Anglo-American owned cattle were driven into New Mexico from Texas in 1865 and 1866 to supply beef to military posts and miners. In 1866, about 7,000 head of cattle were sold to the army, whose increasing demand for beef fueled the cattle drives in the late 1860s and 1870s from Texas to eastern and southern New Mexico. In 1870, there were over 137,000 cattle in New Mexico. Military contracts for beef from New Mexican ranchers ended in the early 1880s (Miller 1989).

Cattle numbers grew to over a half million head by the early 1880s. Some ranchers were attracted to New Mexico following completion of 2 major rail lines in 1879 and 1881. Droughts and overgrazing in west Texas in the 1870s and 1880s also caused many ranchers to drive their herds into New Mexico. Many of the Texas cattle herds that were moved to New Mexico grazed during the summer in the woodlands and forests of the Jemez, Sangre de Cristo, and other mountain ranges in northern and central New Mexico. Other herds went to southeast Arizona and southern Colorado (Scurlock 1997).

In 1870, there were 619,000 sheep in New Mexico (Carlson 1969; table 2). These numbers reached an estimated peak of 4 to 5 million head in the 1880s. At the beginning of the 20th century, due to range deterioration caused by overgrazing and droughts, there was a decrease in sheep to 3.5 million. (Carlson 1969; deBuys 1985; Denevan 1967). Extensive grazing continued in New Mexico uplands until the end of the century. Passage of the General Revision Act on March 3, 1891, authorized the President of the United States to establish Forest Reserves (now called National Forests) on public land, in any state or territory, wholly or partly covered with timber or undergrowth with or without commercial value. Many local residents who lost their grazing rights to the previously common land, continued to graze their stock on the Forest Reserve land (Bahre 1991; Carlson 1969; deBuys 1985). By 1938, about 203,000 sheep were grazing during the summer on public and private lands in northern New Mexico (Workers of the Writers' Program 1940a).

Arizona

The first livestock in Arizona was brought by Franciscan missionaries to the Hopi Pueblo in 1629. Herds of sheep, goats, cattle, oxen, horses, and burros were grazed around the Hopi missions and villages for the next 50 years. By the early 1700s, the Hopi were raising their own livestock; one of the pueblos had 30,000 sheep in 1776 (Schickedanz 1980).

The Spanish brought the first herds of livestock into southern Arizona after 1690. Missions were established with herds of primarily sheep and cattle. Spanish ranching operations were also established in the Santa Cruz and San Pedro drainages (Faulk 1970). Some 100,000 head of cattle were grazing on the headwaters of the San Pedro in southern Arizona in 1694 (Schickedanz 1980). However, Apache raids on Spanish livestock during much of the

1700s prevented settlement of new ranches and kept the number of herds low. In the early 1800s, there were 26,000 sheep and 1,200 horses grazing around Tucson and 1,000 cattle grazing at Tubac. Several Arizona land grants were made in the first 2 decades of the century; one near San Bernardino on the Mexican border grazed 100,000 head of cattle (Faulk 1970). By the early 1820s, large cattle herds were grazing at these locations, but Apache raids forced many to abandon their ranches. Thousands of abandoned cattle became feral and roamed the area into the 1850s (Hirt 1989; Workers of the Writers' Program 1940b).

One Spanish rancher grazed 10,000 sheep and 600 goats in southern Arizona in the mid-1800s. One of the earliest Anglo-American ranch was established on the Santa Cruz River in 1857; another small ranch began operating south of Tucson in 1858. The Apaches increased their livestock raids, which discouraged upland grazing (Hirt 1989).

To the north, on the pinyon-juniper and ponderosa pine-covered Defiance Plateau, the Navajo began herding sheep, cattle, and horses, mules, and burros in the late 1700s. By 1850, about 500,000 sheep, 30,000 cattle, and 10,000 horses, mules and burros were grazing on the plateau. At the same time, the ponderosa pine and conifer forest understories of the Chuska Mountains were intensively grazed by relatively large sheep and other livestock herds (Bailey 1980; Cooper 1960).

United States military posts, mine activity, and settlement growth, increased the demand for beef and mutton, which produced significant growth in southern Arizona's ranching industry (Pratt and Scurlock 1991). The military continued to contract with Arizona ranchers until the mid-1870s. Navajo herds numbered about 225,000 head in 1873. Sheep herds were moved from California and New Mexico to new operations in northern Arizona beginning in the late 1860s and early 1870s.

In 1880, there were 8,000 cattle and 10,000 to 12,000 sheep in the San Pedro Valley, Arizona. The arrival of railroads in the early 1880s caused livestock numbers across most of Arizona to rapidly increase. One sheep rancher near Flagstaff had 50,000 animals grazing in the mid-1880s. By the end of the decade, many ranges were overstocked as the total number of cattle rose from 5,000 head in 1870 to 8,000 head in 1880 to more than a half million head in 1890. By 1891, there were more than 700,000 head of sheep in Arizona. When a drought struck the overgrazed range in 1891, livestock losses averaged 50 to 75 percent in southeastern Arizona.

Introduction of livestock and overgrazing continued on private and public lands into the next century. Sheep outnumbered cattle 10 to 1 in northeastern Arizona, partly due to new Navajo flocks; cattle were common in the south. By 1938, there were 367,000 head of cattle shipped out of Arizona; some 121,000 more were slaughtered in Arizona. There were an estimated 811,000 sheep in the state that same year, with about half of this total on Navajo range-

land (Bahre 1991; Hirt 1989; Workers of the Writers' Program 1940b; Bailey 1980; Cooper 1960; Faulk 1970; Miller 1989).

National Forests

By the time the first Forest Reserves were established in New Mexico and Arizona in the 1890s, most of the understory in accessible ponderosa pine forests had been intensively grazed. Although ranchers thought that free use of public land was a right and stocking was heavy, most realized that limiting herd size on Forest Reserve land was necessary to continue business (Baker et al. 1988; Eastman and Gray 1987).

From 1893 to 1902, 8 Forest Reserves were established in Arizona including Grand Canyon, Prescott, San Francisco Mountains, Black Mesa, Santa Rita, Santa Catalina, Mount Graham, and Chiricahua. These are now part of the Kaibab and Coconino National Forests, Prescott National Forest, Coconino National Forest, Coconino and Sitgreaves National Forests, and Coronado National Forest, respectively (Baker et al. 1988). Twelve more Forest Reserves were added from 1905 to 1906.

In 1900, while surveying grazing at the headwaters of the upper Salt River and its affects on the lower valley, Gifford Pinchot, head of the Bureau of Forestry (now called the Forest Service) in the Department of Agriculture, noted that sheep overgrazing had destroyed young ponderosa pine seedlings (Frome 1962). Although grazing permits for horses and sheep were issued by the Bureau of Forestry during this period, it was not until 1906 that fees were collected for all livestock grazed on the Forest Reserves. From 1901 to 1906, there were 581 permits issued for approximately 98,000 cattle and horses, and 87 permits issued for approximately 347,000 sheep and goats to graze on Forest Reserves in Arizona (Rowley 1985).

In the early years of the 20th century, heavy stocking of Forest Reserves was thought a viable way to reduce vegetation and diminish the fire threat. Protests, noncompliance, and trespass by ranchers hindered effective management of grazing lands (Eastman and Gray 1987; Rowley 1985). Additionally, the demand for food and wool during World War I caused livestock numbers to soar on public and private lands (Brown 1985; deBuys 1985; Donart 1984).

The Forest Service began to reduce the number of permitted livestock on NFS land in the Southwest due to extreme range deterioration and erosion caused by overgrazing; numbers went from approximately 738,000 in 1919 to less than 536,000 in 1929 (Baker et al. 1988; table 3). Many ranchers in the Southwest sold their livestock during the post-war agricultural depression from 1919 to 1921, which further reduced the grazing numbers. Over the remainder of the decade, livestock numbers on NFS land continued to decline. This reduction in numbers grazed and permitted continued into the 1950s (table 3). Increases in grazing fees continued to be controversial (Baker et al. 1988; Rowley 1985).

Table 3. Grazing leases and livestock numbers in the Southwest, 1909–1958.

Year	Permit	Cattle and horses	Sheep and goats	Total
1909	3,376	235,946	512,130	748,076
1914	3,321	270,623	398,134	688,766
1919	3,590	366,520	371,457	737,977
1924,	3,032	279,520	262,492	542,012
1929	a	183,076	352,618	535,694
1934	3,170	189,299	245,189	437,658
1939	a	171,976	193,886	371,862
1944	a	153,217	113,504	266,721
1949	a	a	a	a
1958	2,538	145,247	75,217	223,002

^a Data not recorded.

Source: Baker et al. 1988.

In an attempt to reduce grazing pressure by trespass livestock, fencing of NFS land began in the 1930s and continued into the 1940s. Passage of the Taylor Grazing Act of 1934 was prompted by overgrazing on NFS and Grazing Service (later called the Bureau of Land Management) land. This grazing regulation program resulted in a significant reduction of livestock numbers on public and Pueblo and Navajo land (Bahre 1991; deBuys 1985; Mortensen 1978).

From the 1920s to the 1940s, Forest Service permittees typically grazed more animals than authorized. Also, large livestock operations were buying permits from smaller ranchers. The Forest Service stepped up enforcement to correct these 2 problems. In addition, to prevent control of large areas of rangeland by a small number of individuals, the agency began limiting the maximum number of animals that could be grazed on a single permit. On the Carson and Santa Fe National Forests in New Mexico, the maximum number of animals authorized to graze on 1 permit was 400. In the 1940s, ranchers in New Mexico and southern Colorado began to abandon labor-intensive sheep herding in favor of cattle, which range without herders. Changing economics also resulted in a steady decline in the number of permittees on forest lands (deBuys 1985).

Forest Service reports for the 1950s through 1960s on ponderosa pine grasslands were mixed. According to a 1952 study, ranges on the Kaibab National Forest were improving. A 1964 report noted that the Santa Fe National Forest was overstocked by 20 percent, while a report issued in 1965 for the Lincoln National Forest indicated that range management was improving. Inspectors found that many areas of Coronado National Forest were in unsatisfactory conditions (Baker et al. 1988).

Grazing pressure during this period also resulted from feral horses and burros. Many of these animals sought secluded ranges in the uplands of Southwestern NFS,

Bureau of Land Management (BLM) and National Park Service (NPS) land. Although the Forest Service, BLM, and NPS began round-ups and reductions in the early part of this century, some animals eluded their efforts. Small herds of horses and burros continue to exist on public and American Indian reservation lands in the Southwest (Bahre 1991; deBuys 1985; Symanski 1985).

The long-lasting effect of overgrazing on NFS land during this century was noted in a 1986 Environmental Impact Statement for the grasslands of the Coronado National Forest. The observation was that, "The grazed portion of the range was severely overgrazed" [in 1902] and "to this day ranges show signs of stress" (quoted in Hirt 1989).

Logging

Prehistoric Indian harvesting of ponderosa pine timber was localized. However, extensive use of ponderosa and pinyon pine at Chaco Canyon and other prehistoric population centers between 900 and 1125 resulted in severe environmental degradation. More than 100,000 trees were cut in at least 3 distant mountain ranges and hauled back to Chaco between 1000 and 1125. At other large village complexes (Mogollon, Hohokam, and Hakataya) ponderosa and pinyon pine species were commonly used to construct jacales (a hut in the Southwestern United States with a thatched roof and walls made of upright poles covered with mud or clay), pithouses, or surface houses (Gumerman and Haury 1979; Martin 1979; Schroeder 1979). Both ponderosa and pinyon pine were used to construct and renovate hundreds of other post-500 to 1500 small, prehistoric sites in the Southwest.

Logging by Spanish settlers during the colonial period (1540 to 1821) was limited to local forests near either land-grant villages or mission churches, where the surrounding pinyon juniper woodlands and ponderosa pine forests were commonly exploited. As nearby fuelwood was exhausted, pack mules, burros, and horses transported wood from increasingly greater distances (Adams and Chavez 1956; Fogg 1966). Ponderosa pine was often found in central and northern New Mexico on common land where resources were available for use by the Spanish land grantees. Early mission establishments among the Pueblo, including the Hopi of northeastern Arizona, also used ponderosa pine for building and fuelwood but impacts were limited to small areas (Jones 1932; Scurlock 1997). In southern Arizona, ponderosa pine use was minimal because Spanish land grants and missions, which all dated from the late colonial and Mexican (1821 to 1846) periods, were generally not near ponderosa pine forests.

The first Anglo-American people who arrived in the Southwest in the 1820s and 1830s were fur trappers and traders. Some settled in northern or central New Mexico and southern Arizona. Their small numbers and lifestyle generated minimal impact to ponderosa pine forests,

which they used primarily as a source of fuelwood (Weber 1971).

In 1846, at the beginning of the Mexican War, the United States Army began to establish forts in the Southwest. Posts were established across Arizona and New Mexico over the next 2 decades to protect European settlers against American Indian tribes. Construction and occupation of these forts required lumber and fuelwood. The military set up sawmills or contracted for needed material. Wood cutting by military troops also provided fuel and timber (Giese 1976; Miller 1989; Walker and Bufkin 1979).

Mining in territorial New Mexico and Arizona (1846 to 1880) and construction of the early railroads to New Mexico and Arizona (1879 to 1881) resulted in the first major commercial use of pinyon and ponderosa pine and juniper in the historic period (Scurlock 1997; Walker and Bufkin 1979). Harvesting ponderosa pine for railroad ties, mine timbers, or lumber caused local reduction in woodlands and forests in the late 19th century. One railroad company constructing a line across New Mexico in 1885, used over 930,000 ft of "native pine," which included pinyon and ponderosa (Christiansen 1974; Hirt 1989; Ensign 1888; Perry 1922; Tratman 1889). A logging-sawmill operation was established in the Chiricahua Mountains in 1879 and by 1902, 11 sawmills were operating. About 30 percent of the coniferous forest in the Chiricahuas was logged by 1902 (Bahre 1991).

Timber consumption in New Mexico and Arizona steadily increased over the last 4 decades of the 19th century. Approximately 8 million board feet (MBF) and 22 MBF was cut in 1869 and 1879, respectively. An estimated 5 MBF of lumber was consumed in New Mexico alone in 1886. By 1900, the annual cut in Arizona and New Mexico was 67 MBF (Houk 1993; table 4). Although fuelwood cutting was extensive during this period, little or no ponderosa pine was harvested.

Authorized timber sales from Forest Reserves began in 1897, but the harvest was limited to \$100 worth of timber per year for each permittee. Free use of dead timber was permitted. The Forest Service began timber sales on the 25 reserves in Arizona and New Mexico in fiscal year 1906. Regulations limiting the cut remained until after 1907, when 5 more National Forests (passage of the Act of March 4, 1907, renamed the Forest Reserves) were established in Arizona and New Mexico (Baker et al. 1988); however, unauthorized cutting was widespread. Millions of board feet were illegally cut in the Prescott Forest Reserve in the early years of the century and by 1908, most of the timber in the Manzano National Forest had been harvested illegally for use as railroad construction material (Baker et al. 1988).

In 1907, there was 90 MBF of standing ponderosa pine on the San Francisco Mountains Reserve, now part of the Coconino National Forest in Arizona. That year, this timber was cut and sold, enough mature trees were left to

Table 4. Timber^a consumption in Arizona and New Mexico, 1869-1992.

Year	Lumber production (million board feet)
1869	8,000
1879	22,000
1900	67,000
1909	155,000
1916	173,278
1920	230,477
1925	297,839
1929	322,881
1930	238,382
1932	129,877
1935	226,395
1940	241,562
1945	257,084
1946	384,949
1956	199,827
1964	399,203
1972 ^b	390,825
1980 ^b	365,424
1984 ^b	309,473
1990	433,000
1992	145,000

^a Primarily ponderosa pine.

^b Fiscal year, October 1 - September 30.

Source: Baker et al. 1988; Houk 1993.

seed the cut areas, and a sufficient number of young trees were left to ensure a future cut. Ponderosa pine was also being cut on the Kaibab Plateau. The mill at Fredonia processed about 20 MBF of timber annually from 1910 to 1912. From 1912 to 1926, there were several lumber and timber companies operating in the Flagstaff-Williams area that processed logs from north central Arizona (Tucker and Fitzpatrick 1972).

From 1912 to 1914, intensive logging occurred on Penasco Hill in the Carson National Forest. This operation was producing railroad ties for a second set of tracks across northern New Mexico. The Santa Barbara Pole and Tie Company was established in 1909 in the Santa Fe National Forest. From 1909 to 1926, all of the trees suitable for making railroad ties from the pinyon-juniper zone to the spruce-fir zone were cut on approximately 66,000 acres of this forest (deBuys 1985).

During the latter part of World War I (1916-1918), logging of ponderosa pine in the Southwest increased sharply to meet United States market demands (table 4). Some 6 billion board feet (BBF) of lumber was consumed during the United States war involvement. The regional lumber industry experienced a sharp production decline in 1920 and 1921, but recovered quickly. Timber cutting, mostly ponderosa pine, increased during the remainder of the 1920s (Baker et al. 1988). Sawmills and lumber companies operated in north central Arizona, primarily in the

Coconino National Forest. The Apache Lumber Company purchased 600 MBF in the Sitgreaves and Apache National Forests in 1919 and 1920 (Baker et al. 1988).

Every accessible ponderosa pine forest in New Mexico and Arizona was heavily logged in the 1930s and 1940s. Only stands on steep slopes were spared in Southwestern public and private forests. Logging activity increased during World War II; from 1942 through 1946, the War Department purchased about 8 BBF per year. New Mexico and Arizona contributed from over 242 million to almost 385 MBF during this period (table 4). The Fort Apache Indian Reservation was a major timber source, where over 445 MBF, mainly ponderosa pine, was harvested in 1943. About 75 percent of the 675,000-acre reservation was covered by ponderosa pine (Gomez and Tier 1990; Lindh 1949).

In 1941, there were 72 lumber mills in the upper Rio Grande Basin, New Mexico. These operations processed 60 MBF that year, where 94 percent of the harvest was ponderosa pine. By 1950, the annual cut increased to 70 MBF. This cut was more than 25 percent greater than the net annual tree growth in the watershed (Dortignac 1956).

In 1948, ponderosa pine accounted for 88 percent of the total commercial species cut in the Southwest (Lindh 1949). In 1955, almost 246 MBF of lumber was harvested from public and private lands in New Mexico (Anonymous 1959). Timber production for New Mexico and Arizona in 1964 exceeded 399 MBF (table 4). A decline occurred from 1972 to 1984, but by 1990 a record high of 433 MBF was reached (Baker et al. 1988; Houk 1993). Due to growing concerns for threatened, endangered, and sensitive species and their habitat, timber harvest on NFS land dropped to 145 MBF in 1992 (Houk 1993).

Prehistoric and Historic Ecological Disturbances

Before European settlement, naturally occurring and human-caused fire in ponderosa pine forests was a relatively frequent change agent. Fires, combined with drought, wet years, periodic regeneration, localized clearing, logging, and wood collecting, produced a complex mosaic in the distribution, age, structure, and composition of Southwestern ponderosa pine forests (Covington and Moore 1994).

Fire

Observations from 1850 to 1900, report an understory of abundant or luxuriant bunch grass species in ponderosa pine forests. This vegetation subcommunity generally existed from the beginning of the colonial period to

the early part of this century. This condition, as well as scattered grassy "parks," was maintained by relatively frequent (every 2 to 12 years), low intensity fires and light grazing by indigenous mammals. Interspersed among these grasses were various annual or perennial herbaceous species. Soil erosion was minimal (Cooper 1960). Crown fires in mature timber were rare and some seedlings escaped ground fires. Young trees were generally killed in logged areas as the unburned slash burned hot during fires. Ground fires caused little damage due to "little underbrush and litter" (Plummer 1904).

The effects of fire, both human-caused and natural, and other factors on ponderosa pine forests over the past 150 years have been of interest to a number of investigators in the last 4 decades. Among those who have documented change in the range, structure, and floral composition of historic ponderosa pine forests are Cooper (1960), Johnson (1995), Covington and Moore (1994), and Weaver (1951). Weaver (1951) wrote, "Older whites and Indians remember when the ground under the ponderosa pines was grassy, open, and park-like, with but few windfalls, snags, and other debris." He concluded that fire was a significant factor in the development and maintenance of these conditions in ponderosa pine forests and that the subsequent change was caused by fire suppression beginning in the late 1800s. A policy of fire suppression was adopted for the Forest Reserves beginning in the 1890s, but effective fire control was not developed until after 1900. In that year, a fire in the Santa Fe Forest Reserve burned 40,000 acres (Baker et al. 1988).

Dominance of Gambel oak, New Mexico locust, or piñon-juniper occur following ponderosa pine stand-replacing fires or clear-cutting in some mountain ranges in the northern areas of the region. In the southern portion of the Southwest, ponderosa pine and gray oak or silverleaf oak occur. Associated aspen stand acreage has decreased significantly due primarily to fire suppression (Dick-Peddie 1993). Fire suppression and other human activities have also created oak-juniper thickets or young black-jack pine stands. Fire suppression, intensive livestock grazing, and/or logging, combined with periodic drought, led to regeneration of stands of dense, young pine, commonly called "dog hair thickets." Limited or no seedling regeneration, soil erosion, crown fires, structural changes, and a general decline of forest health also result from fire suppression (Cooper 1960; Covington and Moore 1994; Saab et al. 1995). Recently, ponderosa pine loss due to dwarf mistletoe and bark beetle epidemics, once regulated by periodic fires, has increased significantly (Harrington and Sackett 1992; Johnson 1995).

Other changes in ponderosa pine forest attributed to fire suppression include "decreased decomposition rates, stagnated nutrient cycles, eruption of insects and diseases, decreased herbaceous and shrub forage quality and quantity, ecosystem simplification, increased vertical fuel continuity due to dense sampling and pole patches, higher

severity and destructive potential of wildfire, decreased stream flow and on-site water balance, and less wildlife habitat for species dependent on herbaceous vegetation, and greater canopy closure and landscape homogeneity" (Covington and Moore 1994).

Drought

Drought, combined with changes in fire regime, grazing, and logging, have produced significant changes in Southwestern ponderosa pine forests. The drought from 1896 to 1904 in east central Arizona was severe, killing some ponderosa pine and alligator juniper. Recent, extended droughts, such as the one in the early to mid-1950s, killed juniper and ponderosa pine in the region including the Sevilleta National Wildlife Refuge in central New Mexico. Both of these climatic events resulted in the ponderosa pine zone spreading to higher elevations (Plummer 1904; Scurlock 1996). In contrast, the wet year of 1919 was a time of exceptional ponderosa pine regeneration.

Grazing

As mentioned, the beginning of Spanish settlement and livestock grazing in the Southwest in 1598 brought dramatic changes to riparian, bajada (a long, gradual slope), mesa, mountain grasslands, and other vegetative communities. Grasses and shrubs were decimated by sheep, goats, cattle, and horses for up to several miles around major settlements. Removal of ground cover, soil compaction due to trampling, and droughts, resulted in severe, local sheet erosion and gullying (Ford 1987; MacCameron 1994).

Early in the century, Leiberg et al. (1904) documented livestock damage to seedling ponderosa pine and young aspen shoots. Cattle and sheep trampled young trees, especially in riparian areas. When the grass cover was sparse, sheep nibbled seedlings, which caused stunting. However, goats were the most destructive.

A study of grass plots excluded from grazing for 25 years in ponderosa pine at several National Forests in New Mexico, showed a marked increase in blue grama, Arizona fescue, prairie junegrass, and creeping muhly. Forbs and browse cover increased, but under grazing conditions browse increase was inhibited. Ponderosa pine increased when protected from grazing (Potter and Krenetsky 1967).

More recent studies of ponderosa pine forests have shown that livestock grazing, combined with fire suppression, resulted in denser stands of trees and shrubs that spread due to denudation of understory grass cover (Saab et al. 1995).

Logging

As mentioned, many ponderosa pine forests in the region were extensively cut from the 1870s to the 1940s. In

1898, the U.S. Geological Survey appraised regional forests and estimated that 19 percent of New Mexico and 22 percent of Arizona were forested. By 1924, these figures had decreased due to logging to approximately 16 and 21 percent, respectively. More than 50 years later, the figures had increased to 17 and 25 percent, respectively (Baker et al. 1988).

The estimated amount of canopy coverage of ponderosa pine stands before Anglo-American settlement ranged from 17 to 22 percent (Covington and Sackett 1986). By the early 1990s, the canopy coverage had increased from 40 percent to more than 70 percent (Johnson 1995).

In a recent paper, Johnson (1995) reported that ponderosa pine forests decreased by 206,000 acres from 1962 to 1986 in New Mexico and Arizona, mainly due to logging. Increased density of pines during this period was attributed to partial cutting in some areas and no cutting in others. Effective fire suppression was a third factor in causing this density condition.

Exotic Plants Species

A number of exotic plant species have become established in Southwestern ponderosa pine forests following accidental or intentional introduction (table 5). Two introduced grasses are major understory components in the central and northern portions of the region. These are sheep fescue (*Festuca ovina*), a bunch grass, and Kentucky blue grass (*Poa pratensis*), a sod grass, which are both highly palatable to all livestock (Dick-Peddie 1993; Gay and Dwyer 1970). The fescue may have been introduced early in the colonial period, while the blue grass is a 20th-century introduction (deBuys 1985). Hoarhound (*Marrubium vulgare*), another early naturalized species, is much less common. Yellow and white sweet-clovers (*Melilotus albus* and *M. officinalis*), probably introduced by the Spanish, are found along roadways and other disturbed areas

(Dick-Peddie 1993; Hermann 1966; Hitchcock 1935; Stefferud 1948). Mullein (*Verbascum thaspus*), an important medicinal plant for at least 3 centuries, has thrived in disturbed areas, especially in burned ponderosa pine stands (Scurlock 1997).

Early in this century, the Eurasian crested wheatgrass (*Agropyron cristatum*) was introduced to National Forests in New Mexico and Arizona because of its forage value (Scurlock 1997). This species is now established across the Southwest. These species have diminished the cover of more livestock palatable, native bunch grasses and have altered understory plant composition and general ecology.

Prehistoric and Historic Human Uses of and Impacts on Birds

The uses of and impacts on raptors, game birds, and other non-passerines in ponderosa pine forests is poorly understood. Localized use of birds in forests near large population centers, such as Chaco Canyon, was probably relatively high. Intensive logging may have occurred in the closer stands of ponderosa pine. Spanish modifications to forest habitats in the colonial period were minimal, although growth of major settlements such as Taos, Santa Fe, Albuquerque, Belen, and Tucson steadily increased from 1821 to 1846. The subsequent increase of Anglo-American populations, combined with the Spanish and American Indian populations, adversely affected ponderosa pine forest habitats and associated bird species. Subsequent impacts due to urbanization and recreation after 1945 are addressed by Marzluff in Chapter 5 of this volume.

Table 5. Exotic plant species in the Southwest.

Common name	Scientific name	Date of introduction	Source
Alfalfa	<i>Erodium cicutarium</i>	?	Curtin 1965
Hoarhound	<i>Marrubium vulgare</i>	pre-1600?	Wootton 1915 Tierney 1983
Crested wheatgrass	<i>Agropyron cristatum</i>	post-1935	Hitchcock 1935
Kentucky bluegrass	<i>Poa pratensis</i>	post-1598	Gay and Dwyer 1970
Meadow fescue	<i>Festuca elatior</i>	late 19th c.	Hoover et al. 1948
Sheep fescue	<i>Festuca ovina</i>	1598?	deBuys 1985
Mullein	<i>Verbascum thaspus</i>	post-1800?	Haughton 1978
Shepherd purse	<i>Capsella bursapastoris</i>	?	Reed 1970
Sweetclover(s)	<i>Melilotus alba</i> <i>M. officinalis</i>	pre-1915	Wootton 1915 McKee 1948
Oxeye daisy	<i>Chrysanthemum leucanthemum</i>	?	Reed 1970
Dandelion	<i>Taraxacum officinale</i>	pre-1600?	Reed 1970 Tierney 1983

American Indian

Bird Remains from Archaeological Sites

The close relationship that American Indians in the Southwest have had with local bird species extends back more than 10,000 years and involves activities such as hunting, trapping, gathering eggs, raising and keeping live birds, and using birds or their parts in rituals.

Birds collected by early American Indians living in or near ponderosa pine forests were either used or traded, sometimes over long distances, turning up at archaeological sites far from ponderosa pine forests. Remains of small passerines at Southwestern archeological sites are less common than large birds such as raptors. Remains of Mexican parrots, such as military macaw and thick-billed parrot, were found at excavations at Chaco Canyon in northwestern New Mexico, where they were probably used for their feathers and skins. Also uncovered at Chaco, were sandhill crane, several raptors, black-billed magpie, and common raven bones (Judd 1954; Ladd 1963; Schroeder 1968; Akins 1985).

At Anasazi sites at Canyon de Chelly in northeastern Arizona, the bone or feather remains of 34 wild bird species have been recovered. Among these remains the mourning dove, northern flicker, yellow-bellied sapsucker, common raven, house wren, and western bluebird are found in ponderosa pine forests. Two varieties of domesticated turkey and a scarlet macaw have also been identified (Morris 1986). Nine of the 12 species found at Canyon de Chelly have also been recovered at Mesa Verde National Park and 6 of the 12 species have been found at Wupatki National Monument, a site in east central Arizona with ponderosa pine (Morris 1986).

Spanish documents from the early colonial period (1540 to 1598) for New Mexico and Arizona indicate that geese, cranes, American kestrel, eagles, wild and domesticated turkeys, macaws, parrots, quail, and black-billed magpie were kept in American Indian villages and used for their meat or feathers (Schroeder 1968).

Birds as Spiritual Symbols

Birds were incorporated into every aspect of American Indian life. They were associated with numerous natural elements, such as sky, earth, sun, and moon and with daily activities such as crop planting, hunting, racing, and war. Some birds were thought of as messengers between gods and humans, while others were connected to weather phenomenon. At Taos Pueblo, the saying, "we are in one nest" reflects how closely the Taos Pueblo Indians identified with birds (Hughes 1983).

About 100 bird species had roles in the myths, folklore, rituals, and ceremonies of Pueblo Navajo, Apache, and other tribes (Buskirk 1986; Petit 1990; Schroeder 1968; Tyler 1979; Russell 1975). A majority of these 100 species occurred in the prehistoric and historic ponderosa pine

forests of the Southwest, which were inhabited by various American Indian tribes through time. Among the most important birds to the American Indians were the golden and bald eagles, red-tailed hawks, owls, indigenous and imported parrots, macaws, wild and domestic turkeys, hummingbirds, ravens, pinyon jays, nuthatches, and some warbler species.

Eagles and red-tailed hawks were sky-related. Owls were considered symbols of the dark and, among some Rio Grande Pueblos, were associated with witchcraft. Because the wild turkey was the only domestic native bird, both domestic and wild turkeys were believed "bound to the earth." Brightly colored macaws and parrots were connected to the sun and rainbow, while hummingbirds were "rain birds" due to their association with summer flowers and precipitation. Ravens and crows were affiliated with war and dark rain clouds, while pinyon jays were revered for their aggressive behavior, large "warrior" flocks, and "war cries." The red-shafted northern flicker was associated with war and sunrise because of its red wing feathers and tree "drumming." Nuthatches who move down tree trunks, were also affiliated with war because their movement was opposite normal behavior (Tyler 1979).

Birds in Prehistoric and Historic Art

Fetishes (small-scale likenesses of animals usually shaped from stone) have been made by various Southwestern American Indian tribes for over a thousand years. These objects were believed to bring good luck, power, or protection to the bearer. Eagles, owls, ducks, and ravens were the major bird forms produced as fetishes by American Indians in Arizona and New Mexico (McManis 1995). The Navajo made bird fetishes of stone and cottonwood. Bird forms resembling mourning dove, black-billed magpie, macaw, and an unidentified woodpecker have been recovered (Kluckhohn et al. 1971).

Bird figures or feathers were sometimes painted on pottery; ceramic vessels in the shape of birds were less frequently crafted. The Anasazi fashioned pottery vessels into bird forms such as ducks, parrots, and turkeys (Peckham 1990). Bird figures were commonly used on pottery at Zuni, Acoma, and Zia. The late prehistoric Mimbres of Southwestern New Mexico painted quails, turkeys, parrots, cranes, herons, hummingbirds, owls, crows, ravens, roadrunners, swallows, or swifts on the inside of their pottery (Brody 1977).

Prehistoric and historic petroglyphs (images chiseled into rock) and pictographs (images painted on rock) of birds are relatively common images produced by American Indians across the Southwest. Petroglyphs date from over 3,000 years old to as recent as this century, while pictographs are less common and more recently created. Bird figures occur in southeast Utah, southwest Colorado, and northeast Arizona. Petroglyphs dating from 900 A.D. to

present in north, central, and southern New Mexico commonly have bird forms. The 18th-century Navajo in north-west New Mexico created pictographs and petroglyphs of birds (Schaafsma 1980).

At 2 Anasazi archeological sites near Los Lunas and Bernalillo, New Mexico, 30 bird species have been identified on kiva wall murals including bald eagle, parrots, macaws, whooping and sandhill cranes, hummingbird, mountain bluebird, swallow, raven and/or crow, magpie, jay, and loggerhead shrike (Hibben 1975; Dutton 1963). Many of the mural species are common to ponderosa pine forests and other Southwestern vegetation types, but exotic or unusual species such as quetzal and pileated woodpecker are also featured.

Birds Captured for Feathers, Pets, and Food

The extent that trapping and hunting by early American Indians influenced the bird populations of ponderosa pine forests is difficult to assess without written record and only minimal archeological evidence. Although hunting was not considered a sport, it was practiced by some tribes to control population numbers. Bands or families of Utes were assigned territories where they monitored bird numbers. One section within the territory was hunted only as an emergency food source (Hughes 1983). Birds were taken with bow, traps, snares, and by hand (Kluckhohn et al. 1971).

Feathers and/or skins of numerous species were used in rituals and ceremonies and particular species, such as eagles and parrots, were traded great distances. A presentation of feathers was made by the Pueblo Indians when planting or building. Wild turkey feathers and macaw or parrot feathers decorated Anasazi and Pueblo prayer sticks. Other uses of feathers by the Pueblo included robes, blankets, clothing, fetishes, ceremonial head-dresses, quivers, shields, masks and basket decorations, and arrows (Hill 1982; Ladd 1963; Tyler 1979).

Hill (1982) reported that the Santa Clara Pueblo used feathers of many ponderosa pine passerines for dance and hair ornaments and other ceremonial purposes. He cites feather use of flycatchers, Steller's jay, pinyon jay, black-billed magpie, mountain and western bluebirds, Scott's and Bullock's orioles, western and hepatic tanager, and Grace's warbler. In a more comprehensive account, Ladd (1963) listed 45 bird species found in ponderosa pine forests that were important to Zuni Pueblo people (table 6). Most of these were used for feathers, but parrots, Steller's jay, American robin, and western and mountain bluebird were also considered pets. Turkey, mourning dove, northern flicker, Steller's jay, and common raven, were identified as food sources (table 6).

The Navajo also used feathers from various species of birds (Kluckhohn et al.). The feathers of eagles, which were ritually hunted, and turkeys were used on arrow shafts. Feathers from both of these birds were used to decorate

Table 6. Zuni Indian uses of ponderosa pine birds.

Common name	Feathers	Pets	Food
Turkey	X		X
Mourning dove	X	X	X
Parrot	X	X	
Great horned owl	X		
Common nighthawk	X		
White-throated swift	X		
Broad-tailed hummingbird	X		
Northern flicker	X		X
Lewis' woodpecker	X		
Hairy woodpecker	X		
Downy woodpecker	X		
Cassin's kingbird	X		
Ash-throated flycatcher	X		
Say's phoebe	X		
Violet-green swallow	X		
Rough-winged swallow	X		
Purple martin	X		
Steller's jay	X	X	X
Black-billed magpie	X		
Common crow	X		
Common raven	X	X	X
Pinyon jay	X		
White-breasted nuthatch	X		
Canyon wren	X		
Rock wren	X		
American robin	X	X	
Western bluebird	X	X	
Mountain bluebird	X		
Townsend's solitaire	X		
Loggerhead shrike	X		
Brewer's blackbird	X		
Western tanager	X		
Black-headed grosbeak	X		
Lesser goldfinch	X		
Green-tailed towhee	X		
Spotted towhee	X		
Lark sparrow	X		
Dark-eyed junco	X		

Source: Ladd 1963.

baskets, hats, masks, and prayer and medicine sticks. Feathers or skins of hawks, crows, owls, bluebirds, warblers, blackbirds, and other small birds were used to decorate ceremonial clothing and items such as prayer sticks. Eagle claws were sometimes strung on necklaces.

A number of birds were also used as food by the Apache and Navajo (Mayes et al. 1977). The western Apache ate wild turkey, quail, dove, geese, duck, some small birds, and various bird eggs (Buskirk 1986). Vulture feathers were used by the Mescalero Indians for adornment and ritual ceremonies (Basehart 1973; Opler 1965).

European

Only general references to birds of ponderosa pine forests were recorded by early Spanish explorers in the late 16th and early 17th centuries. The species noted includes waterfowl, wading birds, turkeys, quail, and blackbirds. Spanish impacts on these birds species was limited by seasonal hunting with bow or snares. The earliest reference to birds, specifically turkey, was made by Pedro de Castaneda, one of the chroniclers of Coronado's expedition (1540 to 1542). Castaneda wrote, "There are a very great many native fowl in these provinces, and cocks with great hanging chins" (Hodge 1946). In May 1583, explorer Antonio de Espejo, in the Verde River Valley, Arizona, referred to parrots; several historians have suggested that these were thick-billed parrots (Hammond and Rey 1966; Schroeder 1968).

Spanish bird hunting was minimal in the colonial period; turkeys were usually acquired through trade with the Pueblos. Hunting of quail, partridges, and grouse is mentioned in documents, but was not intensive (Carroll and Haggard 1942). In 1766, one Spanish explorer, Nicolas de Lafora, commented that, "Partridges are abundant and are caught by hand" in New Mexico (Kinnaird 1967). Populations of species, such as wild turkey, prairie chicken, and partridges (probably quail), were larger in the colonial period than in more recent history, and their ranges were more extensive than today (Bolton 1946; Hodge 1956; Kinnaird 1967).

Anglo-American settlers who arrived in the Southwest in the early to mid-1800s used firearms extensively and hunted birds for sport. Most of these settlers, primarily trappers and traders, killed wild turkeys for food. Turkeys, described as abundant, were noted by United States Army contingents in Arizona in 1846 and 1847. In the 1850s, travelers bound for California and boundary and road surveyors also noted the abundance of turkeys. Dr. B.J.D. Irwin observed mourning dove, "wild pigeon" (possibly band-tailed) and wild turkey while stationed at Fort Buchanan in southeastern Arizona (Davis 1982).

From the 1860s to the early 1900s, commercial hunting was practiced by Anglo-American settlers in the Southwest. Army expeditions had hunters, as did railroad work crews. Miners shot or trapped birds for food for boarding house dining rooms, restaurants, and personal use. Although mammals were the main meat species hunted, geese, ducks, wild turkey, grouse, doves, quail, crows, ravens, robins, and blackbirds were also food sources. Bird eggs were intensively collected during this period. Women's fashions, especially feathers or skin for hats, also placed significant demand on bird populations. Passage of the Lacey Act in 1900 ended commercial hunting activity (Borland 1975).

Early Ornithological Surveys

The first scientific studies of birds in New Mexico and Arizona were conducted during the mid- to late 1800s (table 7). Recorded field observations, bird specimen collecting, and, less frequently, egg collecting comprised this work. Some of the earliest field professionals were trained in ornithology or a related field. Some military officers also collected and recorded bird field observations in Arizona and New Mexico. By the late 1800s and into this century, professional ornithologists were conducting field work and specimen collecting.

Dr. Thomas Say, eminent ornithologist and entomologist, was the first trained observer and collector in New Mexico. In 1820, he accompanied Stephen H. Long to Colorado where the expedition split into 2 groups. Say's party traveled south to the headwaters of the Canadian River, then followed the river through northeastern New Mexico, eventually reaching Fort Smith, Arkansas. Among Say's collected specimens were the blue grouse and a flycatcher, later named Say's phoebe (Eifert 1962).

Of the early United States Army observers, Lt. James Abert's collections and descriptions were perhaps the most

Table 7. Ornithologists in New Mexico and Arizona, 1820–1960s.

Ornithologist	Time period
Thomas Say and Edwin James	1820
James Abert	1846
George A. McCall	1850
Samuel Woodhouse	1850–1851
Fullerton Spencer Baird	1850–1887
Caleb Burwell Kennerly	1853
T. Charlton Henry	1853–1854
Dewitt Clinton Peters	1854–1856
W. W. Anderson	1858
Elliott Coues	1860, 1880s
Charles Emil Bendire	1872–1873
Henry Weatherbee Henshaw	1873–1874
Edgar Alexander Mearns	1884–1893
Florence Merriam Bailey	late 1800s–early 1900s
Junius Henderson & John P. Harrington	1910–1913
Fannie Ford	1911
J. Stokely Ligon	1926–1950s
Lyndon L. Hargrave	1926–1970s
Gale Monson	1934–1980s
Allan R. Phillips	1930s–1958
Herbert Brandt	1930s–1940s
Edmund Ladd	1960s

Source: Abert 1962; Brown 1982; Eifert 1962; Henderson and Harrington 1914; Ligon 1961; Norwood 1993.

comprehensive. Abert recorded many mammals and 26 species of birds along the Middle Rio Grande. Ten of these species were found in the montane ponderosa pine including the bald eagle, sparrow-hawk (American kestrel), wild turkey, red-winged flicker (northern), sapsucker (probably red-naped or yellow-bellied), Steller's jay, common raven, Mexican bluebird (possibly western), American robin, and loggerhead shrike (Abert 1962).

Perhaps the earliest naturalist to collect and report on mammals and birds of the Southwest was Samuel Woodhouse, assistant surgeon, United States Army. He accompanied an army expedition in 1850 and 1851 that traveled up the Rio Grande from El Paso to Santa Fe (Ligon 1961). During this trip, Woodhouse became the first to observe and collect white-throated swifts, which he found at El Morro, New Mexico. He also collected the scrub jay, the black-capped vireo, and a finch (Eifert 1962).

In 1853 and 1854, another army doctor, T. Charlton Henry, recorded 170 species of birds while stationed at Forts Thorn, Fillmore, and Webster in New Mexico. His lists include comments on range and seasonal occurrences (Ligon 1961).

Colonel George A. McCall, who conducted an inspection of New Mexico's military posts from March to October 1850, published his observations on birds made during his travels around the territory (McCall 1852). He reported 67 species and collected a few bird specimens such as a peregrine falcon taken at Santa Fe. McCall noted that the brown-headed cowbird was "not numerous" and that the common nighthawk was numerous in the Southwest (McCall 1852).

Army surgeon Elliott Coues collected over 200 species of birds in Arizona and parts of New Mexico in the 1860s and 1880s. Coues, while traveling with an army unit bound for Whipple, Arizona, collected a new species of warbler near Old Fort Wingate, New Mexico. This bird was collected in July 1864 and was later named for his sister Grace (Eifert 1962). He published *A Key to North American Birds* and *Birds of the Colorado Valley*. Coues has been called the "most prodigious of all American ornithologists" (Kastner 1986; Ligon 1961).

One of Arizona's best known ornithologists of the 19th century was Major Charles Emil Bendire who was stationed at Forts Bowie, Lowell, and Whipple, Arizona and Fort Burgwyn, New Mexico from 1872 to 1873. His specialty was bird eggs, which he widely collected. His best known published work was *Life Histories of North American Birds* (1892). Bendire had several bird species named for him; he was also a founder of the American Ornithologists' Union (Ligon 1961).

An early ornithologist who worked in New Mexico was Henry Wetherbee Henshaw who served with the U.S. Geographical and Geological Explorations and Surveys. Henshaw observed and collected birds from 1873 to 1874 in the northern part of New Mexico and around Old Fort Wingate, New Mexico. He published his work in 1885 and 1886 in issues of *The Auk*. (Ligon 1961).

All of the foregoing military ornithologists worked under Fullerton Spencer Baird who was Assistant Secretary, then Secretary of the Smithsonian Institution from 1850 to 1887. Baird, along with T. M. Brewer and R. Ridgway, produced *A History of North American Birds*, published in 1874 (Eifert 1962; Ligon 1961).

The best known woman ornithologist in the Southwest was Florence Merriam Bailey, who conducted field observations, collected bird specimens, and wrote several significant publications from the late 1800s through the early 1900s. Her best known publications are the *Handbook of Birds of the Western United States* (1902) and *Birds of New Mexico* (1928). Bailey was the first female fellow of the American Ornithologists' Union (Behle 1990; Ligon 1961) and the first woman to receive the Brewster Medal for her publication *Birds of New Mexico* (Norwood 1993).

A relatively comprehensive list of New Mexico birds was compiled by Fannie Ford in 1911 for the State Game and Fish Department. She reported 314 species and subspecies. At about the same time, the earliest major work on the ethno-ornithology of an American Indian tribe in the Southwest was conducted by Junius Henderson and John Peabody Harrington of the Bureau of American Ethnology, Smithsonian Institution. This field and literature review, made from 1910 to 1913 and published in 1914, focused on the relationship between the Tewa Pueblo of New Mexico and regional birds and other fauna (Henderson and Harrington 1914).

J. Stokely Ligon, who with Aldo Leopold directed the predator control program in New Mexico, headed up a wild game survey in New Mexico from 1926 to 1927. Birds surveyed included golden eagles, which Ligon viewed as "a serious enemy of certain species of game" and young cattle, goats, and sheep. He noted that killing hawks had severely reduced their numbers. Ligon believed that birds of prey helped control the rodent population and lobbied for protecting legislation. Magpies were considered "enemies" of quail, pheasants, and turkeys, and Ligon recommended that federal and state wildlife personnel initiate control programs for this species (Ligon 1927). Ligon later published his *New Mexico Birds and Where to Find Them*, which includes historical data on 399 bird species in the state. Included with species descriptions are notes on former ranges and status of rare, endangered, or threatened species.

Archeologist-ornithologist Lyndon L. Hargrave, who primarily worked in Arizona from 1926 into the 1970s, accumulated a comparative collection of more than 300,000 bird bones. He conducted field work with ornithologists Alex Wetmore, the late Allan R. Phillips, and Herbert Brandt, and worked with numerous archeologists. Hargrave's best known publication is "Mexican Macaws" (1970).

Phillips and Brandt began fieldwork in Arizona in the 1930s. Phillips' M.A. thesis at the University of Arizona

was, "The Faunal Areas of Arizona: Based on Bird Distribution" (Brown 1982). He moved to Mexico to study birds in 1958 and collaborated with Gale Monson on *An Annotated Checklist of the Birds of Arizona* (1981). Herbert Brandt also worked in Arizona in the middle of this century. His best known work is *Arizona and Its Birdlife* (1951). Monson also began his ornithological investigations in Arizona in the 1930s and worked for the U.S. Fish and Wildlife Service for 29 years. Monson, Phillips, and Joe Marshall collaborated on *The Birds of Arizona* (1964) (Monson and Phillips 1981).

Edmund Ladd of Zuni Pueblo completed a thesis on the ethno-ornithology of his village at the University of New Mexico in 1963. Much of this work focused on the ritual use of bird feathers, especially those decorating prayer sticks, and includes a discussion of specific bird species and their historical uses.

Historical Bird Accounts and Avifaunal Changes

Abundances from Early Studies

The composition, distribution, and populations of avian species in Southwestern ponderosa pine forests have changed over time due to climatic fluctuations, lightning or human-caused fires, and/or other human disturbances that impact birds directly or indirectly through habitat change (Foxy and Tiemey 1984; Hejl 1994; Jehl and Johnson 1994; Johnson 1994; Newman 1979). Human-generated, historical disturbances include snaring or trapping, hunting, poisoning, pesticide use, specimen-collecting, egg-collecting, logging, snag removal, grazing, mining, erecting flight obstacles, exotic species introduction, recreation, and urbanization (Behle 1990; Hejl 1994). The probable impacts of historical human use of birds and their habitats are considered in this section.

By evaluating relative abundances (abundant, common, uncommon, rare, extinct) of birds reported in 3 New Mexico bird publications from 1911 to 1961, species whose abundance changed were identified (Ford 1911; Bailey 1928; Ligon 1961). Because differences in observer style and locale experience is likely to have produced biases, results should be cautiously interpreted. We identified 32 species whose populations in New Mexico ponderosa pine forests were reported as abundant or common in 1911 but less abundant or rare in 1961 (table 8). Species of special interest based on declines or management problems are reported in Hejl's (1994) contemporary analysis and in other chapters of this volume. They include the band-tailed pigeon, olive-sided flycatcher, violet-green swallow, mountain chickadee, golden-crowned kinglet, pygmy

nuthatch, and chipping sparrow. Decreases could be related to habitat loss or modification through logging, fire exclusion, grazing, hunting, and herbicide and pesticide use. However, 14 species reported as rare, uncommon, or common in the 1911 study were potentially more abundant by 1961. Real or apparent increases of these species may have been due to habitat changes, range expansion, observer variability, or incomplete inventories during the late 19th to early 20th centuries. Contemporary accounts report general population increases for Grace's warbler and range expansion for red-faced warbler; 2 of the species noted in table 8 have increased in New Mexico.

To document specific historical information on avifaunas occupying ponderosa pine forests, we listed species surveyed in 4 mountain ranges in New Mexico from the 1920s to the mid-1970s (table 9). In addition, we used Gilman (1908), Mayes et al. (1977), and Bradfield (1974) to compile avifaunal lists for the Navajo Reservation in northeastern Arizona and the Hopi Reservation adjacent to the Navajo lands (table 10). Gilman (1908) recorded presence/absence rather than abundance. Ponderosa pine forests and habitat variety are more extensive on Navajo lands than on Hopi, which may account for the difference in species number listed. These tables are included in this chapter to mark occurrences and relative abundances of bird species in time as a ready historical summary for future investigators of Southwestern ponderosa pine avifaunas.

Changes in Species Ranges

One avian species (thick-billed parrot) and a subspecies (Merriam's turkey) found in the ponderosa pine forest were extirpated historically but have been reintroduced, one unsuccessfully and the other successfully. The thick-billed parrot, which may have ranged as far north as the Verde River Basin in central Arizona in the early colonial period, was exterminated in the 20th century. This species sporadically visited the Animas and Peloncillo Mountains in New Mexico as recently as the early part of this century; it was last seen in 1938 in the Chiricahua Mountains of southeastern Arizona (Ligon 1961; Monson and Phillips 1981). A small number of these parrots were released into the Chiricahuas in 1986 by the U.S. Fish and Wildlife Service, but they have not been seen since the 1989 to 1990 drought (Snyder et al. 1995). Merriam's turkey was historically widespread in riparian woodlands and montane conifer forests in New Mexico and Arizona, but was locally extirpated between 1900 and 1920. Since 1920, reintroduction by game and fish departments in both states has restored viable populations of this subspecies (Ligon 1961; Monson and Phillips 1981).

Table 8. Recorded abundances of ponderosa pine avifauna in New Mexico. A = abundant; C = common; U = uncommon; R = rare; E = extinct.

Common name	Source			Population Increase (I) Decrease (D) Stable (S)
	Ford 1911	Bailey 1928	Ligon 1961	
Blue grouse	C	Locally U	Locally U	D
Merriam's turkey	C	Locally U	U	D
Band-tailed pigeon	C	R to U	Locally C to U	D
Mourning dove	A	C	A	S
Thick-billed parrot	a	Locally R	E	D
Greater roadrunner	a		U	I
Common nighthawk	C		C	S
Poor-will	U	C to U	U to C	I
Common poor-will	U	C to U	U to C	I
Whip-poor-will	U	R	U	S
White-throated swift	C	Locally C	C	S
Calliope hummingbird	C	C	U	D
Broad-tailed hummingbird	C	C	C	S
Rufous hummingbird	C	C	C to A	I
Lewis' woodpecker	Locally U	Locally U to C	Locally U to C	S
Acorn woodpecker	C	C to U	C	S
Williamson's sapsucker	C	U to C	U	D
Yellow-bellied sapsucker	C	C	C	S
Downy woodpecker	U	Locally U	U	S
Hairy woodpecker	C	Fairly U to C	C	S
Three-toed woodpecker	U	Locally U	U to R	S
Northern flicker	C	C	C	S
Olive-sided flycatcher	C	Locally C	U	D
Western wood pewee	C	Locally C	U to C	S
Dusky flycatcher	a	a	C	S
Say's phoebe	C	C	C	S
Cordilleran (western) flycatcher	U	U to C	U to C	I
Ash-throated flycatcher	C	Locally R	C	S
Cassin's kingbird	C		C	D
Purple martin	U	Fairly C	U	S
Tree swallow	a	U	U	S
Violet-green swallow	A	C	C	D
Black-billed magpie	C	Locally U	C	S
Steller's jay	C	C	C	S
Pinyon jay	C	U	U	D
Gray jay	C	R	U	D
Clark's nutcracker		Locally R	U	D
American crow	A	U to A	U	D
Common raven	C	Locally U	U	D
Black-capped chickadee	A	C	C	D
Mountain chickadee	A	A	C	D
Golden-crowned kinglet	C	R	U	D
Ruby-crowned kinglet	C	U	C	D
Red-breasted nuthatch	R	U to R	U	I
White-breasted nuthatch	C	C	C	S
Pygmy nuthatch	A	A	C	D
Brown creeper	U	U to C	C	I
Winter wren	a	R	R	S
Rock wren	C	C	C	S
Canyon wren	Locally C	R	Locally C	S

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Table 8. (continued)

Common name	Source			Population Increase (I) Decrease (D) Stable (S)
	Ford 1911	Bailey 1928	Ligon 1961	
House wren	C	U to C	U	D
Western bluebird	C	Locally C	A	I
Mountain bluebird	C	C	C	S
Townsend's solitaire	C	U	U	D
American robin	C	C	C	S
Hermit thrush	C	U to C	C	S
Northern mockingbird	R	R	R	S
Loggerhead shrike	^a	R	U	I
Solitary vireo	C	Locally C	U	D
Warbling vireo	C	U to C	C	S
Yellow-rumped warbler	A	C to locally A	C	D
Black-throated gray warbler	U	U	U	S
Virginia's warbler	U	U to locally C	U	S
Townsend's warbler	U	U	U	S
Orange-crowned warbler	R	U	U	I
Grace's warbler	R	U	C	I
MacGillivray's warbler	C	U	U	D
Red-faced warbler	R	Locally U	Locally U	S
Painted redstart	^a	Locally U	Locally U	S
Hepatic tanager	R	U	U	I
Western tanager	C	C	C	S
Black-headed grosbeak	C	C	U	D
Spotted towhee	C	C	U	D
Cañon towhee	C	U to R	C	S
Green-tailed towhee	U	Locally U to C	U	S
Dark-eyed junco	C	A	A	I
Yellow-eyed junco	^a	Locally C	Locally A	I
Brewer's blackbird	C	Locally U to C	Locally U	D
Brown-headed cowbird	^a	Locally R	U	I
Pine grosbeak	^a	U	U	S
Cassin's finch	R	U to C	U	I
Rosy finch	R	^a	R	S
Red crossbill	^a	R	U	I
Pine siskin	C	U	C	S
Lesser goldfinch	^a	U	U	S
American goldfinch	U	R	R	D
Evening grosbeak	C	R	U	D
Baird's sparrow	R	C	C	I
Vesper sparrow	C	C	U to C	S
Savannah sparrow	R	^a	U	I
Song sparrow	C	U	U	D
Lark sparrow	^a	U	U	S
Chipping sparrow	A	C	C	D
Brewer's sparrow	^a	C	C	S
White-crowned sparrow	C	C	U	D
Lincoln's sparrow	C	U	U	D

^a Data not recorded.

Table 9. Recorded ponderosa pine avifauna occurrence in 4 New Mexico mountain ranges.

Common name	La Mesa Sangre de Cristo Mtns 1920–1950s ^a	Sandia Mtns 1920s–1950s ^b	Jemez Mtns pre-1977 ^c	Guadalupe Mtns 1972–1974 ^d
Merriam's turkey	X			
Wild turkey	X			
Band-tailed pigeon	X	X	X	
Mourning dove	X	X	X	
Greater roadrunner				
Common nighthawk	X	X	X	X
Poor-will		X		X
Whip-poor-will	X	X		
White-throated swift	X			X
Calliope hummingbird	X	X		
Broad-tailed hummingbird	X	X	X	X
Rufous hummingbird	X		X	
Black-chinned hummingbird	X			
Blue-throated hummingbird				X
Lewis' woodpecker	X	X		
Acorn woodpecker	X	X	X	X
Williamson's sapsucker	X	X		
Yellow-bellied sapsucker	X	X	X	X
Downy woodpecker	X	X	X	
Hairy woodpecker	X	X	X	X
Three-toed woodpecker	X	X	X	
Northern flicker	X	X	X	X
Olive-sided flycatcher	X		X	X
Western wood pewee	X	X	X	X
Dusky flycatcher	X		X	
Say's phoebe		X		X
Gray flycatcher		X		
Cordilleran (western) flycatcher	X	X	X	X
Dusky-capped flycatcher				
Ash-throated flycatcher	X	X	X	X
Wright's flycatcher				
Hammond's flycatcher		X	X	
Cassin's kingbird	X	X		X
Purple martin	X			
Violet-green swallow	X	X	X	X
Black-billed magpie	X			
Steller's jay	X	X	X	X
Pinyon jay	X			X
Gray jay	X			
Clark's nutcracker	X	X		X
American crow	X	X		
Common raven	X	X		
Black-capped chickadee	X	X		
Mountain chickadee		X	X	X
Bushtit	X			
Red-breasted nuthatch	X	X	X	X
White-breasted nuthatch	X	X	X	X
Pygmy nuthatch	X	X	X	X
Brown creeper	X	X	X	X
Winter wren	X		X	
Rock wren	X	X		

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Table 9. (continued)

Common name	La Mesa Sangre de Cristo Mtns 1920–1950s ^a	Sandia Mtns 1920s–1950s ^b	Jemez Mtns pre-1977 ^c	Guadalupe Mtns 1972–1974 ^d
Canyon wren	X	X	X	
House wren	X	X	X	X
Western bluebird	X	X	X	X
Mountain bluebird	X	X	X	
Townsend's solitaire	X	X	X	
Golden-crowned kinglet	X	X		
Ruby-crowned kinglet	X		X	X
Hermit thrush	X	X	X	X
Swainson's thrush		X		
American robin	X	X	X	X
Northern mockingbird	X			
Loggerhead shrike	X	X		
Solitary vireo	X	X	X	X
Warbling vireo	X		X	X
Yellow-rumped warbler	X	X	X	X
Black-throated gray warbler	X	X		
Virginia's warbler	X	X	X	X
Townsend's warbler		X	X	
Orange-crowned warbler	X	X		
Grace's warbler	X	X	X	X
MacGillivray's warbler	X			
Wilson's warbler	X	X		X
Hepatic tanager	X	X		X
Western tanager	X	X	X	X
Black-headed grosbeak	X	X	X	X
Spotted towhee	X	X	X	X
Green-tailed towhee	X	X		X
Dark-eyed junco	X	X	X	X
Brewer's blackbird	X	X		
Brown-headed cowbird	X	X	X	X
Pine grosbeak	X	X		
Cassin's finch	X		X	
Red crossbill	X	X	X	X
Pine siskin	X	X	X	X
Lesser goldfinch	X	X	X	
American goldfinch		X		
Evening grosbeak	X	X	X	
Baird's sparrow	X			
Vesper sparrow	X			
Savannah sparrow	X			
Song sparrow	X	X		
Lark sparrow	X			
Chipping sparrow		X		X
White-crowned sparrow	X			
Lincoln's sparrow	X			

Source:

^a Ligon 1961^b Schwarz 1995^c Foxx & Tierney 1984^d Newman 1979

Table 10. Ponderosa pine avifauna on Navajo and Hopi reservations. A = abundant; C = common; U = uncommon; R = rare; S = sparse; E = extinct; X = abundance not given in paper.

Common Name	Gilman 1908 ^a	Mayes et al. 1977 ^b	Bradfield 1974 ^c
Merriam's turkey	X	U	E
Mourning dove	X	A	C
Common nighthawk		C	C
Whip-poor-will			R
White-throated swift		U	
Broad-tailed hummingbird	X	U	C
Rufous hummingbird		A	A
Lewis' woodpecker	C	U	
Acorn woodpecker		U	
Williamson's sapsucker	X		
Yellow-bellied sapsucker		U	
Downy woodpecker			U
Hairy woodpecker	X	C	C
Northern flicker	X	U	C
Olive-sided flycatcher		U	S
Cassin's kingbird		U	C
Western wood pewee		C	S
Cordilleran (western) flycatcher	U	U	
Say's phoebe	X	U	
Ash-throated flycatcher		C	
Purple martin		U	
Violet-green swallow	X	C	C
Black-billed magpie	E		
Steller's jay	X	C	S
Pinyon jay		U	C
Clark's nutcracker	X	R	
Common raven		C	C
Mountain chickadee	X	C	C
Red-breasted nuthatch		U	S
White-breasted nuthatch		C	S
Pygmy nuthatch	X	C	S
Brown creeper		U	S
Rock wren			U
Canyon wren			U
House wren		U	S
Western bluebird	X	U	C
Mountain bluebird	X	U	C
Townsend's solitaire	X	U	S
Hermit thrush	X	R	U
American robin	X	U	U
Golden-crowned kinglet		U	S
Ruby-crowned kinglet		U	S
Solitary vireo	X	U	C
Warbling vireo			U
Yellow-rumped warbler	X	C	A
Black-throated gray warbler	X	U	
Virginia's warbler	U		
Townsend's warbler			U
Grace's warbler	U	U	
MacGillivray's warbler		U	U
Western tanager	X	U	S
Black-headed grosbeak	X	U	U
Spotted towhee		U	U

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Table 10. (continued)

Common Name	Giiman 1908 ^a	Mayes et al. 1977 ^b	Bradfield 1974 ^c
Green-tailed towhee		U	U
Vesper sparrow		U	
Song sparrow			R
Chipping sparrow		U	
Dark-eyed junco	X	C	C
Brewer's blackbird		U	
Red crossbill		R	S
Cassin's finch			S
Pine siskin		U	S
Lesser goldfinch			S

Year of record:

^a 1907.^b 1958-1976.^c pre-1974.

Source: Bradfield 1974.

Several Southwestern species associated with ponderosa pine have moved north in the last 40 years or so (Jehl and Johnson 1994; Johnson 1994). These include the whip-poor-will, which now ranges across much of Arizona into southwest Utah and over most of New Mexico into south central Colorado, and the red-faced warbler, which is now found over all but northern and eastern New Mexico and northwestern and northeastern Arizona. The summer tanager occupies portions of north central and west central Arizona and New Mexico. The white-winged crossbill has moved southward into the Rocky Mountains of southern Colorado and northern New Mexico where it bred in the late 1970s and 1980s. Two explanations for this phenomenon are: 1) climatic trends with moister and warmer summers since 1965; and 2) reoccupation of former range (Jehl and Johnson 1994; Johnson 1994).

Conclusion

Of the various human activities that have impacted forest composition and structure, logging and fire suppression had the greatest influence on ponderosa pine forest ecosystems since European settlement. Every accessible ponderosa pine forest in New Mexico and Arizona was heavily logged from the 1870s to the 1930s (Baker et al. 1988; Houk 1993). Demand for timber was primarily generated by railroad and mine operations. The effects of logging on southwestern birds were unknown before European settlement; therefore, it is difficult to document alterations of bird populations caused by early American Indian use of ponderosa pine.

Hejl (1994), when reviewing human-induced changes that occurred over the last 100 years in birds inhabiting Western coniferous forests, proposed that logging, fire exclusion, snag removal, loss of herbaceous understory, and/or increased densities of small trees resulted in population declines in bird species associated with burns, old-growth forests, open forests, or snags. Canopy and bark foragers, which historically dominated ponderosa pine forests, were impacted the most. According to Hejl, species exhibiting historical declines include broad-tailed hummingbird, acorn woodpecker, violet-green swallow, purple martin, mountain chickadee, white-breasted nuthatch, pygmy nuthatch, brown creeper, western bluebird, mountain bluebird, American robin, red-faced warbler, lark sparrow, and chipping sparrow.

DeSante and George (1994) identified 9 avian species whose breeding populations in ponderosa pine forests have decreased in Arizona (AZ) or New Mexico (NM) over the last 100 years. These are blue grouse (AZ, NM), wild turkey (AZ, NM), spotted owl (AZ), lesser nighthawk (NM), white-throated swift (AZ), purple martin (AZ), western bluebird (AZ), Lucy's warbler (AZ), and song sparrow (AZ). Since 1890, wild turkey and evening grosbeak have experienced range reductions.

In contrast to those species with historical declines, 10 species (American crow, cordilleran flycatcher, house wren, Townsend's solitaire, hermit thrush, solitary vireo, Virginia's warbler, yellow-rumped warbler, Grace's warbler, and western tanager) have apparently increased in numbers in the Western United States (DeSante and George 1994; Hejl 1994). The downy woodpecker, black-capped chickadee, red-faced warbler, and brown-headed cowbird have increased their breeding distribution. These changes are believed to be caused by climatic shifts, land-

scape modification, grazing, and/or vegetative shifts (Brown and Davis 1995).

Research Needs

Systematic searches of published and unpublished archeological and historic reports that contain data on ponderosa pine avifauna use by prehistoric and historic American Indians is needed. This information would provide a data base for determining: 1) species range; 2) use of native and exotic bird species for food, tools, personal adornment, ritual, pets, etc.; and 3) impacts on populations from existing and future fire history studies.

Little research on the pre-1900 relationship between European settlers and Southwestern ponderosa pine forest birds has been conducted. Various published and unpublished reports, papers, and other documents need to be searched, and pertinent data extracted and synthesized. Careful scrutiny of climatic records, and logging, ranching, farming, and other recorded activities would produce useful information on impacts and population changes. As a baseline for determining these phenomena, early (1850 to 1940) published and unpublished field notes and lists recorded by ornithologists in the Southwest should be examined for seasonal occurrence and population size of species associated with ponderosa pine forests. These data might indicate impacts on avian populations near historic villages and towns or those species obtained from farther distances.

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Chapter 4

Songbird Status and Roles

Linnea S. Hall, Michael L. Morrison, and William M. Block

Introduction

This chapter reviews studies on songbird ecology conducted in Arizona, New Mexico, and Colorado; studies from outside this region are mentioned when they bear direct relevance to our primary region. The studies were conducted in sites where ponderosa pine occurred at least in equal coverage with other trees. We also include studies conducted in pine-oak (pine predominant) or oak-pine (oak predominant) woodlands of southeastern Arizona and Southwestern New Mexico. Our review begins with population studies, including research on distribution, abundance, and trends in population numbers. We then discuss the various roles of birds in the ponderosa pine forest. Next we cover the multifaceted topic of avian natural history and habitat preferences, including use of vegetation and special habitat features, nest predation, foraging habits, and migration habits. We also review the prioritization systems for identifying species of special research and management concern.

Population Status

Research Limitations

Long-term data sets such as Breeding Bird Surveys (Robbins et al. 1986; Peterjohn et al. 1995) and Christmas Bird Counts (Bock and Root 1981) usually allow for indices of relative abundance. Results of many research studies compare absolute or relative abundance of birds among different impacts (such as logging and fire) or conditions (such as varying tree density and season). But few data exist to estimate population parameters such as survival and reproduction. Few data are available to examine nonbreeding or migrating populations because most of the data are collected during the breeding season. Trend data are limited to Breeding Bird Surveys (BBS) and Christmas Bird Counts (CBC); we found no relevant Breeding Bird Census trend data (Marshall 1991). Breeding Bird Atlas data for the Southwest are too recent (collecting started in 1994) to provide trend information (T. Corman, Arizona Dept. of Game and Fish, personal communication).

Therefore, we review here the information on populations by summarizing relevant research results and by summarizing BBS data to examine population trends. Rigorous comparisons of population estimates from different research projects are difficult because of different data collection methods, different sampling intensities, different skill levels of observers, and different analytic techniques. Also, methods used to sample avian populations have inherent biases (compare Verner 1985, for a review of avian census methods). Thus, we limit our discussion of research results to brief descriptions of major studies and to generalizations based on the collective results of these studies.

Research Results

Szaro and Balda (1979) measured breeding bird populations within the Beaver Creek watershed of the Coconino National Forest, Arizona. Vegetation within their study area was dominated by ponderosa pine with Gambel oak and alligator juniper in the understory. They used spot mapping to index densities of individual species and selected guilds (as defined by Root 1967:335) on five plots representing different intensities of logging, from clearcut to control (that is, no logging). As might be expected, bird densities varied among plots and among years. Whether the variations in numbers represented effects of different cutting regimes, however, is difficult to assess; inferences about cause-effect relationships of logging will be covered in the following chapters and we will not duplicate that material here. However, bird populations were generally greatest on the "strip cut" and "silviculturally cut" plots and lowest on the clearcut plots; densities of birds on the control (unlogged) plot were intermediate to these extremes (table 1). Spotted towhees and rock wrens were the most abundant species on the clearcut plot; dark-eyed junco, Steller's jay, and white-breasted nuthatch were most abundant on the "severely thinned" plot; Grace's warbler, solitary vireo, dark-eyed junco, and chipping sparrow on the strip cut plot; dark-eyed junco, pygmy nuthatch, and Grace's warbler on the silviculturally cut plot; and white-breasted nuthatch, pygmy nuthatch, dark-eyed junco, and Grace's warbler on the control plot.

Siegel (1989) examined habitats and populations of breeding birds in old-growth ponderosa pine forests on the Kaibab Plateau, Arizona. He compared bird numbers among stands representing different densities of trees:

Table 1. Comparison of population estimates in ponderosa pine forests. See text for details of each study. Numbers provided are ranges of population estimates from study sites sampled in each study.

Species	Szaro & Balda ^a	Siegel ^b	Overturf ^c	Horton & Mannan ^d	Blake ^e			Haldeman et al!	
					Fall	Winter	Spring	Spring	Winter
Mourning dove	3.0–6.0	0.2–2.6	0.0–10.0		0.0–0.2			7	
Band-tailed pigeon			0.0–0.8				0.0–0.4		
Common poorwill		0.0–0.4			0.0–0.2				
Common nighthawk	0.0–3.0	0.0–0.4	0.0–10.0						
Br-tailed humnringbird	3.0–15.0	4.4–22.1	0.0–15.0				0.0–0.5	3	
Lewis' woodpecker					0.0–2.0	0.0–1.4			
Yellow-bellied sapsucker						0.0–0.2			0.1
Acorn woodpecker	0.0–3.0	0.0–0.4	0.0–5.0	1.1–4.0	0.0–1.2	0.0–0.2	0.0–0.2		
Hairy woodpecker	1.5–6.0	2.8–5.8	2.0–12.0	0.7–1.0	0.0–7.3	0.0–1.2	0.0–2.4	5	1.3
Three-toed woodpecker		0.0–2.3	0.0–5.0						0.04
Northern flicker	1.5–3.8	2.5–8.1	2.0–10.0	1.7–2.6	0.0–0.6		0.0–0.8	9	0.9
Williamson's sapsucker		0.6–6.1							
Cassin's kingbird							0.0–0.2		
Ash-throated flycatcher							0.0–0.2		
Say's phoebe	0.0–3.0								
Western wood pewee	1.5–9.0	0.2–8.2	0.0–15.0		0.0–1.0			4	
Olive-sided flycatcher		0.4–0.8	0.0–5.0				0.0–0.2		
Cordilleran flycatcher	3.0–6.8	0.0–0.4	0.0–3.0	39.2–67.0			0.0–0.2	7	
White-throated swift	0.0–0.4	0.0–0.4							
Violet-green swallow	3.0–9.0	0.4–20.1	0.0–50.0	17.6–37.4			0.0–10.3	30	
American crow									0.1
Common raven		0.0–1.0							
West. scrub jay					0.0–0.2				
Steller's jay	3.0–9.0	1.1–1.8	0.0–10.0		0.0–0.5	0.0–2.0	0.0–0.2	8	0.1
Clark's nutcracker		0.0–0.3							0.04
Mountain chickadee	1.5–9.0	0.4–8.7	0.0–30.0	5.6–12.2	0.0–0.9	0.0–0.4		20	3.4
Plain titmouse						0.0–0.2			
White-breasted nuthatch	3.0–15.0	1.6–3.3	0.0–13.0	2.9–7.0	0.0–4.9	0.0–0.4	0.0–0.8	7	4.1
Red-breasted nuthatch	0.2								
Pygmy nuthatch	1.5–18.0	7.7–16.0	0.0–53.0	14.2–26.2	0.0–0.6		0.0–2.6	26	10.3
Brown creeper		3.4–12.2	0.0–17.0	5.8–9.8			0.0–0.8	8	
House wren	2.3–3.0	0.0–4.4	0.0–54.0	15.0–96.8	0.0–0.2		0.0–1.5		
Canyon wren	0.0–0.2								
Rock wren	3.8–8.3	4.9–16.8	0.0–9.0				0.0–1.0		
Ruby-crowned kinglet					0.0–8.0	0.0–7.1	0.0–0.5		
Loggerhead shrike							0.0–0.2		
American robin	1.0–7.5	2.3–4.2	0.0–17.0		0.0–2.7		0.0–0.2	20	1.1
Townsend's solitaire		0.4–2.6							
Hermit thrush	0.8–2.3	1.9–4.6	0.0–3.0		0.0–0.2			8	
Western bluebird	3.0–15.0	5.8–14.1	5.0–30.0	6.1–12.4	0.0–6.5	0.0–17.4	0.0–5.8	15	3.4
Mountain bluebird	0.0–1.0		0.0–5.0						
Cedar waxwing						0.0–0.2			
Solitary vireo	1.5–12.0	9.1–18.1	0.0–0.7			0.0–0.2	5		
Warbling vireo		1.7–27.6							
Yellow-rumped warbler	3.0–15.0	23.4–47.0	0.0–13.0		0.2–2.8	0.0–1.6	8		
Townsend's warbler							0.0–1.8		
Black-throated gray warbler					0.0–0.2		0.0–0.2		
Red-faced warbler	1.5–4.5								
Grace's warbler	3.8–19.5	29.7–50.2	0.0–7.0				0.0–0.4	5	
Virginia warbler		0.4–0.8					0.0–0.5		
Brown-headed cowbird		0.4–0.8	0.0–7.0				0.0–0.5		

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Table 1. (continued)

Species	Szaro & Balda ^a	Siegel ^b	Overturf ^c	Horton & Mannan ^d	Blake ^e			Haldeman et al.	
					Fall	Winter	Spring	Spring	Winter
Western tanager	1.5–6.7	6.2–10.3	0.0–5.0						
Hepatic tanager	0.0–3.0						0.0–0.2		
White-crowned sparrow					0.0–59.4				
Lark sparrow			0.0–39.0						
Fox sparrow					0.0–0.2				
Chipping sparrow	1.5–12.0	0.6–4.3		0.0–29.0	0.0–0.2		0.0–8.8		
Spotted towhee	5.5–7.3				0.0–0.2		0.0–3.6		
Dark-eyed junco	1.5–22.5	23.8–43.3	5.0–32.0		0.2–44.6	0.0–65.4		23	2.3
Black-headed grosbeak	1.5–4.5	0.0–1.4						1	
Evening grosbeak									0.2
Cassin's finch		1.8–8.2			0.0–2.1	0.0–8.2	0.0–0.4		0.2
Red crossbill	2.0–17.1								
Lesser goldfinch					0.0–1.3				
Pine siskin		0.0–2.6	0.0–37.0				0.5–8.0	9	
Brewer's blackbird								3	

^a Szaro and Balda (1979); units are number of pair/40 ha.

^b Siegel (1989); units are number of birds/40 ha.

^c Overturf (1979); units are number of pair/40 ha.

^d Horton and Mannan (1988); units are number of birds/40 ha.

^e Blake (1982); units represent an index of occurrence based on numbers and distribution of a species with a sampling site.

^f Haldeman et al. 1973.

open, medium, and dense. Species richness showed little difference among stands, although dense stands had more individuals, particularly warbling vireos, violet-green swallows, western wood pewees, and Williamson's sapsuckers. He also found that Grace's warbler, yellow-rumped warbler, and dark-eyed junco were the three most abundant species in all stands, collectively accounting for >40 percent of all birds detected.

Overturf (1979) indexed populations using a spot mapping method to examine the effects of fire on ponderosa pine birds in northern Arizona. Populations were sampled from three to nine years post fire, with the exception of one control area where fire had not occurred recently (table 1). The control area was the Gus Pearson Natural Area, Ft. Valley Experimental Forest. Generally, burned areas supported fewer numbers of birds and fewer species than the unburned area. Species found on the control but not found on the burned areas included violet-green swallow, mountain chickadee, hermit thrush, yellow-rumped warbler, Grace's warbler, and pine siskin. Burned areas, however, tended to have more species that nested or foraged on the ground than were found on the control site. Species that appeared to exhibit positive numerical responses to fire included the chipping sparrow, lark sparrow, dark-eyed junco, green-tailed towhee, western bluebird, northern flicker, and house wren. Overturf attributed this dif-

ference to burned sites possessing a more well developed herbaceous understory than that in the control plot.

In one of the few studies to examine populations of nonbreeding birds, Blake (1982) found pronounced seasonal differences between fall, winter, and spring in bird species composition and bird abundances in ponderosa pine forests of the Prescott National Forest, Arizona (table 1). He also noted spatial differences that corresponded to differences in fire and logging histories. Generally, burned areas contained more individuals, but they were distributed among fewer species than unburned sites. Species restricted to burned areas included common poorwill, western wood-pewee, scrub jay, house wren, hermit thrush, and lesser goldfinch during the fall; and Cassin's kingbird, rock wren, American robin, solitary vireo, Grace's warbler, hepatic tanager, and black-headed grosbeak during the spring. Species restricted to unburned areas included band-tailed pigeon, acorn woodpecker, Lewis' woodpecker, Steller's jay, pygmy nuthatch, canyon wren, American robin, ruby-crowned kinglet, black-throated gray warbler, spotted towhee, chipping sparrow, and fox sparrow during the fall; yellow-bellied sapsucker, Lewis' woodpecker, Steller's jay, plain titmouse, pygmy nuthatch, ruby-crowned kinglet, and cedar waxwing during the winter; and band-tailed pigeon, acorn woodpecker, ash-throated flycatcher, Steller's jay, pygmy nuthatch,

brown creeper, Bewick's wren, ruby-crowned kinglet, loggerhead shrike, Virginia's warbler, black-throated gray warbler, Townsend's warbler, and spotted towhee during the spring.

Haldeman et al. (1973) reported breeding season and wintering populations of birds from a ponderosa pine forest northwest of Flagstaff, Arizona (table 1). Their single study area was the 13-ha Gus Pearson Natural Area that they characterized as undisturbed. They recorded 18 species during winter counts and 69 species during breeding counts. Because they used different methods to calculate relative abundance for each season, comparisons between seasons are difficult. However, of the resident species (that is, those present year round), the pygmy nuthatch was the most common species during both seasons. Other common wintering birds were the mountain chickadee, white-breasted nuthatch, western bluebird, and dark-eyed junco. Besides the pygmy nuthatch, other common breeding birds included the violet-green swallow, dark-eyed junco, mountain chickadee, American robin, and western bluebird.

Horton and Mannan (1988) sampled populations of cavity-nesting birds in the Santa Catalina Mountains, southeastern Arizona, as part of a study to evaluate the effects of prescribed fire. The violet-green swallow and northern flicker exhibited population declines following the fire, whereas the mountain chickadee population appeared to increase. Horton and Mannan (1988) speculated that the population shifts were possibly attributable to changes in prey abundance and shifts in habitat use following fire.

Bennetts (1991) investigated the relationship of breeding birds and dwarf mistletoe in Colorado ponderosa pine forests. He found positive correlations between mistletoe and total bird abundance and number of species, as well as with abundances of eight foraging guilds. He also found strong positive correlations of mistletoe with snag numbers and the abundance of cavity nesting birds.

General Comparisons Among Studies

As noted previously, differences in how studies were conducted preclude rigorous comparisons. However, some generalizations are possible. Species richness (number of species) during the breeding season ranged from 23 (Haldeman et al. 1973) to 47 (Siegel 1989). Fewer species were detected during winter (14 to 16, Blake 1982 and Haldeman et al. 1973) or fall (27, Blake 1982) than during the breeding season. The range in species richness during the breeding season could have resulted from temporal or geographic differences, or variations in methodologies or skill levels of observers.

Across the studies, there was a mixture of responses to heavy alteration of forest vegetation. In regard to fire, abundances of birds either increased (Blake 1982) or decreased (Overturf 1979), whereas species composition was lower on burned sites in both studies. In clearcuts studied by Szaro and Balda (1979), bird numbers decreased,

but in open stands studied by Siegel (1989), species richnesses were similar among open and "closed" stands. These differences indicate that treatments can elicit variable responses from bird species, probably because of variations in geographic location, and because of the historic (prior) conditions of the areas.

Population Trends

BBS data provide one of only a few sources of long-term population data from which trends may be inferred. However, without going into details here, it must be noted that many problems have been identified with BBS data and analyses (Peterjohn et al. 1995, Thomas and Martin 1996). These problems include observer bias and biases associated with sampling design. Furthermore, a lot of discussion has been devoted to identifying the correct way to analyze BBS data (Thomas and Martin 1996).

Regardless of these potential limitations, Miller (1992) evaluated population trends of ponderosa pine birds using BBS data. BBS routes were selected from Colorado ($n = 5$), Utah ($n = 5$), Arizona ($n = 5$), and New Mexico ($n = 6$) that sampled managed ponderosa pine forests. Whether or not these managed pine forests were a representative sample of pine forest of the southwest is unknown, but population trends in unmanaged pine forests (for example, old-growth forest, wilderness lands) may have differed from those in managed forests. To ensure that standardized methods were used, analyses were done by the U.S. Fish and Wildlife Service, Patuxent Research Center.

Miller examined trends of individual species and groups of species as defined by nesting strategy (for example, primary-cavity, secondary-cavity, or cup nesters), nesting habitat (woodland or coniferous forest), or residency status (resident, short-distant migrant, neotropical migrant). Analyses were done at the state level for New Mexico (because this was the only state with adequate samples); New Mexico and Arizona combined; Colorado and Utah combined; and all four states combined. For New Mexico, Miller found declining populations of 77 percent of all birds examined (46 of 61), and from 50 to 100 percent of the species within any of the groups that he evaluated (table 2). Fewer population declines were noted when census routes from states were pooled (table 2). Of particular interest was that about two-thirds (50) of the species found in New Mexico and Arizona (75 total bird species) exhibited significant population declines (table 2), and many of these were birds that nested in open cups and species that tended to be year-round residents. Miller identified 50 species that exhibited declines and 25 that exhibited population increases (table 3).

The Christmas Bird Count program, sponsored by the National Audubon Society, provides information on the abundance of birds wintering in various locations in North America. There are, however, only two count locations

Table 2. Proportion of bird species declining 1968 to 1990 along managed ponderosa pine breeding bird survey routes, for species with ≥ 5 routes counted, and an average of 20.5 birds per route (modified from Miller 1992).

Guild	New Mexico	New Mexico & Arizona	Colorado & Utah	All four states
Woodland nesting	11 of 13 (85%)	9 of 16 (56%)	5 of 11 (45%)	6 of 19 (32%)
Coniferous nesting	8 of 8 (100%)	6 of 11 (55%)	5 of 7 (71%)	4 of 14 (29%)
Primary cavity nesting	1 of 2 (50%)	2 of 3 (67%)	1 of 2 (50%)	1 of 4 (25%)
Secondary cavity nesting	9 of 12 (75%)	7 of 14 (50%)	3 of 6 (50%)	8 of 15 (53%)
Open cup nesting	23 of 26 (88%)	20 of 31 (65%)	10 of 18 (56%)	26 of 41 (63%)
Permanent resident	11 of 11 (100%)	10 of 12 (83%)	3 of 5 (60%)	10 of 14 (71%)
Short distance migrant	15 of 25 (60%)	16 of 33 (48%)	10 of 22 (45%)	20 of 39 (51%)
Neotropical migrant	10 of 13 (77%)	9 of 15 (60%)	4 of 11 (36%)	12 of 22 (55%)
All birds	46 of 61 (77%)	50 of 76 (66%)	21 of 45 (47%)	54 of 97 (57%)

that have been regularly surveyed in Southwestern ponderosa pine forest: one centered near Flagstaff, Arizona, which has been surveyed since 1968, and another centered near Mormon Lake, Arizona, which has been surveyed since 1982. CBC data have been shown to produce reliable indications of trends in bird abundance when a count has been conducted for a sufficient period of time (that is, about 20 years), and when a sufficient count effort has been expended each year (Bock and Root 1981). Although the Flagstaff count meets these requirements, trend analyses should not be based on only one or a few counting locations (Bock and Root 1981). Therefore, we have not included analyses of CBC data in this report.

Several authors have recently documented range and population shifts for particular Southwestern bird species. For example, Johnson (1994) suggested northward expansion of the ranges of Grace's warbler, painted redstart, hepatic tanager, and summer tanager in response to "natural" climate change over the past century. Based on an extensive literature review, DeSante and George (1994) concluded that willow flycatcher, buff-breasted flycatcher, western bluebird, Bell's vireo, summer tanager, and song sparrow populations were decreasing across the west, whereas berryline hummingbird, violet-crowned hummingbird, black phoebe, European starling, red-faced warbler, and brown-headed cowbird populations were increasing. Whether or not these range shifts and population trends apply to Southwestern ponderosa pine forest is unclear, however, because the western region reviewed

by DeSante and George encompasses many different vegetation types.

Brawn and Balda (1988a) reviewed the population status of Southwestern ponderosa pine birds and suggested that broad-tailed hummingbird, acorn woodpecker, three-toed woodpecker, purple martin, violet-green swallow, mountain chickadee, white-breasted nuthatch, pygmy nuthatch, brown creeper, western bluebird, mountain bluebird, American robin, red-faced warbler, chipping sparrow, and lark sparrow populations would also be likely to decline over time in response to past and present land-use activities. Many of these species are ones that nest in cavities or rely on a well-developed herbaceous understory. We can presume that the synergistic and cumulative effects of natural vegetation change, livestock grazing, logging, fuelwood harvest, and fire suppression will underlie many of the predicted population declines (discussed in detail in Finch et al., this volume).

Carothers et al. (1973a) briefly summarized the status of selected species in northern Arizona. They noted that the Lewis' woodpecker had become a fairly common permanent resident, and the evening grosbeak a locally common permanent resident in ponderosa pine forest around Flagstaff. In contrast, they noted a decline in numbers of red-breasted nuthatches in ponderosa pine. They also noted that the exotic European starling had changed in status from a rare winter visitor or transient to a common winter resident and an uncommon summer resident in the Flagstaff area.

Table 3. Increasing and decreasing bird species on managed ponderosa pine Breeding Bird Survey routes in Arizona and New Mexico, for species with ≥ 5 routes and 20.5 birds per route (modified from Miller 1992). These lists include both songbirds and non-songbirds.

Decreasing	Increasing
Mallard	Turkey vulture
Killdeer	Red-tailed hawk
Band-tailed pigeon	American kestrel
Mourning dove	Northern flicker
Hairy woodpecker	Cassin's kingbird
Acorn woodpecker	Cordilleran flycatcher
Common nighthawk	Steller's jay
Broad-tailed hummingbird	European starling
Western Kingbird	Brown-headed cowbird
Ash-throated flycatcher	Vesper sparrow
Say's phoebe	Spotted towhee
Western wood-pewee	Green-tailed towhee
Gray flycatcher	Blue grosbeak
Horned lark	Western tanager
Western scrub jay	Hepatic tanager
Common raven	Purple martin
American crow	Barn swallow
Clark's nutcracker	Rough-winged swallow
Pinyon jay	Bewick's wren
Red-winged blackbird	House wren
Eastern meadowlark	Red-breasted nuthatch
Western meadowlark	Townsend's solitaire
Brewer's blackbird	Hermit thrush
House finch	American robin
Red crossbill	Western bluebird
Lesser goldfinch	
Pine siskin	
Lark sparrow	
Chipping sparrow	
Canyon towhee	
Black-headed grosbeak	
Cliff swallow	
Violet-green swallow	
Loggerhead shrike	
Warbling vireo	
Solitary vireo	
Virginia's warbler	
Yellow-rumped warbler	
Grace's warbler	
Black-throated gray warbler	
House sparrow	
Northern mockingbird	
Rock wren	
White-breasted nuthatch	
Pygmy nuthatch	
Plain titmouse	
Mountain chickadee	
Common bushy tit	
Ruby-crowned kinglet	
Mountain bluebird	

Ecological Roles

Seed Dissemination

Mistletoe

Hudler et al. (1979) studied the role of birds in the spread of dwarf mistletoe (*Arceuthobium* spp.) in a Colorado ponderosa pine forest. Long-distance seed transmission (that is, farther than possible by normal seed discharge) occurred infrequently; successful infection occurred once every four years on average. Mountain chickadees and pygmy nuthatches were the primary vectors of the parasite. Laboratory studies showed that seeds seldom remained viable when ingested by birds. Rather, successful movement of the seeds occurred when they became attached to bird feathers and later transferred to foliage.

Bennetts (1991) and Bennetts and Hawksworth (1991) studied the indirect effects of dwarf mistletoe on birds in a Colorado ponderosa pine forest. The total number of birds and the total number of bird species detected increased with increasing levels of mistletoe infestation; this pattern was consistent across most foraging assemblages of birds. In addition, the number of snags and the abundance of cavity-nesting birds increased with increasing levels of mistletoe. The authors suggested that dwarf mistletoe should not be viewed solely as a forest pest (because of its often negative influence on commercial timber volume), but rather in the context of an ecological disturbance process and its influence on wildlife communities. That is, mistletoe is a disturbance process that changes the structure and function of ponderosa pine and other host communities. In their review of the literature, they also found that the witches' brooms caused by the mistletoe are an important nesting and roosting substrate for many species of birds and squirrels, and that some species use mistletoe as a food source. Mistletoe has been shown to serve as a nesting substrate by Forsman et al. (1984), Bull and Henjum (1990), Bull et al. (1989); as a roosting substrate by Martinka (1972); and as a food source for birds and other animals by Taylor (1935), Broadbooks (1958), Urness (1969), Farentinos (1972), Craighead et al. (1973), Currie et al. (1977), Hall (1981), and Severson (1986).

Pine Seeds

Balda and his coworkers (for example, Balda and Bateman 1971; Balda 1973, Bateman and Balda 1973) conducted a long-term, intensive study of the ecology and behavior of the pinyon jay in a northern Arizona ponderosa pine forest. Pinyon jays are year-round residents and obtain part of their winter food from pine seeds that they cached during the fall. This caching behavior helps spread pine seeds and thus plays a major role in the population dynamics of these trees. Clark's nutcrackers are also a

seed-predator and a very important seed-disperser for wingless seeds (for example, *Pinus edulis*) (Tomback and Linhart 1990). Nutcrackers have been found to affect forest regeneration and to possibly extend the range of piñon pines (reviewed in Christensen et al. 1991). They also forage on ponderosa pine seeds, when they are available, and may therefore play a part in the dynamics of ponderosa pine forests. Another ponderosa pine seed-predator is the red crossbill. The crossbill is nomadic, following sporadic, scattered pine seed crops (Gill 1995:290). In the Rocky Mountains, crossbills will nest in January and February if pine seeds are abundant (Gill 1995:275).

Indicators of Forest Conditions

Szaro and Balda (1982) discussed the selection and subsequent monitoring of birds as indicators of environmental change, using their data from a ponderosa pine forest of northern Arizona as an example. They noted that many different definitions have been applied to the term "indicator" for use in environmental management, including: 1) endangered and threatened plants and animals; 2) species commonly hunted, fished, or trapped; 3) species with specialized habitat needs; and 4) plants or animals selected because changes in their populations are thought to indicate the effects of natural- or human-induced changes on the collective species of a major biological community. The use of birds as indicators is controversial (for example, see Morrison et al. 1992), primarily because indicator species may be affected differently from other species by habitat changes. Nevertheless, the concept is important here because there are diverse opinions on the subject, and because in certain situations (for example, chemically polluted environments) birds can indicate habitat conditions (Morrison 1986).

Szaro and Balda (1982) found that species such as the hermit thrush, red-faced warbler, Cordilleran flycatcher, and pygmy nuthatch, which are found in old-growth ponderosa pine forest and only lightly disturbed areas, are replaced in moderately to heavily cut areas by species such as the western wood-pewee, yellow-rumped warbler, and rock wren. Therefore, those species that are most sensitive to habitat perturbations may potentially make the best indicator species. Some species that are too rare to be useful as indicators of the general community—such as Virginia's warbler, brown creeper, and hepatic tanager—may be useful indicators of special habitat needs because they breed in ponderosa pine. Szaro and Balda concluded that the two species that best indicated the overall "health" of the bird community were the pygmy nuthatch and violet-green swallow. They based this finding on the fact that, when they found high densities of pygmy nuthatches and violet-green swallows, they also found high densities of most of the other ponderosa pine forest bird species (see Szaro and Balda 1982, table 1).

"Habitat specialists" as indicator species are discussed in Rich and Mehlhop (this volume).

Roost and Nest Cavity Formation

Scott (1978) summarized the frequent use of cavities in dead or partially dead trees in ponderosa pine forest and mixed pine woodlands in Arizona and New Mexico by the American kestrel, 7 species of owls, the elegant trogon, 11 species of woodpeckers, 2 flycatchers, 3 swallows, 5 chickadees and titmice, 3 nuthatches, the brown creeper, 4 wrens, and 3 bluebirds. Similarly, Ffolliott (1983) summarized the scant literature on cavity-nesting animals in Southwestern ponderosa pine forests and found that at least 49 species of birds, 10 species of mammals, and numerous species of insects and herpetofauna used tree cavities in these forests. In addition, he noted that 63 percent of the birds and 75 percent of the mammals that are snag-dependent in Southwestern forests are insectivorous. This diet preference is important because birds and mammals have been credited with insect control that helps maintain ecosystem functioning.

An important interaction exists in ponderosa pine forests involving the location and suitability of potential nest trees, the type and number of primary cavity excavating species (especially woodpeckers), and the number and distribution of secondary cavity nesting species. Although secondary cavity nesting species will use non-bird excavated holes (for example, holes resulting from disease or broken branches) for nesting, their frequent use of bird-excavated holes indicates a likely preference for such cavities or a limitation of alternative nest sites.

Brawn and Balda (1988b; see also Brawn 1985, Brawn and Balda 1983) tested the common assumption that nest sites limit the breeding density of secondary cavity nesters in an Arizona ponderosa pine forest. They found this assumption to be only partially correct. They found that secondary cavity nesters, as a group, can indeed be limited by nest sites. But only three of the six species they studied significantly increased in density when provided with artificial nest boxes; these were the violet-green swallow, pygmy nuthatch (which can also be a primary cavity-nesting species), and western bluebird. Numbers of house wrens, mountain chickadees, and white-breasted nuthatches did not differ. They concluded that a given population appears to be limited by nest sites if it is sufficiently common during the breeding season and dependent upon snags as a source of nest sites. Within species that are nest site limited, availability of food or foraging substrates and territoriality may determine an upper limit to breeding densities if nest sites are in ample supply. Thus, a dynamic exists between nest sites, food availability, and intra- and interspecific competition for nest sites.

A study of secondary cavity nesters in northern Arizona by Cunningham et al. (1980) found pronounced in-

terspecific variation in the use of snags for nest sites; certain species were reliant on snags, whereas others rarely used snags. For example, nearly all violet-green swallows and pygmy nuthatches nested in snags, whereas white-breasted nuthatches were not so dependent upon snags. Cunningham et al. also found that mountain chickadees, white-breasted nuthatches, and house wrens were relatively uncommon regardless of the availability of snags and foraging substrate. It is the common species that seem to increase the most after provision of nest boxes. Brawn and Balda (1988b) speculated that this was because relatively rare populations do not contain enough non-breeding individuals (that is, floaters) to be able to take advantage of the increase in nesting sites. Common species thus can be nest-site limited, whereas rare species are being suppressed by other factors. Brawn et al. (1987) also found that, during the breeding season, interspecific competition for food among secondary cavity nesters appeared to be unimportant in ponderosa pine bird communities. The factors holding down numbers of rare species are still generally unknown.

There is apparently an interaction between the species of snag retained after treatments and the response of birds to total snag density. Scott (1979) found that populations of some species of cavity-nesting birds can be reduced significantly by removal of conifer snags even when some aspen snags are left. Other hardwoods, such as oak, provide nesting sites for some species of birds within the ponderosa pine type. Some birds such as swallows, however, may not make the change from ponderosa pine snags to the smaller hardwood snags.

Hay and Guntert (1983) examined the seasonal requirements for snags by pygmy nuthatches in northern Arizona ponderosa pine forest. They found that trees with nest cavities were shorter and consequently had a small diameter at breast height (dbh) compared to those used for roosting during other seasons. Greater cavity height of the fall and spring roosts compared to summer roosts was related to more absorption of spring-fall radiation by the former. In contrast, nest cavities appeared to be positioned to obtain moderate insolation and shielding from the wind. Hay and Guntert stated that cavity selection is interrelated with the overall biology of the species, and management should emphasize snag and/or cavity quality, rather than the absolute quantity of snags available. They also concluded that additional baseline research into the seasonal quality of cavities and snags needed for cavity-dependent species in ponderosa pine forests was needed.

Horton and Mannan (1988) studied the interrelationship between fire and snag dynamics in southeastern Arizona ponderosa pine and mixed pine-oak forest. Natural fires burned every 2 to 12 years in Southwestern ponderosa pine before suppression by humans beginning in the late 19th century (for more details, see Moir et al. and Finch

et al., this volume). These fires were usually light surface fires that produced generally open, park-like conditions. Modern forest management uses broadcast understory fires to reduce accumulations of woody debris left by logging or natural processes to reduce the risk of catastrophic crown fires. These fires also impact snag dynamics by consuming existing snags and creating others by killing trees. Horton and Mannan found that a single application of moderately intense surface fire resulted in a net decrease of 33 percent of snags preferred for nesting. However, no species of cavity-nesting bird disappeared in the first breeding season following the fires, and only the northern flicker and violet-green swallow declined in abundance. They concluded that these changes were not due to a shortage of snags. Their study, however, was conducted for only one year following fire treatment.

Snag Management

According to Scott (1978), little information existed on management guidelines for cavity nesting birds in Southwestern ponderosa pine forests prior to the late 1970s. Before that time, snags were removed during forest harvest because of potential fire and safety hazards, and many thought they had poor aesthetic value and were indicative of an unhealthy forest. Using his own research and that of Balda (1975), Scott (1978) concluded that, on average, at least 2.5 large (243 cm dbh) snags per acre should be retained in ponderosa pine forests. In addition, all naturally occurring snags should be left during timber harvest. Specifically, he found that 1) snags usually did not become suitable for nesting until 6 years after the trees died; 2) snags that retained more than 40 percent of their bark were used more frequently and contained more holes than those with less bark; 3) snags in higher dbh classes (243 cm) were used significantly more than smaller snags and the larger snags also contained more holes; 4) snags on northern and southern aspects were used at about the same frequency, but those on northern exposures averaged more holes per snag; and 5) snags over 23 m tall were used at a significantly higher rate than shorter snags, but comprised only 16 percent of the available snags.

Balda (1975) found that 4.2 snags/ha were necessary in ponderosa pine forests to achieve average densities and natural species diversity of secondary cavity nesters. He also stated that 6.7 snags/ha were necessary to maintain maximum densities and natural species diversity of these birds.

Ffolliott (1983) examined the implementation of USDA Forest Service snag guidelines on study areas across the ponderosa pine belt of northern Arizona, examining both present conditions and simulated (modeled) conditions at the end of a 20-year period. Snags were defined as standing dead trees at least 30 cm dbh and 3.1 m in height; no differentiation was made between hard and soft snags. His analyses showed that none of his study areas that had been subjected to various silvicultural treatments met any

of the suggested policies for snag retention (USDA Forest Service 1977). From his analysis, only virgin forest would meet a retention policy of 2.5 to 5.0 snags/ha through natural mortality.

Rosenstock (1996) found that snags >46 cm dbh and >10 m tall were frequently used for nesting in ponderosa pine forest. Cunningham et al. (1980) found a preference for snags >58 cm dbh and >20 m tall on the Beaver Creek Watershed in northern Arizona. Paine and Martin (1995, as cited in Rosenstock 1996) found that 84 percent of ponderosa snags used for nesting on their Mogollon Rim study sites were >30 cm dbh and >10 m tall. Horton and Mannan (1988) found a preference for snags >51 cm dbh.

This review indicates that little research has been conducted on snag requirements in ponderosa pine forests. Studies that have been conducted demonstrate that at least 5 large snags/ha may be necessary to maintain populations of cavity-nesting species. However, it also appears that these guidelines are not being attained on at least some of the forested lands.

Predator-Prey Relationships/Pest Control

As reviewed by Holmes (1990), numerous bird species respond both functionally and numerically to increasing prey densities. While birds seem unable to prevent population epidemics of their prey, they do appear to have a substantial impact when prey populations are at endemic levels. From his review of the literature, Holmes concluded that birds could delay the onset of an insect outbreak. For example, modeling of spruce budworm populations suggested that predation by birds may be a significant factor in maintaining endemic population levels of this species.

As reviewed by Dahlsten et al. (1990) for western mixed-conifer forests (which include ponderosa pine as a major component), many species of forest birds concentrate their foraging activities on insect species considered to be forest pests. In addition, Koplín (1969) demonstrated a functional response of woodpeckers to insect outbreaks. Insectivorous birds may also increase the fitness of the plants on which they forage for arthropod prey. For example, Marquis and Whelan (1994) examined the effect of insectivorous birds on white oak (*Quercus alba*) growth in a deciduous forest in Missouri. Through experimental manipulations they demonstrated that the presence of birds enhanced the growth of juvenile oaks via bird consumption of leaf-chewing insects (primarily Lepidopteran larvae). They suggested that forest management practices that promote the conservation of insectivorous bird species will help maintain forest productivity. The extension of this to ponderosa pine forests (with or without an oak component) is obvious. Marquis and Whelan further suggest that although insecticide spraying and handpicking insects off trees can reduce their numbers, these are not necessarily feasible alternatives for controlling arthropod numbers in forests.

Insect consumption of cones and seeds can negatively impact vertebrate use of such resources. Christensen and Whitham (1993) found that stem- and cone-boring insects, birds (Clark's nutcrackers, pinyon jays, and [western] scrub jays), and mammals competed for pinyon pine seeds. And insect herbivores indirectly affected resource use by the vertebrates through a 57 percent average reduction in crop sizes. Thus, the foraging of birds on insects plays several important roles and is a significant factor to consider in the management of ponderosa pine forests. There is a paucity of information on this subject, however, so this is an important area for research.

Habitat Use

General Habitat Use

Balda (1967, 1969) studied the use of foliage by breeding birds in ponderosa pine and oak-juniper forests of the Chiricahua Mountains, Arizona. He found that certain species (such as the pygmy nuthatch) were closely associated with ponderosa pine of many heights, whereas other species (such as the chipping sparrow) were found in specific height layers regardless of the tree species involved. Other species such as Grace's warbler were restricted to particular heights in pines. The models for pines strongly suggested that foliage volume may be an important factor in limiting the densities of the pygmy nuthatch and Grace's warbler, even though the former species is a cavity nester. Balda (1970) also described the bird community present in oak and oak-juniper-pine woodlands.

Marshall (1957) summarized surveys he conducted in pine-oak woodlands during the summers of the early 1950s from the Pinaleno and Santa Catalina mountains in Arizona, south into central Sonora and to the Sierra Madre Occidental of northwestern Chihuahua, Mexico. Ponderosa pine entered his pine-oak woodlands only occasionally. The related Apache pine was more frequently encountered on his sites, along with chihuahua pine (*P. leiophylla*). Marshall provided descriptions of the overall relationship between the distribution of birds and plants in the region and summarized his observations in annotated species notes. Of particular interest are his observations of pine (and pine-oak) forest birds of current special concern, including the thick-billed parrot, buff-breasted flycatcher, elegant trogon, spotted owl, and Montezuma quail, because he details the population status and describes the habitat affinities of these species.

Carothers et al. (1973a) edited a volume that summarized the status and general habitat preferences of birds in the San Francisco and White mountains of Arizona, concentrating on breeding birds. A paper by Haldeman et al. (1973) included a brief section on wintering birds, where 18 species were observed during the winter in ponderosa pine forest, and 69 species were observed during summer, of which 23 were known to nest. They consid-

ered the following species to be exclusive users of the ponderosa pine forest during their study in this region: solitary vireo, western bluebird, and Brewer's blackbird. The pygmy nuthatch, violet-green swallow, American robin, white-breasted nuthatch, and Grace's warbler were considered to be "characteristic" of ponderosa pine forest (that is, found to be two to three times as abundant than in a comparison area).

Franzreb published a series of papers (1978, 1983, 1984) that detailed results of her study of birds in a mixed Douglas-fir, ponderosa pine, and Southwestern white pine forest in the White Mountains, Arizona. In this mixed-conifer forest, she found that ponderosa pine and Southwestern white pine were used less frequently than expected based on total foliage volume, whereas use exceeded availability for Douglas-fir, white fir, and Engelmann spruce. She also showed, however, that certain species, especially the Grace's warbler, relied upon pines for foraging. Franzreb's 1978 and 1983 papers also discussed the influence of logging on bird abundance and foraging behavior. Her 1984 paper detailed the foraging behaviors of the ruby-crowned and golden-crowned kinglets. Both species strongly preferred spruce and Douglas-fir and avoided pines for foraging.

Salomonson and Balda (1977) examined the winter behavior of the Townsend's solitaire in a pinyon-juniper-ponderosa pine ecotone in northern Arizona. Territory size, and ultimately survival, were related to the abundance of juniper berries. Laudenslayer and Balda (1976; also Laudenslayer 1973) studied the breeding birds of a pinyon-juniper-ponderosa pine ecotone in northern Arizona. They concentrated on five bird species and described their densities, foliage preferences, and foraging habitats. The mountain chickadee and solitary vireo preferred ponderosa pine; the bushtit and plain titmouse preferred pinyon-juniper; and chipping sparrows were found throughout the ecotone.

Overturf (1979) compared the breeding bird communities on burned and unburned sites in ponderosa pine of northern Arizona. The burned sites showed a decreased number of bird species and bird abundance, which were related to the decrease in habitat heterogeneity and loss of the canopy and shrub-sapling vegetation layer. In addition, burning caused a shift in bird species composition from foliage users to ground-using birds because burning caused an increase in herbaceous plants. Overturf concluded that burning in this "pyroclimatic monoculture" would be an effective management strategy because it simulated natural fires and increased the overall habitat heterogeneity in the forest (for more details, see Finch et al., this volume).

Szaro and Balda (1979, 1986) and Szaro et al. (1990) found that significant temporal variations occurred in habitat use and foraging behavior of ponderosa pine birds in northern Arizona. Szaro and Balda (1986) showed that

bird density and species richness were influenced by both weather and timber harvest. The effects of weather on birds varied depending on the type of timber harvest conducted, although the harvest type was of primary importance in determining community structure. The impact of harvest was clearly more pronounced after the mildest winter and tended to be minimized after the severest winter. They concluded that studies must be conducted during a variety of weather conditions (over many years) to determine the trend of bird responses in different forest types (including different harvest types). Similarly, Szaro et al. (1990) showed that weather and harvest type significantly influenced foraging behaviors of ponderosa pine birds over a three-year period. They urged that studies be conducted that identified the proximate mechanisms that caused this variation in foraging behavior. They suggested that such causes would include resource availability, weather conditions, predation, and plant phenology.

Szaro and Balda (1982) summarized the habitat preferences of ponderosa pine forest species based on their study of various seral stages (see also Szaro and Balda 1986; Szaro et al. 1990; and as summarized above). The disturbance regime they used to simulate seral stages ranged from uncut, mature forest to severely thinned forest (see table 4). Six species (of 25 total species, or 24 percent) showed no distinct habitat preferences: the northern flicker, hairy woodpecker, Steller's jay, common nighthawk, mourning dove, and white-breasted nuthatch. Six species (24 percent) preferred undisturbed or only lightly thinned mature forest: the red-faced warbler, hermit thrush, Cordilleran flycatcher, pygmy nuthatch, violet-green swallow, and black-headed grosbeak. Similarly, two additional species (8 percent; dark-eyed junco and mountain chickadee) preferred undisturbed to moderately disturbed (cut) forest, and another four species (16 percent) preferred lightly to moderately disturbed areas (Grace's warbler, yellow-rumped warbler, western tanager, western bluebird). Thus, up to 18 species (72 percent) seemed to prefer mature forest with some disturbance (includes those species showing no distinct preferences). An additional six species (24 percent) preferred lightly to heavily disturbed (chipping sparrow and solitary vireo), moderately to heavily disturbed (western wood-pewee, American robin, and broad-tailed hummingbird), or heavily disturbed (rock wren) areas. Finally, the acorn woodpecker was confined to oak groves. The authors concluded that the hermit thrush, red-faced warbler, Cordilleran flycatcher, and pygmy nuthatch showed strong preference for undisturbed to only slightly disturbed forest.

Stallcup (1968) studied habitat segregation of foraging nuthatches and woodpeckers in a Colorado ponderosa pine forest and described the density and composition of this group of birds throughout the year. Birds studied were the white-breasted, red-breasted, and pygmy nuthatches, hairy woodpecker, northern (red-shafted) flicker, and

Table 4. Habitat preferences of birds in selected ponderosa pine stands in northern Arizona (from Szaro and Balda 1982). The disturbance regime ranged from (in increasing intensity of disturbance): untreated mature forest, silviculturally cut, irregular strip cut, to severely thinned cut.

Preference Species
None
Northern flicker
Hairy woodpecker
Steller's jay
Common nighthawk
Mourning dove
White-breasted nuthatch
Nondisturbed or lightly disturbed areas
Red-faced warbler
Hermit thrush
Cordilleran flycatcher
Pygmy nuthatch
Violet-green swallow
Black-headed grosbeak
Nondisturbed to moderately disturbed areas
Dark-eyed junco
Mountain chickadee
Moderately to heavily disturbed areas
Western wood pewee
American robin
Broad-tailed hummingbird
Heavily disturbed areas
Rock wren
Lightly or moderately disturbed areas
Grace's warbler
Yellow-rumped warbler
Western tanager
Western bluebird
Lightly to heavily disturbed areas
Chipping sparrow
Solitary vireo
Oak groves
Acorn woodpecker

Williamson's sapsucker. Red-naped sapsuckers, downy woodpeckers, and northern three-toed woodpeckers were present but rare. The absence of the red-breasted nuthatch during breeding may have resulted from a shortage of nest sites, or more likely, a lack of foraging space because of competition from other species. Stallcup suggested that food shortages might be responsible for segregating bird species.

Apparently the most recent study available on the general habitat affinities of ponderosa pine birds was conducted by Rosenstock (1996). He noted that previous studies on the effects of forest treatments on birds in Southwestern ponderosa pine (for example, Szaro and Balda 1979) examined treatments that are no longer in common use (for example, clear-cuttings, strip cuttings).

As such, he examined the abundance of birds across a wider gradient of pine and pine-oak seral stages than had previously been conducted. In summary, he found 43 species in pine-oak, and 38 in pine. Two rather uncommon species (Clark's nutcracker and evening grosbeak) were found only in pine, whereas seven species were unique to pine-oak (dusky flycatcher, downy woodpecker, lesser goldfinch, rock wren, spotted towhee, Virginia's warbler, and warbling vireo), and all but the Virginia's warbler were rare or uncommon. Four common species—acorn woodpecker, black-headed grosbeak, house wren, and red-faced warbler—were found primarily in pine-oak. Densities of violet-green swallows and western wood pewees were higher in pine patches, whereas American robins, hermit thrushes, and white-breasted nuthatches were more abundant at pine-oak sites. By vegetative structural stage (VSS; see Moir et al., this volume, for definitions of VSSs), neotropical migrant abundances and species richness were similar across VSS classes at pine-oak sites but were highest at VSS class 4 and 6 in pine. Residents and short-distance migrants had similar abundances and species richness in all VSS classes in pine-oak. At pine sites, however, abundance of these groups of species was lower in VSS class 3 stands but similar in all other classes; class 6 had a higher species richness than the other classes. Cavity nesting species had similar abundances and richnesses across all pine-oak classes, and across all pine classes except class 6, which had considerably higher values.

Although Rosenstock noted that previous studies in Southwestern ponderosa pine were conducted before the importance of spatial variables on bird communities was widely acknowledged, he was not able to determine the influence of patch size and other spatial attributes on the bird community he studied.

Nesting Habitat

Martin (1988) studied the ability of nest predation to explain patterns of covariation in species numbers with area and habitat in mixed ponderosa pine forest and maple-dominated stands in central Arizona. Variation in numbers of species among drainages was positively correlated with variation in the density of foraging and nesting substrates. His results were consistent with a prediction that birds select nest sites based in part on the availability of sites that minimized their risk of nest predation, and that these sites increase in number with density of foliage at nest height. His results were also consistent with a hypothesis that availability of suitable nest sites is one of the bases for the relationship between species numbers and foliage density for foliage-nesting species. In a related study, Martin and Roper (1988) detailed their findings for the hermit thrush. They found that hermit thrushes had low nesting success (7 to 20 percent), due mostly to nest predation. The structure of vegetation around the nest influenced the predation rate and likely

the nest-site availability. Likewise, Li and Martin (1991) presented results from the same study region for cavity-nesting species. Although aspens accounted for only 12 percent of all trees present in the study area, dead aspen accounted for 88 percent of all nest sites. Li and Martin also identified specific aspen-conifer patches that were chosen for nesting and foraging. Nest cavity height influenced nesting success, with the lower nests showing the lowest success. The authors noted that populations of cavity nesters might decrease if aspen snags decreased in height and abundance; alternative conifer snags were rare because most large trees were harvested before they died.

Siegel (1989) examined the distribution and abundance of birds in virgin old growth and mature managed ponderosa pine forest in northern Arizona (table 1). The mature managed stands met the "minimum" USDA Forest Service standards for old-growth forest. Siegel reached the following conclusions. First, brown creepers used large (>20 inches dbh) snags, in denser stands of older trees, with large pieces of sloughing bark. Such conditions provided the necessary microsites for nest placement and also served as foraging sites. Second, hermit thrushes nested in the canopies of mature trees, in contrast to the much smaller trees this species uses in other parts of its range. Siegel felt that small pine were not used because they did not provide the necessary support branches for their nests nor the foliage necessary to conceal the nests. He also thought that placement of nests in the canopy served better to regulate nest temperatures. In addition, hermit thrushes also foraged in moist, cool sites. Third, a higher total density of birds was found in dense stands of pine compared to other stands and was apparently due to the greater abundance of aspen and the concomitant wetter conditions in these stands. The warbling vireo, violet-green swallow, western wood-pewee, Williamson's sapsucker, and three-toed woodpecker were more common in the dense stands because they used the groves of pine-aspens for nesting and foraging. Also, the mesic, dense stands may have supported higher bird abundances because of their greater total foliage volume, and concomitantly, higher densities of invertebrate prey. In contrast, species richness was only slightly higher in older and denser stands, indicating that this situation did not follow the standard positive relationship between foliage height diversity and bird species diversity.

Finally, Siegel (1988) concluded that the mesic conditions created in dense old growth likewise created conditions that were more characteristic of forests at higher elevations or latitudes (that is, Canadian and Hudsonian life zones). These conditions apparently provided the resources used by the brown creeper, hermit thrush, three-toed woodpecker, northern goshawk, and saw-whet owl in ponderosa pine. Warm and dry exposures in more open old-growth stands were either unsuitable or marginal locations for these species.

McEllin (1979) compared the demography, territorial spacing, and foraging behavior of white-breasted and pygmy nuthatches in Colorado ponderosa pine and mixed ponderosa pine-aspen stands. White-breasted nuthatches nested primarily in natural cavities in live pines, whereas pygmy nuthatches nested in pre-existing cavities in dead pines; cavity availability was higher for the latter species. Significant differences were shown for the foraging behaviors, within sexes of each species and between species: differences in foraging heights, and foraging locations within trees (for example, limbs versus trunks). McEllin concluded that these species exploited different aspects of forest structure; that is, white-breasted nuthatches were more specialized in the vertical, horizontal, and tree structure dimensions, whereas pygmy nuthatches showed greater specialization in food items and prey acquisition behaviors. With regard to forest management, McEllin stated that careful analyses of these ecological relationships is a necessary requirement of any program. Artificial reproduction of favorable conditions for one species or one season might result in unfavorable conditions for another species or season. Detailed analyses of space utilization patterns within and between species under different forest conditions can provide ecological information that will be important in designing forest management strategies.

Brawn (1991) studied the reproduction and foraging of western bluebirds on two ponderosa pine sites in northern Arizona and found that breeding phenology and allocation of parental care were adjusted by bluebirds in response to local environmental conditions. Brawn also found that feeding rates of nestlings and fledging success were greater on the moderately logged site than on the heavily logged site.

Migrant Use of Ponderosa Pine

Very little information exists on use of stopover areas by migrant birds, including what vegetation types and habitats are most important to birds during migration, where these sites occur, and how their distribution and abundance are changing over time (Moore et al. 1995). Also, because more migrants pass through the eastern two-thirds of the United States, most of the literature on stopover sites concern eastern migrants. Hence, there are few papers describing the specific use of Southwestern ponderosa pine forests as stopover sites. For example, Phillips et al. (1964) presented information on bird species in Arizona; and although in the species accounts they implied that several of the species migrated through ponderosa pine forests in the state, they did not state it explicitly (table 5). Hejl (1994, table 3), summarizing Brawn and Balda (1988a), also listed species that occur in Southwestern ponderosa pine forests but did not indicate those that were only migrating through the forests. On the other hand, Hutto (1985) found that stopover periods for transient (migrant) birds in fall and spring rarely exceeded

Table 5. Breeding (B), wintering (W), and probable strictly migrant (M) birds in ponderosa pine forests (with oak or other plant species co-dominant) in Arizona and New Mexico, based on Phillips et al. (1964) and the New Mexico Partners in Flight list of sensitive bird species. Includes both Cordilleran (ponderosa pine) and Madrean (ponderosa and Apache) pine-oak forest types together. An asterisk (*) indicates a species for which there is some question about its use of ponderosa pine when it is in Arizona.

State Species	State Species	State Species	State Species
Arizona	Rock wren* (B)	New Mexico	Red-tailed hawk (B,W)
Band-tailed pigeon (B)	American robin (B,W)	Virginia's warbler (B)	American kestrel (B,W)
Mourning dove (B)	Hermit thrush (B)	Olive-sided flycatcher (B)	American robin (B,W)
Whip-poor-will (B)	Eastern bluebird (B,W)	Grace's warbler (B)	
Vaux's swift* (M)	Western bluebird (B,W)	Band-tailed pigeon (B)	
White-throated swift (B)	Mountain bluebird (B,W)	Red-naped sapsucker (B,W)	
Black-chinned hummingbird (M)	Townsend's solitaire (B,M)	Willow flycatcher (B)	
Broad-tailed hummingbird (B)	Blue-gray gnatcatcher* (M)	Hammond's flycatcher (B)	
Rufous hummingbird* (M?)	Golden-crowned kinglet* (W)	Peregrine falcon (B)	
Allen's hummingbird* (M?)	Ruby-crowned kinglet* (M)	Williamson's sapsucker (B,W)	
Calliope hummingbird (M)	Olive warbler (B)	Dusky flycatcher (B)	
Rivoli's hummingbird (B)	Water pipit* (M)	Cordilleran flycatcher (B)	
Elegant trogon (B)	Cedar waxwing* (M)	Olive warbler (M)	
Northern flicker (B,W)	Loggerhead shrike (M)	Hepatic tanager (B)	
Acorn woodpecker (B,W)	Hutton's vireo (W)	Broad-tailed hummingbird (B)	
Lewis' woodpecker (B,M)	Solitary vireo (B,M)	Cassin's kingbird (B)	
Red-naped sapsucker (W)	Warbling vireo (B,M)	Western bluebird (B,W)	
Yellow-breasted sapsucker (W)	Orange-crowned warbler (B)	Townsend's solitaire (B,W)	
Williamson's sapsucker* (B?,W,M)	Virginia's warbler (B)	Northern goshawk (B,W)	
Hairy woodpecker (B,W)	Yellow-rumped warbler (B,M)	Flammulated owl (B)	
Downy woodpecker (B,W)	Townsend's warbler (M)	Mountain bluebird (B,W)	
Three-toed woodpecker (B,W)	Hermit warbler (M)	Swainson's thrush (B)	
Cassin's kingbird (B)	Grace's warbler (B)	Wilson's warbler (B)	
Sulphur-bellied flycatcher (B)	Common yellow-throat* (M)	Cooper's hawk (B,W)	
Dusky-capped flycatcher (B)	Red-faced warbler (B)	White-throated swift (B)	
Black phoebe' (B,W?)	Wilson's warbler* (M)	Magnificent hummingbird (M)	
Buff-breasted flycatcher (B)	Painted redstart (B)	Greater pewee (M)	
Cordilleran flycatcher (B)	Red-winged blackbird (B,W)	Purple martin (B)	
Southwest willow flycatcher (B)	Brown-headed cowbird (B)	Golden-crowned kinglet (B,W)	
Greater pewee (B)	Bronzed cowbird (B)	Hermit thrush (B,W)	
Olive-sided flycatcher (B,M)	Western tanager (B,M)	Veery (B)	
Western wood-pewee (B)	Hepatic tanager (B)	Warbling vireo (B)	
Violet-green swallow (B)	Black-headed grosbeak (B,M)	Orange-crowned warbler (B)	
Tree swallow* (B?)	Evening grosbeak (B,W)	Western tanager (B)	
Rough-winged swallow (B)	Red crossbill (B,W)	Black-headed grosbeak (B)	
Purple martin (B)	Cassin's finch (B,W)	Sharp-shinned hawk (B,W)	
Steller's jay (B,W)	House finch* (B,W)	Western wood-pewee (B)	
Western scrub jay* (M?)	Pine siskin (B)	Cassin's finch (B,W)	
Mexican jay (B,W)	Lesser goldfinch (B,W)	Ash-throated flycatcher (B)	
Common raven* (B,W)	Green-tailed towhee* (B)	Tree swallow (B,W)	
Pinyon jay (B,W)	Spotted towhee (B)	Violet-green swallow (B)	
Mexican chickadee (B,W)	Savannah sparrow* (W)	Ruby-crowned kinglet (B,W)	
Mountain chickadee (B,W)	Lark sparrow* (B)	Spotted towhee (B,W)	
White-breasted nuthatch (B,W)	Tree sparrow* (W)	Chipping sparrow (B)	
Red-breasted nuthatch (W)	Chipping sparrow (B,M,W)	Lincoln's sparrow (B)	
Pygmy nuthatch (B,W)	Dark-eyed junco (B,M,W)	Brown creeper (B,W)	
Brown creeper (B,W)	Yellow-eyed junco (B,W)	Yellow-rumped warbler (B,W)	
American dipper* (B,W)	White-crowned sparrow* (M)	Northern flicker (B,W)	
Winter wren (W)	Lincoln's sparrow* (B)	Dark-eyed junco (B,W)	
House wren (B)	Song sparrow* (B,W)	Pine siskin (B,W)	
Canyon wren* (B)		House wren (B)	

four to six days in pine (mostly Apache; *P. engelmannii*) and other vegetation in the Chiricahua Mountains, Arizona; and Moore et al. (1995) demonstrated that riparian or riverine areas in the southwest are vital for Southwestern migrants, notably the woodland species.

In general, stopover sites are used for depositing and replenishing lipid stores, molting, and resting (Moore et al. 1995). Stopover sites are crucial to a migrant bird's survival, especially long-distance migrants. Migration, although it allows birds to avoid overwintering in harsh environments, also has large costs associated with it, including the high energetic demands of transport (especially when there are climatic stresses); the multiple adjustments necessary to exploit unfamiliar sites; the conflicting demands of predator avoidance and food acquisition at stopover sites; and competition with other migrants and resident species for resources (Morse 1989:205; Moore et al. 1995).

Various features may cue migrants into selecting stopover sites in ponderosa pine forests, such as the proximity to riparian corridors, the forest structure, or the feeding rates or numbers of other migrants at sites (Moore et al. 1995). In a study of spring migrants crossing the Gulf of Mexico, Moore et al. (1995) found that the birds clearly selected areas with greater structural diversity following the flight. The areas were comprised of forests with complex mixed-shrub layers and contained the greatest diversity and abundance of migrants. However, Morse (1989:96) summarized studies of habitat selection by migrating warblers and found that habitat selection is subject to immediate and major fitness payoffs, indicating that selection of stopover sites may be influenced by factors other than vegetative structure. Climate changes, for example, may affect the choice of stopover sites, and ultimately wintering sites. Terrill and Ohmart (1984) found that the wintering ranges of yellow-rumped warblers differed from year to year in Arizona and adjacent Mexico apparently because the birds were retreating farther south in years when the winters were severe.

The amount of habitat actually available to migrants along the migration route is probably inherently limited, however, because migrants cannot take the time to search extensively for the "best" stopover sites (Moore and Simons 1992). This is due to a bird's need to reach the breeding area before it is saturated with conspecifics, or to reach the wintering area before the onset of severe weather. Studies of warbler species have demonstrated that some species use stopover sites that resemble those used on the breeding grounds, whereas other species do not use similar sites (reviewed in Morse 1989, chapter 9). Furthermore, the distributions of migrant birds are often correlated with changes in food availabilities (Morse 1989; Martin and Karr 1990; Moore et al. 1995). Because migration is a period of exceptional energy demand, it probably exerts strong selective pressures on the maximiza-

tion of foraging efficiency (Moore and Simm 1985). Hutto (1985) found that the distribution of most insectivorous migrant birds in the Chiricahua Mountains, Arizona, was correlated with the abundance of arthropods in those vegetation types. He concluded that birds forage where they can be most efficient, unless interspecific competitive interactions force them to modify their first choice.

Species of Special Concern in Ponderosa Pine Forests

In this section we summarize current information on species of special concern in Southwestern ponderosa pine forests. To identify such species, we consulted the 1995 Arizona Partners in Flight (AZPIF) and 1994 New Mexico Partners in Flight (NMPIF) lists of sensitive breeding and wintering terrestrial bird species in the states. For these lists, bird species were ranked according to scores derived from their local and global distributions and abundances; the severity of threats on their breeding and wintering grounds; and the "importance" of Arizona and New Mexico to their overall distributions.

AZPIF and NMPIF also summarized the primary vegetation associations used by each bird species. The lists were created based on species accounts in the literature (for example, Phillips et al. 1964), as well as unpublished data. We did not consult state wildlife agency publications on threatened and sensitive species (for example, Threatened Native Wildlife in Arizona, Arizona Department of Game and Fish, 1988; BISON-M database, New Mexico Department of Game and Fish, 1996) because Atwood (1994) demonstrated that these publications were often incomplete and erroneous. We caution that the AZPIF and NMPIF lists may also suffer from the same weaknesses, but at a **minimum** the lists have been reviewed by authorities who are familiar with the distribution of birds in each state.

Arizona

Species of special concern received ranks from 1 to 100. Of the approximately 240 species given ranks in Arizona, 100 of these use ponderosa pine for breeding, wintering, and/or migrating. Of these hundred, 11 species were given ranks 150 (table 6), indicating that they are very high priority species—ones of special concern in the state—either because of low local or global abundances; restricted global or Arizona breeding distributions; substantial potential for extirpation on the breeding or wintering grounds; and/or a high importance of Arizona to the total breeding distribution of the species. Of these species, the whip-poor-will, elegant trogon, buff-breasted flycatcher, and sul-

phur-bellied flycatcher are at the northern edge of their ranges in Arizona, with the majority of their numbers occurring in Mexico. Atwood (1994) suggested that the inclusion of these species based solely on their limited occurrence at the northern extension of their ranges may ultimately divert research and management attention that should be given to truly threatened species. Two species on the list, the southwest willow flycatcher and olive-sided flycatcher, have shown declines in the state (and elsewhere), probably due to habitat destruction, and for the willow flycatcher, cowbird parasitism (Robinson et al. 1995). The remaining species on the list were placed there because of perceived moderate to extensive threats on the breeding and/or wintering grounds, and/or localized and isolated breeding distributions.

Another 20 ponderosa pine species were given ranks between 51 and 100 (table 6), indicating that they are of moderate concern but not exposed to threats as severe as the species with scores ≤ 50 . These species were mostly considered uncommon (in abundance) in Arizona and globally. They were also considered to have moderate threats on their breeding and/or wintering grounds.

The 69 remaining species had ranks >100 , indicating that their populations may be stable.

New Mexico

Of the 156 total species given ranks in New Mexico, 52 of these use ponderosa pine for breeding, wintering, and/or migrating. Of these fifty-two, 31 species were given ranks >2.50 (table 6) by NMPIF, indicating that they either had experienced declines in abundances over the past 26 years; their trends were unknown; they had low local or global abundances; they had restricted global or New Mexico breeding distributions; there was substantial potential for extirpation on the breeding or wintering grounds; and/or New Mexico is important to the total breeding distribution of the species. Of the special concern species occurring in ponderosa pine forests, only the peregrine falcon is currently listed as federally endangered or threatened. Another 12 species occurring in ponderosa pine were given ranks between 2.10 and 2.45 (table 6), indicating that their status is of moderate, rather than high, concern in the state.

Comparison of Lists

In both Arizona and New Mexico, the (southwest) willow flycatcher, olive-sided flycatcher, olive warbler, Virginia's warbler, and Grace's warbler were given high priority ranks. The NMPIF database listed six species of high concern that were considered of only moderate concern in Arizona: the band-tailed pigeon, Cordilleran flycatcher, greater pewee, Townsend's solitaire, orange-crowned warbler, and hepatic tanager. The NMPIF list also contained an additional 21 species of high concern, versus Arizona's six other species of high concern. For species of moderate concern, the AZPIF database listed an

Table 6. Southwestern ponderosa pine forest birds in Arizona and New Mexico with ranks indicating that they are of high or moderate concern in each state. Criteria for rankings are given in the text.

Rank Species	Rank Species
Arizona	New Mexico
≤ 50	>2.50
Whip-poor-will	Virginia's warbler
Elegant trogon	Olive-sided flycatcher
Buff-breasted flycatcher	Grace's warbler
Southwest willow flycatcher	Band-tailed pigeon
Olive-sided flycatcher	Red-naped sapsucker
Olive warbler	Willow flycatcher
Solitary vireo	Hammond's flycatcher
Virginia's warbler	Peregrine falcon
Red-faced warbler	Williamson's sapsucker
Sulphur-bellied flycatcher	Dusky flycatcher
Grace's warbler	Cordilleran flycatcher
51–100	Olive warbler
Band-tailed pigeon	Hepatic tanager
Northern (glided) flicker	Broad-tailed hummingbird
Lewis' woodpecker	Cassin's kingbird
Red-naped sapsucker	Western bluebird
Yellow-breasted sapsucker	Townsend's solitaire
Williamson's sapsucker	Northern goshawk
Three-toed woodpecker	Flammulated owl
Cordilleran flycatcher	Mountain bluebird
Greater pewee	Swainson's thrush
Tree swallow	Wilson's warbler
Pygmy nuthatch	Cooper's hawk
Eastern bluebird	White-throated swift
Townsend's solitaire	Magnificent hummingbird
Loggerhead shrike	Greater pewee
Orange-crowned warbler	Purple martin
Painted redstart	Golden-crowned kinglet
Hepatic tanager	Hemit thrush
Lazuli bunting	Veery
Red crossbill	Warbling vireo
Green-tailed towhee	Orange-crowned warbler
	2.10–2.45
	Western tanager
	Black-headed grosbeak
	Sharp-shinned hawk
	Western wood-pewee
	Cassin's finch
	Ash-throated flycatcher
	Tree swallow
	Violet-green swallow
	Ruby-crowned kinglet
	Spotted towhee
	Chipping sparrow
	Lincoln's sparrow

other 14 beyond the six mentioned above, whereas New Mexico had only 12 total species listed (table 6).

Changes in Abundance

Hejl (1994), summarizing Brawn and Balda (1988a), proposed that 15 Southwestern ponderosa pine forest bird species have probably decreased in abundance from presettlement times to the present because of decreases in the prevalence of these forest conditions. Hejl based this on the birds' requirements for burned sites, old-growth forests, and/or snags. The species were the broad-tailed hummingbird (AZPIF ranking # 113; NMPIF ranking # 48), acorn woodpecker (AZPIF #129), three-toed woodpecker (AZPIF #52), purple martin (#116, #82), violet-green swallow (#172, #119), mountain chickadee (AZPIF #170), white-breasted nuthatch (AZPIF #206), pygmy nuthatch (AZPIF #68), brown creeper (#189, #138), western bluebird (#132, #51), mountain bluebird (#160, #66), American robin (#225, #156), red-faced warbler (#16, #17), chipping sparrow (#205, #129), and lark sparrow (#177, #93). For the most part, however, Hejl's projections do not coincide with the species of special concern on the AZPIF and NMPIF lists, and the purple martin, western bluebird, and American robin were shown by Miller (1992) to be increasing in Arizona and New Mexico. Hejl (1994) also proposed that nine other bird species have probably increased in abundance from presettlement times to the present because of fire suppression and increased amounts of second-growth forests. These species were the Cordilleran flycatcher (AZPIF #74, NMPIF #37), house wren (#224, #152), Townsend's solitaire (#98, #52), hermit thrush (#150, #85), solitary vireo (#45, #53), Virginia's warbler (#33, #11), yellow-rumped warbler (#217, #140), Grace's warbler (#49, #16), and western tanager (#145, #91). Miller (1992) found that numbers of solitary vireos, Virginia's warblers, and Grace's warblers have actually decreased in managed ponderosa pine forests. However, Johnson (1994) determined that Grace's warblers, painted redstarts, and hepatic tanagers have expanded their ranges northward in this century. On the AZPIF and NMPIF lists, these latter two species are considered fairly high priority ones for study because of their rarity and localization. In addition, the solitary vireo and Virginia's warbler are also ranked as species of special concern in Arizona and New Mexico, despite Hejl's indications that they should be responding positively to habitat changes in Southwestern forests.

As mentioned previously for the southwest willow flycatcher, a significant factor in the decline of some other bird species in the western United States is the increase in parasitism by brown-headed cowbirds. This species, along with two grackle species, has experienced the greatest rate of increase and largest expansion of any native bird species in the United States (Marzluff 1994). There are about 11 to 20 cowbirds per Breeding Bird Survey route in Ari-

zona and 0 to 10 per route in New Mexico (Robinson et al. 1995). Because of their parasitic nature, cowbirds can breed in a wider range of vegetation types than probably any other North American passerine (Robinson et al. 1995). In the west, cowbirds occur regularly in coniferous forests but in fewer numbers than in other nearby areas such as meadows and riparian zones (for example, Rothstein et al. 1984).

Host species of cowbirds tend to be small-sized, open-cup-nesting birds with long incubation periods, including *Empidonax* flycatchers and phoebes, vireos, warblers, and sparrows such as the chipping sparrow. Hosts inhabiting forest edges and/or second-growth forests also tend to be more heavily parasitized. The largest declines in host numbers are seen in species with restricted geographic breeding ranges and with habitat that is fragmented, is threatened by direct destruction (such as that of the southwest willow flycatcher), and/or has been subject to fire suppression (reviewed in Robinson et al. 1995; see also Moir et al., this volume).

Despite concerns about increased parasitism by cowbirds in the western United States, parasitism has not been documented in several birds that would seem to be likely candidates. For example, Martin (1992, table 1) summarized reproductive data for neotropical migrant birds in Arizona and New Mexico. Black-headed grosbeaks in deciduous (oak) forests in New Mexico were not parasitized by cowbirds. Neither were warbling vireos, orange-crowned warblers, Virginia's warblers, yellow-rumped warblers, MacGillivray's warblers, red-faced warblers, western tanagers, and black-headed grosbeaks in mixed-conifer/deciduous forests in Arizona according to several recent studies. On the other hand, parasitism rates in other small flycatchers and warblers (such as western woodpeewees and painted redstarts in Arizona) can be quite high (L. Christoferson, unpubl. manuscript, University of Arizona). For example, Marvil and Cruz (1989) documented the fate of solitary vireo nests in ponderosa pine/Douglas-fir forests in Colorado. Approximately 49 percent of all vireo nests were parasitized with one to three brown-headed cowbird eggs during the breeding seasons of 1984–1986, leading to a significant decrease in the reproductive success of the nests.

Conclusions

We found specific information on the use of Southwestern ponderosa pine forests by approximately 50 bird species. However, of these species, only about 35 percent appear to restrict their vegetation use to primarily ponderosa pine, whereas about 65 percent are associated with other plant components (for example, aspen, oak, Douglas-fir,

fir, spruce, and pinyon-juniper) within ponderosa pine forests. This shows that most ponderosa pine bird species require features in addition to pine. It also implies that forest management must include consideration of these features if the retention of diverse bird communities is desired. Although many species are declining in abundance, few species are nearing extirpation. More effort could thus be expended on monitoring trends of species of special concern and on monitoring their demographics. The factors causing the apparent declines are still largely speculative and thus need to be investigated.

In regard to "disturbed" sites (either from fire or logging), bird species showed different responses, although most species appeared to tolerate (at least in terms of their abundances) light to moderate disturbance. With heavy alteration of the forest structure (for example, via fires, clearcutting, or strip-cutting), species composition varied in a predictable way, with more understory species using cleared forest stands. Nest predation apparently influenced the placement of nests to the extent that birds selected denser foliage. Nest success—as might be expected—varied among species and study areas, but bluebird nesting success decreased on heavily altered sites. Forest management must be site- and time-specific and management objectives must consider all of the different components that are used by the numerous species of ponderosa pine forests. Data also indicate a strong need for intensive studies of the reproductive success of ponderosa pine birds; without these data, any conclusions about the current status or current habitat requirements of the species are tenuous.

We know little specifically about the use of ponderosa pine forests by migrating birds. However, we can estimate that Southwestern pine forests are probably used as stopover sites by at least 25 migrant bird species in a given year. Research on migratory birds in other vegetation types suggests that forest structure, food availability, inter- and intraspecific competition for resources, and climate conditions all influence the use of these forests by migrant species. Therefore, we can probably assume that these same factors would influence the use of Southwestern ponderosa pine forests as stopover sites. And as such, the number of species that may depend on ponderosa pine forests for replenishment of lipids or as resting sites makes this vegetation type important to their survival. However, we need more research on how migratory birds use ponderosa pine forests. Most studies have also concentrated on breeding birds; more work needs to be conducted on non-breeding (wintering) birds. This information is critical for developing appropriate forest management plans because of the role that stopover sites can play in maintaining bird populations.

Natural expansions and increases in populations of some ponderosa pine forest species have been documented (DeSante and George 1994, Johnson 1994); how-

ever, a large percentage of species have declined, due probably to various causes. The many factors that may affect ponderosa pine songbird numbers (such as fire, logging, grazing, and climate change) and the variations in local site conditions make it difficult to predict exact trends in bird numbers. Again, the implications of this for management of ponderosa pine forests are that one treatment, or one management style, will not elicit the same population response from all bird species. Similarly, effects of past management practices may vary depending on location.

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Chapter 5

Effects of Urbanization and Recreation on Songbirds

John M. Marzluff

Introduction

The world's population has grown to over 5 billion people and shows no sign of slowing (Horiuchi 1992). Our increasing population and natural resource use is the fundamental reason that much of the natural world is in crisis (Mangel et al. 1996). In the United States, the greatest recent increases in human population are in the Western states. Nevada leads in population growth, followed by Arizona; New Mexico ranks ninth (U.S. Department of Commerce). As a result, human impacts on western bird communities, which are already severe (Jehl and Johnson 1994), will probably increase.

The human population in the ponderosa pine forests of Arizona and New Mexico, although currently low, is on the rise due to tourism and retirement industries (Raish et al. this volume). Computers have enabled many people to conduct business remotely. Work-at-home individuals are choosing ponderosa pine forest towns because of their small size, safety, cleanliness, scenic beauty, and friendly inhabitants (J. Burding, Flagstaff Chamber of Commerce, personal communication). Moreover, cool temperatures and scenic beauty attract large numbers of recreationists to the forests, especially during the summer months when desert dwellers want to escape extreme temperatures. The importance of ponderosa pine forests as recreation sites (Raish et al. this volume) indicates that the potential impacts of humans on the forest will probably be greater than resident population censuses might suggest.

Human pressures on ponderosa pine forests will continue to increase (Boyle and Samson 1985; Anderson 1995; Flather and Cordel 1995; Raish et al. this volume). The potential effects of these increases on songbirds in ponderosa pine forests are not well studied, but many results are predictable if human use of the forests can be quantified (Foin et al. 1977). This chapter discusses how urbanization and recreation in Southwestern ponderosa pine forests might influence songbirds and comments on the research necessary to provide an assessment of future affects. Other important human impacts on ponderosa pine forest birds, including fire suppression, logging, and grazing, are discussed in Chapters 2, 6, and 7 of this publication.

Effects of Urbanization and Recreation on Songbirds

There have been few studies documenting the effects of urbanization and recreation on songbirds and only 2 that test the affects on Southwestern ponderosa pine forests (Aitchison 1977; Yarnell 1993). However, a general study review is useful because many affects are consistent over large geographic areas (Rosenberg et al. 1987) and are predictable given knowledge of local avian natural history (Foin et al. 1977).

In this chapter, the words "urban" and "urbanization" reference towns and their associated affects. Concentrated human presence is the key feature that distinguishes urbanization from other forms of disturbance.

Urbanization

Urbanization directly influences songbird populations and communities by changing ecosystem processes, habitat, and/or food supply. Urbanization indirectly influences songbirds by affecting their predators, competitors, or disease organisms. Individual birds may adjust their behavior in response to human factors in urban environments. In forested North America, urbanized habitats typically support larger (measured by biomass) and richer (more species) but less even in relative abundance avian communities because they are dominated by a few, abundant species (Pitelka 1942; Emlen 1974; DeGraff and Wentworth 1981; Rosenberg et al. 1987; Mills et al. 1989). Urbanization also favors some species but selects against others so that the composition of urban avian communities differs from those in native environments (Beissinger and Osborne 1982; Rosenberg et al. 1987; Mills et al. 1989; Blair 1996). While many studies have documented these findings, none have specifically measured the effects of urbanization on avian demography. Many urban populations may be sink (area of population decline) populations (Pulliam 1988) that attract many recruits but produce few (Blair 1996). Marzluff and Balda (1992) suggested that this was the case for pinyon jays in Flagstaff, Arizona during the 1980s, and this is probably also true for many flycatchers, Steller's jays, wrens, thrushes, warblers, tanagers, grosbeaks, and sparrows.

Changes in Ecosystem Processes

The affects likely to have the greatest impact on ponderosa pine forest birds are changes in the basic functioning of the ponderosa pine ecosystem; specifically, reduction in natural processes such as fire, altered nutrient cycling, and disrupted water cycling. These changes are accentuated by urbanization and can lead to long-term forest degradation.

Existence of buildings has prompted intense efforts to suppress fire near urban areas, which disrupts the natural fire regime that has evolved with ponderosa pine forest birds. Detailed discussion of the effects of fire suppression on forest structure and function and forest avifauna are in Chapters 1 and 6, respectively.

The energy and building requirements of humans disrupts the natural nutrient cycling of ponderosa pine forests. Forests are thinned to reduce the fire threat and some dead woody material is removed for fuelwood. Loss of snags leads to reductions in insectivores, which can lead to a reduction in forest health (Hall et al. this volume). The combination of fire suppression, logging, and fuel wood harvest has created a new, unbalanced nutrient cycle where nutrients in living trees are removed from the forest as wood products and nutrients in dead debris are removed as firewood. The most important effect of urbanization on nutrient cycling is probably a lengthening of cycles. Fire suppression around urban areas has eliminated the primary mechanism of nutrient cycling in ponderosa pine forests. The lack of fire causes living and dead biomass to accumulate much faster than it degrades and recycles (Covington and Moore 1994). Prescriptions to reduce the Future fire threat, such as thinning (Edminster and Olsen 1996), are then used rather than prescribed burning. As a result, the urban pine forest, although accumulating nutrients and energy, typically exports them rather than recycles them. This nutrient and energy loss may steadily degrade forest growth with long-lasting affect on forest birds.

Water is an important, often limiting, resource in ponderosa pine forests. Permeable, volcanic soils hold little water above ground and permanent streams, lakes, and ponds are rare. Runoff patterns are affected by urbanization as native soils are replaced by impermeable concrete and surrounding forest substrates are compacted by vehicular and foot traffic. Urban centers have tremendous water requirements that affect water distribution and cycling in surrounding forests. Water tables are lowered as aquifers are used at greater than replacement rates (Thorn et al. 1993; Haneberg and Friesen 1995). As forest health declines, springs and seeps important to wildlife may dry up causing bird reductions or redistributions. Songbirds that are able to tolerate human activity will become increasingly dependent on urban areas for water.

Habitat Changes

Vegetation in moderately urban environments is typi-

cally more fragmented, includes less coverage at mid- and upper levels, and has more ground level coverage than in natural environments (Beissinger and Osborne 1982; Blair 1996). Not only are patches of vegetation isolated in urban environments, they also rarely include the full complement of species found in natural forests (Beissinger and Osborne 1982). Native plant species are often removed from urban environments and replaced by exotic ornamentals (Beissinger and Osborne 1982; Rosenberg et al. 1987). Even moderately urban environments contain few standing or downed dead trees to provide nest and foraging sites for cavity nesters and timber drillers. Extreme urbanization leads to decreases in vegetation at all levels as man-made structures replace vegetation (Blair 1996). In heavily urbanized areas, forest structure may be modified well beyond the city boundaries (Kamada and Nakagoshi 1993).

Urbanization in ponderosa pine forests produces most of the vegetation effects previously noted. Native shrub and oak understories are usually replaced by lawns and ornamental shrubs. The ponderosa pine canopy is fragmented by houses and roads, but this forest type is not typified by a closed canopy. Even with fragmentation, the actual density of trees in and around urban centers is probably much greater than during presettlement times because of smaller average tree size and fire suppression (Morgan 1994). Snags and downed woody debris are found at low densities in urban ponderosa pine forests because of safety, fire, and aesthetic concerns. Exotic junipers and Colorado pinyon pine trees, commonly planted in urban yards, supply food for wintering Townsend's solitaires, western bluebirds, American robins, and jays. However, exotic plant communities disproportionately favor a few bird species at the expense of preserving the entire native avifauna. Despite these changes, towns in ponderosa pine are less likely to modify natural habitat than other urban centers (eastern United States, West Coast, desert Southwest) because they are modestly sized and have housing developments that are often widely dispersed to enjoy the natural scenic beauty. Where heavily urbanized areas do occur, opportunities for ground foragers are greatly reduced.

Direct habitat modification by urbanization in ponderosa pine forests will likely: 1) benefit ground-gleaning and probing birds that are tolerant of human activity (American robin, European starling, Brewer's blackbird, and American crow); 2) benefit species that nest in man-made structures or ornamental vegetation (rock dove, house sparrow, European starling, house wren, purple martin, barn swallow, house finch, and eastern kingbird); 3) reduce shrub and canopy nesters and foragers (warblers, vireos, tanagers, grosbeaks, wrens, creepers, chickadees, and nuthatches); and 4) reduce burn specialists, cavity nesters, and bark drillers (olive-sided flycatcher, swallows, woodpeckers, chickadees, nuthatches, creepers,

and bluebirds). These effects have been noted on similar species in other environments (Beissinger and Osborne 1982; Rosenberg et al. 1987; Mills et al. 1989; Blair 1996). Yarnell's (1993) study of annual trends in birds counted on Flagstaff's National Audubon Society's Christmas Bird Count suggests that urban obligates and grassland species have increased around Flagstaff from 1967 to 1991.

Food Changes

Urban centers provide food to birds directly at feeders and indirectly at areas of waste treatment, collection, and transfer. Seed eaters and nectivores (hummingbirds, jays, woodpeckers, chickadees, nuthatches, juncos, sparrows, finches, and grosbeaks) benefit from feeders. Scavenging omnivores (gulls, jays, crows, and ravens, blackbirds, and European starlings) benefit from spilled waste (Robbins et al. 1986; Boarman 1993; Marzluff et al. 1994).

Food resources are also affected indirectly by changes in vegetation as previously discussed. In particular, exotic plants have fewer insects than native plants and urban lawns are rich and consistent feeding grounds (Rosenberg et al. 1987). These changes favor ground foragers and granivores while selecting against shrub and mid-canopy foliage gleaners as previously mentioned.

Predator Changes

Introduced predators (cats, dogs) are more abundant in urban areas than in native forests and may have substantial effects on the avifauna (Churcher and Lawton 1987). Other avian predators (sharp-shinned hawk, northern pygmy owl, merlin, and Cooper's hawk) may increase in urban areas and concentrate their activities at feeders where prey are abundant. Human predators can also seriously deplete local songbirds, sometimes just for sport. An example of this occurred in Flagstaff when a teenager shooting pinyon jays during one breeding season caused most of the nest failure and mortality experienced by the flock that year (Marzluff and Balda 1992). Large predators are usually eliminated from areas of human habitation. If northern goshawks in urban ponderosa pine forests are also reduced, songbird populations may increase. Coyotes (*Canis latrans*) and mountain lions (*Felis concolor*) have increased in and around urban areas recently. These predators may benefit many songbirds by reducing mammalian nest predators, especially cats (Quinn 1992).

Perhaps even more important than the increasing mortality experienced by free-flying birds, urbanization reduces nesting productivity by escalating the number of predators that destroy bird nests. Nest predation is probably the most important limiting factor on songbirds (Martin 1993a, b), even outweighing winter mortality for migratory species (Bohning-Gaese et al. 1993). Nest predators, often more abundant in urban areas than native habitats, have increased dramatically in the Western United States during the last century (Robbins et al. 1986; Boarman 1993;

Marzluff et al. 1994). As predator density increases so does the predation rate (Andren 1992; Marzluff et al. 1995).

Important nest predators in ponderosa pine include domestic cats, striped skunks (*Mephitis mephitis*), rock squirrels (*Citellus variegatus*), Abert squirrels (*Sciurus aberti*), gopher snakes (*Pituophis melanoleucus*), Steller's jays, American crows, and common ravens (Marzluff and Balda 1992). Surveys of jays, crows, and ravens conducted at several locations in and adjacent to Southwest ponderosa pine each winter since about 1960, suggest that ravens are more abundant and increasing quicker at urban than at rural sites (figure 1; Yarnell 1993). Moreover, the greatest densities of ravens in rural areas are at sites near urban areas. Figure 1b shows that Mormon Lake, which is 25 km from Flagstaff, has the highest density of ravens of the rural sites studied. American crows are also more typically abundant at urban than rural sites (figure 2). Crows in Flagstaff continued to increase in 1996 (R. Balda, personal communication). However, Prescott, Arizona has yet to be colonized by crows and rural areas near urban centers (Sandia Mountains, New Mexico; Mormon Lake, Arizona) are occasionally visited by many crows. Steller's jays vary greatly in abundance from year to year at rural and urban sites without a consistent tendency to be more abundant in urban sites (figure 3). Other jays, such as scrub and Mexican, may actually respond positively to urbanization (Marzluff et al. 1994). These lower-elevation species are invading ponderosa pine towns most notably Payson, Prescott, and Flagstaff, Arizona (Yarnell 1993). Counts during the breeding season at rural sites (none are available for urban sites) suggest that crows, ravens, and Steller's jays are common, and that typically urban nest predators, such as crows, can be abundant in rural sites (figure 4).

The increasing number of nest predators, especially ravens, in urban ponderosa pine forests reduces productivity of native songbirds. Nearly half of all pinyon jay nests in Flagstaff failed from predation in the 1980s. This was a significant increase over predation in the 1970s and was closely correlated with increasing raven populations in the city (Marzluff and Balda 1992). Reduced jay productivity led to a decrease in population size and an increased reliance on immigration to sustain the Flagstaff population. Thus, the population functioned as a sink population during the 1980s although it was probably a source (area of population increase) population in the 1970s. Perhaps other open-nesting songbirds suffer similar fates in urban environments.

Disease

Disease rarely regulates temperate bird populations. Urban populations are probably more susceptible to disease than those in native forests because artificial feeders concentrate birds and increase the incidence of disease spread. Moreover, some urban species, such as rock doves and

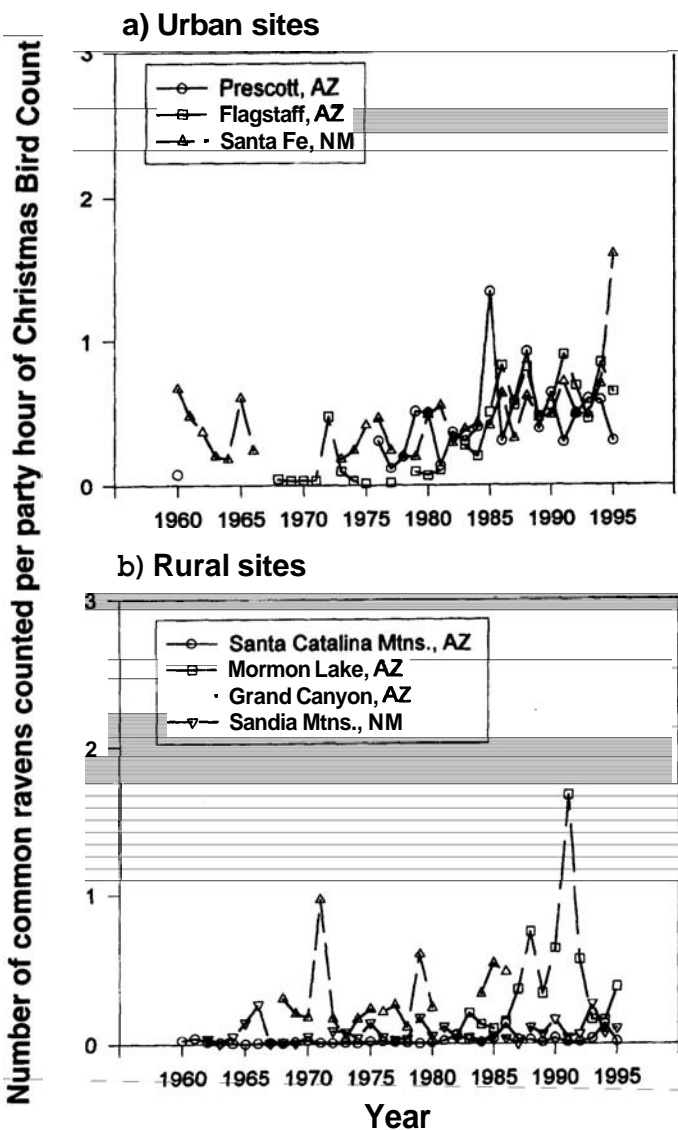


Figure 1. Number of common ravens counted during winter surveys in Southwestern ponderosa pine areas. Birds were counted each winter at the same location as part of the National Audubon Society's Christmas Bird Count. Counts were standardized by observers, which varies annually, by dividing the total number of birds counted by total observation time (party hours). All sites in Arizona and New Mexico that had relatively complete counts from 1960 through 1995 were used. Sites inside the city limits of urban centers are plotted in the top panel and those outside city limits are plotted in the bottom panel.

blackbirds, may be reservoirs for disease (Garner 1978). Rock doves, more common in urban ponderosa pine forests than in natural forests (figure 5; Yarnell 1993), are known to carry diseases such as *Trichomonas*. This protozoan may survive in urban settings better than in rural areas because of the large rock dove population. In addition,

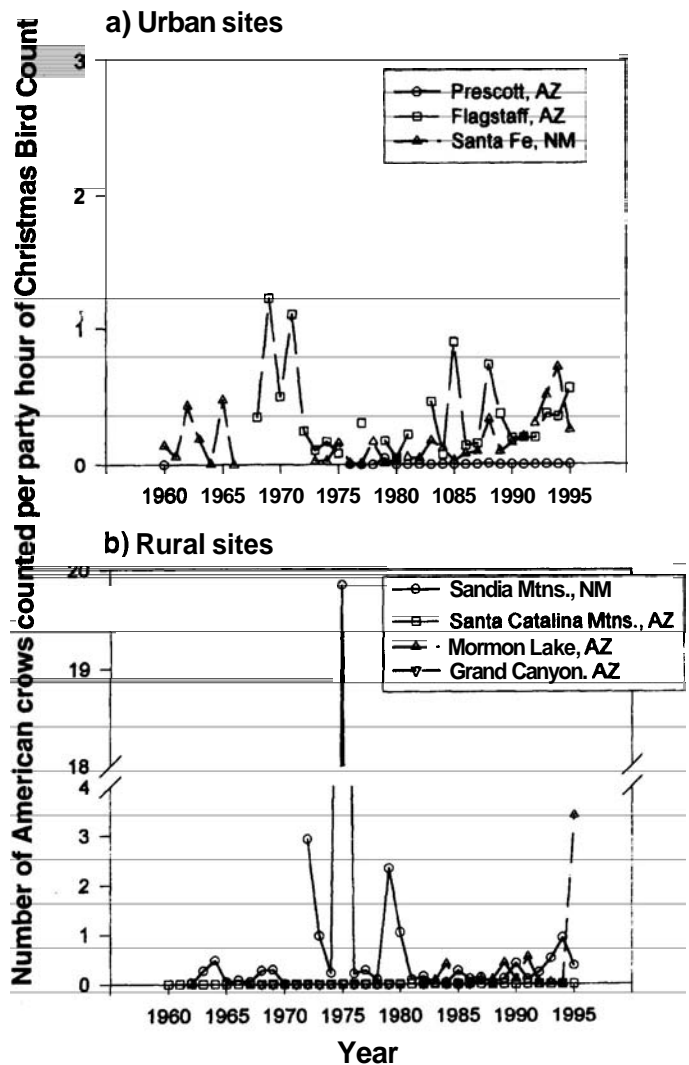


Figure 2. Number of American crows counted at urban and rural sites during the annual National Audubon Society's Christmas Bird Counts. Counts were standardized by observers, which varies annually, by dividing the total number of birds counted by total observation time (party hours). All sites in Arizona and New Mexico that had relatively complete counts from 1960 through 1995 were used. Sites inside the city limits of urban centers are plotted in the top panel and those outside city limits are plotted in the bottom panel.

tion, when environmental conditions, such as warm springs, favor *Trichomonas* growth, it is quickly transmitted at communal feeding sites. During the spring of 1996 in Flagstaff, *Trichomonas* growth and transmission resulted in the death of several evening grosbeaks and pine siskins (Bill Watt, Arizona Department of Fish and Game, personal communication). Seed eaters and nectivores are most susceptible to such diseases because they frequent urban feeders.

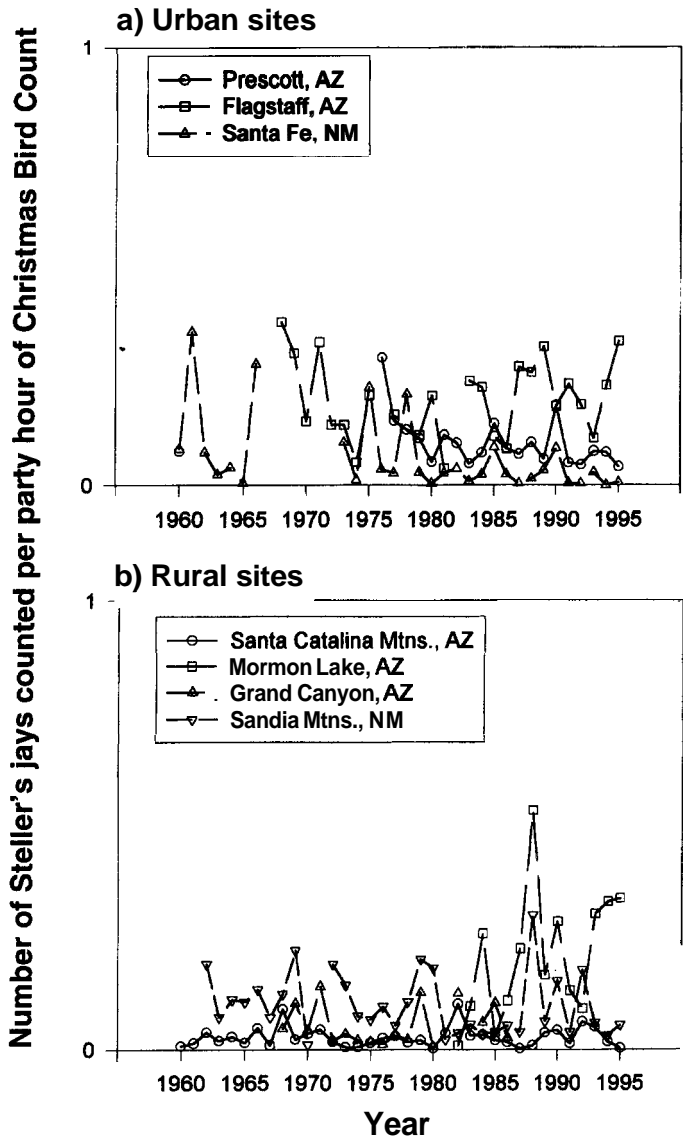


Figure 3. Number of *Steller's jays* counted at urban and rural sites during the annual National Audubon Society's Christmas Bird Counts. Counts were standardized by observers, which varies annually, by dividing the total number of birds counted by total observation time (party hours). All sites in Arizona and New Mexico that had relatively complete counts from 1960 through 1995 were used. Sites inside the city limits of urban centers are plotted in the top panel and those outside city limits are plotted in the bottom panel.

Competition

Availability of nest sites helps determine the population density of cavity-nesting birds in ponderosa pine forests (Brawn and Balda 1988). Cavity nest sites are usually at a premium in urban sites because of snag removal. The increased abundance of European starlings at urban sites (Johnston and Garrett 1994) suggests that the limited num-

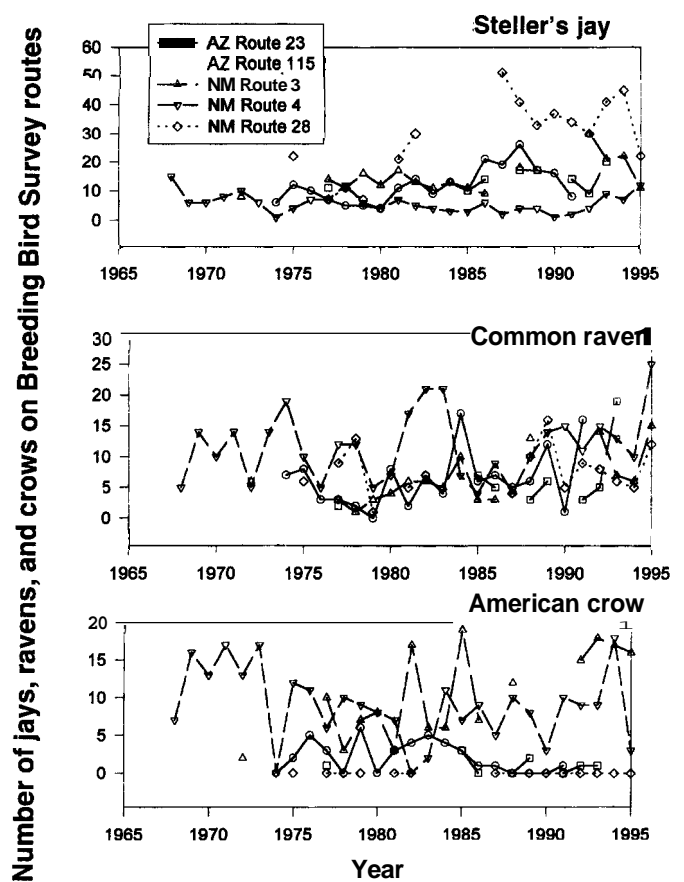


Figure 4. Number of nest predators counted during breeding season surveys in ponderosa pine forests of New Mexico and Arizona. These counts are part of the National Biological Service's Breeding Bird Survey program that began in 1966. Birds are counted along a 49.5 mile route that is driven by an observer once per year. The observer counts birds while stopping for 3 minutes at each of 50 locations spaced at 0.5 mile intervals along the route. All routes with fairly complete data in New Mexico and Arizona were in rural locations.

ber of urban cavity nest sites may be difficult for native birds to obtain. Starlings commonly outcompete native birds for cavities (Feare 1984), which affects native cavity-nester populations in urban forests. Even the best public intentions can exacerbate this problem; nest boxes for native birds often support breeding starlings and house sparrows. House wrens may also use these boxes and prey on eggs and nestlings of other species.

Behavioral Adjustment to Urbanization

Individuals may adjust their behavior in response to features of urban environments. Such adjustments may enhance a species' ability to persist in the urban environment and may have ramifications beyond the urban setting.

The best documented behavior changes in urban environments involve nesting. Birds breeding in urban environments often nest earlier than those in rural environments because of supplemental food (Balda and Bateman 1972). This may be detrimental in ponderosa pine forests where late spring snow storms often destroy early nests

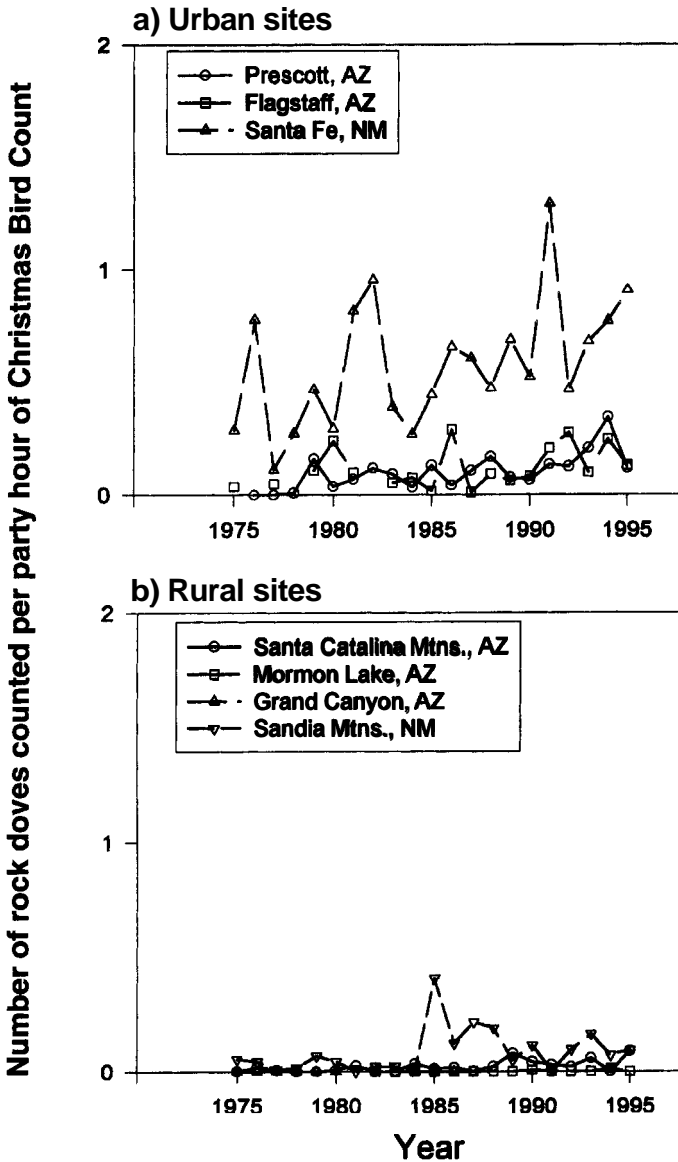


Figure 5. Number of rock doves counted at urban and rural sites during the annual National Audubon Society's Christmas Bird Counts. Counts were standardized by observers, which varies annually, by dividing the total number of birds counted by total observation time (party hours). All sites in Arizona and New Mexico that had relatively complete counts from 1960 through 1995 were used. Sites inside the city limits of urban centers are plotted in the top panel and those outside city limits are plotted in the bottom panel.

(Marzluff and Balda 1992). Songbirds that are repeatedly disturbed at their nest may increase their aggressiveness (Knight and Temple 1986). Persecution by humans may select for reduced aggressiveness (Knight et al. 1989). Species that live closely with humans, such as American crows, may become accustomed to human presence in urban areas (Knight et al. 1987). Increased nest predation in urban areas may cause some birds to change nest placement to minimize losses (Knight and Fitzner 1985; Marzluff 1988).

Foraging behavior also may be modified in urban environments. Species that use human food sources may reduce their use of natural foods and change their temporal and spatial foraging behavior to include provisioning sites. Reduced reliance on natural foods may interrupt seed dispersal and pollination far beyond the urban center. Clark's nutcrackers, for example, are important dispersal agents for whitebark pine in Colorado. Nutcracker reliance on human handouts in Rocky Mountain National Park may have decreased the dispersal of whitebark pine in the region (Tomback and Taylor 1986). This may also occur with pinyon pine, which depends on jays, crows, and ravens, especially the pinyon jay, for dispersal (Marzluff and Balda 1992). However, pinyon jays in Flagstaff that regularly visited feeders, abandoned them in the fall when pinyon pine seeds were ripe. They cached seeds from the lower elevation pinyon pine forest in the ponderosa forest. Many of the pinyon seeds germinated and became established trees. Pinyon pine is now encroaching into ponderosa pine habitat because of the actions of this bird. Ironically, the pinyon jay may only survive in ponderosa pine forests because of urbanization and supplemental food provided at bird feeders.

Recreation

Recreation can affect wildlife through harvest, habitat modification, predation, and disturbance (Knight and Cole 1995b). Habitat modification and disturbance are most relevant for songbirds because their effects on behavior may modify vigor, productivity, or survival of individuals. Individual demographics and behavior may affect abundance, distribution, and population viability (Anderson 1995; Knight and Cole 1995b). Populations may influence community organization and interactions among community members (Gutzwiller 1995). The general effect of and impacts on specific types of recreation in ponderosa pine forests are discussed in this section.

Habitat Modification

Habitat modification indirectly affects wildlife and can have long-lasting effects. Recreationists modify habitat primarily by trampling vegetation and harvesting fire wood. Trampling from hiking, camping, fishing, and nature study compacts soil, decreases its porosity, and increases erosion (Cole and Landres 1995). This, along with

vegetation crushing, reduces seed germination, seedling establishment, plant growth, and reproduction. Trails may be used by predators and parasites, such as cowbirds, to gain access to forest interiors. Plant species composition often changes in recreation sites as disturbance favors very small or very large species, low growing species, species with tough leaves, and annuals with rapid growth and copious seed production (Cole and Landres 1995). Above-ground vegetation, dead wood, and brush piles are reduced. Plant species diversity is reduced under extreme disturbance but may increase with low to moderate recreation levels (Cole and Landres 1995; Blair 1996). Recreationists may increase the spread of exotic plants by acting as dispersal agents. Habitat contiguity and horizontal and vertical diversity is reduced by recreation. Habitat changes will generally cause the greatest reduction in bird species that rely on shrub and ground cover (juncos, thrushes, warblers, sparrows, vireos, and wrens) and those that depend on standing dead and downed woody debris (woodpeckers, secondary cavity nesters).

Human Disturbance

Disturbance from recreation on wildlife depends on the recreationist and the animals (Knight and Cole 1995a). The predictability, frequency, magnitude, timing, and location of recreation are important to songbirds. Birds may habituate to predictable disturbances such as walking, driving, or camping in consistent locations. This may reduce the recreation disturbance, but it can also be detrimental if habituated birds later approach humans and are persecuted (Snyder and Snyder 1974). The potential influence of disturbance increases with its frequency and intensity. Increases in visitor use of a park in the Netherlands was correlated with reductions in songbird density (van der Zande and Vos 1984). Most songbirds use ponderosa pine forests only during the breeding season, so the timing of recreation has important implications. Effects may be especially pronounced during the early part of the nesting cycle when nest construction and incubation occur (Gotmark 1992). Disturbance during the winter may be important to permanent residents, especially when cold temperatures and deep snow increase energetic requirements and decrease foraging efficiency.

Ponderosa pine songbirds are less affected by recreation than many animals because of their life history traits. The degree of ecological specialization, body size, and sociality of animals may influence their responses to recreation (Knight and Cole 1995a). Specialized birds that require specific foods or habitats (hummingbirds, cavity nesters, pinyon jays, Clark's nutcrackers, and crossbills) are more vulnerable to disturbance because they have less ability to respond to environmental changes (Croonquist and Brooks 1991). The variable temperature, precipitation regime, and seed crops characteristic of ponderosa pine forests (Marzluff and Balda 1992), has favored birds' abili-

ties to exploit alternative resources when necessary. Thus, even specialists in ponderosa pine forests may be more resilient to change than species in less variable climates. This is especially relevant for permanent residents that may adjust better to recreational disturbance than migrants. Large animals are more affected by disturbance than small ones possibly because of historical persecution and energetics (Knight and Cole 1995a). This suggests that most songbirds will tolerate recreational disturbance better than larger birds or mammals. Animals that feed in social groups may respond quicker to disturbance than solitary ones because of increased vigilance and the past experiences of other individuals (Knight and Cole 1995a). Therefore, although songbirds in general may tolerate disturbance from recreation, social species in ponderosa pine forests (pygmy nuthatch, pinyon jay, red crossbill, evening grosbeak, pine siskin) may be less tolerant than solitary species.

The influence of recreation on individuals and populations can affect communities by altering competitive, symbiotic, and predator-prey relationships (Gutzwiller 1995). If interacting species differ in their tolerance of humans, then recreation may affect some participants more than others and unbalance the relationship. Scavenging birds include tolerant crows and wary ravens and raptors. In one study, disturbance by fisherman favored crows because eagles and ravens quickly flushed when humans approached allowing crows to obtain more meat from salmon carcasses (Knight et al. 1991; Skagen et al. 1991). A similar effect could occur in ponderosa pine forests where eagles are flushed by nature viewers from big game carcasses during the winter. Recreationists may upset predator-prey relationships by disturbing nesting birds and advertising nest locations to predators (Gutzwiller 1995). Predators may be more tolerant of human activity than nesting birds or may actually cue in on human activity to locate nests (Gotmark 1992).

Effects of Recreation in Ponderosa Pine Forests

Motorized travel and scenery viewing — Although motorized travel and scenery viewing are the most popular forms of recreation in Southwestern ponderosa pine forests (Raish et al. this volume), they probably have minor, indirect effects on songbirds. Forest fragmentation by unimproved roads is unlikely to significantly affect songbird movements because the nonforested areas around such roads are small and ponderosa pine forests do not naturally have closed canopies. Paved, heavily-traveled roads may constrain movement by relatively sedentary songbirds, such as winter wrens, and affect their selection of breeding habitat (S. J. Hejl, personal communication). Roads may decrease songbird productivity because increased road-kills and litter may subsidize nest predators and provide them with foraging corridors into the forest interior (Knight et al. 1995). People stopping at scenic overlooks also may subsidize jays, crows, and ravens

and perhaps disrupt nearby breeding songbirds. Seed-eating songbirds (finches, sparrows, juncos) may benefit from roads that concentrate rain water run-off and increase annual plant productivity along roadsides. However, such benefits may be countered by increases in cowbirds that may also use annual plant seeds.

Camping — Camping, one of the most common forms of recreation in Southwestern ponderosa pine forests (Raish et al. this volume), is perhaps the most destructive recreational pursuit (Jim 1989). Most responses by songbirds to camping are indirect reactions to human intrusion; songbirds respond directly to habitat change and food supplementation (Foin et al. 1977). Although these responses are usually concentrated in relatively small areas, how far they extend beyond the campground is poorly understood. Vegetation in newly established campsites usually changes within a year as it is trampled and soil becomes compacted (Cole and Landres 1995; Marion and Cole 1996). Cover declines, especially in ground and shrub layers, and erosion increases. Dead and downed wood is quickly scavenged for fires or removed for safety (Foin et al. 1977; Cole and Landres 1995). Plant species diversity and horizontal and vertical structural diversity decline.

Bird communities change in response to habitat changes. Bird species richness and density increases, but evenness of abundance generally declines as campgrounds become dominated by a few widespread, permanent, generalist residents (Foin et al. 1977; Boyle and Samson 1985; Guth 1978). Density and diversity declined at one Arizona campground immediately after it was opened to the public for the summer season (Aitchison 1977). Brewer's blackbirds, mountain chickadees, Steller's jays, American crows, and common ravens will probably increase at campgrounds in ponderosa pine forests, as they have elsewhere in the West (Foin et al. 1977; Marzluff et al. 1995). However, Aitchison (1977) noted a severe decline in Steller's jays after an Arizona campground was opened, primarily because many nests were destroyed by removal of trees and slash. Dark-eyed juncos, American robins, hermit thrushes, warblers, vireos, wrens, and deep forest species will decline as ground, shrub, and mid-canopy cover is removed and isolated (Aitchison 1977; Foin et al. 1977; Guth 1978; Blakesley and Reese 1988). Cavity nesters, bark drillers, and other birds that forage on downed woody debris will decline. Productivity of open-nesting birds will decline as nest predators and parasites (brown-headed cowbirds) increase in response to food supplementation (Clevenger and Workman 1977; Rothstein 1994; Marzluff et al. 1995).

Pack animals have the potential to disrupt ponderosa pine forest bird communities. Spilled feed, feces, and litter attracts and supports brown-headed cowbirds that parasitize native songbirds reducing their productivity (Rothstein 1994). Establishment of pack stations or corals in remote ponderosa pine locations could pave the

way for these parasites into areas with minimal human disturbance. Warblers, vireos, and flycatchers are most susceptible to cowbird parasitism (Rothstein 1994). Although it is unlikely that parasitism alone would cause significant declines in such species, it could contribute to declines in conjunction with habitat destruction, nest predation, and disruption of ecosystem functioning (Rothstein 1994).

Hiking, Nature Study, and Wildlife Photography — These nonconsumptive recreational pursuits are usually thought inconsequential to wildlife. However, their recent surge in popularity (Boyle and Samson 1985; Raish et al. this volume) has prompted evaluation of their impacts (Boyle and Samson 1985; Riffell et al. 1996). These activities can affect songbirds as humans intrude into their territories to observe nests or unique behavioral activities. Nature study and photography may be of special concern because they tend to repeatedly disturb rare and unusual species (Boyle and Samson 1985).

Repeated intrusions in songbird territories during the breeding season can decrease singing (Gutzwiller et al. 1994), increase or decrease nest defense (Knight and Temple 1986; Keller 1989), and increase predation (Gotmark 1992). These changes may reduce the productivity of individuals and influence community composition (Riffell et al. 1996). In fact, intrusion involving 8 to 37 people/ha/day was correlated with declining songbird (warblers, wrens, thrushes) density in the Netherlands (van der Zande and Vos 1984; van der Zande et al. 1984). More dispersed intrusions (1 person for 1 to 2 hrs/ha/week), even if repeated for up to 5 breeding seasons, did not cause widespread impacts to the birds living in mixed-conifer forests in Wyoming (Riffell et al. 1996). Such widespread recreation may influence songbirds as community diversity and density of common species declined in some years. Nearly all songbirds in Southwestern ponderosa pine forests were included in this study, but no effects on individual species were noted. Therefore, although common species may be affected by disturbance in a given year, the effects of hiking, nature study, and photography are unlikely to be cumulative in ponderosa pine forests except where visitor densities are high such as in Grand Canyon National Park and large recreation areas.

Resorts and Recreation Residences — The number of resorts, established camps, and recreational residences in Southwestern national forests has fluctuated and recently declined (Raish et al. this volume). However, the effects of the substantial number of resorts and residences that remain are similar to the impacts from urbanization, camping, and hiking. The most important results of these developments are habitat loss and fragmentation, supplementing nest predators, habitat structure simplification, snag removal, and increased intrusion into surrounding forests by residents. Birds near resorts often have breeding disrupted (Lehtonen 1973; Vermeer 1973; Robertson

and Flood 1980). Avian diversity decreases and density increases as common, widespread species dominate these areas (Robertson and Flood 1980).

Winter Sports and Mechanized Off-road Travel — Snowmobiling and off-road vehicles, which are increasing in popularity across the United States (Boyle and Samson 1985), have great potential to destroy vegetation, alter habitat, and increase wildlife harassment (Berry 1980; Boyle and Samson 1985; Cole and Landres 1995). These forms of recreation are less common in ponderosa pine forests than in higher or lower elevation areas and do not appear to significantly affect songbirds in Southwestern ponderosa pine forests.

More important to ponderosa pine forests is ski-area development in adjacent, higher elevations. There is an increased abundance of scavengers that prey on nests at such developments (Watson 1979). More importantly, ski-area development often increases urbanization in ponderosa pine towns. Flagstaff, Showlow, Pinetop, Ruidoso, and Taos are all expanding (Raish et al. this volume), partly because of increased recreation at nearby ski areas.

Cumulative Effects of Urbanization and Recreation

Table 1 qualitatively assesses the variety of the potential effects of urbanization and recreation on songbirds in the ponderosa pine forest. This assessment summarizes the affects discussed in this chapter and are hypotheses rather than known influences; many potential affects are unknown and many may depend on context.

The following assumptions were made based on studies conducted elsewhere and species natural history: 1) disease negatively affects seed eaters and nectarivores that frequent urban feeders; 2) nest predation negatively influences open nesters, especially those in urban areas; 3) competition with European starlings negatively affects urban cavity nesters; 4) habitat for species that nest in ornamental vegetation or man-made structures improves with urbanization, but habitat for natural cavity, canopy, shrub, and ground nesters is degraded by urbanization; 5) urbanization provides increased food for species using feeders, lawns, and those able to scavenge refuse; 6) road construction favors scavengers and small seed eaters; 7) campgrounds are associated with reduced ground and shrub coverage, increased nest predation, and supplemental food; 8) hiking, nature study, and photography have minor, negative affects on open-nesting species that are relatively intolerant of humans; and 9) resorts and recreation residences favor scavengers and birds able to exploit lawns and feeders.

Few species benefit from urbanization and recreation. Large jays, crows, and ravens, human commensals (purple martin, brown-headed cowbird, house sparrow, house wren, barn swallow, rock dove), and widespread generalists (European starling, Brewer's blackbird) will probably increase in ponderosa pine forests as human populations continue to increase. Several other species (hummingbirds, jays and nutcrackers, chickadees, nuthatches, American robin, grosbeaks, juncos, small finches, and chipping sparrow) that exploit some aspect of human activity (primarily food supplements) should remain stable with increasing human populations. The remaining species require habitat features that humans disrupt most severely. These species (flycatchers, swallows, brown creeper, wrens, bluebirds, Townsend's solitaire, hermit thrush, vireos, warblers, tanagers, song sparrow, and red crossbill) will probably decline in areas of high human use and perhaps throughout the ponderosa pine forest if human activities continue to increase.

Research Needs

Future research should investigate the potential effects of urbanization and outdoor recreation in ponderosa pine forests. None of the studies reviewed in this chapter directly assessed urbanization and recreation in Southwestern ponderosa pine forests. Nearly every relationship hypothesized in table 1 should be tested with designed experiments. Studies of urbanization are especially important because affects on birds are significant and human populations are expanding rapidly in ponderosa pine forests. In addition, even though many forms of recreation may have minor affects on birds, recreation is widespread and increasing in popularity throughout the ponderosa pine forest.

Investigations should be rigorous, carefully designed experiments to establish causal relationships between human activity and songbird population viability (Gutzwiller 1995; Knight and Cole 1995b). Experiments should address the direct and indirect effects of humans on songbirds and identify short-term, behavioral and long-term affects on inclusive fitness. Demonstration of human impacts on avian fitness is crucial to understand how people affect bird populations (Van Horne 1983; Vickery et al. 1992). Experiments must be designed to consider natural factors, such as weather and food availability, and should test the interaction of natural factors with recreation and urbanization on bird populations. An adaptive management approach should be used where managers implement ideas in a controlled, experimental way and researchers test specific management hypotheses.

Critical evaluation of human influence requires long-term monitoring of abundance, distribution, and fitness

of uniquely-marked songbirds. Rather than focusing on a single species, researchers should monitor all members of the avian community simultaneously, perhaps conducting detailed fitness measurements on representatives of those species most likely to be affected by human activities. Species, such as American crows, common ravens,

European starlings, and house wrens that appear to benefit from human activities, should be carefully monitored because they can affect songbirds that may not decline from direct human actions.

Some of the most important research questions concerning urbanization impacts are: 1) How do bird communi-

Table 1. Hypothesized changes in songbird abundance in response to urbanization and recreation in Southwestern ponderosa pine forests. Species groups are listed if all members are expected to respond in similar ways; otherwise individual species are listed.

Species	Urbanization						Recreation		
	Disease	Predation	Competition	Habitat	Food	Roads	Camp/ Picnic	Hike/ Study/Photo	Resort/ Residence
Hummingbirds	—	—			++				+
Woodpeckers			—	—	+		—		—
Olive-sided flycatcher		—		—					
Western kingbird		—		+	+				+
Other flycatchers		—		—			—	—	
Purple martin ^a			—	++					+
Barn swallow				++					+
Other swallows				—				—	
American crow	—			++	++	+	++		++
Common raven				++	++	++	++		++
Pinyon jay	—	—		—	++		—	—	
Clark's nutcracker				—	+		+		+
Steller's jay	—	—		—	++		+	—	+
Chickadees	—		—	—	++		+		+
Nuthatches	—		—	—	++		—		+
Brown creeper				—			—	—	
House wren			—	++	+				+
Other wrens		—	—	—			—	—	
Bluebirds			—	—			—	—	—
Townsend's solitaire		—		—			—		
Hermit thrush		—		—			—	—	
American robin		—		+	++	—	—	+	
Vireos		—		—			—	—	
Ground nesting warblers		—		—		—	—	—	
Shrub nesting warblers		—		—		—	—	—	
Canopy nesting warblers		—		—		—	—	—	
Tanagers		—		—		—	—	—	
Grosbeaks	—	—		—	+	—	—	+	
Song sparrow		—		—	+	—	—	—	
House sparrow	—	—		++	++	++		+	
Chipping sparrow		—		—	+		—	—	+
Juncos		—	—		—	+	+	—	—
Blackbirds/cowbirds	—	—		+	++		++	—	+
European starling	—			++	++		++		+
Red crossbill		—		—		+	—	—	
Other finches	—	—		+	++	+	—	—	+

^a Natural purple martin nesting sites are reduced with snag removal, but this may be overcompensated for by martin houses placed near urban residences.

+Affects that may moderately increase a species' abundance or productivity.

++ Affects that may strongly increase a species' abundance or productivity.

—Affects that may moderately decrease a species' abundance or productivity.

—Affects that may strongly decrease a species' abundance or productivity.

Blank, no affect suspected.

ties change with increasing urbanization? Standardized surveys should be expanded to include urban areas and similar rural controls so that changes through time can be assessed. Specific comparisons of bird abundance and productivity in towns of various size and through time would help answer this question. 2) How does a particular type and level of urban development affect birds? Comparisons of bird abundance and productivity among different intensities of urbanization have not been done in ponderosa pine forests. In particular, the effects of dispersed housing in the forest, which is growing rapidly, should be studied. 3) What types of urban developments are most compatible with native songbirds? Research about the benefits of landscaping with native plants, using alternative energy sources, and educating homeowners would help identify long-term adjustments that government could encourage to minimize human impacts on the ponderosa pine avifauna. 4) Do nest predators disproportionately decrease productivity in urban areas relative to rural areas? If so, how does this affect various types of birds (open nesters versus cavity nesters, ground versus canopy nesters, social versus solitary species, etc.)? 5) How do birds respond to the urban/rural interface? How far from urban centers do the effects of urbanization extend into the surrounding forest? How important is the impact from house cats and other subsidized predators at varying distances from urban sources? Detailed studies of radio tagged predators are needed.

Some of the more important research questions about recreation impacts are: 1) What motivates people to pursue various recreational activities? This information will better quantify the behavior of people in the forest and improve estimation of the amount and projected increase in the activity. 2) How do various forms of recreation synergistically affect songbirds? Many forms of recreation occur at the same place and at the same or different times, yet we know nothing about how they combine to influence songbirds (Gutzwiller 1995). Comparisons of bird abundance and productivity across areas with increasing multiple recreation use could address this question. 3) What influence does Grand Canyon National Park, which attracts millions of visitors for a variety of recreational pursuits, have on songbirds? This question could be addressed in a broad study comparing bird abundance and productivity in and around recreation areas of various size in ponderosa pine forests. 4) How long should camps be closed to reduce subsidized predator populations? How much recovery is needed in camps before sensitive ground foragers or cavity nesters return? Assuming that camping affects songbirds as hypothesized, research should be conducted to determine how various degrees of camp closure would reduce affects. 5) How can campsites be made more beneficial to forest birds and less attractive to human commensals? Research is needed to determine how to effectively reduce food supplementation at camp-

grounds and pack stations, and how to determine if actions, such as increasing habitat diversity or erecting nest boxes, would benefit shrub, canopy, and cavity nesters.

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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; Koplín 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 (Mannan 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 Mannan 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; Mannan 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 Mannan 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 reas 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 (2ha) 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	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	C AZ	NB	More common on unburned plots	2
Nuthatch 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	N AZ	B	More common on burned plots	1
Towhee 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; Koplín 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 (Granholtm 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 for 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/foilage 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 (*Ame-lanchier* 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 (Soggeet 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 Neuenchwander 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 effects 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 wildfires. 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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Chapter 7

Landscape Dynamics and Considerations

Kevin M. Rich and Patricia Mehlhop

Introduction

Landscape ecology is the study of spatial heterogeneity and its influence on organisms and ecological processes (Risser et al. 1984). Recent advances in remote sensing technologies, computer software and hardware, and methods for quantifying spatial heterogeneity have contributed to the emergence of landscape ecology as a powerful approach for analyzing spatial patterns and their ecological consequences. The following references provide a good overview of the field of landscape ecology: Forman and Godron (1986), Naveh and Lieberman (1994), Pickett and Cadenasso (1995), Risser et al. (1984), Turner and Gardner (1991), and Urban et al. (1987).

Table 1 defines key terms in landscape ecology used in this chapter. Exact definitions of landscape, patch type, and patch depend on the specific organisms and processes being studied (Dunning et al. 1992; McGarigal and Marks 1995; Wiens 1976; Wiens and Milne 1989). Typically, landscapes occupy a spatial scale intermediate between an organism's home range and its regional distribution (Dunning et al. 1992). Thus, for songbirds in the Southwest, landscapes may be defined ranging in size from a few hectares to thousands of square kilometers. The patch type

of primary interest here is ponderosa pine forest, or forest in which ponderosa pine is the sole dominant plant species. Individual patches may range in size from a few trees to hundreds of square kilometers, depending on the phenomena and species under investigation, the scale of the study and the resolution of any remote sensing imagery used.

Landscape ecologists generally divide spatial patterns observed in landscapes into two categories: landscape composition and landscape configuration. Landscape composition refers to the variety and abundance of patch types within a landscape without considering the location of individual patches (Dunning et al. 1992; McGarigal and Marks 1995). An example of a measure of landscape composition is the proportion of a given landscape covered by ponderosa pine forest. Landscape configuration refers to the spatial relationships between patches in a landscape (McGarigal and Marks 1995). For example, one might be interested not only in the total amount of ponderosa pine present in a landscape but also in the degree to which individual ponderosa pine patches are isolated from each other. Both landscape composition and configuration have been shown to have significant influences on the distribution and abundance of songbirds (Freemark et al. 1995).

Many studies in Southwestern ponderosa pine forests have investigated the relationships between songbirds and

Table 1. Definition of several key terms used in landscape ecology.

Term	Definition	Reference ^a
landscape	a mosaic of patches relevant to the phenomenon under consideration (at any scale)	1
patch	distinguished by discontinuities in environmental character states from its surroundings; implicit is the notion that the discontinuities have biological significance	2
patch type	a description of the environmental character states differentiating a patch or group of similar patches from surrounding areas ^b	1
landscape composition	features associated with the presence and amount of each patch type within the landscape but without being spatially explicit	1
landscape configuration	physical distribution or spatial character of patches within the landscape	1
grain	the resolution of the data, that is, the area represented by each data unit ^c	3
extent	the overall size of the study area ^c	3
local population	set of individuals that all interact with each other with a high probability	4
metapopulation	set of local populations that interact via individuals moving among populations	4

^a References: 1. McGarigal and Marks (1995); 2. Wiens (1976); 3. Turner et al. (1989); 4. Hanski and Gilpin (1991).

^b Our definition. The term is used, although not explicitly defined, by McGarigal and Marks (1995).

^c The terms "grain" and "extent" are also used to refer to the smallest and largest scales at which an organism responds to spatial heterogeneity (Kotliar and Wiens 1990). We present the above definitions because we use these terms in describing spatial data sets in the text.

habitat characteristics at the level of individual patches (Hall et al. and Finch et al., this volume). To date, though, no published studies from Southwestern ponderosa pine forests have examined the relationships between songbirds and spatial patterns at the level of entire landscapes. In this chapter, we will discuss the importance of scale in ecological research, highlight several tools available for characterizing landscape patterns in Southwestern ponderosa pine forests, and describe specific research needs at fine, intermediate, and large spatial scales. We will also address research needs relevant to habitats and species of special concern.

The Importance of Scale

Different ecological processes occur at different spatial scales (Kotliar and Wiens 1990; Urban et al. 1987; Wiens 1989). Factors affecting habitat selection by individuals within patches may differ from factors influencing the distribution and abundance of organisms across landscapes (Wiens 1989; Wiens et al. 1987; McGarigal and McComb 1995). To fully understand the ecology of songbirds in Southwestern ponderosa pine forests, additional research is needed at multiple spatial scales, including fine-scale studies at the level of individual patches; intermediate-scale studies at the level of landscapes several hundred hectares in size; and large-scale studies at the level of landscapes hundreds to thousands of square kilometers in size.

At different scales, different spatial patterns emerge for ponderosa pine forests in the Southwest. At a scale of several hundred hectares, ponderosa pine forests generally appear as integral components of larger forests. Ponderosa pine forests often meet and blend with pinyon-juniper along lower elevational boundaries and with Douglas-fir and mixed-conifer along upper elevational boundaries. At a scale of hundreds to thousands of square kilometers, though, Southwestern ponderosa pine forests tend to appear highly fragmented.

How these spatial patterns influence the songbirds that use these forests is unknown. Many studies in forests of eastern and central North America have found that smaller, more isolated patches tend to have fewer songbird species and fewer individuals of those species than larger, less isolated patches (for example, Ambuel and Temple 1983; Askins and Philbrick 1987; Blake 1986; Blake 1991; Blake and Karr 1984; Blake and Karr 1987; Freemark and Collins 1992; Freemark and Merriam 1986; Lynch and Whigham 1984; Robbins et al. 1989; Whitcomb et al. 1981). These studies have generally focused on patches of forest surrounded by non-forested agricultural and suburban areas. In contrast, several studies in western North America have shown little relationship between patch size

and songbird species richness or abundance in forest patches surrounded by forests of different species composition or age and size class (Aney 1984; Lehmkuhl et al. 1991; Rosenberg and Raphael 1986). Conceivably, songbirds in ponderosa pine forests may show responses characteristic of birds in Eastern fragmented forests at large spatial scales, while showing responses characteristic of birds in other Western forests at intermediate spatial scales. Until landscape-level research on songbirds in Southwestern ponderosa pine forests is carried out, though, such comparisons will remain speculative.

Characterization of Landscape Patterns

A prerequisite for most research in landscape ecology is the availability of data on the spatial patterns of interest. All spatial data sets have a certain grain and extent. "Grain" refers to the resolution of the data (Turner et al. 1989). For example, on a relatively fine-grain map, it might be possible to distinguish features 1 m in size, while on a relatively coarse-grain map these features might not be visible. Extent refers to the area covered by the data set. A spatial data set is only useful for a given study if it has a grain and extent appropriate for the research being carried out (McGarigal and Marks 1995; Turner et al. 1989). The data must have a fine enough grain that patch types and patches relevant to the organisms and phenomena being investigated can be readily distinguished. In addition, the extent must be large enough that meaningful spatial patterns can be identified.

Table 2 provides information on several spatial data sets currently available or soon to be available that include data on Southwestern ponderosa pine forests. The USDA Forest Service General Ecosystem Survey and Terrestrial Ecosystem Surveys are limited in their applicability for research on songbirds since only Forest Service land is included, and since map units are based on potential natural vegetation rather than current vegetation. The data sets based on advanced very high resolution radiometer (AVHRR) imagery are limited in their applicability, as well. They are very coarse-grain, with a resolution of 1 km. Keitt et al. (1995) suggest that some details of the Earth Resources Observation Systems (EROS) classification are rather suspect from a biogeographic standpoint, and they use the USDA Forest Service classification in their analysis of potential habitat patches for the Mexican spotted owl. However, the Forest Service classification does not distinguish between forest dominated by ponderosa pine and forest dominated by Douglas-fir, rendering it inadequate for studies focusing on ponderosa pine forest.

Table 2. Selected data sets currently available or soon to be available for characterizing landscape patterns influencing songbirds in Southwestern ponderosa pine forests.

Data set	Source of imagery	Scale or resolution	Availability ^a	References ^b
USDA Forest Service (Southwestern Region) General Ecosystem Survey	aerial photography	1:250,000	currently available	1
USDA Forest Service Terrestrial Ecosystem Surveys	aerial photography	1:24,000	currently available	2
Vegetative cover types from EROS	AVHRR	1 km	currently available	3
USDA Forest Service forest cover types	AVHRR	1 km	currently available	4, 5, 6
AZ Gap Analysis	TM	30 m	fall 1997	7
NM Gap Analysis	TM	30 m	currently available	8, 9

^a Currently available refers to data sets available as of August 1996.

^b References: 1. USDA Forest Service (1989); 2. USDA Forest Service (1986); 3. Loveland et al. (1991); 4. Evans and Zhu (1993); 5. Powell et al. (1993); 6. Zhu and Evans (1992); 7. K. Thomas, personal communication; 8. Muldavin (1994); 9. B. Thompson, personal communication.

The Arizona and New Mexico Gap Analysis data sets will provide a valuable addition to the spatial data available for landscape ecological studies of songbirds in ponderosa pine forests. Since they are based on Landsat thematic mapper (TM) imagery with a 30-m resolution, though, they will be somewhat limited in their usefulness for addressing questions requiring very detailed, fine-grain data on forest composition and structure. The development of spatial data sets with a relatively high resolution, on the order of 1 m, would provide an extremely useful resource for studies on the effects of fine-grain forest attributes on songbirds in the Southwest.

McGarigal and Marks (1995) have published a computer program called FRAGSTATS that provides researchers with a powerful tool for quantifying landscape composition and configuration. Versions of FRAGSTATS are available for use with either vector or raster image files. FRAGSTATS computes a comprehensive array of landscape metrics including area metrics, patch size metrics, edge metrics, shape metrics, core area metrics, nearest neighbor metrics, patch diversity metrics, and contagion and interspersion metrics. The accompanying documentation includes a thorough description of each metric, including mathematical definitions and a discussion of each metric's ecological applications and limitations (McGarigal and Marks 1995).

Fine-Scale Studies

Although studies of the relationships between habitat characteristics and songbird species' richness and abundance have been carried out at the individual patch level in Southwestern ponderosa pine forests, more research is needed to clarify these relationships. More research is

needed to determine the effects of vegetation species composition, tree size and age class, density of overstory and understory vegetation, and fire and grazing history on songbird diversity and abundance at the patch level (Hall et al. and Finch et al., this volume). Such information will be useful for managing forest patches (for example, forest stands) to maintain local songbird diversity and abundance.

In addition, research is needed to determine the extent to which individual species are obligate users of ponderosa pine forest. Many songbird species are known to occur in ponderosa pine forest. Some species, such as Grace's warbler, appear to be ponderosa pine specialists and may require the presence of ponderosa pine forest to survive and reproduce (Hall et al., this volume). Other species, such as the mountain chickadee, appear to be forest generalists and may be able to thrive in a variety of forest types. Still other species, such as the American robin, appear to be extreme generalists and are frequently found in a wide variety of forest and non-forest habitats. Clearly, individual songbird species can differ greatly in their habitat requirements, and research is needed to elucidate the specific habitat requirements for songbirds found in ponderosa pine forests. Information is needed on the extent to which individual songbird species require ponderosa pine habitat in the breeding season, during migration, and as winter residents.

The degree to which songbird species are ponderosa pine specialists versus broader habitat generalists has potential implications for the scale at which those species respond to spatial heterogeneity. Ponderosa pine specialists are likely to respond to spatial heterogeneity at a finer scale than habitat generalists. For example, Grace's warblers may be more sensitive than American robins to differences in tree size and age class, density of overstory and understory vegetation, and grazing intensity within a ponderosa pine forest. Such hypotheses need to be tested

in field studies that compare the responses of habitat specialists and generalists to different fine-scale patterns of spatial heterogeneity. This type of study will likely reveal indicator species (presumably habitat specialists) useful for monitoring ponderosa pine forest habitat quality.

Ponderosa pine specialists also undoubtedly differ from habitat generalists in their responses to broad-scale patterns of spatial heterogeneity. For a Grace's warbler, a series of ponderosa pine forests separated by pinyon-juniper woodland might appear to be a fragmented landscape. For an American robin, however, the same landscape may appear relatively continuous. Understanding the fine-scale habitat requirements of individual species is an important element in understanding the responses of those species to spatial patterns at broader scales.

Intermediate-Scale Studies

In addition to studies at the patch level in which individual patches represent independent data points, studies at the landscape level in which landscapes represent independent data points are needed to examine the relationships between landscape characteristics and songbird distribution and abundance. Examples of such studies carried out in other regions include a study by McGarigal and McComb (1995) in mixed-conifer forest in the central Oregon Coast Range, and a study by Evans (1995) in mixed-conifer forest in west-central Idaho. In both studies, landscapes were defined at a scale of several hundred hectares and chosen to represent a wide spectrum of spatial patterns reflecting different forest management regimes. McGarigal and McComb (1995) used ground-truthed aerial photographs for baseline data on spatial attributes, while Evans (1995) used a ground-truthed timber strata map generated from a Payette National Forest timber inventory. In both studies, FRAGSTATS (McGarigal and Marks 1995) was used to compute measures of landscape composition and configuration.

McGarigal and McComb (1995) and Evans (1995) both found significant relationships between several measures of landscape composition and configuration and the abundance of one or more songbird species. Interestingly, McGarigal and McComb (1995) found that for species strongly associated with a particular patch type at the patch level, the relationships between abundance and the amount of preferred patch type present at the landscape level varied greatly. McGarigal and McComb's (1995) study supports the idea that different processes occur at different spatial scales, and that relationships seen at the patch level cannot necessarily be extrapolated over landscapes.

Large-Scale Studies

Research is also needed at a relatively large scale of hundreds to thousands of square kilometers to determine patterns of songbird distribution and abundance and shed light on ecological processes at this scale. Ecological interactions between individuals of a given species and biotic and abiotic factors in the environment are likely to vary across the range of that species. To understand the ecology of a species, one must understand ecological processes occurring throughout its range. Thus, to fully understand the ecology of songbirds in Southwestern ponderosa pine forests, one must understand ecological processes occurring across the ranges of these species.

At large spatial scales, ponderosa pine forests in the Southwest tend to occur within "Sky Islands" of mountain forest surrounded by seas of arid grassland and desert (DeBano et al. 1995; Gehlbach 1981). One area of potential interest in studying songbirds in these forests is the area of metapopulation dynamics. Metapopulations are groups of two or more populations connected by infrequently dispersing individuals, and they typically occur when populations occupy areas of suitable habitat separated by areas of unsuitable habitat (Hanski and Gilpin 1991). Some metapopulations may exhibit "source-sink" characteristics (Brawn and Robinson 1996; Howe et al. 1991; Pulliam 1988; Pulliam and Danielson 1991). In these cases, it is believed that individuals from source populations, in which productivity exceeds mortality, disperse to sink populations, which would go locally extinct in the absence of such migration.

Little is known about the extent to which songbird species in Southwestern ponderosa pine forests exhibit metapopulation dynamics. Given the fragmented patterns of ponderosa pine forest found at large spatial scales in the Southwest, it is likely that at least some songbird species found in this habitat exist as metapopulations. However, the degree to which a given species exists as a metapopulation is no doubt influenced by the habitat preferences and requirements of the species and the extent to which it can disperse through unsuitable habitat. Overall, one would predict that ponderosa pine specialists, such as Grace's warbler, would exhibit very different metapopulation dynamics than broader forest generalists, such as the mountain chickadee. Mountain chickadees may in turn exhibit very different metapopulation dynamics than extreme habitat generalists, such as the American robin.

Likewise, the nature of source-sink dynamics within metapopulations undoubtedly varies from species to species. For some species, ponderosa pine forest may represent source habitat in which productivity is relatively high. For other species, ponderosa pine forest may represent sink habitat in which mortality and emigration exceed productivity. Source-sink dynamics are further compli-

cated in migratory species by the fact that some areas may be unimportant for breeding but critical as stopover sites during migration or as wintering habitat.

Attempting to understand metapopulation dynamics is an ideal example of an endeavor that requires research at multiple spatial scales. Studies at fine scales are needed to determine exactly how the species in question uses different habitat types. Studies at intermediate scales are needed to learn more about habitat requirements, including how landscape composition and configuration affect habitat selection. Studies at larger scales are needed to determine overall patterns of habitat availability, how habitat use varies throughout the range, and how patterns of habitat availability and use relate to metapopulation dynamics. For migratory species, information at each spatial scale is needed for breeding areas, for stopover sites used during migration, and for wintering habitat.

One key aspect of understanding the population dynamics of a species is understanding dispersal patterns of individuals through different habitat types. We know that most songbirds are capable of traveling great distances (many migrate to the tropics for the winter). However, vagility, or the physical ability of a species to move, should not be equated with dispersal, or the movement of individuals to new areas to settle there and breed (Villard et al. 1995). Little is known about dispersal in songbirds. Some studies (Drilling and Thompson 1988; Holmes and Sherry 1992; Kendeigh 1941) suggest that typical dispersal distances for adults in some species of songbirds may be less than 350 m. However, these studies provide limited data for a small number of species. Even less is known about dispersal in first-year songbirds, that is, how far first-year birds tend to nest from their birth sites. Greenwood and Harvey (1982) suggest that the median first-year dispersal for both sexes is usually less than 10 territories away from the birth site. However, Villard et al. (1995) argue that this generalization may not be valid since recapture rates of songbirds banded as nestlings are usually lower than 10 percent. In forest patches of central Illinois, Robinson (1992) observes that songbirds have very low reproductive success, and he suggests that populations in the area may be maintained by individuals dispersing from forests over 200 km away.

To date, no studies have been published estimating dispersal distances for songbirds in ponderosa pine forests in the Southwest. Information on dispersal distances could potentially be gathered through extensive banding operations and attempts at recapture across large areas. Another alternative would be to identify isolated patches in which one or more species have been extirpated due to stochastic processes, forest fires, or human activities such as logging, and then survey those patches to determine whether those species reappear over time. If those species do reappear, this would suggest that they were able to disperse from an area at least as far away as the nearest suitable

habitat (Villard et al. 1995). Such studies would be especially useful when the areas of nearest suitable habitat are a considerable distance away (for example, in another Sky Island), as they might provide insights into maximum dispersal distances for songbirds over different habitat types.

Spatial data sets from the Arizona and New Mexico Gap Analysis projects should provide information useful for large-scale studies on songbirds in Southwestern ponderosa pine forests (table 2). To adequately study most ecological patterns and processes important for songbirds in ponderosa pine forests, though, analyses of spatial data from imagery will need to be accompanied by field investigations. This will likely present some logistical challenges at scales of hundreds to thousands of square kilometers. Nonetheless, data from imagery are generally of little use unless they are ground-truthed and closely linked with data collected in the field. The collection of field data across large spatial scales may be facilitated by collaboration among researchers and by the careful selection of field sites based on high-quality imagery.

Habitats and Species of Special Concern

Because of the relatively small area of old-growth ponderosa pine forests remaining in the Southwest and economic pressures to harvest these forests, research into songbird responses to landscape characteristics of old-growth ponderosa pine forests at multiple scales should be a top priority. At the patch level, more research is needed to determine exactly how songbirds use old-growth ponderosa pine forests and the extent to which they depend on them. At larger landscape levels, research is needed to determine how the proportion and spatial configuration of old-growth ponderosa pine forest in a landscape influences songbird distribution and abundance.

Research on songbird responses to landscape composition and configuration at multiple scales is needed that considers both overall songbird diversity and the abundance of individual species. Measuring the local diversity of songbird species in an area provides insight into the ability of that area to support a variety of different kinds of songbirds. However, from a regional perspective, the number of species in a given area may not be as important as which species are present. For example, a clearcut patch may be found to have a relatively high diversity of songbird species, but those species may be common throughout the region. Thus, widespread clearcutting in the region might produce areas of high local species diversity while dramatically reducing overall regional diversity.

Studies that focus on individual songbird species are necessary for understanding the relationships between individual species and different types of habitat and for gaining insights into population and metapopulation dynamics. Landscape-level studies focusing on those songbird species most vulnerable to local extirpation or rangewide extinction are especially urgent. No such studies have been carried out, and landscape-level information is needed to inform management decisions affecting regional avian diversity and the long-term viability of those species.

A list of bird species on managed ponderosa pine Breeding Bird Survey routes in Arizona and New Mexico whose populations have been declining is provided in Chapter 4 of this volume (from Miller 1992), as is a list of bird species found in ponderosa pine forests ranked as being of high or moderate concern by the Arizona and New Mexico Partners in Flight programs. These lists offer a starting point for identifying target species for landscape-level studies in Southwestern ponderosa pine forests.

Typically, landscape-level studies of songbirds in other regions have involved sampling all songbird species encountered across different landscapes using standardized techniques. In many studies, rare species were not considered in the analysis of abundance data because they did not lend themselves well to the statistical methods used (for example, Evans 1995; Hagan et al. 1996; Knick and Rotenberry 1995; McGarigal and McComb 1995; Rosenberg and Raphael 1986). To overcome this problem in Southwestern ponderosa pine forests, research must be carried out over broad enough spatial and temporal scales that sufficient data on rare species are gathered for statistical analysis.

Rare species form a critical component of bird communities. In most studies of bird communities, a small number of species are found at all or most sites while many species occur at only a few (for example, Evans 1995; Hansen et al. 1995; Hejl and Woods 1991; Rosenberg and Raphael 1986; Verner and Larson 1989). Landscape-level research that focuses on rare species is needed to gather more information about these species and to provide a scientific basis for managing rare species and their habitats. Maintaining viable populations of rare species is essential for maintaining overall avian diversity in the Southwest, as well as for maintaining healthy, intact communities and ecosystems.

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Chapter 8

Summary

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Most ornithological studies in Southwestern ponderosa pine forests have yielded results that are applicable only to the specific location and particular conditions of the study areas (for example, Green 1979 and Hurlbert 1984). In addition, varying interpretation of similar study results by investigators has limited our ability to extend or synthesize research results from Southwestern ponderosa pine forests beyond the scope of any individual study. In studies that address similar questions and have similar results, broader inferences are possible.

Isolated studies of selected aspects of songbird ecology will not provide the level of resolution required to answer complex research questions and management problems. Therefore, decision makers should review our research recommendations and commit adequate financial and institutional support to incorporate them into a coordinated research program that systematically addresses these research needs. Developing management approaches to research needs that also meet societal demands will only occur when the USDA Forest Service, USDI Fish and Wildlife Service, state resource agencies, public advocacy groups, and other organizations agree that a more comprehensive understanding of ponderosa pine forest ecology is mandatory for management of Southwestern ponderosa pine forests and their avifauna.

Ponderosa Pine Forest Ecology

Ponderosa pine forests today differ drastically from those before European settlement of the Southwest (Covington and Wagner 1996; Moir et al., this volume). Many of these changes resulted from past land-use activities, primarily since European settlement (Raish et al., this volume; Scurlock and Finch, this volume). The foremost activities leading to forest change include logging, fuelwood harvest, fire suppression, livestock grazing, and urban development (Finch et al., this volume; Raish et al., this volume; Scurlock and Finch, this volume). The singular, synergistic, and cumulative impacts of these land uses have resulted in overstocked forests that exhibit 1) size-class distributions skewed toward smaller trees, 2) unnaturally high levels of disease and pathogens, 3) high susceptibility to catastrophic crown fires, 4) depleted woody and herbaceous understories, and 5) altered ecological relationships and ecosystem processes (Moir et al., this volume).

If we hope to evaluate population changes of birds inhabiting ponderosa pine forests, we must understand how their habitats have changed. Our knowledge of presettlement or reference ponderosa pine forests is limited to the results of retrospective studies, archaeological records, and exploration narratives (for example, Covington and Wagner 1996; and Scurlock and Finch, this volume). Although these descriptions provide useful models of presettlement forest patterns, the models are general, lacking detail about the range of variation that existed before intensive forest management (Reynolds et al. 1996). Presettlement or reference states for Southwestern forests are typically inferred from conditions existing in the late 1800s (Covington and Moore 1994). This assumes that historical conditions recorded during this time period are representative of prehistoric and Mexican periods, but as Scurlock and Finch (this volume) described, American Indians and Spanish people used Southwestern forests and wildlife to varying degrees before Anglo-American colonization of the Southwest through the 1800s. Therefore, we question the reliance on the late 1800s as the appropriate period for inferring reference forest conditions demonstrating minimal human impact.

Ponderosa pine occupies a gradient from the upper elevation of the pinyon-juniper woodland to mixed-conifer forests. Most knowledge of presettlement conditions is derived from studies conducted within the mid-elevation zone (between pinyon-juniper and mixed-conifer) where ponderosa occurs as a climax species. Researchers generally agree that xerophytic ponderosa pine forests were more open with clumps of pine trees interspersed among grassy openings. These conditions were maintained by low-intensity ground fires every 2 to 12 years that limited tree regeneration and dense forests (Moir et al., this volume). Given these conditions and disturbance regimes, much of the presettlement xerophytic pine forest probably tended toward older, mature conditions (Covington and Moore 1994). Descriptions of mesophytic forests (for example, mixed conifer) where ponderosa pine is a seral species are less available, but many of these forests were more open before 1880 (Moir et al., this volume).

Our ability to characterize existing ponderosa pine forests is also somewhat limited. We have detailed information on forest structure and composition for some areas, but information is limited for most. From what we do know, much of the existing ponderosa pine forests are relatively dense because small, relatively young (<100 years old) trees have proliferated in response to human use of forested lands. Logging, fuelwood harvest, and cata-

strophic fire have reduced the numbers of large, mature ponderosa pine trees and snags over time (Raish et al., this volume). Areas where the forest was originally a mosaic of tree clumps and grassy openings have become continuous tree canopies as trees have invaded these openings. Fire regimes and disease pathways have been altered, rendering these forests at far more risk than they were historically. Where fire, insects, and disease once played key roles in maintaining forests, they can now devastate forests.

We are also observing shifts in the composition of these forests as a result of past forest management. In some ponderosa pine stands, the number of shade-tolerant conifers is increasing, moving the classification of some stands from ponderosa pine to mixed-conifer (Johnson 1994a). In existing mixed-conifer forests, an emphasis on harvesting mature ponderosa pine trees over other conifer species may be altering both stand structure and composition in favor of more shade-tolerant conifers such as Douglas-fir and white fir (USDI 1995).

A cornerstone to conserving avian populations in ponderosa pine forests is acquiring more detailed information about past and current forest conditions. Published research and existing knowledge (this volume) provide a good foundation from which we can proceed, but significant information gaps remain. In particular, we must understand the range of variation in key forest attributes both in reference ponderosa pine forests and in the forests that exist today. Managing ponderosa pine forests for one ecological condition may not provide the variation in conditions needed to support the variety of birds native to Southwestern pine forests (Miller 1996). Also required is the information and technology needed to evaluate forest conditions over large geographic areas. The ability to quantify and model spatial relationships of vegetative conditions, especially at the landscape and regional scales, is critical to understanding the dynamics of ponderosa pine ecosystems and evaluating areas in greatest need of remedial management actions.

Songbird Ecology

Most insightful studies of the ecology of ponderosa pine birds have been conducted within the past 40 years. These studies have been largely descriptive, although some small-scale experiments have been conducted. The most extensive descriptive study examined bird-habitat relationships within 23 stands representing gradients of ecological conditions in ponderosa pine and pine-oak forests of northern Arizona (Rosenstock 1996). This work with major studies by Szaro, Brawn, Blake, Balda, and others (for example, T. Martin's study in progress through the

Montana Cooperative Wildlife Research Unit, University of Montana) provides the basis for much of our current knowledge of songbird community ecology in Southwestern ponderosa pine forests (Finch et al., this volume; Hall et al., this volume). Knowledge gaps not addressed by community-level studies are captured to some extent by single-species studies conducted by investigators such as Marzluff and Martin (Marzluff, this volume; Finch et al., this volume; Hall et al., this volume).

Because most published studies of passerines are relatively recent, their results largely reflect ecological relationships in forests altered by human activities over the past century. Although archaeological records from prehistoric periods and historical ornithological accounts from expeditions and collections exist for the Southwest (Scurlock and Finch, this volume), these records document mostly presence and absence of bird species rather than avian abundances. Therefore, bird use of ponderosa pine forests reported in contemporary studies cannot be readily compared to historical accounts or archaeological finds. Consequently, we do not know if patterns of abundance and species composition of birds that we see today are similar to those of presettlement forests. Because the Southwest has undergone extensive climatic changes such as warming over geologic time, contemporary avifaunas in Southwestern ponderosa pine forests likely differ from prehistoric or historical avifaunas in response to natural forest changes alone (Johnson 1994b). That the Southwest was settled by different cultural groups at different periods of time, each group using forest and avian resources to different extents (Scurlock and Finch, this volume), further confounds interpretation of temporal and spatial changes in avifaunas.

If we assume, however, that the strongest or most consistent relationships that we detect in contemporary studies also existed in the past, then it could be instructive to evaluate whether habitat resources essential for specific bird species were available in presettlement forests. We could then speculate whether temporal changes in resource distributions or quantities would have been beneficial or detrimental to species' populations. For example, species that rely on large trees for an important aspect of their life history (such as nesting) may have been more abundant in the past when large trees were more abundant, whereas species that favor dense stands may have been less abundant historically.

Cavity-nesting species are perhaps the most studied group of birds in the Southwest (Balda 1975; Cunningham et al. 1980; Ffolliot 1983; Brawn and Balda 1983, Rosenstock 1996). Collectively, these studies emphasize the importance of snags, particularly large snags, as potential nesting substrates for these species. Results of Brawn's (1985) experimental research on secondary cavity-nesting birds and Rosenstock's (1996) observational research on both primary and secondary cavity nesters concur that snags

and nest substrates are limiting factors for many of these species. Miller's (1992) analysis of Breeding Bird Survey (BBS) data suggests that populations of the hairy woodpecker, acorn woodpecker, violet-green swallow, white-breasted nuthatch, pygmy nuthatch, mountain chickadee, and mountain bluebird are declining in the Southwest. If these declines are indeed real, then loss of snags that provide nest, foraging, and perch sites could be a contributing or even a primary factor explaining declining populations.

The loss of large trees in many ponderosa pine forests has also likely impacted populations and habitats of numerous species. Rosenstock (1996) found positive relationships between the relative abundance of large trees and breeding populations of violet-green swallows, brown creepers, house wrens, chipping sparrows, pygmy nuthatches, and northern flickers. All of these species except the chipping sparrow are bark-foraging species or require snags for nesting. Large trees may provide habitat for many arthropod prey of bark-foraging birds, and these bark-foraging birds may be morphologically adapted to forage more efficiently on the bark furrows of larger trees (Richardson 1942). For species such as the chipping sparrow and perhaps Grace's warbler, large trees provide elevated song posts and substrates for their open-cup nests. Thus, the loss of large trees not only curtails the sustained supply of large snags and nest cavities but may also reduce foraging substrates, song perches, and substrates for open-cup nests.

Changes to the forest understory, mainly the loss of structural and floristic diversity, have also altered habitats of a number of species. Gambel oak is an important understory component in pine-oak forests (Rosenstock 1996), and aspen is an important component of some early successional ponderosa pine forests. Unlike pines, large oaks and aspens often have natural or excavated cavities while still live. Characteristics of these cavities appear to be favored by some bird species over cavities in pine snags (Finch et al., this volume). Gambel oak provides acorn mast, and arthropods found on oaks add to the diversity of prey for insectivorous birds. We are observing loss of large Gambel oaks to fuelwood harvest and loss of aspen to pine succession in fire-excluded forests. Increased competition with pines for light as forest canopy cover increases may also explain declines of these deciduous trees. Further, heavy browsing by wildlife and livestock may be limiting regeneration of oak, aspen, and shrubs to replace those lost by natural or human causes (USDI 1995).

Grasses, forbs, and shrubs provide cover for ground-foraging and ground-nesting species. They also provide a variety of seeds, fruits, and nectar for granivorous (such as juncos, towhees, sparrows), frugivorous (such as thrushes), and nectivorous (such as hummingbirds) species. Since 1880, these herbaceous understories have been heavily impacted by livestock, elk, increased tree densities, and altered fire regimes. Undoubtedly, these changes

have affected the avifauna. Reductions in the amounts of seeds and fruits may be particularly important during the winter, when these foods are generally more available than arthropods.

Studies should continue to emphasize habitat and population ecology but must provide greater consideration of geographic variation, seasonality, spatial scale, and population demographics. Past management activities have reduced the amount of mature/old-growth ponderosa pine forest in the Southwest and the openness of stands. Older forests and open forests provide unique conditions used by various species (Siegel 1989, Finch et al. this volume). Researchers have identified some general habitat correlates for birds in late-successional forests, but additional research—especially experimental—that details the ultimate and proximate factors underlying avian selection of different ponderosa pine habitats could help to identify key forest attributes that might be emphasized in future forest management. New research should examine bird-habitat relationships in different ponderosa pine types, successional stages, and patch sizes across a gradient of spatial scales and management situations (commercial forests, wilderness areas, research natural areas, experimental forests). Research should also identify key site-level characteristics. At larger landscape scales, for example, bird-habitat relationships should consider patch size and shape, distance between patches, number of patches, and landscape mosaic patterns (Rich and Mehlhop, this volume).

Published information on bird-habitat relationships is limited both spatially and temporally. As noted by Rich and Mehlhop (this volume), knowledge of habitat relationships and population characteristics of ponderosa pine birds at the landscape level is virtually nonexistent for the Southwest. Many earlier studies suffer from little or no replication (number of sample plots within a similar condition or treatment), restricting the level of inference possible from the results. Also, most studies were relatively short-term (1–4 years) and were typically restricted to the breeding season. In addition, most breeding bird studies did not evaluate reproductive success or survival rates in relation to habitat elements. As a result, the full range of habitat use by resident species has not been sampled; habitat use by species that do not occupy Southwestern ponderosa pine forests during the breeding season (for example, most wintering and many migrating birds) has rarely been studied; temporal variation in bird communities is not well understood (Gaud et al. 1986; Hejl and Beedy 1986; Hall et al., this volume); and avian demographic responses to habitat variation need further study. Thus, our knowledge of habitat associations of birds in ponderosa pine is a credible start but is far from what we require to describe desired conditions to land managers.

Existing information on population trends and the population ecology of ponderosa pine birds provides good

baseline information but leaves many questions unanswered. Results from analyses of BBS and Christmas Bird Count (CBC) data, despite their weaknesses, can be used as a starting point to focus future monitoring and research efforts (which is indeed their intent). A logical start would be to increase the number of samples in ponderosa pine forests for both BBS and CBC and to allocate samples throughout the range of conditions found in these forests. Further, results from BBS or CBC data could be used as a basis for more intensive sampling efforts (see also Manley et al. 1993). For example, Miller's (1992) preliminary analysis of BBS data suggests that more species have declined than have increased in abundance over the past 30 years. Greater effort should be devoted to monitoring bird populations exhibiting these perceived declines. This more intensive monitoring should not be restricted to measures of absolute or relative abundance, but should also include estimates of other population parameters such as survival, reproduction, or turnover rates. Likely, research will be needed to determine which population parameter is the most sensitive index of population status prior to initiating intensive monitoring efforts.

Effects of Land-Use Activities

Numerous types of land and natural resource use have the potential of altering bird habitats, leading to spatial and temporal changes in bird populations (Rotenberry et al. 1995; Saab et al. 1995; Thompson et al. 1995). The primary current land uses discussed in this volume include timber harvest, fire, fire suppression, grazing by wildlife and livestock, recreation, and urbanization. At least three major factors complicate a study addressing the effects of any of these factors. The first is that natural events such as climate, succession, and numerous stochastic disturbances occur simultaneously with human impacts. Separating effects of natural events from human activities is extremely difficult. Second, where human activities occur, more than one type of activity usually takes place. For example, many forests that have undergone timber harvest have also been subjected to fire suppression and livestock grazing. Thus, the real effects of land use are likely synergistic rather than the results of any one factor acting singly. Third, effects of activities can become additive or even multiplicative over time. These cumulative effects, coupled with synergistic effects and effects of natural events, create a difficult and complicated puzzle to solve. That has not prevented researchers from attempting to address these questions in the past, nor should it dissuade researchers from doing so in the future. Limiting the number of variables under study can help to reduce the complexity of a study, and developing coopera-

tive research partnerships to conduct studies that address interactions among land uses may be the key to interpreting complex bird-habitat relationships. Regardless of how studies might be approached, understanding interactive cause-effect relationships of land use is critical for future management of Southwestern ponderosa pine forests and the conservation of the associated avifauna.

Observational studies are basically correlative and may not elucidate cause-effect relationships. Although the studies reviewed in this book have provided useful information, the interpretations that we have drawn from them are limited. The effects of various land uses, singly and in combination, are best studied using well-designed experiments. The need for experiments to understand the effects of land management on specific ecosystem attributes (including birds) is not a new concept (see Eberhardt and Thomas 1991; James and McCulloch 1995; USDI 1995). Such studies are rarely conducted because costs and logistical obstacles associated with implementing large-scale forest manipulations limit their application.

We recognize that the design and implementation of experiments is a daunting challenge (Carpenter et al. 1995). Granted, we can develop educated guesses based on available evidence as to how particular land uses might affect bird habitats, populations, and perhaps community dynamics, but we can rarely assign levels of assurance that our guesses are correct. Given that such studies would need to be both well replicated and conducted at large spatial scales, success of implementing experiments requires commitment and collaboration by public participants, resource-management agencies, and researchers. Treatments such as logging, fire, and grazing manipulations would need to be implemented by management agencies, following experimental designs developed in cooperation with researchers. Numerous opportunities exist to plan and design management treatments that allow for the implementation of research experiments (Carpenter et al. 1995). Taking advantage of these opportunities would resolve many key issues on forest passerine ecology.

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Appendix: Birds Referenced in This Book

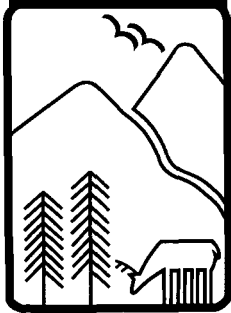
Common name	Scientific name	Common name	Scientific name
Acorn woodpecker	<i>Melanerpes formicivorus</i>	Downy woodpecker	<i>Picoides pubescens</i>
American crow	<i>Corvus brachyrhynchos</i>	Dusky flycatcher	<i>Empidonax oberholseri</i>
American dipper	<i>Cinclus mexicanus</i>	Dusky-capped flycatcher	<i>Myiarchus tuberculifer</i>
American goldfinch	<i>Carduelis tristis</i>	Eastern bluebird	<i>Sialia sialis</i>
American kestrel	<i>Falco sparverius</i>	Eastern kingbird	<i>Tyrannus tyrannus</i>
American robin	<i>Turdus migratorius</i>	Eastern meadowlark	<i>Sturnella magna</i>
Ash-throated flycatcher	<i>Myiarchus cinerascens</i>	Elegant trogon	<i>Trogon elegans</i>
Baird's sparrow	<i>Ammodramus bairdii</i>	European starling	<i>Sturnus vulgaris</i>
Bald eagle	<i>Haliaeetus leucocephalus</i>	Evening grosbeak	<i>Coccothraustes vespertinus</i>
Band-tailed pigeon	<i>Columba fasciata</i>	Flammulated owl	<i>Otus flammeolus</i>
Barn swallow	<i>Hirundo rustica</i>	Fox sparrow	<i>Passerella iliaca</i>
Bell's vireo	<i>Vireo bellii</i>	Golden-crowned kinglet	<i>Regulus satrapa</i>
Berylline hummingbird	<i>Amazilia beryllina</i>	Golden eagle	<i>Aquila chrysaetos</i>
Bewick's wren	<i>Thryomanes bewickii</i>	Grace's warbler	<i>Dendroica graciae</i>
Black-billed magpie	<i>Pica pica</i>	Gray flycatcher	<i>Empidonax wrightii</i>
Black-capped chickadee	<i>Parus atricapillus</i>	Great horned owl	<i>Bubo virginianus</i>
Black-capped vireo	<i>Vireo atricapillus</i>	Greater peewee	<i>Contopus pertinax</i>
Black-chinned hummingbird	<i>Archilochus alexandri</i>	Greater roadrunner	<i>Geococcyx californianus</i>
Black-headed grosbeak	<i>Pheucticus melanocephalus</i>	Green-tailed towhee	<i>Pipilo chlorurus</i>
Black-throated gray warbler	<i>Dendroica nigrescens</i>	Hairy woodpecker	<i>Picoides villosus</i>
Black phoebe	<i>Sayornis nigricans</i>	Hammond's flycatcher	<i>Empidonax hammondii</i>
Blue grouse	<i>Dendragapus obscurus</i>	Hepatic tanager	<i>Piranga flava</i>
Blue-gray gnatcatcher	<i>Poliotila caerulea</i>	Hermit thrush	<i>Catharus guttatus</i>
Blue grosbeak	<i>Guiraca caerulea</i>	House finch	<i>Carpodacus mexicanus</i>
Blue-throated hummingbird	<i>Lampornis clemenciae</i>	House sparrow	<i>Passer domesticus</i>
Brewer's blackbird	<i>Euphagus cyanocephalus</i>	House wren	<i>Troglodytes aedon</i>
Brewer's sparrow	<i>Spizella breweri</i>	Hutton's vireo	<i>Vireo huttoni</i>
Broad-tailed hummingbird	<i>Selasphorus platycercus</i>	Killdeer	<i>Charadrius vociferus</i>
Brown creeper	<i>Certhia americana</i>	Lark sparrow	<i>Chondestes grammacus</i>
Brown-headed cowbird	<i>Molothrus ater</i>	Lazuli bunting	<i>Passerina amoena</i>
Buff-breasted flycatcher	<i>Empidonax fulvifrons</i>	Lesser goldfinch	<i>Carduelis psaltria</i>
Bullock's orioles	<i>Icterus bullockii</i>	Lesser nighthawk	<i>Chordeiles acutipennis</i>
Bushtit	<i>Psaltriparus minimus</i>	Lewis' woodpecker	<i>Melanerpes lewis</i>
California spotted owl	<i>Strix occidentalis occidentalis</i>	Lincoln's sparrow	<i>Melospiza lincolnii</i>
Calliope hummingbird	<i>Stellula calliope</i>	Loggerhead shrike	<i>Lanius ludovicianus</i>
Canada jay	<i>Perisoreus canadensis</i>	Lucy's warbler	<i>Vermivora luciae</i>
Canyon wren	<i>Catherpes mexicanus</i>	Mallard	<i>Anas platyrhynchos</i>
Cañon towhee	<i>Pipilo fuscus</i>	MacGillivray's warbler	<i>Oporornis tolmiei</i>
Cassin's finch	<i>Carpodacus cassinii</i>	Magnificent hummingbird	<i>Eugenes fulgens</i>
Cassin's kingbird	<i>Tyrannus vociferans</i>	Merriam's turkey	<i>Meleagris gallopavo merriami</i>
Cedar waxwing	<i>Bombycilla cedrorum</i>	Mexican chickadee	<i>Parus sclateri</i>
Chipping sparrow.	<i>Spizella passerina</i>	Mexican parrot	<i>Amazona</i> spp.
Clark's nutcracker	<i>Nucifraga columbiana</i>	Mexican spotted owl	<i>Strix occidentalis lucida</i>
Common crow	<i>Corvus brachyrhynchos</i>	Merlin	<i>Falco columbarius</i>
Common nighthawk	<i>Chordeiles minor</i>	Military macaw	<i>Ara militaris</i>
Common raven	<i>Corvus corax</i>	Montezuma quail	<i>Cyrtonyx montezumae</i>
Common poorwill	<i>Phalaenoptilus nuttallii</i>	Mountain bluebird	<i>Sialia currucoides</i>
Cooper's hawk	<i>Accipiter cooperii</i>	Mountain chickadee	<i>Parus gambeli</i>
cordilleran (western) flycatcher	<i>Empidonax difficilis</i>	Mourning dove	<i>Zenaida macroura</i>
Curve-billed thrasher	<i>Toxostoma curvirostre</i>	Northern flicker	<i>Colaptes auratus</i>
Dark-eyed junco	<i>Junco hyemalis</i>	Northern goshawk	<i>Accipiter gentilis</i>

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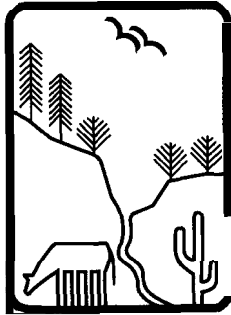
Common name	Scientific name	Common name	Scientific name
Northern mockingbird	<i>Mimus polyglottos</i>	Spotted towhee	<i>Pipilo maculatus</i>
Northern pygmy owl	<i>Glaucidium gnoma</i>	Steller's jay	<i>Cyanocitta stelleri</i>
Northern woodpecker	<i>Picoides</i> spp.	Sulphur-bellied flycatcher	<i>Myiodynastes luteiventris</i>
Olive-sided flycatcher	<i>Contopus borealis</i>	Summer tanager	<i>Piranga rubra</i>
Olive warbler	<i>Peucedramus taeniatus</i>	Swainson's thrush	<i>Catharus ustulatus</i>
Orange-crowned warbler	<i>Vermivora celata</i>	Thick-billed parrot	<i>Rhynchopsitta pachyrhyncha</i>
Painted redstart	<i>Myioborus pictus</i>	Three-toed woodpecker	<i>Picoides tridactylus</i>
Peregrine falcon	<i>Falco peregrinus</i>	Townsend's solitaire	<i>Myadestes townsendi</i>
Pileated woodpecker	<i>Dryocopus pileatus</i>	Townsenb's warbler	<i>Dendroica townsendi</i>
Pine grosbeak	<i>Pinicola enucleator</i>	Tree swallow	<i>Tachycineta bicolor</i>
Pine siskin	<i>Carduelis pinus</i>	Turkey vulture	<i>Cathartes aura</i>
Pinyon jay	<i>Gymnorhinus cyanocephalus</i>	Vaux's swift	<i>Chaetura vauxi</i>
Plain titmouse	<i>Parus inornatus</i>	Veery	<i>Catharus fuscescens</i>
Prairie chicken	<i>Tympanuchus</i> spp.	Vesper sparrow	<i>Poocetes gramineus</i>
Purple martin	<i>Progne subis</i>	Voilet-crowned hummingbird	<i>Amazilia violiceps</i>
Pygmy nuthatch	<i>Sitta pyhmaea</i>	Violet-green swallow	<i>Tachycineta thalassina</i>
Quetzal	<i>Pharomachrus</i> spp.	Virginia's warbler	<i>Vermivora virginiae</i>
Red-breasted nuthatch	<i>Sitta canadensis</i>	Warbling vireo	<i>Vireo gilvus</i>
Red crossbill	<i>Loxia curvirostra</i>	Water pipit	<i>Anthus spinoletta</i>
Red-faced warbler	<i>Cardellina rubrifrons</i>	Western bluebird	<i>Sialia mexicana</i>
Red-naped sapsucker	<i>Sphyrapicus varius nuchalis</i>	Western kingbird	<i>Tyrannus verticalis</i>
Red-tailed hawk	<i>Buteo jamaicensis</i>	Western meadowlark	<i>Sturnella neglecta</i>
Red-shafted northern flicker	<i>Colaptes auratus</i>	Western screech owl	<i>Otus kennicotti</i>
Rivoli's hummingbird	<i>Eugenes fulgens</i>	Western tanager	<i>Piranga ludoviciana</i>
Rock dove	<i>Columba livia</i>	Western wood pewee	<i>Contopus sordidulus</i>
Rock wren	<i>Salpinctes obsoletus</i>	Whip-poor-will	<i>Caprimulgus vociferus</i>
Rosy finch	<i>Leucosticte arctoa</i>	White-breasted nuthatch	<i>Sitta carolinensis</i>
Rough-winged swallow	<i>Stelgidopteryx serripennis</i>	White-crowned sparrow	<i>Zonotrichia leucophrys</i>
Ruby-crowned kinglet	<i>Regulus calendula</i>	White-throated swift	<i>Aeronautes saxatalis</i>
Rufous hummingbird	<i>Selasphorus rufus</i>	White-winged crossbill	<i>Loxia leucoptera</i>
Sandhill crane	<i>Grus canadensis</i>	Whooping crane	<i>Grus americana</i>
Savannah sparrow	<i>Passerculus sandwichensis</i>	Wild turkey	<i>Meleagris gallopavo</i>
Saw-whet owl	<i>Aegolius acadicus</i>	Williamson's sapsucker	<i>Sphyrapicus thyroideus</i>
Say's phoebe	<i>Sayornis saya</i>	Willow flycatcher	<i>Empidonax traillii</i>
Scarlet macaw	<i>Ara macao</i>	Wilson's warbler	<i>Wilsonia pusilla</i>
Scott's orioles	<i>Icterus parisorum</i>	Winter wren	<i>Troglodytes troglodytes</i>
Scrub jay	<i>Aphelocoma coerulescens</i>	Wright's flycatcher	<i>Empidonax wrightii</i>
Sharp-shinned hawk	<i>Accipiter striatus</i>	Yellow-bellied sapsucker	<i>Sphyrapicus varius</i>
Solitary vireo	<i>Vireo solitarius</i>	Yellow-eyed junco	<i>Junco phaeonotus</i>
Song sparrow	<i>Melospiza melodia</i>	Yellow-rumped warbler	<i>Dendroica coronata</i>

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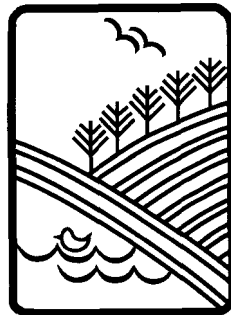
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Rocky Mountain Forest and Range Experiment Station

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