FIRE AND AVIAN ECOLOGY IN NORTH AMERICA

VICTORIA A. SAAB AND HUGH D. W. POWELL, EDITORS

Studies in Avian Biology No. 30
A Publication of the Cooper Ornithological Society

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Cover drawing: Black-backed Woodpecker (*Picoides arcticus*), Grasshopper Sparrow (*Ammodramus savannarum*), and Northern Bobwhite (*Colinus virginianus*). Drawing by Joyce V. VanDeWater.

STUDIES IN AVIAN BIOLOGY

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Studies in Avian Biology is a series of works too long for *The Condor*, published at irregular intervals by the Cooper Ornithological Society. Manuscripts for consideration should be submitted to the editor. Style and format should follow those of previous issues.

Price $18.00 including postage and handling. All orders cash in advance; make checks payable to Cooper Ornithological Society. Send orders to Cooper Ornithological Society, *c/o* Western Foundation of Vertebrate Zoology, 439 Calle San Pablo, Camarillo, CA 93010.

ISBN: 0-943610-64-8

Library of Congress Control Number: 2005925879
Printed at Cadmus Professional Communications, Ephrata, Pennsylvania 17522
Issued: 27 July 2005

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PREFACE

Many North American ecosystems evolved under the influence of wildfire. Nevertheless, for much of the twentieth century, land managers concentrated their fire management activities on minimizing the amount of land that burned. The 1980s saw wider acceptance of fire with both wild and managed fire commonly incorporated into land management plans. Interest in this topic grew over the course of several years during informal discussions between the editors and organizers of the Third International Partners in Flight Conference in Asilomar, California in 2002. Those discussions led to a half-day symposium organized by one of us (VAS) that was held during the Partners in Flight Conference.

The focus of the symposium was to evaluate patterns in the way humans have altered fire regimes and to examine the consequences on populations of birds and their habitats throughout North America. The symposium was intended from the onset to serve as the basis for a volume of *Studies in Avian Biology*. Most of the 11 chapters contained in this volume are based on symposium presentations, although not all topics discussed in the symposium are represented here (e.g., Mexico).

We thank the Cooper Ornithological Society for providing logistical support and an excellent outlet for the symposium, and our colleagues who graciously served as peer reviewers for the chapters in this volume: Robert Askins, Bill Block, Carl Bock, Greg Butcher, Mary Chase, Courtney Conway, Richard DeGraff, Jane Fitzgerald, Luke George, Matt Vander Haegen, Chuck Hunter, Dick Hutto, Frances James, Rudy King, John Lehmkuhl, Ed Murphy, Ken Rosenberg, Robin Russell, Janet Ruth, Tom Sisk, and Joel Sauder. We are grateful to the United States Forest Service for generously providing funds to support the publication of this volume, facilitated by Beatrice Van Horne and Carl Edminster, and for awarding funds through the National Fire Plan. We also thank the Joint Fire Sciences Program for their financial support. We appreciate the editing contributions of *Studies in Avian Biology* editors John Rotenberry and especially Carl Marti. The research reported in this volume has not been subjected to Agency review, and therefore does not necessarily reflect the views of the U.S. Forest Service. We thank Dan Huebner for creating the maps, Joyce VanDeWater for producing the cover artwork, and Cecilia Valencia for translating the abstracts into Spanish.

Victoria A. Saab
Hugh D. W. Powell

Studies in Avian Biology No. 30:1–13

FIRE AND AVIAN ECOLOGY IN NORTH AMERICA: PROCESS INFLUENCING PATTERN

VICTORIA A. SAAB AND HUGH D. W. POWELL

Abstract. We summarize the findings from 10 subsequent chapters that collectively review fire and avian ecology across 40 North American ecosystems. We highlight patterns and future research topics that recur among the chapters. Vegetation types with long fire-return intervals, such as boreal forests of Canada, forests at high elevations, and those in the humid Pacific Northwest, have experienced the least change in fire regimes. The spatial scale of fires has generally decreased in eastern and central North America, while it has largely increased in the western United States. Principal causes of altered fire regimes include fire suppression, cessation of ignitions by American Indians, livestock grazing, invasion by exotic plants, and climate change. Each chapter compiles the responses of birds to fire in a specific region. We condensed these responses (203 species) into a summary table that reveals some interesting patterns, although it does not distinguish among fire regimes or time since fire. Aerial, ground, and bark insectivores clearly favored recently burned habitats, whereas foliage gleaners preferred unburned habitats. Species with closed nests (i.e., cavity nesters) responded more favorably to newly burned habitats than species with open-cup nests, and those nesting in the ground and canopy layers generally favored burned habitats compared to shrub nesters. Future directions for research suggested by authors of individual chapters fell into two broad groups, which we characterized as habitat-centered questions (e.g., How does mechanical thinning affect habitat?) and bird-centered questions (e.g., How does fire affect nest survival?).

Key Words: alterations in fire regimes, avian ecology, bird responses, fire ecology, historical fire regimes, North American vegetation.

FUEGO Y ECOLOGÍA DE AVES EN NORTEAMÉRICA: PROCESO INFLUENCIANDO EL PATRÓN

Resumen. En este capítulo resumimos distintos descubrimientos de 10 capítulos subsecuentes, los cuales revisan la ecología del fuego y de las aves a través de 40 ecosistemas de Norte América. Subrayamos los patrones y temas para la investigación recurrentes entre los capítulos. Tipos de vegetación con intervalos largos de recurrencia de incendios, tales como los bosques boreales de Canadá, bosques de altas elevaciones, y aquellos en la parte húmeda del Pacífico Noroeste, han experimentado el menor cambio en los regimenes de incendios. La escala espacial de incendios generalmente ha disminuido en el este y centro de Norte América, mientras que ha incrementado enormemente en la par oeste de los estados Unidos. La principales causas de regimenes de incendio alterados incluyen la supresión de incendios, la terminación por parte de los Indios de Norte América de la provocación de incendios, el pastoreo, la invasión de plantas exóticas, y el cambio climático. Cada capítulo compila las respuestas de las aves al fuego de una región en particular. Condensamos dichas respuestas (203 especies) en una tabla, la cual revela algunos patrones interesantes, a pesar de que no reconoce regimenes de incendio o el tiempo transcurrido a partir del incendio. Insectívoros aéreos, de suelo y de la corteza claramente se favorecen de habitats recientemente incendiados, en donde especies de follaje espigado prefieren habitats sin incendiar. Especies con nidos cerrados (ej. que anidan en cavidades) respondieron más favorablemente a habitats recientemente quemados que aquellas especies con nidos de copa abierta, y las especies que anidan en el suelo y en las copas, generalmente se favorecieron de habitats quemados, en comparación con los que anidan en arbustos. Futuras direcciones para la investigación, sugeridas por los autores de cada capítulo recaen en dos grandes grupos, los cuales caracterizamos como preguntas centradas en el habitat (ej. cómo las prácticas mecánicas para aclareo afectan el hábitat? Y preguntas centradas en las aves (ej. Cómo el fuego afecta a la supervivencia de nidos?)

Many North American ecosystems evolved under the influence of wildfire. Nevertheless, for much of the twentieth century, land managers concentrated on minimizing the amount of land that burned. The wisdom of fire suppression seemed self-evident after the 1910 wildfires ravaged much of the West, despite dissenting opinion by prominent forest scientists as early as the 1920s (Carle 2002). For nearly a century, the widespread suppression of fire and the rise of other land uses, particularly livestock grazing and timber harvest, slowly altered ecosystems and ultimately led to larger wildfires in many places (Dombeck et al. 2004).

Scientific and political attitudes toward fire and fire suppression developed as a result of lessons learned in specific regions of the continent such as the importance of frequent, low-severity fire (and the possibility of prescribing it) in the pine forests of the Southeast. Gradually, these lessons were applied to other geographic regions, such as the ponderosa pine forests of the Southwest and the mixed-conifer forests of the Sierra Nevada (Carle 2002). Wider acceptance of fire as a natural disturbance was seen during the 1980s when wild and managed fires were commonly incorporated into land management plans. Continued research described the variability inherent in fire regimes, even within a single vegetation type, and underscored the importance of keeping local conditions in mind when applying principles learned elsewhere (e.g., Ehle and Baker 2003).

The earliest research to recognize the negative effects of fire suppression on bird communities of North America was conducted by Stoddard (1931, 1963; see Engstrom et al*., this volume*). Stoddard demonstrated the critical role of wild and managed fire in maintaining the health of pine ecosystems and of bird populations in the southeastern United States. Early studies in the American Southwest also demonstrated the influence of fire suppression on avian communities. Marshall (1963) neatly documented some first principles in the effects of fire suppression by comparing coniferous-forest bird communities in northern Mexico, where fires were not suppressed, to fire-suppressed forests of Arizona and New Mexico. Species common to heavier forest cover were more abundant in the denser U.S. forests, whereas species typical of relatively open conditions were more abundant in Mexican forests. Other seminal work on the ecological relationships of fire and birds was conducted by Bock and Lynch (1970) in mixed-conifer forests of the Sierra Nevada, California. Their study was the first to contrast species richness and composition in recent wildfires to unburned forests, a powerful approach that remains underutilized today.

Along with concern about the influence of fire suppression on ecological systems (Laverty and Williams 2000, USDA Forest Service 2000), interest in fire effects on bird communities has also increased in the last 25 yr (Lotan and Brown 1985, Krammes 1990, Ffolliott et al. 1996). The following 10 chapters gather what we have learned about fire history, fire regimes and their alterations, and the ensuing responses of the bird communities. Taking our cue from the geographically specific lessons of the past, each chapter describes the fire regimes of a particular region of the continent. We hope that this organizational scheme will allow regional patterns to emerge from each chapter, and a reading of the volume will reveal patterns with a wider applicability. In this chapter, we highlight some of these recurrent patterns and summarize future research topics.

FIRE REGIMES AND ECOSYSTEMS COVERED IN THIS VOLUME

The next 10 chapters review over 40 major ecosystems, their corresponding fire regimes, and the associated bird communities (Fig. 1). Bock and Block (Chapter 2) describe the most floristically diverse region, the eight major ecosystems of the southwestern United States and northern Mexico, which span desert grasslands to high-elevation spruce forests. Purcell and Stephens (Chapter 3) treat the fire regime of the unique oak woodlands that exist in the central valley of California. Finishing our treatment of the Pacific coast, Huff et al. (Chapter 4) describe 12 vegetation types of the maritime Pacific Northwest.

Knick et al. (Chapter 5) summarize research for five vegetation types of the vast intermountain shrub-steppe, where alteration to the fire regime has recently gained attention as a pressing management problem (Knick et al. 2003, Dobkin and Sauder 2004). Saab et al. (Chapter 6) describe fire regimes in five Rocky Mountain forest types that occur between the desert Southwest and the southern edge of the Canadian boreal forests. Hannon and Drapeau discuss fire in the immense boreal forest of Canada (Chapter 7). Moving eastward from the Rocky Mountain front, Chapter 8 (Reinking) addresses changes to the natural fire regime of the tallgrass prairie region. Artman et al. discuss four vegetation types in eastern deciduous forests (Chapter 9). Vickery et al. take on the volume's smallest region, the grasslands and shrublands of the Northeast, which are largely of human origin and so present special challenges in management (Chapter 10). Engstrom et al. (Chapter 11) close the volume with the topic of fire and birds in pine savannas and prairies of the Southeast, where many of the questions we are still asking about the relationship between ecosystems, fire, and bird communities were first raised.

Most of these vegetation types have fire as some component of their natural disturbance regime, although natural fire is extremely rare in some types (e.g., Sonoran desert of the Southwest and coastal forests of the maritime Pacific Northwest). The diversity of climate, topography, and vegetation across North America results in a wide range of wildfire regimes, as described by fire severity and fire frequency. These range from frequent, low-severity fires (e.g., southeastern longleaf pine forests) to infrequent, high-severity fires (e.g., the Canadian boreal forest). Across vegetation types,

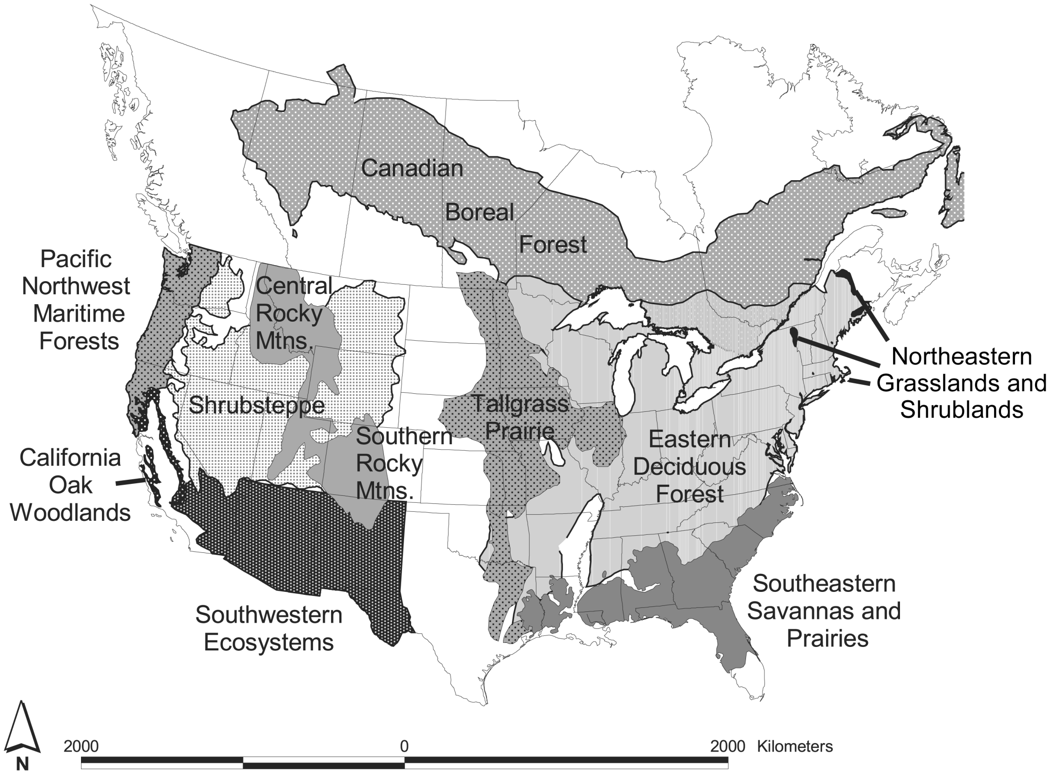

FIGURE 1. Spacial extent of the 10 geographic regions covered in this volume.

similar fire severities can occur at very different frequencies (see Figs. 1–2; Brown 2000).

FIRE TERMINOLOGY

To provide an understanding of terms repeatedly used in this volume, we summarize the most common terminology in describing fire effects. Fuels are vegetative biomass, living or dead, which can be ignited (Brown 2000). Fuel components refer to items such as dead woody material (usually subdivided into size classes), litter, duff, herbaceous vegetation, and live foliage. Fire regime is defined by the historical variability in fire frequency, extent or size, magnitude, and timing (seasonality) (Agee 1993). For this volume, we define historical to mean prior to European settlement in North America. Fire frequency is the number of fires occurring per unit time (usually years) in a given area. Fire frequency is often described by an alternate measurement, the fire-return interval, which is the time (in years) between two successive fires in the same area. Prescribed fires (distinct from naturally caused wildfires) are planned by forest managers and deliberately ignited to meet specific objectives.

A fire's magnitude is characterized by two complementary measures: fire intensity, a simple measure of heat released per unit area (and often roughly characterized by flame lengths); and fire (or burn) severity, a measure of a fire's long-term effects on plants or whole ecosystems. The intensity of a fire depends on topography, climate and weather, and vegetation or fuels. High-severity fires, also termed stand-replacement or crown fires, are defined by the widespread death of aboveground parts of the dominant vegetation, changing the aboveground structure substantially in forests, shrublands, and grasslands (Smith 2000). High-severity fires typically burn treetops, but very hot surface fires can also kill trees by burning root systems without ever rising above the forest floor. In contrast, low-severity or understory fires consume ground-layer vegetation and duff, but rarely kill overstory trees and do not substantially change the structure of the dominant vegetation (Smith 2000, Schoennagel et al. 2004). Mixed-severity fires either cause selective mortality in dominant vegetation, depending on different plant species' susceptibility to fire, or burn different patches at high or low severity, imprinting the

Table 1. Summary of likely changes in fire regimes since European settlement in major vegetation types across North America. Changes are summarized from each of the chapters in this volume; chapter authors are given in parentheses after each region designation. Decreases are indicated by –, increases indicated by +, and no change by 0 for each characteristic of the fire regime. See individual chapters for full descriptions of vegetation types.

Vegetation type	Frequency	Severity	Spatial scale
Southwestern United States (Bock and Block)			
Chihuahuan desertscrub and desert grassland	–	–	–
Sonoran desert	+	+	+
Madrean evergreen savanna	–	–	–
Interior chaparral	–	–	–
Pinyon-juniper woodland	–	+	+
Ponderosa pine and pine-oak woodland	–	+	+
Mixed conifer forests	–	+	+
Riparian woodlands	+	+	+
California oak woodland (Purcell and Stephens)	–	+	+
Maritime Pacific Northwest (Huff et al.)			
Mixed conifer	–	+	+
Coastal forests[a]	0	0	0
Oak woodland and dry grassland	–	–	–
Shrubsteppe (Knick et al.)			
Mesic shrubsteppe	–	–	–
Xeric shrubsteppe	+	+	+
Rocky Mountains (Saab et al.)			
Pinyon-juniper, upper ecotone[b]	–	+	+
Pinyon-juniper, closed woodland[a, b]	0	0	0
Ponderosa pine	–	+	+
Mixed conifer	+	0	+
Lodgepole pine	0	0	0
Spruce-fir	0	0	0
Boreal forests of Canada (Hannon and Drapeau)			
Boreal plains	–	0	–
Boreal shield	–	0	–
Central tallgrass prairie (Reinking)	–/+[c]	0	–
Eastern deciduous forest (Artman et al.)			
Oak-hickory and oak-pine	–		–
Maple-beech and birch-aspen[a]	0	0	0
Grasslands and shrublands of the Northeast (Vickery et al.)	–		–
Southeastern pine savannas and prairies (Engstrom et al.)	–	+	–

[a] Historical fire was extremely rare in these vegetation types with fire-return intervals in the hundreds of years.

[b] Evidence conflicts concerning changes in fire regimes of pinyon-juniper woodlands (Baker and Shinneman 2003).

[c] Although fire frequency has declined in most of the tallgrass prairie, it has increased due to prescribed burning for livestock forage in a portion of the Flint Hills.

landscape with fire's characteristic mosaic signature (Smith 2000).

Fire suppression is the act of preventing fire from spreading, whereas fire exclusion is the policy of suppressing all wildland fires in an area (Smith 2000). For more information on fire terminology see the glossary web pages of the Fire Effects Information System (USDA Forest Service 2004).

PATTERNS AND CAUSES OF ALTERED FIRE REGIMES

The frequency, severity, and spatial scale (i.e., size and distribution) of fires across most of North America have changed over the last century (Table 1). The vegetation types in which there has been little change lie primarily outside the United States, in boreal forests of Canada (Hannon and Drapeau, *this volume*), and pine/grasslands of northern Mexico (Marshall 1963, Minnich et al. 1995, Bock and Block, *this volume*). Within the United States, the least change to fire regimes can be found in vegetation types with long fire-return intervals, including vegetation types at high elevations and in the humid Pacific Northwest. The spatial scale of fires has generally decreased in eastern and central North America, while it has largely increased in the western United States (Table 1). Fire has become less frequent throughout North America, except in vegetation types where fire was always rare historically (e.g., Sonoran desert, riparian woodlands, and xeric shrubsteppe; Bock and Block, *this volume*; Knick et al., *this volume*). Fire frequency has actually increased in some portions of the tallgrass prairie region, where annual fire is often used for range management (Reinking, *this volume*). Fire severity has primarily increased in the western United States, while little change in severity was reported in central and eastern North America.

Principal causes of altered fire regimes include fire suppression, livestock grazing, invasive plant species, climate change, and an absence of ignitions by American Indians (Table 2). Fire suppression and livestock grazing are the most pervasive disruptions of natural fire regimes, although livestock grazing is primarily a problem in the western United States. Next most common are the spread of invasive plants and climate change. Habitat fragmentation is also a common cause of changes in fire regimes throughout the continent (Table 2).

Historical fire patterns generally differ from contemporary fire regimes, at least where historical fire regimes are well understood (e.g., Baker and Ehle 2001). In some regions, long-standing practices of burning by American Indians have greatly complicated the task of distinguishing natural from human-altered fire regimes. Where this is the case, the authors of two chapters in this volume (Engstrom et al., Purcell and Stephens) argue that understanding past fire regimes is of less practical value than investigating how present-day fires fit into the landscape, and how they can be used to achieve management objectives.

PATTERNS OF AVIAN RESPONSE TO ALTERED FIRE REGIMES

To a large extent, researchers are still describing the responses of birds to differing fire regimes in detail. This work is a necessary prerequisite to measuring the effects of fire regime alterations (or restorations) on bird populations. Until such experiments have been conducted, we can summarize the ways in which various species, guilds, or communities are known to respond to fire and then hypothesize how changes in fire regimes may be expected to affect them. To do this, the authors of each chapter summarized studies from their region that described fire effects on one or more bird species. Fire effects were interpreted as adverse, neutral, beneficial, or mixed depending on the species and time frame considered. The great majority of studies reported fire effects in terms of change in relative abundance, during the breeding season, within 5 yr after fire.

In this chapter, we summarize the species responses reported from each of the 10 chapters in this volume. We classify responses for 203 North American bird species as either positive, negative, inconclusive (i.e., not enough data to determine the response), or mixed (i.e., data suggest both a positive and negative response) (Table 3, Appendix). Species were categorized by nest type (open vs. closed [cavity]), nest layer (canopy, shrub, ground or near ground), and foraging guild based on the *Birds of North America* accounts (Poole and Gill 2004) and Ehrlich et al. (1988). Although this type of summary is necessarily coarse resolution (e.g., does not distinguish between fire regimes or time since fire), we feel it offers valuable insights.

Inconclusive responses were prevalent among the 203 species, but some patterns were apparent. Aerial, ground, and bark insectivores clearly favored burned habitats, whereas foliage gleaners preferred unburned habitats. Species with closed nests responded more favorably to burned habitats than species with open-cup nests, and those nesting in the ground and canopy layers generally favored burned habitats compared to shrub nesters.

Each region clearly supported assemblages of fire specialists as well as groups of species that primarily occupy unburned habitats. For example, species recorded more often in burned habitats included fairly well-known fire specialists such as the Northern Bobwhite (*Colinus virginianus*), Black-backed Woodpecker (*Picoides arcticus*), Red-cockaded Woodpecker (*Picoides borealis*), Western Bluebird (*Sialia mexicana*), and Mountain Bluebird (*Siala currucoides*). In addition, authors identified a range of species with less well-appreciated associations with burned habitat, including Wild Turkey (*Meleagris gallopavo*), Northern Flicker (*Colaptes auratus*), Eastern Wood-Pewee (*Contopus virens*) and Western Wood-Pewee (*Contopus sordidulus*), Tree Swallow (*Tachycineta bicolor*), House Wren (*Troglodytes aedon*), Rock Wren (*Salpinctes obsoletus*), American Robin (*Turdus migratorius*), Connecticut Warbler (*Oporornis agilis*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Chipping Sparrow (*Spizella passerina*), Grasshopper Sparrow (*Ammodramus savannarum*), Vesper Sparrow (*Pooecetes gramineus*), and Horned Lark (*Eremophila alpestris*) (for a complete listing of species responses, see the summary table in each chapter). Species found more often in unburned habitats included Montezuma Quail (*Cyrtonyx montezumae*), Ash-throated Flycatcher (*Myiarchus cin-*

TABLE 2. REPORTED CAUSES OF ALTERED FIRE REGIMES IN MAJOR VEGETATION TYPES ACROSS NORTH AMERICA, AS SUMMARIZED IN EACH CHAPTER OF THIS VOLUME (AUTHORS APPEAR IN PARENTHESES FOLLOWING EACH REGION NAME). SEE INDIVIDUAL CHAPTERS FOR FULL DESCRIPTIONS OF VEGETATION TYPES.

Vegetation type	Fire suppression	Livestock grazing	Invasive plants	Climate change	Fire practices of American Indians	Other causes
Southwestern United States (Bock and Block)						
Chihuahuan desertscrub and desert grassland	X	X	X	X		Control of prairie dogs
Sonoran desert			X			
Madrean evergreen savanna	X	X				
Interior chaparral	X	X		X		Drought
Pinyon-juniper	X	X				
Ponderosa pine and pine-oak woodland	X	X				Logging
Mixed conifer	X					
Riparian woodland		X	X			Water impoundment
California oak woodland (Purcell and Stephens)	X	X	X		X	Habitat fragmentation
Maritime Pacific Northwest (Huff et al.)						
Mixed conifer	X	X			X	
Coastal forests[a]						
Oak woodland and dry grassland	X				X	Habitat fragmentation from agricultural and rural development
Shrubsteppe (Knick et al.)						
Mesic shrubsteppe	X	X	X			
Xeric shrubsteppe		X	X	X		Habitat fragmentation
Rocky Mountains (Saab et al.)						
Pinyon-juniper—upper ecotone[b]	X	X		X		
Pinyon-juniper—closed woodland zone[a, b]						
Ponderosa pine	X	X				Logging
Mixed conifer	X	X		X		
Lodgepole pine[a]						
Spruce-fir[a]						
Boreal forests of Canada (Hannon and Drapeau)						
Boreal plains	X			X		Logging and habitat fragmentation
Boreal shield				X		Logging and habitat fragmentation
Central tallgrass prairie (Reinking)	X	X	X	X	X	Habitat fragmentation from agricultural and residential development; drought; prescribed fire
Eastern deciduous forests (Artman et al.)						
Oak-hickory and oak-pine forests	X		X		X	Habitat fragmentation from agricultural and rural development
Maple-beech and birch-aspen[a]						
Northeastern grasslands and shrublands (Vickery et al.)	X				X	
Southeastern pine savannas and prairies (Engstrom et al.)	X				X	Habitat fragmentation from agricultural and urban development

[a] Little to no change in fire regimes reported for these forest types because historical fire was rare in these vegetation types with fire-return intervals in the hundreds of years.

[b] Evidence conflicting for documented changes in fire regimes of pinyon-juniper woodlands (see review by Baker and Shinneman 2003).

TABLE 3. SUMMARY OF BIRD RESPONSES TO FIRE FOR 203 NORTH AMERICAN SPECIES. THIS TABLE DOES NOT DISTINGUISH BETWEEN FIRE TYPES (WILDLAND, PRESCRIBED, STAND-REPLACING, UNDERSTORY, VARIOUS SEVERITIES), VEGETATION TYPES, OR TIME SINCE FIRE.

		Response (% of studies)			
	N[a]	Positive	Negative	No response	Mixed response
Nest Type					
Closed nesters	244	36	18	40	5
Open nesters	544	29	23	39	9
Cowbirds	6	50	0	50	0
Nest layer					
Ground nesters	215	35	21	37	7
Shrub nesters	150	25	33	35	7
Canopy nesters	423	31	18	42	9
Cowbirds	6	50	0	50	0
Foraging guild					
Aerial insectivores	90	48	9	34	9
Bark insectivores	103	34	20	38	8
Ground insectivores	120	31	22	39	8
Foliage insectivores	164	17	30	47	5
Carnivores	17	35	18	41	6
Nectarivores	4	50	0	25	25
Omnivores	296	32	21	37	9

[a] Number of species-study combinations.

erascens), Steller's Jay (*Cyanocitta stelleri*), Winter Wren (*Troglodytes troglodytes*), Chestnut-backed Chickadee (*Poecile rufescens*), Golden-crowned Kinglet (*Regulus satrapa*), Varied Thrush (*Ixoreus naevius*), Hooded Warbler (*Wilsonia citrina*), Black-and-white Warbler (*Mniotilta varia*), Spotted Towhee (*Pipilo maculatus*), and Field Sparrow (*Spizella pusilla*). Interestingly, differing responses were reported among regions for some species, such as Williamson's Sapsucker (*Sphyrapicus thyroideus*), Brown Creeper (*Certhia americana*), Hermit Thrush (*Catharus guttatus*), and Henslow's Sparrow (*Ammodramus henslowii*).

Although experiments have yet to document actual changes to bird communities stemming from changes to fire regimes, the above patterns can help make informed guesses about the direction of some changes. Where fire suppression makes forests less open, we might expect more shrub nesters, open-cup nesters, and foliage gleaners. Fire suppression has reduced the amount of recently burned habitat on the landscape, possibly reducing populations of postfire-habitat specialists (Hutto 1995). When fire-suppressed ecosystems burn at higher severities than normal, as is a concern in southeastern and southwestern pine forests and some grasslands or shrublands, insectivores (other than foliage gleaners) may benefit. At the same time, regions with low-severity fire regimes may lie outside the geographic or elevational range of some high-severity postfire specialists, meaning that such uncharacteristically high-severity burns may not be recolonized by the same suite of postfire specialists seen elsewhere. In addition, such an alteration of fire regime would likely reduce suitability for the species already there (i.e., low-severity specialists). These sorts of hypotheses are admittedly speculative, and we are confident that data from experiments involving specific vegetation types and fire regimes can greatly improve them.

MANAGEMENT TOOLS FOR RESTORING FIRE REGIMES

Management tools for restoring fire regimes center around prescribed fire. Some ecosystems may be able to be managed solely or at least primarily by prescribed fire, particularly nonforest ecosystems such as northeastern grasslands, tallgrass prairie, and shrubsteppe. Forests that evolved under frequent low-severity fire, such as southwestern ponderosa pine, should be amenable to management by prescribed fire that mimics the frequency and severity of natural (or at least historic, pre-European settlement) fire regimes (Schoennagel et al. 2004). However, a return to frequent fires in these ecosystems will require careful planning, since fire exclusion has led to well-documented increases in fuel loads in many of these forests, and fires are now likely to burn with greater severity than was typical in the past (e.g, Covington et al. 1997, Fulé et al. 2002). Forests that historically burned at mixed or high severity are much more problematic: prescribed low-severity fires will not restore a natural fire regime to these ecosystems, but high-severity fires present the real danger of destroying human settlements as well as the practical problem of public opposition to large swaths of blackened land and reduced air quality.

To aid the safe reintroduction of fire, managers have at their disposal the tools of mechanical fuels reduction and selective ignition. The once-prevalent view that logging and thinning (and mowing in grasslands) can mimic the effects of fire no longer holds much sway, but these methods do hold promise for reducing fuel loads before prescribed fire is applied (Imbeau et al. 1999; Wikars 2002; Zuckerberg 2002; Hannon and Drapeau, *this volume*; Vickery et al., *this volume*). Fuels reduction requires much different prescriptions than commercial logging, because fine ground fuels and saplings, not large-diameter trees, are most capable of carrying fire over large areas and up into the forest canopy (Agee 1993, Schoennagel 2004).

RECOMMENDATIONS FOR FUTURE WORK

A clear result of this literature survey is that, despite much work in describing bird communities in various habitats, precious few controlled comparisons between burned and unburned habitats have been conducted. Much of what we expect birds to do in response to fire restoration comes as logical inferences made from what we know about plant community responses to fire (Purcell and Stephens use this approach in their chapter of this volume). It should be our next task to design experiments that test these inferences so that management decisions can be based on actual data.

In this respect, future directions for research can be divided into two groups: habitat-centered questions (e.g., How does mechanical thinning affect habitat? [Purcell and Stephens, Vickery et al., Huff et al., *this volume*]; How will supply of burned vs. old-growth forest change with climate change and development? [Hannon and Drapeau, Huff et al., *this volume*]), and bird-centered questions (see below). Both sets of questions are pressing, and authors in the chapters that follow have included both types in their recommendations for future research. Interested readers can find excellent habitat-centered reviews and discussions of the state of fire research elsewhere (e.g., *Conservation Biology* Vol. 15 No. 6 December 2001, Pp. 1536–1567 [Conservation Forum, five papers] and *Conservation Biology* Vol. 18 No. 4 August 2004, Pp. 872–986 [Special Section edited by Williams and DellaSala, 13 papers]). For this summary, we identify bird-centered questions that were identified as pressing issues in at least three chapters.

How do bird responses vary with severity, season, size, and age of the burn and with postfire management activities?

The most important next step is to understand the effects of these variables in shaping bird responses to fire. The many interactions among these variables dictate the need for carefully designed experimental studies rather than continued descriptive work.

How does fire affect reproductive success and nest survival?

Of nearly equal importance is the need to move away from measuring abundance and toward measuring reproductive success as dependent variables (Van Horne 1983, Bock and Jones 2004).

How does prescribed fire affect vegetation and birds?

Prescribed fire is widely seen as the most promising tool for reintroducing fire to North American ecosystems. At the same time, we know little about how differing fire prescriptions affect bird populations. Of particular importance is determining how dormant-season fires, which are relatively easily controlled, differ from growing-season fires, which are typical of natural fire regimes (Engstrom et al*., this volume*).

What are the landscape-level responses of species to fire?

Because fire influences landscapes, it is important that we study fire at large spatial scales. Ongoing advances in radio-telemetry and remote sensing technology and increasing precision in stable-isotope and population-genetics techniques (Clark et al. 2004) offer new avenues of inquiry into metapopulations of fire-associated species.

What mechanisms drive population change postfire?

Along with understanding how populations change in response to fire, we need to address why they change. Do foraging opportunities change

(Powell 2000)? Are nest sites created or destroyed (Li and Martin 1991)? Does predation pressure increase with time since fire (Saab et al. 2004)?

Despite growing awareness that fire exclusion and fire suppression have caused their own profound disturbances to the continent's forests and grasslands, as much as a billion dollars is still spent annually in fighting fires (i.e., in each of four of the last 10 yr; Dombeck et al. 2004). We agree with other recent authors that the indiscriminate fighting of fires, entrenched as it is in popular culture and in politics, is at best an inefficient use of scarce land management funds and at worst needlessly endangers the lives of firefighters. We believe that firefighting holds greatest promise for protecting the urban parts of the urban-wildland interface and for avoiding unnaturally severe fires in the few ecosystems adapted to a low-severity regime (DellaSala et al. 2004). The fractal nature of both exurban development and fire behavior means that in any given area the amount of this interface is large, and this certainly complicates this problem. Nevertheless, it clearly seems reactive to continue battling naturally ignited fires burning within historic ranges of severity (Schoennagel et al. 2004). Both economically and ecologically, the proactive alternative would be to fund research programs that will guide fire prescriptions, clarify the specific fuel treatments that can help restore fire to the landscape, and reveal the contributions of fire severity, size, season, and succession to the persistence of bird communities in landscapes across the continent.

ACKNOWLEDGMENTS

We thank Carl Marti and Robin Russell for reviewing this manuscript and Scott Story for technical assistance. We extend our heartfelt thanks to the volume authors for lending their expertise and effort to each of their chapters. We also thank the many experts who reviewed the chapters for their time and helpful comments.

Appendix. Foraging guild, nest layer, and nest type for 211 North American bird species whose responses to fire are reported in chapters 2–10 of this volume. Foraging guilds: AI = aerial insectivore, BI = bark insectivore, FI = foliage insectivore, GI = ground insectivore, CA = carnivore, NE = nectarivore, OM = omnivore. Nest layers: GR = ground, SH = shrub, CA = subcanopy to canopy. Nest types: O = open, C = closed (including cavity nesters as well as species nesting in crevices and domed or pendent nests). Categories were assigned according to Poole and Gill (2004) and Ehrlich et al. (1988).

Species	Forage guild	Nest layer	Nest type
Wood Duck (*Aix sponsa*)	OM	CA	C
Ruffed Grouse (*Bonasa umbellus*)	OM	GR	O
Blue Grouse (*Dendragapus obscurus*)	OM	GR	O
Greater Prairie-Chicken (*Tympanuchus cupido*)	OM	GR	O
Wild Turkey (*Meleagris gallopavo*)	OM	GR	O
Scaled Quail (*Callipepla squamata*)	OM	GR	O
Northern Bobwhite (*Colinus virginianus*)	OM	GR	O
Montezuma Quail (*Cyrtonyx montezumae*)	OM	GR	O
Black Vulture (*Coragyps atratus*)	CA	GR	C
Turkey Vulture (*Cathartes aura*)	CA	CL[a]	C
Northern Harrier (*Circus cyaneus*)	CA	GR	O
Sharp-shinned Hawk (*Accipiter striatus*)	CA	CA	O
Red-shouldered Hawk (*Buteo lineatus*)	CA	CA	O
Red-tailed Hawk (*Buteo jamaicensis*)	CA	CA	O
American Kestrel (*Falco sparverius*)	CA	CA	C
Upland Sandpiper (*Bartramia longicauda*)	OM	GR	O
Long-billed Curlew (*Numenius americanus*)	OM	GR	O
Wilson’s Snipe (*Gallinago delicata*)	OM	GR	O
White-winged Dove (*Zenaida asiatica*)	OM	SH	O
Mourning Dove (*Zenaida macroura*)	OM	SH	O
Yellow-billed Cuckoo (*Coccyzus americanus*)	FI	SH	O
Spotted Owl (*Strix occidentalis*)	CA	CA	O
Short-eared Owl (*Asio flammeus*)	CA	GR	O
Common Nighthawk (*Chordeiles minor*)	AI	GR	O
Calliope Hummingbird (*Stellula calliope*)	NE	CA	O
Broad-tailed Hummingbird (*Selasphorus platycercus*)	NE	CA	O
Rufous Hummingbird (*Selasphorus rufus*)	NE	CA	O
Lewis’s Woodpecker (*Melanerpes lewis*)	AI	CA	C
Red-bellied Woodpecker (*Melanerpes carolinus*)	BI	CA	C
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	AI	CA	C
Williamson’s Sapsucker (*Sphyrapicus thyroideus*)	OM	CA	C
Yellow-bellied Sapsucker (*Sphyrapicus varius*)	OM	CA	C
Red-naped Sapsucker (*Sphyrapicus nuchalis*)	OM	CA	C
Ladder-backed Woodpecker (*Picoides scalaris*)	BI	CA	C
Downy Woodpecker (*Picoides pubescens*)	BI	CA	C
Hairy Woodpecker (*Picoides villosus*)	BI	CA	C
Red-cockaded Woodpecker (*Picoides borealis*)	BI	CA	C
American Three-toed Woodpecker (*Picoides dorsalis*)	BI	CA	C
Black-backed Woodpecker (*Picoides arcticus*)	BI	CA	C
Northern Flicker (*Colaptes auratus*)	OM	CA	C
Pileated Woodpecker (*Dryocopus pileatus*)	OM	CA	C
Olive-sided Flycatcher (*Contopus cooperi*)	AI	CA	O
Eastern Wood-Pewee (*Contopus virens*)	AI	CA	O
Western Wood-Pewee (*Contopus sordidulus*)	AI	CA	O
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	AI	GR	O
Acadian Flycatcher (*Empidonax virescens*)	AI	CA	O
Alder Flycatcher (*Empidonax alnorum*)	AI	SH	O
Willow Flycatcher (*Empidonax traillii*)	AI	SH	O
Least Flycatcher (*Empidonax minimus*)	AI	SH	O
Hammond’s Flycatcher (*Empidonax hammondii*)	AI	CA	O
Gray Flycatcher (*Empidonax wrightii*)	AI	SH	O

APPENDIX. CONTINUED.

Species	Forage guild	Nest layer	Nest type
Dusky Flycatcher (*Empidonax oberholseri*)	AI	SH	O
Pacific-slope Flycatcher (*Empidonax difficilis*)	AI	CA	C
Ash-throated Flycatcher (*Myiarchus cinerascens*)	AI	SH	O
Great Crested Flycatcher (*Myiarchus crinitus*)	AI	CA	C
Eastern Phoebe (*Sayornis phoebe*)	AI	CA	O
Eastern Kingbird (*Tyrannus tyrannus*)	AI	CA	O
Loggerhead Shrike (*Lanius ludovicianus*)	CA	SH	O
White-eyed Vireo (*Vireo griseus*)	FI	SH	O
Yellow-throated Vireo (*Vireo flavifrons*)	FI	CA	O
Blue-headed Vireo (*Vireo solitarius*)	FI	CA	O
Plumbeous Vireo (*Vireo plumbeus*)	FI	CA	O
Cassin's Vireo (*Vireo cassinii*)	FI	CA	O
Warbling Vireo (*Vireo gilvus*)	FI	CA	O
Philadelphia Vireo (*Vireo philadelphicus*)	FI	CA	O
Red-eyed Vireo (*Vireo olivaceus*)	FI	CA	O
Gray Jay (*Perisoreus canadensis*)	OM	CA	O
Steller's Jay (*Cyanocitta stelleri*)	OM	CA	O
Blue Jay (*Cyanocitta cristata*)	OM	CA	O
Pinyon Jay (*Gymnorhinus cyanocephalus*)	OM	CA	O
Black-billed Magpie (*Pica hudsonia*)	OM	CA	O
Clark's Nutcracker (*Nucifraga columbiana*)	OM	CA	O
American Crow (*Corvus brachyrhynchos*)	OM	CA	O
Common Raven (*Corvus corax*)	OM	CA	O
Horned Lark (*Eremophila alpestris*)	GI	GR	O
Tree Swallow (*Tachycineta bicolor*)	AI	CA	C
Violet-green Swallow (*Tachycineta thalassina*)	AI	CA	C
Chickadee (*Poecile* spp.)	FI	CA	C
Carolina Chickadee (*Poecile carolinensis*)	FI	CA	C
Black-capped Chickadee (*Poecile atricapillus*)	FI	CA	C
Mountain Chickadee (*Poecile gambeli*)	FI	CA	C
Chestnut-backed Chickadee (*Poecile rufescens*)	FI	CA	C
Boreal Chickadee (*Poecile hudsonicus*)	FI	CA	C
Tufted Titmouse (*Baeolophus bicolor*)	FI	CA	C
Verdin (*Auriparus flaviceps*)	FI	SH	C
Brown Creeper (*Certhia americana*)	BI	CA	C
Red-breasted Nuthatch (*Sitta canadensis*)	BI	CA	C
White-breasted Nuthatch (*Sitta carolinensis*)	BI	CA	C
Pygmy Nuthatch (*Sitta pygmaea*)	BI	CA	C
Brown-headed Nuthatch (*Sitta pusilla*)	BI	CA	C
Cactus Wren (*Campylorhynchus brunneicapillus*)	OM	SH	C
Rock Wren (*Salpinctes obsoletus*)	GI	GR	C
Carolina Wren (*Thryothorus ludovicianus*)	GI	CA	C
House Wren (*Troglodytes aedon*)	GI	CA	C
Winter Wren (*Troglodytes troglodytes*)	GI	CA	C
Golden-crowned Kinglet (*Regulus satrapa*)	FI	CA	O
Ruby-crowned Kinglet (*Regulus calendula*)	FI	CA	O
Blue-gray Gnatcatcher (*Polioptila caerulea*)	FI	CA	C
Eastern Bluebird (*Sialia sialis*)	AI	CA	C
Western Bluebird (*Sialia mexicana*)	AI	CA	C
Mountain Bluebird (*Sialia currucoides*)	AI	CA	C
Townsend's Solitaire (*Myadestes* townsendi)	AI	GR	O
Swainson's Thrush (*Catharus ustulatus*)	FI	SH	O
Hermit Thrush (*Catharus guttatus*)	GI	SH	O
Wood Thrush (*Hylocichla mustelina*)	GI	CA	O
American Robin (*Turdus migratorius*)	GI	CA	O
Varied Thrush (*Ixoreus naevius*)	GI	CA	O

APPENDIX. CONTINUED.

Species	Forage guild	Nest layer	Nest type
Gray Catbird (*Dumetella carolinensis*)	FI	SH	O
Northern Mockingbird (*Mimus polyglottos*)	GI	SH	O
Sage Thrasher (*Oreoscoptes montanus*)	GI	SH	O
Brown Thrasher (*Toxostoma rufum*)	GI	SH	O
European Starling (*Sturnus vulgaris*)	GI	CA	C
Cedar Waxwing (*Bombycilla cedrorum*)	FI	CA	O
Lucy's Warbler (*Vermivora luciae*)	FI	CA	C
Nashville Warbler (*Vermivora ruficapilla*)	FI	GR	O
Orange-crowned Warbler (*Vermivora celata*)	FI	GR	O
Tennessee Warbler (*Vermivora peregrina*)	FI	GR	O
Virginia's Warbler (*Vermivora virginiae*)	GI	GR	O
Northern Parula (*Parula americana*)	FI	CA	C
Bay-breasted Warbler (*Dendroica castanea*)	FI	CA	O
Black-throated Green Warbler (*Dendroica virens*)	FI	CA	O
Cape May Warbler (*Dendroica tigrina*)	FI	CA	O
Cerulean Warbler (*Dendroica cerulea*)	FI	CA	O
Chestnut-sided Warbler (*Dendroica pensylvanica*)	FI	SH	O
Grace's Warbler (*Dendroica graciae*)	FI	CA	O
Magnolia Warbler (*Dendroica magnolia*)	FI	CA	O
Palm Warbler (*Dendroica palmarum*)	GI	GR	O
Pine Warbler (*Dendroica pinus*)	BI	CA	O
Prairie Warbler (*Dendroica discolor*)	FI	SH	O
Townsend's Warbler (*Dendroica townsendi*)	FI	CA	O
Yellow-rumped Warbler (*Dendroica coronata*)	FI	CA	O
Yellow-throated Warbler (*Dendroica dominica*)	BI	CA	O
Yellow Warbler (*Dendroica petechia*)	FI	SH	O
Black-and-white Warbler (*Mniotilta varia*)	BI	GR	O
American Redstart (*Setophaga ruticilla*)	FI	CA	O
Worm-eating Warbler (*Helmitheros vermivorus*)	FI	GR	O
Northern Waterthrush (*Seiurus noveboracensis*)	GI	GR	O
Ovenbird (*Seiurus aurocapillus*)	GI	GR	C
Louisiana Waterthrush (*Seiurus motacilla*)	GI	GR	O
Mourning Warbler (*Oporornis philadelphia*)	FI	GR	O
MacGillivray's Warbler (*Oporornis tolmiei*)	FI	SH	O
Connecticut Warbler (*Oporornis agilis*)	GI	GR	O
Kentucky Warbler (*Oporornis formosus*)	GI	GR	O
Common Yellowthroat (*Geothlypis trichas*)	FI	SH	O
Canada Warbler (*Wilsonia canadensis*)	FI	GR	O
Wilson's Warbler (*Wilsonia pusilla*)	FI	GR	O
Hooded Warbler (*Wilsonia citrina*)	FI	SH	O
Yellow-breasted Chat (*Icteria virens*)	FI	SH	O
Scarlet Tanager (*Piranga olivacea*)	FI	CA	O
Summer Tanager (*Piranga rubra*)	FI	CA	O
Western Tanager (*Piranga ludoviciana*)	FI	CA	O
Canyon Towhee (*Pipilo fuscus*)	OM	SH	O
Eastern Towhee (*Pipilo erythrophthalmus*)	OM	GR	O
Green-tailed Towhee (*Pipilo chlorurus*)	OM	SH	O
Spotted Towhee (*Pipilo maculatus*)	OM	GR	O
Bachman's Sparrow (*Aimophila aestivalis*)	OM	GR	O
Botteri's Sparrow (*Aimophila botterii*)	OM	GR	O
Cassin's Sparrow (*Aimophila cassinii*)	OM	GR	O
Brewer's Sparrow (*Spizella breweri*)	OM	SH	O
Chipping Sparrow (*Spizella passerina*)	OM	SH	O
Clay-colored Sparrow (*Spizella pallida*)	OM	SH	O
Field Sparrow (*Spizella pusilla*)	OM	GR	O
Vesper Sparrow (*Pooecetes gramineus*)	OM	GR	O

APPENDIX. CONTINUED.

Species	Forage guild	Nest layer	Nest type
Lark Sparrow (*Chondestes grammacus*)	OM	GR	O
Sage Sparrow (*Amphispiza belli*)	GI	SH	O
Lark Bunting (*Calamospiza melanocorys*)	GI	GR	O
Savannah Sparrow (*Passerculus sandwichensis*)	OM	GR	O
Baird's Sparrow (*Ammodramus bairdii*)	OM	GR	O
Henslow's Sparrow (*Ammodramus henslowii*)	OM	SH	O
Grasshopper Sparrow (*Ammodramus savannarum*)	OM	GR	O
LeConte's Sparrow (*Ammodramus leconteii*)	OM	GR	O
Sharp-tailed Sparrow (*Ammodramus caudacutus*)	OM	GR	O
Black-throated Sparrow (*Amphispiza bilineata*)	OM	SH	O
Fox Sparrow (*Passerella iliaca*)	OM	GR	O
Lincoln's Sparrow (*Melospiza lincolnii*)	OM	GR	O
Song Sparrow (*Melospiza melodia*)	GI	SH	O
Swamp Sparrow (*Melospiza georgiana*)	OM	SH	O
White-crowned Sparrow (*Zonotrichia leucophrys*)	OM	GR	O
White-throated Sparrow (*Zonotrichia albicollis*)	OM	GR	O
Dark-eyed Junco (*Junco hyemalis*)	OM	GR	O
Northern Cardinal (*Cardinalis cardinalis*)	OM	SH	O
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	OM	CA	O
Blue Grosbeak (*Passerina caerulea*)	OM	SH	O
Pyrrhuloxia (*Cardinalis sinuatus*)	OM	SH	O
Lazuli Bunting (*Passerina amoena*)	OM	SH	O
Indigo Bunting (*Passerina cyanea*)	OM	SH	O
Dickcissel (*Spiza americana*)	GI	GR	O
Bobolink (*Dolichonyx oryzivorus*)	OM	GR	O
Brewer's Blackbird (*Euphagus cyanocephalus*)	OM	SH	O
Rusty Blackbird (*Euphagus carolinus*)	OM	CA	O
Red-winged Blackbird (*Agelaius phoeniceus*)	OM	SH	O
Eastern Meadowlark (*Sturnella magna*)	GI	GR	O
Western Meadowlark (*Sturnella neglecta*)	GI	GR	O
Common Grackle (*Quiscalus quiscula*)	OM	CA	O
Brown-headed Cowbird (*Molothrus ater*)	OM	–	P[b]
Baltimore Oriole (*Icterus galbula*)	OM	CA	C
Orchard Oriole (*Icterus spurius*)	FI	CA	C
Pine Grosbeak (*Pinicola enucleator*)	OM	CA	O
Red Crossbill (*Loxia curvirostra*)	OM	CA	O
House Finch (*Carpodacus mexicanus*)	OM	CA	O
Cassin's Finch (*Carpodacus cassinii*)	OM	CA	O
American Goldfinch (*Carduelis tristis*)	OM	SH	O
Pine Siskin (*Carduelis pinus*)	OM	CA	O
Evening Grosbeak (*Coccothraustes vespertinus*)	OM	CA	O

[a] Cliff.

[b] Parasitic.

Studies in Avian Biology No. 30:14–32

FIRE AND BIRDS IN THE SOUTHWESTERN UNITED STATES

Carl E. Bock and William M. Block

Abstract. Fire is an important ecological force in many southwestern ecosystems, but frequencies, sizes, and intensities of fire have been altered historically by grazing, logging, exotic vegetation, and suppression. Prescribed burning should be applied widely, but under experimental conditions that facilitate studying its impacts on birds and other components of biodiversity. Exceptions are Sonoran, Mojave, and Chihuahuan desert scrub, and riparian woodlands, where the increased fuel loads caused by invasions of exotic grasses and trees have increased the frequency and intensity of wildfires that now are generally destructive to native vegetation. Fire once played a critical role in maintaining a balance between herbaceous and woody vegetation in desert grasslands, and in providing a short-term stimulus to forb and seed production. A 3–5 yr fire-return interval likely will sustain most desert grassland birds, but large areas should remain unburned to serve species dependent upon woody vegetation. Understory fire once maintained relatively open oak savanna, pinyon-juniper, pine-oak, ponderosa pine (*Pinus ponderosa*), and low elevation mixed-conifer forests and their bird assemblages, but current fuel conditions are more likely to result in stand-replacement fires outside the range of natural variation. Prescribed burning, thinning, and grazing management will be needed to return fire to its prehistoric role in these habitats. Fire also should be applied in high elevation mixed-conifer forests, especially to increase aspen stands that are important for many birds, but this will be an especially difficult challenge in an ecosystem where stand-replacement fires are natural events. Overall, surprisingly little is known about avian responses to southwestern fires, except as can be inferred from fire effects on vegetation. We call for cooperation between managers and researchers to replicate burns in appropriate habitats that will permit rigorous study of community and population-demographic responses of breeding, migrating, and wintering birds. This research is critical and urgent, given the present threat to many southwestern ecosystems from destructive wildfires, and the need to develop fire management strategies that not only reduce risk but also sustain bird populations and other components of southwestern biological diversity.

Key Words: birds, chaparral, desert, fire, grassland, mixed-conifer, pine-oak, prescribed burning, riparian, savanna, Southwest, wildfire.

FUEGO Y AVES EN EL SUROESTE DE ESTADOS UNIDOS

Resumen. El fuego es una fuerza ecológica importante en varios ecosistemas sur-occidentales, pero sus frecuencias, tamaños e intensidades han sido alteradas históricamente por el pastoreo, aprovechamientos forestales, vegetación exótica y supresión. Las quemas prescritas deberían ser aplicadas, pero bajo condiciones experimentales las cuales faciliten el estudio de sus impactos en aves y otros componentes de biodiversidad. Algunas excepciones son el matorral xerófilo de Sonora, Mojave y Chihuahua, y bosques de galería, donde el incremento del material combustible causado por invasiones de pastos y árboles exóticos ha incrementado la frecuencia e intensidad de incendios, los cuales generalmente son dañinos para la vegetación nativa. Alguna vez el fuego jugó un papel importante para mantener el balance entre la vegetación herbácea y forestal en pastizales del desierto, así como para estimular el retoño y la producción de semilla en el corto plazo. Una repetición de incendio con intervalos de 4–5 años, sustentaría a la mayoría de las aves de pastizales, pero grandes áreas deberían permanecer sin incendiarse para servir a las especies dependientes de la vegetación forestal. El fuego algún tiempo mantuvo relativamente abierta la sabana de encinos, piñón-juníperos, pino-encino, pino ponderosa *(Pinus ponderosa)*, y bosques de coníferas mixtos de bajas elevaciones, así como sus aves correspondientes, pero las condiciones actuales de combustible tienden mas a resultar en reemplazos del crecimiento de plantas fuera del rango natural de variación. Se requerirían quemas preescritas, aclareos y el manejo de pastizales para regresar al papel que jugaba el fuego en la prehistoria en estos habitats. El fuego también debería ser aplicado en bosques de coníferas mixtos de alta elevación, especialmente para incrementar el crecimiento de aspen, el cual es importante para varias aves, pero esto sería un reto sumamente importante en ecosistemas donde el reemplazo del crecimiento de plantas en incendios es un evento natural. Es sorprendente lo poco que se conoce acerca de las respuestas de las aves a los incendios sur-occidentales, a excepción en lo que se refiere a la respuesta de la vegetación al fuego. Pedimos cooperación entre los manejadores e investigadores para replicar incendios en habitats apropiados, que permitan rigurosos estudios de respuestas demográficas de comunidades y poblaciones, de aves reproductoras, migratorias y aves que permanecen en estas regiones durante el invierno. Este estudio es crítico y urgente, dado el presente peligro que varios ecosistemas sur-occidentales enfrentan debido a incendios destructivos, así como por la necesidad de desarrollar estrategias de manejo las cuales no solo disminuyan el riesgo, sino también sustenten las poblaciones de aves y otros componentes de diversidad biológica de los ecosistemas sur-occidentales.

The conditions necessary and sufficient for fire in natural ecosystems include a source of ignition, such as lightning or anthropogenic burning, and an adequate quantity of dry fuel (Pyne et al. 1996). These conditions are met in most ecosystems of the southwestern United States (McPherson and Weltzin 2000), and the ecological importance of fire in the region has long been recognized (Leopold 1924, Humphrey 1958). We also know that humans have drastically altered historic frequencies, sizes, and intensities of fire by anthropogenic disturbances such as logging, livestock grazing, introduction of exotics, landscape fragmentation, and suppression efforts (Covington and Moore 1994, Bahre 1985, 1995, McPherson 1995, Moir et al. 1997). In 1988 and again in 1996, groups of researchers and managers assembled to synthesize the known effects of fire on natural resources in the southwestern United States, including its plant communities and wildlife, and to recommend ways to respond to wildfire and to use prescribed burning (Krammes 1990, Ffolliott et al. 1996). This paper is a follow-up to the results of those conferences, with a specific emphasis on populations and communities of southwestern birds.

For purposes of this review, we define the Southwest as that portion of the United States adjacent to Mexico, from the Mojave desert of southern Nevada and southeastern California eastward across Arizona and New Mexico and into trans-Pecos Texas (Fig. 1). Our definitions and descriptions of major ecosystems in the Southwest are taken largely from Brown (1982a) and Barbour and Billings (2000). We consider eight major ecosystems in this review: (1) Chihuahuan desert and associated desert grasslands, (2) Sonoran and Mojave deserts, (3) Madrean evergreen savanna, (4) interior chaparral, (5) pinyon-juniper woodland, (6) pine and pine-oak woodland, (7) mixed-conifer forest, and (8) riparian woodlands. For each of these ecosystems we describe the distribution, elevation, size, major vegetation, and characteristic birds, including those identified as priority species (Partners in Flight 2004). We describe the prehistoric importance of fire, fire-return interval, and its effects on vegetation. We then review how prehistoric fire regimes have been altered by recent human activities. We discuss known and probable effects of fire on birds under present conditions. At the end of each section, we suggest how both wild and prescribed fire should be managed for the benefit of birds, and identify the major unanswered questions and research priorities regarding the impact of fire on avian communities.

CHIHUAHUAN DESERT SCRUB AND DESERT GRASSLANDS

The Chihuahuan desert includes more than 45,000,000 ha, distributed mostly between 1,000 and 2,000 m elevation, from the Valley of Mexico north into Trans-Pecos Texas, southern New Mexico, and extreme southeastern Arizona (MacMahon 2000). Desert grassland (about 50,000,000 ha) generally surrounds the Chihuahuan Desert, forming a patchy belt that grades from desert scrub up into Madrean evergreen woodland, pinyon-juniper woodland, and pine-oak woodland from Mexico City north to the southwestern United States (McClaran 1995). We consider these ecosystems together because they are similar in vegetation (Axelrod 1985, Burgess 1995, MacMahon 2000, McLaughlin et al. 2001), they interdigitate on a fine geographic scale (Lowe and Brown 1982), and desert scrub has replaced large areas of southwestern grasslands within historic time, due at least in part to altered fire regimes (Humphrey 1974, McPherson 1995, Whitford 2002, Turner et al. 2003).

Dominant vegetation of the Chihuahuan desert includes shrubs and small trees, especially creosotebush (*Larrea tridentata*), tarbush (*Flourensia cernua*), mesquite (*Prosopis* spp.), and acacia (*Acacia* spp.), along with various species of *Yucca* and *Agave* (Brown 1982a, MacMahon 2000, Whitford 2002). Each of these plants extends into desert grasslands as well, along with smaller shrubs such as burroweed (*Isocoma tenuisecta*) and various species of *Baccharis* (McClaran 1995). Black grama (*Bouteloua eriopoda*) and tobosa (*Hilaria mutica*) are predominant grasses of the Chihuahuan desert, and these also extend into desert grasslands where they mix with a variety of warm-season perennial bunchgrasses, especially those in the genera *Bouteloua*, *Eragrostis*, and *Aristida* (McClaran 1995, McLaughlin et al. 2001).

Characteristic birds of desert grassland and Chihuahuan desert include species with a spectrum of habitat requirements, from those associated primar-

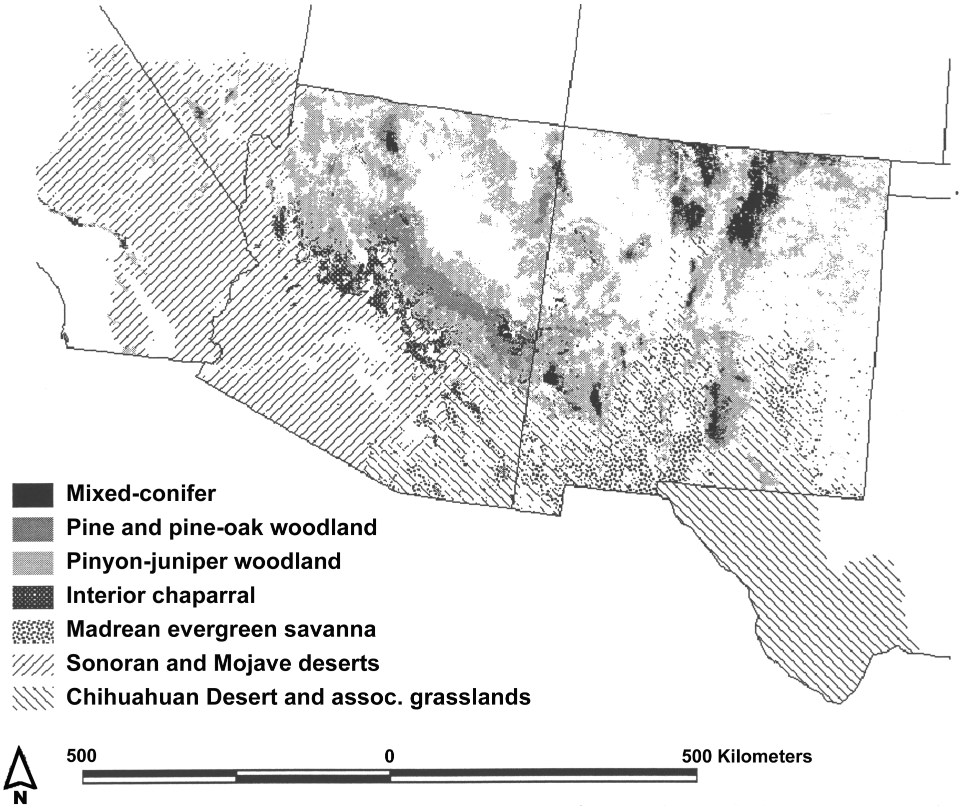

FIGURE 1. Ecosystems of the southwestern United States considered in this review.

ily with shrubs, such as Gambel's Quail (*Callipepla gambelii*) and Cactus Wren (*Campylrorhynchus brunneicapillus*), to those associated with relatively open grasslands, such as Horned Lark (*Eremophila alpestris*) and Grasshopper Sparrow (*Ammodramus savannarum*) (Brown 1982a). Desert grasslands are particularly important wintering habitat for a number of migratory sparrows, because of their seed production (Pulliam and Dunning 1987). Given historic conversions of grassland to desert scrub, it is not surprising that many Partners in Flight priority species for this region are associated with grasslands, or at least with areas that include significant grass cover. Examples include Ferruginous Hawk (*Buteo regalis*), Aplomado Falcon (*Falco femoralis*), Sprague's Pipit (*Anthus spragueii*), Cassin's Sparrow (*Aimophila cassinii*), Botteri's Sparrow (*Aimophila botterii*), Grasshopper Sparrow, and Baird's Sparrow (*Ammodramus bairdii*), and two birds restricted to grasslands of Arizona and Sonora, the endangered Masked Bobwhite (*Colinus virginianus ridgwayi*), and the Rufous-winged Sparrow (*Aimophila carpalis*).

Fire in Chihuahuan Desert Scrub and Desert Grasslands

Fires probably were very uncommon in Chihuahuan desert proper, and its dominant grass, black grama, is damaged by fire (Gosz and Gosz 1996). However, fires probably occurred once every 7–10 yr in higher, cooler, and wetter desert grasslands above the fringes of the Chihuahuan desert, and prehistoric fire served to keep these areas relatively free of trees and shrubs (McPherson 1995, McPherson and Weltzin 2000).

Southwestern grasslands from west Texas to southeastern Arizona almost universally experienced major invasions of woody plants over the course of the twentieth century (Buffington and Herbel 1965, Bahre and Shelton 1993, Archer 1994). These events have been attributed to climate change, livestock grazing, prairie dog (*Cynomys* spp.) control, and fire exclusion resulting from suppression efforts and loss of fine fuels to domestic grazers (Archer et al. 1995, Bahre 1995, Weltzin et al. 1997, Whitford 2002). Historical conversion of desert grassland to desert scrub has been nearly complete, and apparently permanent, in many black grama grasslands at the margins of the Chihuahuan desert (Schlesinger et al. 1990, Whitford 2002). However, recovery of native desert grasslands can occur after long-term livestock exclusion in relatively mesic areas (Valone et al. 2002), although it is not yet clear what role fire might play in this process (Valone and Kelt 1999).

Fire Effects on Chihuahuan Desert Scrub and Desert Grassland Birds

Birds associated with grasslands have declined more than other avian groups, both nationally and in the Southwest (Brown and Davis 1998, Vickery and Herkert 2001) begging the questions: (1) What have been the effects of contemporary fires on vegetation and birds in desert grasslands, and (2) What should be the role of prescribed burning in maintenance and restoration of southwestern grassland bird habitats?

Fire can have two categorically different effects on desert grassland vegetation and these in turn can have very different effects on birds. In the short term, fire reduces grass cover for one to three postfire growing seasons, while stimulating the abundance and variety of forbs, and generally increasing seed production (Bock et al. 1976, Bock and Bock 1978, Bock and Bock 1992a, McPherson 1995). Results of several studies in Arizona grasslands indicate that these short-term effects can improve habitat for seedeaters and open-ground species such as Scaled Quail (*Callipepla squamata*), doves, Horned Larks, and a variety of wintering sparrows (Table 1; Bock and Bock 1978, Bock and Bock 1992b, Gordon 2000, Kirkpatrick et al. 2002). At the same time, fire-caused reductions of grass cover temporarily reduce habitat quality for species dependent upon heavy ground cover, such as Montezuma Quail (*Cyrtonyx montezuma*), Cassin's Sparrow, Botteri's Sparrow, and Grasshopper Sparrow (Table 1).

Over the longer term, fire potentially can reduce (but probably not eliminate) cover of woody vegetation in desert grassland communities, although fire effects on vegetation are species-specific and related to season, grazing history, recent precipitation, and fire frequency (McPherson 1995, Valone and Kelt 1999, Drewa and Havstad 2001). Desert grasslands that include mesquite and other woody plants usually support a higher abundance and species richness of birds than open desert grasslands (Whitford 1997, Lloyd et al. 1998, Pidgeon et al. 2001). However, with the possible exception of the Cactus Wren (Table 1; Kirkpatrick et al. 2002), these negative effects have not yet been seen following fire, probably because fire frequencies and intensities have been insufficient to result in much long-term loss of woody cover.

Fire clearly had a historical importance in keeping southwestern desert grasslands relatively free of shrubs, but it has not yet been demonstrated that prescribed burning can be used to restore these conditions. This should be a high research priority. Given the vulnerability of black grama to fire in the most arid sites, the major application of prescription burning probably should be in relatively mesic areas dominated by a variety of other native perennial bunchgrasses. Some birds of the desert grassland depend upon woody vegetation that is a natural part of most Chihuahuan environments, while others require relatively open areas with substantial grass cover, and still others are attracted to the bare ground and heavy seed crops that come in the first 2–3 yr after a burn. All of this argues for maintaining a mosaic of landscapes in various stages of postfire succession, with some areas unburned for decades and others burned perhaps on a rotation of 3–5 yr.

In summary:

1. Prehistoric fires probably were uncommon in the Chihuahuan desert itself, but were important in sustaining the surrounding desert grasslands, and in determining the desert-grassland boundary.
2. Woody plants have increased in formerly open desert grasslands, following introduction of livestock and resulting decreases in fire frequency and intensity.
3. Contemporary fire in relatively mesic desert grasslands has the effect of reducing grass cover, while increasing bare ground, forb cover, and seed production for 2-3 yr postfire; over the longer term and with repeated burning, prescribed fire likely also could be used to reduce woody vegetation and benefit grasses.
4. Desert grassland and Chihuahuan desert avifaunas include some birds that depend on woody vegetation, others that require heavy grass cover, and still others that benefit from open ground and high seed production; the goal of prescription burning should be to restore and sustain this sort of habitat mosaic, with some areas rarely if ever burned, and others burned on a 3–5 yr rotation.
5. A research priority should be to determine if repeated fire in desert grassland can reduce woody vegetation to something resembling prehistoric levels, and to better understand the effects of such a fire regime on the abundance and demography of desert grassland birds.

TABLE 1. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSE OF BREEDING BIRDS (CHANGE IN ABUNDANCE) TO FIRE IN SOUTHWESTERN HABITATS OF NORTH AMERICA.

Species	State	Years after fire	Size (ha)	No. of sites	Response[a]	Type of fire	Reference[b]	Comments[c]
Scaled Quail (*Callipepla squamata*)	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 1-yr increase.
Montezuma Quail (*Cyrtonyx montezumae*)	AZ	1–2	100, 150, 350	4	–	wild	1	Sacaton grassland; 1-yr decline.
Sharp-shinned Hawk (*Accipiter striatus*)	AZ	3	10,000	14	–	wild	2	Ponderosa pine; nonbreeding season.
White-winged Dove (*Zenaida asiatica*)	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 1-yr increase; breeding season.
Mourning Dove (*Zenaida macroura*)	AZ	3	10,000	14	0	wild	2	Ponderosa pine; breeding season.
	AZ	1, 3, 9, 20	350–2,890	4	+	wild	3	Ponderosa pine; breeding season.
	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 2-yr increase.
	AZ	1–2	1,596	14	+	prescr.	4	Mesquite grassland; breeding season.
	AZ	1–4	1,000	4	+	wild	5	Mesquite grassland; 1–3 yr increase.
	AZ	1–2	240, 120	4	+	wild	6	Oak savanna.
Broad-tailed Hummingbird (*Selasphorus platycerus*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; breeding season.
Lewis's Woodpecker (*Melanerpes lewis*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; breeding season; response to severe fire.
Ladder-backed Woodpecker (*Picoides scalaris*)	AZ	1–2	1,596	14	+	prescr.	4	Mesquite grassland; winter.
Hairy Woodpecker (*Picoides villosus*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; larger increase following severe fire than moderate fire.
	AZ	7	10,000	14	+	wild	7	Ponderosa pine; same area as above; population in severe fire areas greater than unburned areas, but lower than that recorded after 3 yr.
	AZ	1, 3, 9, 20	350–2,890	4	+	wild	3	Ponderosa pine; breeding season.
	AZ	1	4,800	6	+	wild	8	Ponderosa pine; nonbreeding season.
Northern Flicker (*Colaptes auratus*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine.
	AZ	1–2	100	6	–	prescr.	9	Ponderosa pine & mixed-conifer; breeding season.
Olive-sided Flycatcher (*Contopus cooperi*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; breeding season; response to severe fire.
Western Wood-Pewee (*Contopus sordidulus*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; breeding season; positiive response to severe and moderate fire.
Ash-throated Flycatcher (*Myiarchus cinerascens*)	NM	14	6,250	4	–	wild	10	Ponderosa pine; breeding season.
	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; breeding season.
Loggerhead Shrike (*Lanius ludovicianus*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland.
Plumbeous Vireo (*Vireo plumbeus*)	AZ	3	10,000	14	–	wild	2	Ponderosa pine; breeding season; negative response to severe fire.
Steller's Jay (*Cyanocitta stelleri*)	AZ	3	10,000	14	0	wild	2	Ponderosa pine.
	AZ	1, 3, 9, 20	350–2,890	4	+	wild	3	Ponderosa pine; breeding season.

TABLE 1. CONTINUED.

Species	State	Years after fire	Size (ha)	No. of sites	Response[a]	Type of fire	Reference[b]	Comments[c]
Pinyon Jay (*Gymnorhinus cyanocpehalus*)	AZ	3	10,000	14	0	wild	2	Ponderosa pine.
Clark's Nutcracker (*Nucifraga columbiana*)	AZ	3	10,000	14	0	wild	2	Ponderosa pine.
American Crow (*Corvus brachyrhynchos*)	AZ	3	10,000	14	0	wild	2	Ponderosa pine; nonbreeding season.
Common Raven (*Corvus corax*)	AZ	3	10,000	14	0	wild	2	Ponderosa pine.
Horned Lark (*Eremophila alpestris*)	AZ	1–4	1,000	4	+	wild	5	Mesquite grassland; 1–3 yr increase.
	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 2nd yr increase.
Violet-green Swallow (*Tachycineta thalassina*)	AZ	1–2	100	6	–	prescr.	9	Ponderosa pine & mixed-conifer; breeding season.
	AZ	1	4,800	6	+	wild	8	Ponderosa pine; nonbreeding season.
Mountain chickadee (*Poecile gambeli*)	AZ	3	10,000	14	–	wild	2	Ponderosa pine; drastic decline in severe burns.
	AZ	1	10,000	14	–	wild	11	Ponderosa pine; drastic decline in severe burns.
	AZ	1–2	100	6	+	prescr.	9	Ponderosa pine & mixed-conifer; breeding season.
	NM	14	6,250	4	–	wild	10	Ponderosa pine & mixed-conifer; breeding season.
Verdin (*Auriparus flaviceps*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; winter.
White-breasted Nuthatch (*Sitta carolinensis*)	AZ	3	10,000	14	–	wild	2	Ponderosa pine; negative response to severe fire.
	AZ	1	10,000	14	–	wild	11	Ponderosa pine; negative response to severe fire.
	AZ	1	4,800	6	–	wild	8	Ponderosa pine; nonbreeding season.
Pygmy Nuthatch (*Sitta pygmaea*)	AZ	3	10,000	14	–	wild	2	Ponderosa pine; negative response to severe fire.
	AZ	1, 3, 9, 20	350–2,890	4	–	wild	3	Ponderosa pine; breeding season.
Brown Creeper (*Certhia americana*)	AZ	3	10,000	14	0/–	wild	2	Ponderosa pine; no change in breeding season; declines in severe areas during nonbreeding season.
	AZ	1, 3, 9, 20	350–2,890	4	–	wild	3	Ponderosa pine; breeding season.
Cactus Wren (*Campylorhynchus brunneicapillus*)	AZ	1–2	1,596	14	–	prescr.	4	Mesquite grassland.
House Wren (*Troglodytes aedon*)	NM	14	6,250	4	+	wild	10	Ponderosa pine & mixed-conifer; breeding season.
Ruby-crowned Kinglet (*Regulus calendula*)	AZ	1	4,800	6	–	wild	8	Ponderosa pine; nonbreeding season.
Western Bluebird (*Sialia mexicana*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; positive responses to severe and moderate fires.
	AZ	1	10,000	14	+	wild	11	Ponderosa pine; positive responses to severe and moderate fires.
	AZ	1	4,800	6	+	wild	8	Ponderosa pine; nonbreeding season.
	NM	14	6,250	4	+	wild	10	Ponderosa pine & mixed-conifer; breeding season.
Hermit Thrush (*Catharus guttatus*)	NM	14	6,250	4	–	wild	10	Ponderosa pine & mixed-conifer; breeding season.
American Robin (*Turdus migratorius*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; positive responses to severe and moderate fires.

TABLE 1. CONTINUED.

Species	State	Years after fire	Size (ha)	No. of sites	Resp-onse[a]	Type of fire	Reference[b]	Comments[c]
Northern Mockingbird (*Mimus polyglottos*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; breeding season.
Virginia's Warbler (*Vermivora virginiae*)	NM	14	6,250	4	–	wild	10	Ponderosa pine & mixed-conifer; breeding season.
Lucy's Warbler (*Vermivora luciae*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; breeding season.
Yellow-rumped Warbler (*Dendroica coronata*)	AZ	3	10,000	14	–	wild	2	Ponderosa pine; breeding season; negative response to severe fire.
Grace's Warbler (*Dendroica graciae*)	AZ	3	10,000	14	–	wild	2	Ponderosa pine; breeding season; avoidance of severe fire.
	AZ	1, 3, 9, 20	350–2,890	4	–	wild	3	Ponderosa pine; breeding season.
	AZ	1, 3, 9, 20	350–2,890	4	–	wild	12	Ponderosa pine; breeding season.
	NM	14	6,250	4	–	wild	10	Ponderosa pine & mixed-conifer; breeding season.
Common Yellowthroat (*Geothlypis trichas*)	AZ	1–2	150, 350, 100	4	–	wild	1	Sacaton grassland; 2-yr decline; breeding season.
Western Tanager (*Piranga ludoviciana*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; breeding season; positive response to moderate fire.
Green-tailed Towhee (*Pipilo chlorurus*)	AZ	1, 3, 9, 20	350–2,890	4	+	wild	3	Ponderosa pine; breeding season.
Spotted Towhee (*Pipilo maculatus*)	NM	14	6,250	4	+	wild	10	Ponderosa pine & mixed-conifer; breeding season.
Canyon Towhee (*Pipilo fuscus*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; winter.
Cassin's Sparrow (*Aimophila cassinii*)	AZ	1–2	1,596	14	–	prescr.	4	Mesquite grassland; breeding season.
	AZ	1–4	1,000	4	m	wild	5	Mesquite grassland; 2-yr decline in native grassland; breeding season.
	AZ	1	?	6	–	prescr.	13	Mesquite grassland; winter.
	AZ	1–2	150, 350, 100	4	+	wild	1	Sacaton grassland; 2-yr increase; breeding season.
Botteri's Sparrow (*Aimophila botterii*)	AZ	1–2	1,596	14	–	prescr.	4	Mesquite grassland; breeding season.
	AZ	1–4	1,000	4	–	wild	5	Mesquite grassland; 2-yr decline; breeding season.
	AZ	1–2	100, 150, 350	4	–	wild	1	Sacaton grassland; 1-yr decline; breeding season.
Chipping Sparrow (*Spizella passerina*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; breeding season.
	AZ	1, 3, 9, 20	350–2,890	4	+	wild	3	Ponderosa pine; breeding season.
	AZ	1–2	240, 120	4	+	wild	6	Oak savanna; winter.
Brewer's Sparrow (*Spizella breweri*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; winter.
	AZ	1	?	6	0	prescr.	13	Mesquite grassland; winter.
Vesper Sparrow (*Pooecetes gramineus*)	AZ	1–2	1,596	14	+	prescr.	4	Mesquite grassland; winter.
	AZ	1–4	1,000	4	+	wild	5	Mesquite grassland; 2–3 yr increase; winter.
	AZ	1	?	6	+	prescr.	13	Mesquite grassland; winter.
	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 2-yr increase; winter.
	AZ	1–2	240, 120	4	+	wild	6	Oak savanna; winter.

TABLE 1. CONTINUED.

Species	State	Years after fire	Size (ha)	No. of sites	Resp-onse[a]	Type of fire	Reference[b]	Comments[c]
Lark Sparrow (*Chondestes grammacus*)	AZ	1–4	1,000	4	+	wild	5	Mesquite grassland; 2- yr increase; breeding season.
Black-throated Sparrow (*Amphispiza bilineata*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland.
Savannah Sparrow (*Passerculus sandwichensis*)	AZ	1–4	1,000	4	+	wild	5	Mesquite grassland; 1-yr increase; winter.
	AZ	1	?	6	+	prescr.	13	Mesquite grassland; winter.
	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 2-yr increase; winter.
Grasshopper Sparrow (*Ammodramus savannarum*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; winter.
	AZ	1–4	1,000	4	–	wild	5	Mesquite grassland; 2-yr decline.
	AZ	1	?	6	0	prescr.	13	Mesquite grassland; winter.
Baird's Sparrow (*Ammodramus bairdii*)	AZ	1	?	6	0	prescr.	13	Mesquite grassland; winter.
Lincoln's Sparrow (*Melospiza lincolnii*)	AZ	1	?	6	0	prescr.	13	Mesquite grassland; winter.
White-crowned Sparrow (*Zonotrichia leucophrys*)	AZ	1	?	6	0	prescr.	13	Mesquite grassland; winter.
	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 1-yr increase; winter.
	AZ	1	4,800	6	+	wild	8	Ponderosa pine; winter.
Dark-eyed Junco (*Junco hyemalis*)	AZ	3	10,000	14	0	wild	2	Ponderosa pine.
Pyrrhuloxia (*Cardinalis sinuatus*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; breeding season.
Blue Grosbeak (*Passerina caerulea*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland; breeding season.
	AZ	1–2	100, 150, 350	4	–	wild	1	Sacaton grassland; 2-yr decline; breeding season.
Eastern Meadowlark (*Sturnella magna*)	AZ	1–2	1,596	14	0	prescr.	4	Mesquite grassland.
	AZ	1–4	1,000	4	m	wild	5	Mesquite grassland.
	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 2-yr increase.
Western Meadowlark (*Sturnella neglecta*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; breeding season.
Brown-headed Cowbird (*Molothrus ater*)	AZ	3	10,000	14	+	wild	2	Ponderosa pine; breeding season; increase with moderate fire.
House Finch (*Carpodacus mexicanus*)	AZ	1–2	100, 150, 350	4	+	wild	1	Sacaton grassland; 1-yr increase.
Red Crossbill (*Loxia curvirostra*)	AZ	3	10,000	14	–	wild	2	Ponderosa pine; decline with severe and moderate fire.

[a] Change in abundance: + = increase; – = decrease; 0 = no effect or study inconclusive; m = mixed response.

[b] References: 1 = Bock and Bock (1978); 2 = Bock and Block (in press); 3 = Lowe et al. (1978); 4 = Kirkpatrick et al. (2002); 5 = Bock and Bock (1992b); 6 = Bock et al. (1976); 7 = Block and Covert (unpubl. data); 8 = Blake (1982); 9 = Horton and Mannan (1988); 10 = Johnson and Wauer (1996); 11 = Dwyer and Block (2000); 12 = Overturf (1979); 13 = Gordon (2000).

[c] Unless otherwise indicated, includes data from both breeding and nonbreeding seasons.

SONORAN AND MOJAVE DESERT SCRUB

The Sonoran desert includes about 27,500,000 ha in the lowlands of southeastern California, southwestern Arizona, most of Baja California, and the western half of Sonora, Mexico (Robichaux 1999, MacMahon 2000). At its northwestern limits, Sonoran desert grades into Mojave desert, which includes another 14,000,000 ha of the lowest elevations in southeastern California, southern Nevada, and northwestern Arizona (MacMahon 2000). These deserts include species-rich, structurally complex, and in many ways similar mixtures of shrubs, trees, succulents, and annual forbs (Turner 1982, Turner et al. 1995, MacMahon 2000). Dominant shrubs common to both deserts include creosote bush (*Larrea tridentata*) and bur sage (*Ambrosia dumosa*). Characteristic taller vegetation includes small trees such as palo verde (*Cercidium* spp.) and columnar cacti such as the saguaro (*Cereus giganteus*) in the Sonoran Desert, and the Joshua tree (*Yucca brevifolia*) in the Mojave desert.

The avifaunas of these deserts are species rich compared to nearby desert grasslands (Tomoff 1974, Davis and Russell 1990), and they include a variety of cavity-nesting species such as the Elf Owl (*Micrathene whitneyi*), Ferruginous Pygmy-Owl (*Glaucidium brasilianum*), Gila Woodpecker (*Melanerpes uropygialis*), and Gilded Flicker (*Colaptes chrysoides*) that depend upon large trees and cacti for nest sites (Brown 1982a, Cartron and Finch 2000, Hardy and Morrison 2001). At least in the Sonoran desert, there is a strong positive relationship between vegetation volume and complexity, and the overall abundance and diversity of birds (Tomoff 1974, Mills et al. 1991). Partners in Flight priority species for one or both deserts include Gambel's Quail, Gilded Flicker, Gila Woodpecker, Costa's Hummingbird (*Calypte costae*), Cactus Wren, Black-tailed Gnatcatcher (*Polioptila melanura*), Rufous-winged Sparrow, and all four Southwestern thrashers (*Toxostoma bendirei*, *T. curvirostre*, *T. crissale*, and *T. lecontei*).

FIRE IN SONORAN AND MOJAVE DESERT SCRUB

Wildfires probably were relatively uncommon in the Sonoran and Mojave deserts prehistorically, and restricted to periods following wet winters, when residual fine fuels left from annual forb production were sufficient to carry a burn across the otherwise sparse desert floor (McLaughlin and Bowers 1982). In the absence of dendrochronological data, Rogers and Steele (1980) attempted to use degree of fire adaptation in perennial plants as evidence for historical fire frequency in the Sonoran desert. They concluded that such adaptations were widespread but relatively weak, and that a fire-return interval of anything less than 20 yr would be highly destructive of most native trees, shrubs, and especially cacti (see also McLaughlin and Bowers 1982).

The introduction and spread of exotic grasses such as red brome (*Bromus rubens*) and buffelgrass (*Pennisetum ciliare*), and a variety of exotic forbs, increased both the frequency and intensity of fire in the Sonoran and Mojave deserts over the past century, causing substantial mortality of woody plants and succulents (Rogers 1985, Brown and Minnich 1986, Schmid and Rogers 1988, Burgess et al. 1991, Miller et al. 1995). Furthermore, both seed and foliar production of these exotics are likely to be enhanced by increased levels of carbon dioxide, so that anticipated climate changes may increase the frequency of fire in these ecosystems even beyond their present unnaturally high levels (Smith et al. 2000).

FIRE EFFECTS ON SONORAN AND MOJAVE DESERT SCRUB BIRDS

We could find no studies that compared avian species richness or abundance in burned versus unburned Sonoran and Mojave desert landscapes. However, there is little doubt that fire-caused mortality of desert woody plants and succulents would have a strongly negative impact on the majority of native bird populations, especially those dependent upon trees and cacti for nest sites.

The principal management objective for Sonoran and Mojave desert ecosystems should be to prevent and suppress wildfires that kill the native trees, shrubs, and succulents. A critical research need is to develop and test methods for limiting the spread and abundance of exotic grasses and forbs responsible for increased fuel loads. Cool-season, prescribed burning is one possible method for reducing fuels, but the risks are high because of the inherent fire-vulnerability of the native vegetation.

In summary:

1. Fires were historically uncommon in the Sonoran and Mojave deserts, and much of the native vegetation is relatively intolerant of the effects of burning.
2. Introduction and spread of exotic forbs and especially grasses have increased both the frequency and intensity of fire in these deserts, threatening many of the shrubs, trees, and succulents that are critical habitat components for birds.

3. The highest management and research priority is to find ways of reducing the frequency and intensity of wildfire in Sonoran and Mojave desert scrub habitats, by controlling the spread and abundance of exotic forbs and grasses.

MADREAN EVERGREEN SAVANNA

This oak-dominated ecosystem includes about 1,500,000 ha of the Sierra Madre Occidental, largely in Mexico, but extending north into southeastern Arizona, southern New Mexico, and Trans-Pecos Texas (Brown 1982a, McPherson 1997). Distributed mostly between 1,000 and 2,000 m elevation, Madrean evergreen savanna grades into desert grassland and mesquite savanna at its lower elevational limits, and into pine-oak woodland at its upper bounds. It is a typical savanna, with scattered broad-crowned trees and a grassy understory. The common oaks include *Quercus emoryi*, *Q. arizonica*, and *Q. grisea*, frequently with scattered populations of juniper (*Juniperus deppeana*, and *J. monosperma*), and pinyon pine (*Pinus cembroides*).

Typical birds of southwestern oak savannas include acorn-dependent species such as Acorn Woodpecker (*Melanerpes formicivorus*) and Mexican Jay (*Aphelocoma ultramarina*), foliage gleaners and insect hawkers such as Bridled Titmouse (*Baeolophus wollweberi*) and bluebirds (*Sialia* spp.), and species dependent on the grassy understory such as Montezuma Quail. Among these, the Montezuma Quail, Mexican Jay, Bridled Titmouse, and Eastern Bluebird (*Sialia sialis*) have been identified as Partners in Flight species of priority.

Fire in Madrean Evergreen Savanna

Fire almost certainly maintained Madrean evergreen savanna in a relatively open condition prehistorically, favoring grasses over understory shrubs and young trees (McPherson and Weltzin 2000). Cattle grazing and fire suppression have virtually eliminated wildfire from an ecosystem that probably evolved with a return interval of about 10 yr (McPherson 1997). The result has been a substantial increase in woody vegetation at the expense of the understory grasses, over the past century (Humphrey 1987, Turner et al. 2003). There have been few studies examining the effects of recent wildfires or prescribed burns on this habitat. Limited work suggests that the oaks can be top-killed by fire, but that they frequently resprout from the lower trunk or root crown (Johnson et al. 1962, Barton 1995).

Fire Effects on Madrean Evergreen Savanna Birds

Two cool spring wildfires in savannas at the distributional limits of oak in southeastern Arizona killed no mature trees, but they reduced grass cover and increased forb cover and seed production for two postfire years (Bock et al. 1976). Total bird abundance was greater on the burned areas, especially of winter seedeaters such as Mourning Dove (*Zenaida macroura*), Vesper Sparrow (*Pooecetes gramineus*), and Chipping Sparrow (*Spizella passerina*). This result is generally consistent with those from studies of wildfire and prescribed burning in mesquite grassland (Table 1). However, these results tell us virtually nothing about the likely responses of birds to hotter fires that change woodland structure, and we found no other published studies about fire effects on birds in Madrean evergreen savannas. In the midwestern United States, fires play a critical role in shaping the composition of oak savannas and their avifaunas (Davis et al. 2000, Brawn et al. 2001). Fires in Madrean oak savannas likely have similar effects, but they have not yet been documented.

The goal of fire management in Madrean evergreen savannas should be to prevent stand-replacement wildfires that kill mature oaks to the ground, since these events would eliminate a structural component of the habitat that is critical for most of its bird species. Cool-season, prescribed burning could have the double benefit of reducing fuels and the risk of catastrophic wildfire, and improving habitat for birds such as the Montezuma Quail that depend on dense understory grasses for escape cover (Brown 1982b). Determining avian responses to prescribed understory fire should be a research priority for Madrean evergreen savanna.

In summary:

1. Wildfire likely maintained oak-dominated Madrean evergreen savanna in a relatively open condition, with scattered broad-crowned trees and grassy understory.
2. Fire suppression and fuel reductions caused by livestock grazing have favored woody vegetation over grasses.
3. The risk of catastrophic wildfire has increased historically, and birds dependent upon open woodlands and grassy understory probably have declined, although this has not been studied.
4. Cool-season prescribed burning could reduce the risk of catastrophic wildfire and improve habitat for a variety of bird species in this habitat, but there has been virtually no research on this subject.

INTERIOR CHAPARRAL

North of Mexico, interior chaparral is best developed in a band south of the Mogollon Rim extending from northwestern to east-central Arizona, where it occupies about 1,400,000 ha (Pase and Brown 1982, Keeley 2000). This shrubby habitat is more patchily distributed to the south and east, across southeastern Arizona, southern New Mexico, southwest Texas, and onto the western slopes of the Sierra Madre Oriental of northeastern Mexico, where it again becomes a major vegetation type. Interior chaparral is distributed from 1,000–2,000 m elevation in the north, and from 2,000–3,000 m in the south. It usually intergrades with pine-oak woodland and with grassland-desertscrub at its upper and lower elevational limits, respectively (Pase and Brown 1982, Keeley 2000).

Interior chaparral consists primarily of a mixture of dense perennial shrubs, especially live oak (*Quercus turbinella*) and various species of manzanita (*Arctostaphylos* spp.) and *Ceanothus* (Keeley 2000). Some characteristic birds of interior chaparral given priority status by Partners in Flight include Crissal Thrasher (*Toxostoma crissale*), Virginia's Warbler (*Vermivora virginiae*), Green-tailed Towhee (*Pipilo chlorurus*), Canyon Towhee (*Pipilo fuscus*), and Black-chinned Sparrow (*Spizella atrogularis*).

FIRE IN INTERIOR CHAPARRAL

Fire-return interval for interior chaparral may be 50–100 yr, much longer than that for the better-studied California chaparral, and probably related to its relatively low productivity (Keeley 2000). Nevertheless, shrubs of interior chaparral recover well from fire, either by seed or by re-sprouting, and postfire recovery may take only 5–10 yr (Pase and Granfelt 1977, Carmichael et al. 1978). Drought, livestock grazing, and suppression have reduced fire frequency over the past century, resulting in increased shrub and reduced perennial grass cover in Arizona interior chaparral (Brejda 1997). Research and management have focused on effects of wildfire, prescription burning, grazing, and herbicide application on attributes of chaparral ecosystems such as livestock forage production, soil quality, and watershed function (Bolander 1981, Davis 1989, Overby and Perry 1996, Brejda 1997).

FIRE EFFECTS ON INTERIOR CHAPARRAL BIRDS

We found no published information on responses of bird populations to fire alone in interior chaparral. Szaro (1981) compared bird populations between two stands of Arizona interior chaparral, one unburned and un-manipulated for 20 yr, and the other burned, treated with herbicides, and seeded with exotic grasses. The avian assemblage in the undisturbed chaparral was dominated by species such as Gambel's Quail, Mexican Jay (*Aphelocoma ultramarina*), Bewick's Wren (*Thryomanes bewickii*), Crissal Thrasher and Spotted Towhee (*Pipilo maculatus*). The manipulated watershed supported only two common birds, the Rock Wren (*Salpinctes obsoletus*) and Rufous-crowned Sparrow (*Aimophila ruficeps*). However, the herbicide and seeding treatments doubtless obscured fire effects, so the results of this study cannot be taken as indicative of avian responses to prescribed burning alone. In studies of California chaparral, postfire bird assemblages included higher proportions of grassland species than those in unburned stands, but the overall variety and abundance of birds were comparable (Lawrence 1966, Wirtz 1982).

Complete conversion of interior chaparral to grassland, by whatever means, almost certainly would negatively impact most birds. Prescribed burning might benefit birds and other wildlife in interior chaparral if it is used to create relatively small openings in areas of heavy shrub growth, in order to increase grass cover and habitat structural heterogeneity. This possibility should be tested, using a series of replicated cool-season burns, matched with unmanipulated control sites, and sampled both before and up to 5 yr after fire.

In summary:

1. Wildfire probably occurred prehistorically in interior chaparral once every 50–100 yr, and native shrubs are adapted to recover relatively quickly; these fires likely maintained patchiness in this habitat, and facilitated development of native grass cover.
2. Shrub cover has increased historically, as a result of livestock grazing and fire suppression, reducing habitat heterogeneity and increasing the likelihood of unnaturally large and intense wildfires.
3. Prescribed burning might be used to reduce the risk of wildfire and to increase landscape heterogeneity beneficial to chaparral birds, but this possibility needs much more study.

PINYON-JUNIPER WOODLANDS

Pinyon-juniper woodland occurs throughout the northern two-thirds of Arizona and New Mexico, an area encompassing over 10,000,000 ha (Conner et al. 1990, Van Hooser et al. 1993). These woodlands are found between 1,200 and 2,700 m elevation and are dominated by various pinyon pines (*Pinus edulis, P. discolor,* and *P. californiarum*) and junipers (*Juniperus deppeana*, *J. osteosperma*, *J. monosperma*, and *J. scopulorum*). Tree species composition and structure vary geographically and according to topography, ranging from closed-canopy, mesic woodland to open savanna (Moir and Carleton 1986).

Balda and Masters (1980) reported 73 bird species that breed in pinyon-juniper woodland. Of these, they concluded that 18 were highly dependent on this habitat, including Western Screech-Owl (*Otus kennicotti*), Black-chinned Hummingbird (*Archilochus alexandri*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Gray Flycatcher (*Empidonax wrightii*), Western Scrub-Jay (*Aphelocoma californica*), Pinyon Jay (*Gymnorhinus cyanocephalus*), Juniper Titmouse (*Baeolophus ridgwayi*), Bushtit (*Psaltriparus minimus*), Bewick's Wren (*Thryomanes bewickii*), Northern Mockingbird (*Mimus polyglottos*), Blue-gray Gnatcatcher (*Polioptila careulea*), Gray Vireo (*Vireo vicinior*), Black-throated Gray Warbler (*Dendroica nigrescens*), House Finch (*Carpodacus mexicanus*), Spotted Towhee, Canyon Towhee, Lark Sparrow (*Chondestes grammacus*), and Black-chinned Sparrow (*Spizella atrogularis*). Species of concern within this ecosystem include Ferruginous Hawk (*Buteo regalis*), Gray Flycatcher (*Empidonax wrightii),* Pinyon Jay, Bendire's Thrasher (*Toxostoma bendirei*), Juniper Titmouse, Gray Vireo, and Black-throated Gray Warbler.

Fire in Pinyon-Juniper Woodlands

Historically, the primary role of fire in pinyon-juniper woodlands was more to limit its extent and distribution, and to regulate tree densities, than to change its composition or structure. This fire regime maintained large expanses of grassland, and grassy openings within an open woodland. In addition to regulating forest structure, fire played important roles in nutrient cycling, and in stimulating sprouting and fruiting that led to increased food production, especially for wintering populations of non-game birds (Balda and Masters 1980). Grassland birds, frugivores, and those that favored the interface between woodland and grassland almost certainly benefited from historical fire regimes.

More recently, fire suppression and the removal of fine herbaceous fuels by grazing livestock have facilitated expansion of pinyon-juniper woodlands into formerly open grasslands, and led to increased tree densities within existing woodlands (Pieper and Wittie 1990). Concomitantly, the fire regime has changed from low-severity, stand-maintenance burns to high-severity, stand-replacement burns. Bird species most likely to be negatively affected by this altered fire regime are those that require live trees for some aspect of their life history (O'Meara et al. 1981, Sedgwick and Ryder 1987).

Fire Effects on Pinyon-Juniper Woodlands Birds

Little information is available on fire effects in pinyon-juniper woodlands, particularly as related to birds (Balda and Masters 1980, Pieper and Wittie 1990, Severson and Rinne 1990). Although the ecological effects of chaining on bird habitats are not equivalent to those of fire, we consider effects of chaining as they relate to tree removal. As one would guess, species that depend on trees for foraging or nesting, such as Black-throated Gray Warbler, Plumbeous Vireo (*Vireo plumbeus*), White-breasted Nuthatch (*Sitta carolinensis*), and Gray Flycatcher, responded negatively to chaining (O'Meara et al. 1981, Sedgwick and Ryder 1987). Two species that favor more open habitats, Rock Wren (*Salpinctes obsoletus*) and Chipping Sparrow, appeared to benefit. However, we are reluctant to equate chaining with burning. Chaining removes all standing trees and snags, and reduces biomass and nutrients in the system. In contrast, some trees and snags remain standing following fire. Residual snags, for example, provide ephemeral (within 6 yr postfire) nesting substrates for cavity-nesting birds such as Hairy Woodpecker (*Picoides villosus*) and Western Bluebird (*Sialia mexicana*). As snags fall and are no longer available as nesting substrates, populations of cavity-nesting birds decline (Block, unpubl. data). Fire also plays important roles in nutrient cycling, and in stimulating sprouting and fruiting, which can lead to increased food production, especially for wintering populations of non-game birds (Balda and Masters 1980).

Ideally, pinyon-juniper woodland should be managed to restore ecosystem structure and function, which would include returning to the historical fire regime. The practicality of doing so is dubious given that it would entail concerted efforts to reduce both grazing intensity and tree densities to provide conditions needed to sustain low-severity, ground fires.

Given the near absence of information on fire effects on birds in pinyon-juniper woodland, there are numerous opportunities for research in this habitat type. Priority, however, should be given to understanding how disruption of natural fire regimes has altered bird habitats and affected bird populations. This research would focus on two general topics: (1)

the habitat and population ecologies of birds in areas that have lacked fire for the past century, and (2) the effects of recent large-scale, stand-replacement fires on bird habitats, populations, and communities. Once these studies are completed, research experiments should be conducted to elucidate effects of potential management options to reduce fuels and move toward conditions resulting from a more natural fire regime.

In summary:

1. Fire once maintained pinyon-juniper woodlands in a savanna-like condition, with numerous grassy openings.
2. Fire suppression and loss of fuels to livestock grazing reduced fire frequency, resulting in increased woodland density, and a shift to stand-replacement fires.
3. Almost nothing is known about bird responses to fire in pinyon-juniper woodland.
4. Research and management should focus on understanding the ecology of birds in existing unburned pinyon-juniper woodlands, on the effects of recent stand-replacement fires, and eventually on ways to restore these woodlands to their historic structural condition, including the use of prescribed burning.

PONDEROSA PINE AND PINE-OAK WOODLANDS

Southwestern montane forests include both Cordilleran and Madrean flora. Cordilleran flora dominates more northern latitudes, whereas Madrean flora is largely restricted to basin-and-range mountains in southeastern Arizona, southwestern New Mexico, and along the Mogollon escarpment (Brown 1982a). The primary differences between the two systems are the particular pine and oak species; the overall structure is similar. Regardless of the flora, woodland and forest vegetation generally occur in gradients influenced by topography, aspect, soils, and climate.

Ponderosa pine (*Pinus ponderosa*) is the most common forest type in the Southwest, comprising approximately 70% of the forested land base (Conner et al. 1990, Van Hooser et al., 1993). At lower elevations, ponderosa pine forest is bounded by pinyon-juniper woodlands or oak savannas (Whitaker and Niering 1964, 1965). These lower forests are xerophytic, and ponderosa pine is the climax tree species. Various pinyon pines (*Pinus edulis, P. discolor, P. californiarum*), junipers (*Juniperus deppeana*, *J. osteosperma*, *J. monosperma*, and *J. scopulorum*), and oaks (*Quercus grisea, Q. arizonica, Q. emoryi, Q. hyperleucoides, Q gambelii,* and *Q. undulata*) occur as subdominant trees. Big sagebrush (*Artemisia tridentata*), rabbitbrush (*Chrysothamnus nauseosus*), and New Mexican locust (*Robinia neomexicana*) are common shrubs, with blue grama (*Bouteloua gracilis*), Arizona fescue (*Festuca arizonica*), and mountain muhly (*Muhlenbergia montana*) as the primary grasses. With increasing elevation, ponderosa pine forests become more mesophytic and, although still the dominant tree, ponderosa pine is a seral species amid mixed-conifer forests (Moir et al. 1997).

Hall et al. (1997) list over 100 bird species using ponderosa pine forest. Some characteristic species include Mourning Dove, Broad-tailed Hummingbird (*Selasphorus platycercus*), Northern Flicker (*Colaptes auratus*), Hairy Woodpecker, Western Wood-Pewee (*Contopus sordidulus*), Violet-green Swallow (*Tachycineta thalassina*), Steller's Jay, Common Raven (*Corvus corax*), Mountain Chickadee (*Popecile gambeli*), White-breasted Nuthatch, Pygmy Nuthatch (*Sitta pygmaea*), Western Bluebird, Plumbeous Vireo, Yellow-rumped Warbler (*Dendroica coronata*), Grace's Warbler (*Dendroica graciae*), Western Tanager (*Piranga ludoviciana*), Red Crossbill (*Loxia curvirostra*), Cassin's Finch (*Carpodacus cassinii*), Pine Siskin (*Carduelis pinus*), Chipping Sparrow, and Dark-eyed Junco (*Junco hyemalis*). Bird species of special concern within southwestern pine forests include Northern Goshawk (*Accipiter gentilis*), Mexican Spotted Owl (*Strix occidentalis lucida*), Flammulated Owl (*Otus flammeolus*), Greater Pewee (*Contopus pertinax)*, Olive-sided Flycatcher (*Contopus cooperi*), Cordilleran Flycatcher (*Empidonax occidentalis*), Purple Martin (*Progne subris*), Olive Warbler (*Peucedramus taeniatus*), Virginia's Warbler, and Grace's Warbler.

FIRE IN PONDEROSA PINE FORESTS AND PINE-OAK WOODLANDS

Fire is perhaps the most important natural disturbance in southwestern pine forests (Moir and Dieterich 1988, Covington and Moore 1994, Moir et al. 1997), and it influences plant composition, forest structure, and successional pathways. Frequent, low-intensity fires were part of the evolutionary history of many lower-elevation forests, extending up through mesophytic ponderosa pine and lower elevation mixed-conifer (Savage and Swetnam 1990, Moir et al. 1997). Crown fires seldom occurred, and they were confined to relatively small patches (Pyne 1996). Within the xerophytic pine, fire occurred every 2–12 yr and maintained an open grassy understory and a patchy tree pattern. Given the frequency at which fires occurred, little wood debris accumulated on the forest floor, and most fire was fueled by dead herbaceous vegetation. These low-intensity fires reduced understory fuel levels and killed small trees, preserving the characteristic open stand structure (Cooper 1960, 1961; White 1985).

Within the past century, management and economic activities, primarily fire suppression, livestock grazing, and logging, have had profound effects, altering natural fire disturbance regimes and their effects on forest structure and composition (Cooper 1960, 1961, Covington and Moore 1994). The synergistic effects of these practices have resulted in dense forests consisting mostly of small trees, reductions in fine fuels, heavy accumulations of ground and ladder fuels, and forests at high risk of large-scale, stand-replacement fires (Cooper 1960, 1961, Covington and Moore 1994). In addition, fire exclusion has led to changes in forest composition. For example, lack of fire has allowed shade-tolerant firs (*Abies* spp.) to compete with dominant pines for nutrients, thereby moving mesophytic pine forests toward mixed-conifer forests (Moir et al. 1997). Over-topping by pines has shaded out oaks and aspen (*Populus tremuloides*), reducing their prevalence on the landscape (Moir et al. 1997). In other areas, pines are encroaching upon open meadows and parks, converting them to forest (Moir et al. 1997). These changes have combined to increase continuities of fuels within and among stands, thereby increasing the risk and prevalence of large-scale, stand-replacement fire (USDI 1995).

Given large-scale fires of the past decade and risks to lives and properties, land-management agencies are beginning to implement fuels reduction programs with the goal of abating fire risk. Fuels reduction includes tree thinning and prescribed fire, used singly or in combination. Little information is available on the response of birds to such treatments.

FIRE EFFECTS ON PONDEROSA PINE AND PINE-OAK WOODLANDS BIRDS

Generalizing fire effects on birds in pine and pine-oak forests is difficult, given differences in fire severity, intensity, and size, as well as the scale and season of study. Short-term responses may differ from long-term responses; breeding bird response may differ from wintering bird response; and effects observed at the stand scale may differ from those at the landscape or regional scale. Lowe et al. (1978) examined a series of fires representing a chronosequence ranging from 1–20 yr postfire, and found that fire effects changed with time (Table 1). Ground-foraging birds and woodpeckers increased immediately following fire, presumably in response to increased food and nesting substrates, and then declined once canopy cover began to recover and food supplies diminished. Flycatchers reached their greatest abundance about seven years following fire, and then decreased. Concomitant with population responses might also be shifts in habitat-use patterns. Current studies indicate that Hairy Woodpeckers occupy smaller winter home ranges in forests 2 yr postfire than they use in forests 6 yr postfire (Covert and Block, unpubl. data). Presumably the amount of area used corresponds to that needed for adequate food.

Populations of secondary cavity-nesting birds responded differently to fires of varying severities in southwestern pine forests (Dwyer and Block 2000). Mountain Chickadee, Pygmy Nuthatch, and White-breasted Nuthatch populations were lower 2 yr postfire in areas of severe wildfire, whereas only the Mountain Chickadee declined in response to moderate understory fire. Western Bluebird populations were greater in severely burned forest than in unburned forest. Dwyer (2000) also found that populations of Western Bluebirds increased in a severely burned forest following introduction of nest boxes, suggesting that nest cavities might be limiting after fire. This situation might change in time, once primary cavity-nesting species reestablish themselves.

In one of the few published studies of responses by non-breeding birds, Blake (1982) found that, in the year following a wildfire, burned areas contained more individuals but fewer species than unburned areas. Some migrant and wintering species were unique to burned areas during the fall, including Common Poorwill (*Phalaenoptilus nuttalli*), Western Wood-Pewee, Western Scrub-Jay, House Wren (*Troglodytes aedon*), Hermit Thrush (*Catharus guttatus*), and Lesser Goldfinch (*Carduelis psaltria*).

Bird response to wildfire varies by season and fire severity. Bock and Block (in press) present data 3 yr post-wildfire from an ongoing study in northern Arizona (Table 1). Northern Flicker and Hairy Woodpecker populations increased in both moderately and severely burned areas, but increases were greater in response to severe fire. In contrast, Broad-tailed Hummingbird, Western Wood-Pewee, Plumbeous Vireo, and Western Tanager breeding populations increased following moderate-severity fire. When population declines were observed, most were in response to severe fire, including Williamson's Sapsucker (*Sphyrapicus thyroideus*; nonbreeding), Steller's Jay (breeding), Mountain

Chickadee (breeding and nonbreeding), Brown Creeper (nonbreeding), White-breasted Nuthatch (breeding and nonbreeding), Pygmy Nuthatch (breeding and nonbreeding), Plumbeous Vireo (breeding), Yellow-rumped Warbler (breeding), and Grace's Warbler (breeding).

Most studies of fire effects on birds in pine systems have focused on stand-replacement burns. These investigations provide little insight into the probable effects of understory burning, or on avian responses to habitat alterations associated with prescribed fire. Two studies are exceptions. Horton and Mannan (1988) examined effects of prescribed fire on cavity-nesting birds in a pine-oak forest in the Santa Catalina Mountains of Arizona. They sampled birds prior to prescribed fire, and then for one and two years afterwards. They found few changes in bird abundance, with Northern Flickers and Violet-green Swallows decreasing, and Mountain Chickadees increasing. In the other study, Marshall (1963) conducted a retrospective comparison of bird communities within the Madrean Archipelago in forests where natural fire had occurred in Mexico, versus similar forests north of the border where fire had been suppressed. He found that species common to brush or heavier forest cover, such as Ash-throated Flycatcher, Black-throated Gray Warbler, Scott's Oriole (*Icterus parisorum*), and Spotted Towhee were more abundant in the denser forests of Arizona and New Mexico. In contrast, species typical of relatively open conditions, American Kestrel (*Falco sparverius*), Cassin's Kingbird (*Tyrannus vociferans*), Purple Martin, Chipping Sparrow, and Western and Eastern bluebirds, were more abundant in Mexican forests.

Knowledge of the effects of wild and prescribed fire on birds is far less than what is needed to provide a basis for management of southwestern ponderosa pine forests. In particular, more studies are needed to better understand effects of understory wildfire and prescribed fire on birds. Meanwhile, we advocate that fire management strive to move toward historical fire regimes, wherever possible. The most immediate need is to reduce fuel continuity and the threats of large, stand-replacing crown fires. Research should continue on ramifications of past management so we have a basis for developing future management that ensures viable populations of species native to Southwestern ponderosa pine forests. As management options are developed, they should be applied within an adaptive management framework that monitors the response of bird populations and communities to enable adjustments to management through time.

In summary:

1. Wildifire once maintained most southwestern pine forests as relatively open stands, with large scattered trees and a grassy understory.
2. The combined effects of fire suppression, livestock grazing, and logging have caused most southwestern pine forests to become crowded by smaller trees, with a greatly-increased risk of stand-replacement fire.
3. The principal management objective for southwestern pine forests should be to return them to their open condition, using prescribed fire and other methods, both to reduce their vulnerability to catastrophic fire and to enhance their habitat value for birds and other wildlife.
4. Most research on avian responses to fire in southwestern ponderosa pine forests has centered on the results of high-intensity burns; future emphasis should be on results of low-intensity, ground fires that once characterized these forests, and that will be an essential aspect of their future management.

MIXED-CONIFER FORESTS

Mixed-conifer forests occur on approximately 20% of forested land in the Southwest (Conner at al. 1990, Van Hooser et al. 1993). This represents an increase since the 1960s, due in part to effects of fire suppression and the conversion of pine forest and aspen stands to mixed conifer. The reduction of wildfire disturbance in mesophytic ponderosa pine forests favors shade-tolerant Douglas-fir (*Pseudotsuga menziesii*) and white fir (*Abies concolor*) which become the dominant tree species. Once this happens, the forest is more appropriately described as mixed conifer.

At lower elevations (2,000–2,400 m), mixed-conifer stands are warm-climate forests dominated by Douglas-fir, white fir, ponderosa pine, and southwestern white pine (*Pinus strobiformis*), with various broadleaf trees (e.g., *Populus* spp., *Quercus* spp., *Acer* spp.) in the sub-canopy. At higher elevations (2,400–3,000 m), ponderosa pine is no longer present, and mixed-conifer forests grade into spruce-fir forests consisting of Engelmann spruce (*Picea engelmanni*), corkbark fir (*Abies lasiocarpa*), white fir, and Douglas-fir (Moir 1993). Trembling aspen occurs as a seral species in most montane forest types, where it can occur as a subdominant tree in conifer forests, or as monotypic stands embedded within a matrix of conifer forests.

Some birds characteristic of mixed-conifer in the Southwest are Northern Goshawk, Mexican Spotted Owl, Broad-tailed Hummingbird, Northern Flicker, Hairy Woodpecker, Williamson's Sapsucker, Cordilleran Flycatcher, Steller's Jay, Mountain Chickadee, Red-breasted Nuthatch (*Sitta canadensis*), Golden-crowned Kinglet (*Regulus satrapa*), Hermit Thrush, Plumbeous Vireo, Warbling Vireo (*Vireo gilvus*), Yellow-rumped Warbler, Grace's Warbler, Olive Warbler, Red-faced Warbler (*Cardellina rubifrons*), Dark-eyed Junco, and Western Tanager. Birds of special management concern include Northern Goshawk, the threatened Mexican Spotted Owl, Williamson's Sapsucker, Olive-sided Flycatcher, Dusky Flycatcher (*Empidonax oberholseri*), and Red-faced Warbler.

FIRE IN MIXED-CONIFER FORESTS

In lower elevation mixed-conifer forests, the historical fire regime was very similar to that occurring in ponderosa pine, in that most events were low-severity ground fires (Grissino-Mayer et al. 1995, Moir et al. 1997). In contrast, many fires that occurred at higher elevations within mixed-conifer and spruce-fir forests were stand-replacing, providing opportunities for establishment of aspen. Since it is a seral species, aspen will persist as long as disturbance continues. In the absence of disturbance, conifers will eventually overtop and outcompete aspen for light and nutrients.

FIRE EFFECTS ON MIXED-CONIFER FORESTS BIRDS

We found few studies from the Southwest that specifically address the response of birds to fire in mixed-conifer forests. What little we can suggest is extrapolated from studies in the Sierra Nevada (Bock and Lynch 1970, Raphael et al. 1987) or Rocky Mountains (Hutto 1995, Kotliar et al. 2002). Certainly, fire provides opportunities for a number of species that occur in much lower numbers in unburned forest. Bock and Lynch (1970) found that 28% of 32 regularly breeding species occurred only in burned forest, and 19% only in unburned forest; overall, species richness was highest in the burned forest. Species restricted to burned forest included Willamson's Sapsucker, Olive-sided Flycatcher, House Wren, Mountain Bluebird (*Sialia currucoides*), Lazuli Bunting (*Passerina amoena*), Green-tailed Towhee, Chipping Sparrow, and Brewer's Sparrow; those restricted to unburned forest were Hermit Thrush, Golden-crowned Kinglet, Plumbeous Vireo, and Nashville Warbler (*Vermivora ruficapilla*).

Hutto (1995) identified 15 species, primarily woodpeckers, flycatchers, and seedeaters, that were more abundant in postfire, mixed-conifer forest in the Rocky Mountains. Of species mostly confined to recent postfire conditions, four also occur in the Southwest: Olive-sided Flycatcher, American Three-toed Woodpecker (*Picoides dorsalis*), Clark's Nutcracker (*Nucifraga columbiana*), and Mountain Bluebird. Species found more frequently in areas 10–40 yr postfire included Common Nighthawk (*Chordeiles minor*), Calliope Hummingbird (*Stellula calliope*), Northern Flicker, Orange-crowned Warbler (*Vermivora celata*), and Chipping Sparrow. The American Robin, Yellow-rumped Warbler, and Dark-eyed Junco were detected in all early and mid-successional forest studies that Hutto (1995) reviewed.

Kotliar et al. (2002) summarized results from 11 published and unpublished studies in conifer forests of the western US, where severe, stand-replacement wildfire had occurred within 10 yr of data collection. Of these, only one (Johnson and Wauer 1996) occurred in the Southwest. The studies occurred in various forest types, although mixed-conifer appeared best represented in their sample. Kotliar et al. (2002) found that 9 of 41 species were more abundant in recently burned forests, including American Three-toed Woodpecker, Black-backed Woodpecker (*Picoides arcticus*), Northern Flicker, Hairy Woodpecker , Olive-sided Flycatcher, Mountain Bluebird, Western Wood-Pewee, House Wren, and Tree Swallow (*Tachycineta bicolor*). All of these except the Black-backed Woodpecker are found commonly in the Southwest.

Clearly, wildfire in mixed-conifer forests creates habitats and provides resources that otherwise would not be available for a variety of birds in these ecosystems. However, not all species are favored by fire. Some, such as the Mexican Spotted Owl, require older forests that result from years of fire exclusion (May and Gutiérrez 2002).

Following fire, many mixed-confer forests transition into aspen. Given fire suppression, aspen has less opportunity to become established, and existing stands succeed to mixed-conifer. Aspen forest is a dwindling forest type in the Southwest that often supports more species than surrounding conifer forests, thereby contributing to greater landscape diversity (Finch and Reynolds 1987, Griffis 1999). Management priorities should emphasize maintaining and restoring aspen forests on the landscape.

More field research specific to southwestern conditions needs to be conducted to understand fire effects on birds in mixed-conifer forests. Clearly, the various successional stages of mixed-conifer forests support distinctive avifaunas, and thus all succcessional stages should be represented in appropriate quantities in the landscape (Kotliar et al. 2002). This requires management that emulates natural fire regimes to the extent possible (Kotliar et al. 2002). At lower elevations, this would require reducing ladder fuels and increasing fine fuels needed to carry ground fire. Potential tools to achieve these conditions include reductions in grazing pressures, thinning, and prescribed fire.

At higher elevations, fire management might entail a combination of prescribed and natural fire, with well-planned fuel breaks consisting of topographic or vegetation barriers that impede fire spread. Fire management at higher elevations is best achieved with a mosaic of long-unburned stands mixed with other areas that are burned with varying frequencies and intensities. The resulting landscape should possess the heterogeneity to provide habitat for numerous species.

Future research should focus on the effects of past management so we have a basis for ensuring viable populations of species native to mixed-conifer forests. As management options are developed, they should be applied within an adaptive management framework that monitors the response of bird populations and communities to treatments, to enable adjustments to management through time. Research should be structured in such a way to address questions at the appropriate scale in time and space. Wildfire in mixed-conifer forest results in a shifting mosaic of seral stages through time. To understand the dynamics of wildfire, research cannot be restricted to short-term studies but must continue for decades. Similarly, research cannot be restricted to small plots, but must be extended to landscapes to better understand relationships at the scale at which disturbance regimes manifest themselves.

In summary:

1. Ground fires once maintained low-elevation southwestern mixed-conifer forests in a relatively open condition, whereas higher-elevation forests experienced stand-replacement burns that created heterogeneous landscapes, including openings for aspen regrowth.
2. Historical reductions in fire frequencies caused low-elevation forests to become dense, and all southwestern mixed-confer forests to experience occasional large stand-replacement fires.
3. Few studies have been done of avian responses to fire in southwestern mixed-conifer forests; however, studies in this habitat in the Sierra Nevada and Rocky Mountains indicate that each type of mixed-conifer forest supports a distinctive avifauna, from unburned mature forests, to aspen groves that follow stand-replacement fires, to open park-like forests maintained by ground fires.
4. Research goals should be to learn more about habitat requirements of birds in southwestern mixed-conifer forests, by conducting long-term studies at appropriate landscape scales.
5. Management goals should be to return low elevation forests to the historic relatively open condition, and to create high-elevation mosaics of unburned forests and those burned with varying frequencies and intensities, especially including those that provide opportunities for aspen.

RIPARIAN WOODLANDS

Riparian woodlands follow stream and river channels that cross all the southwestern ecosystems discussed previously in this chapter. Dominant native trees in southwestern riparian woodlands include cottonwood (*Populus* spp.), sycamore (*Platanus wrightii*), willow (*Salix* spp.), ash (*Fraxinus velutina*), walnut (*Juglans* spp.), mesquite, and a variety of others that can be locally common at different elevations (Johnson and Jones 1977, Patten 1998, Cartron et al. 2000).

Southwestern riparian woodlands support an abundance and variety of breeding birds greater than the relatively arid ecosystems adjacent to them. Riparian avifaunas include some of the highest bird densities ever reported, and many species that are rare or missing elsewhere in the region (Carothers et al. 1974, Strong and Bock 1990, Rosenberg et al. 1991, Nabhan 2000). Low and mid-elevation gallery forests of large mature trees are particularly important for both breeding and migratory birds (Bock and Bock 1984, Szaro and Jakle 1985, Skagen et al. 1998, Powell and Steidl 2000). Riparian species that appear most frequently on state and regional Partners in Flight priority lists include Common Black-Hawk (*Buteogallus anthracinus*), Yellow-billed Cuckoo (*Coccyzus americanus*), Elegant Trogon (*Trogon elegans*), Bell's Vireo (*Vireo bellii*), Lucy's Warbler (*Vermivora luciae*), and Abert's Towhee (*Pipilo aberti*), along with the endangered Southwestern Willow Flycatcher (*Empidonax trailii extimus*; Sedgwick 2000).

Fire in Riparian Woodlands

The frequencies and effects of prehistoric wildfires in southwestern riparian woodlands are very poorly understood (Dwire and Kauffman 2003). While such fires usually are assumed to have been rare (Busch 1995), most riparian corridors cross upland ecosystems that burned relatively frequently, and dominant native trees such as cottonwood and willow have shown considerable ability to resprout after fire (Ellis 2001). Much more certain is that the frequency and especially the intensity of fires have increased historically. While livestock grazing may have reduced fuels somewhat, two other factors have combined to make these ecosystems more likely to experience intense fire: the spread of exotic saltcedar trees (*Tamarix ramosissima*); and increasing aridity resulting from reduced flows and altered flooding regimes (Busch and Smith 1995, Ellis et al. 1998).

Fire Effects on Riparian Woodlands Birds

We found no studies describing the response of birds to fire in southwestern riparian habitats. However, we do not recommend prescribed burning as a research or management priority. Recent fires have been highly destructive of most native riparian vegetation, while facilitating the spread of saltcedar, which fails to provide habitat for many native birds (Rosenberg et al. 1991, Busch 1995). Research and management efforts should be directed at finding ways to control saltcedar, and to restore flow and flood patterns conducive to reproduction in the native trees, especially cottonwood, willow, and sycamore.

In summary:

1. Southwestern riparian woodlands support an extraordinary variety and abundance of birds, many of which have a high conservation priority.
2. Many of these ecosystems have been altered historically by water impoundments and diversions that reduce flows, change flood regimes, encourage the spread of exotic saltcedar, and increase the frequency and intensity of fire.
3. Research and management priorities should not involve fire, but should be directed at returning flood regimes that favor native trees such as cottonwood, willow, and sycamore that in turn provide critical habitat for many southwestern birds.

RESEARCH AND MANAGEMENT RECOMMENDATIONS

We have described habitat-specific research and fire management issues in the preceding sections of this review. In summary, we do not recommend application of prescribed fire in Sonoran, Mojave, or Chihuahuan deserts, and associated xeric desert grasslands, or in southwestern riparian woodlands. Major threats to these ecosystems are the increased fuel loads caused by invasions of exotic grasses and trees, and the resulting increase in wildfire frequency and intensity. Managers and researchers must find ways to reverse these invasions, for the sake of southwestern desert and riparian woodland ecosystems and their associated avifaunas.

Wildfire doubtless once played a highly significant role in (1) sustaining mesic desert grasslands in a relatively shrub-free state, (2) maintaining structural heterogeneity of interior chaparral, (3) limiting the distribution and density of pinyon-juniper woodland, (4) maintaining oak, pine, and low-elevation mixed-conifer ecosystems as open stands of relatively mature trees, and (5) opening dense stands of high-elevation, mixed-conifer forests and providing opportunities for aspen regrowth. Whenever possible, prescribed fire should be applied to mimic these effects. This will have the double benefit of reducing fuels and the risks of large wildfires, and sustaining habitats upon which many southwestern birds depend.

Successful implementation of prescribed burning programs in southwestern ecosystems will not be easy. In formerly open woodlands, such as pine and oak, the challenge will be to keep fire on the ground where it can open the forest floor without harming the mature trees. In higher-elevation mixed-conifer forests, where stand-replacement fires were a part of the natural ecosystem dynamic, the challenge will be to create landscapes with sufficient fuel breaks so that prescribed fire can be contained in a desired area.

Finally, it is important to recognize that certain kinds of birds require or prefer unburned areas, even in ecosystems that have a long evolutionary association with fire. That is why burning all of any particular landscape would be just as undesirable as preventing fire altogether. For every sparrow that depends upon the seeds produced by recently burned desert grassland, there is another that requires heavy grass cover that a fire temporarily destroys. For every bluebird that prefers an open pine forest, there is a towhee that does best where understory foliage is dense. For every sapsucker that nests in fire-dependent aspen, there is a Mexican Spotted Owl that prefers a mature stand of mixed-coniferous forest. In all of these cases, the overall objective of management must be to maintain landscape-level mosaics of stands in various stages of postfire ecological succession, including some areas long spared from fire.

Given the prevalence and ecological importance of fire in the Southwest, there have been remarkably few studies of the effects of fire on southwestern birds, especially of prescribed burning and for ecosystems other than ponderosa pine (Table 1). Also scarce are studies about birds outside the breeding season, or on demographic attributes other than abundance, such as nesting success. Most of our conclusions and recommendations about fire and birds in the Southwest are based on extrapolations from known fire effects on vegetation and generally understood habitat requirements of particular bird species. We believe most of our conclusions are reasonable, but they would be strengthened and doubtless greatly refined by the results of more replicated, large-scale, properly controlled field studies. It always appears self-serving when scientists call for more research, but in this case the need is self-evident. Given increased public awareness and concern about the destructive aspects of wildfire in the Southwest, there is a real danger that fire prevention and suppression policies will be implemented that are as ecologically unfortunate as those of the past century.

ACKNOWLEDGMENTS

We thank H. Powell, V. Saab, and two anonymous reviewers for helpful comments on an earlier draft of this chapter.

Studies in Avian Biology No. 30:33–45

CHANGING FIRE REGIMES AND THE AVIFAUNA OF CALIFORNIA OAK WOODLANDS

Kathryn L. Purcell and Scott L. Stephens

Abstract. Natural and anthropogenic fire once played an important role in oak woodlands of California. Although lightning-ignited fires were infrequent, the California Indians used fire to modify oak woodland vegetation for at least 3,000 yr. These high-frequency, low-intensity fires likely resulted in little mortality of mature oaks, low but continuous tree recruitment, an open understory, and a fine-grained mosaic of vegetation patches. Following settlement by Europeans in the mid-1800s, ranchers burned to reduce shrub cover and to increase grassland area and forage production; surface fires were common with average fire-return intervals of 8–15 yr. Fire suppression, begun in the 1940s to 1950s, led to increases in surface and crown fuels, invasion of woody vegetation in the understory, and increased tree density. In the absence of demonstrated fire effects on oak woodland birds, we used changes in vegetation structure expected to result from fire and fire suppression to predict the response of oak woodland birds to fire and fire suppression based on nesting habitat of 17 common oak woodland species breeding at the San Joaquin Experimental Range, Madera County, California. Our results suggest that populations of Western Kingbirds (*Tyrannus verticalis*), Western Bluebirds (*Sialia mexicana*), and Violet-green Swallows (*Tachycineta thalassina*), would increase in abundance following fire, because they consistently nested in habitat similar to that expected to result from frequent, low-intensity fire. The species predicted to respond negatively to changes resulting from fire differed among the variables examined. If fire produces a mosaic of habitat patches rather than a homogeneous landscape, we expect that the differing habitat needs of most species will be provided for. As with fire, the most obvious change resulting from excluding livestock was an increase in shrub cover. The question naturally arises to what extent livestock grazing creates habitat similar to that created by historical fire, but this question remains unstudied. More fire-history research is needed to understand past fire regimes of oak woodlands and the effects of fire, including prescribed fire, on the vegetation and the bird community. The effects of grazing and the extent to which grazing mimics fire clearly require more study. We encourage others to test our hypotheses regarding responses of birds to variables expected to be altered by fire: shrub cover, tree density, and numbers of snags, saplings, and logs. Finally, we need to test our working hypothesis that a mosaic of habitat patches will provide the habitat conditions needed to sustain the high avian diversity characteristic of oak woodlands.

Key Words: anthropogenic, avian diversity, fire, fire frequency, fire intensity, fire suppression, livestock grazing, oak woodlands, Violet-green Swallow, Western Bluebird, Western Kingbird.

REGÍMENES DEL FUEGO Y AVIFAUNA CAMBIANTE DE LOS BOSQUES DE ENCINO DE CALIFORNIA

Resumen. Alguna vez los incendios tanto naturales, como antropogénicos jugaron un importante papel en los bosques de encino de California. A pesar de que los incendios causados por relámpagos eran infrecuentes, los Indios de California utilizaban el fuego para modificar los bosques de encino por al menos 3,000 años. La elevada frecuencia y baja intensidad de incendios causó poca mortandad en encinos maduros, un renuevo bajo, pero continuo, vegetación secundaria abierta y un fino mosaico de parches de vegetación. Después del asentamiento de los Europeos a mediados de 1800s, quienes manejaban las tierras, quemaban para reducir la cobertura de arbustos y para incrementar el área de pastizales, así como la producción de forraje; eran comunes las superficies de incendios con un promedio de repetición de intervalos de 8–15 años. La supresión del fuego comenzó en 1940–1950,lo cual causó el incremento de combustible (tanto en superficie, como en copas), la invasión de vegetación forestal en la vegetación secundaria y un aumento en la densidad de árboles. En ausencia de demostraciones de los efectos del fuego en aves de bosques de encino, usamos cambios en la estructura de la vegetación, esperando lo que resulte del incendio, así como la supresión del mismo, para predecir la respuesta de las aves en bosques de encino a los incendios y a la supresión de estos, basados en habitats de anidamiento de 17 especies comunes reproductivas de aves de bosques de encino en el Rancho Experimental de San Joaquín, Condado de Madera, California. Nuestros resultados sugieren que las poblaciones de Tirano Pálido (*Thyrannus verticalis*), Azulejo Gorjiazul (*Sialia mexicana*), y Golondrina Cariblanca (*Tachycineta thalassina*), incrementarían en abundancia después de un incendio, dado que ellas constantemente anidan en habitats similares a aquellos esperados después de incendios frecuentes de baja intensidad. Las especies que se espera que respondan negativamente a los cambios resultantes de los incendios, difieren según las variables examinadas. Si el fuego produce un mosaico de parches de habitat, en lugar de un paisaje homogéneo, esperamos que los necesidades de la mayoría de las especies del habitat que difiere serán proveídas. Así como con en el fuego, el cambio más obvio que resulta de la exclusión del ganado, es un incremento en la cobertura de arbustos. La pregunta surge naturalmente; hasta qué punto el pastoreo crea un habitat similar a aquel creado por el fuego históricamente? Pero esta pregunta permanece aún sin estudiar. Se requiere mayor investigación en la historia de los incendios, para entender regimenes pasados de incendios en bosques de encino y los efectos de estos (incluyendo quemas preescritas) en la vegetación y en las comunidades de aves. Nosotros animamos a otros a comprobar nuestra hipótesis, tomando en cuenta las respuestas de las aves a las variables que se espera sean alteradas por el fuego: cobertura arbustiva, densidad de árboles y número de tocones, muestreos y trozas. Finalmente, necesitamos comprobar la hipótesis con la cual trabajamos: un mosaico de parches de un habitat proveería las condiciones que requiere el habitat para sustentar una alta diversidad de aves, característico de bosques de encino.

Oak woodlands comprise some of the richest and most diverse ecosystems in California, providing habitat during all or part of the year for more than 110 bird species (Verner et al. 1980, Block and Morrison 1990). These woodlands encircle the Central Valley and extend south along the coast to Mexico (Fig. 1). Managing oak woodlands for avian diversity requires a long-term perspective of disturbance regimes.

Fire was once an important component of the disturbance regime in oak woodlands of California. In addition to lightning-ignited fires, anthropogenic sources of ignition have been important historically (Stewart 1955, Lewis 1973, 1977, 1982, Timbrook et al. 1982, Anderson 1993, Pyne 1993, Kay 1995). American Indians used fire to modify vegetation for thousands of years (Johnston 1970, Lewis 1993). European settlement brought the introduction of livestock, the introduction of non-native annual grasses and other plant species, which resulted in a loss of native plant species, and the decimation of the California Indian population (Byrne et al. 1991). As a result, fire regimes have changed as well, but quantitative data are scarce.

Few fire-history studies have addressed oak woodlands (McClaran and Bartolome 1989, Mensing 1992, Stephens 1997, Fry 2002). Pre-European burning patterns and their impacts on stand structure and landscape patterns are more difficult to determine with confidence, as they are based on historical records and interviews with informants (Lewis 1977, 1980). Studies of the effects of fire on birds of oak woodlands are even scarcer.

Here we review existing information on how fire as a disturbance regime has changed in California's oak woodlands, and how the various fire regimes and changes to them have affected the vegetation. We discuss existing information on historic burning by California Indians and the resulting effects on oak woodlands. Although prehistoric fire regimes are difficult to reconstruct and disagreement on the specific impacts of anthropogenic fires exists, most now agree that burning by American Indians had a major influence on the vegetation over thousands of years. We then discuss the evidence for burning by early Euro-American settlers, their differing objectives, and effects on vegetation. We briefly touch on the results of suppression efforts begun from 1940–1950 and the issues of implementing prescribed fire in a modern landscape. We review the general effects of high-frequency, low-intensity fire on vegetation and the results of previous studies on the effects of fire on birds. Finally, we use our knowledge of habitat requirements of oak woodland birds and data from our studies of nesting habitat of birds at the San Joaquin Experimental Range, Madera County, California, to attempt to predict the response of the bird community to vegetation change from fire and fire suppression. These results are intended to provide hypotheses and to stimulate research on the effects of fire and fire suppression on birds of oak woodlands.

CALIFORNIA OAK WOODLANDS

We define oak woodlands as oak-dominated plant communities in California lowland and foothill regions. The major oak communities considered here include blue oak (*Quercus douglasii*) woodland, blue oak-foothill pine (*Pinus sabiniana*), coast live oak (*Quercus agrifolia*) woodland, and valley oak (*Quercus lobata*) woodland (Fig. 1) but do not include the montane mixed hardwood-conifer vegetation types. Although we briefly describe individual vegetation types here and discuss their differences, not enough work is available on the individual types to warrant separate discussion of each and, for the most part, they are referred to collectively throughout this chapter.

Blue oak woodlands occur in dry, hilly terrain in the western foothills of the Sierra Nevada and Cascade Ranges, the Tehachapi Mountains, and the

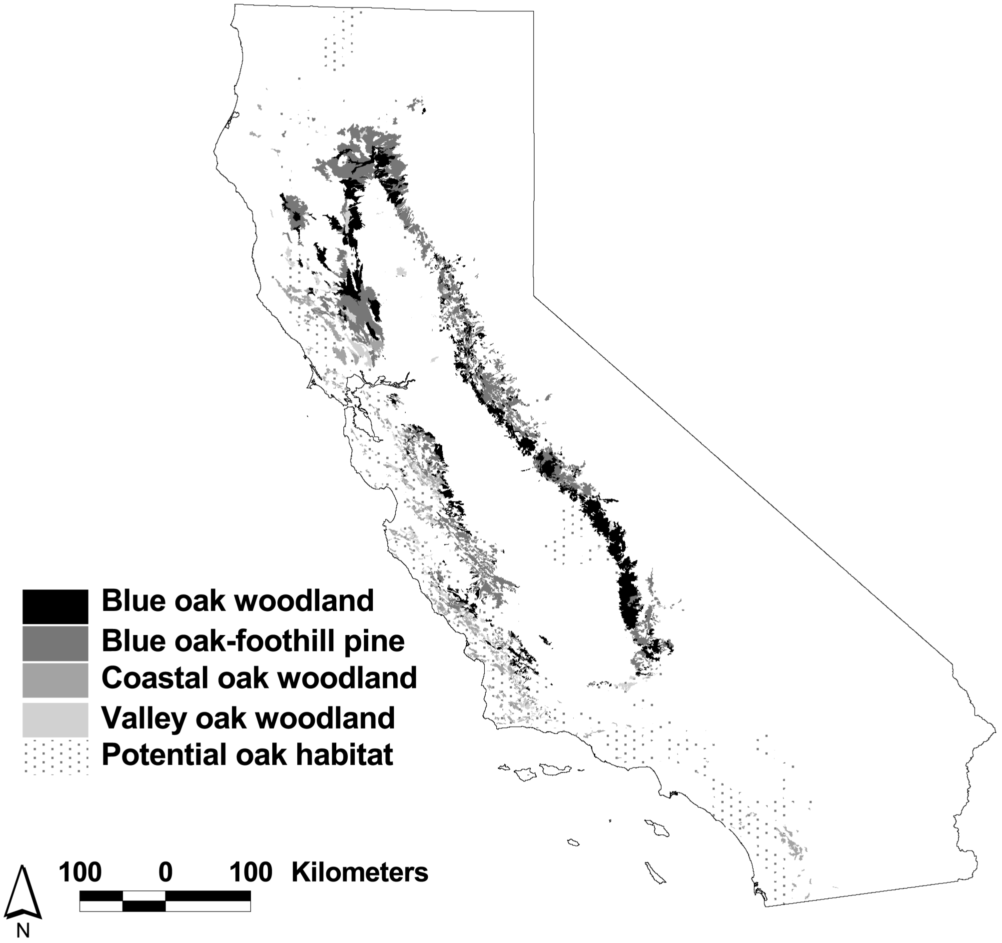

FIGURE 1. Approximate current coverage of valley and foothill oak woodland habitats throughout California based on the California GAP Analysis Project (Davis et al. 1998) and potential coverage based on Kuchler (1976) (adapted from California Partners in Flight 2002).

eastern foothills of the Coast Ranges. They range from open woodlands of scattered trees to stands with nearly closed canopies (Ritter 1988a). Blue oak is the dominant tree species, and the understory consists of annual grasses and forbs. Blue oak-foothill pine woodlands are more diverse both structurally and floristically (Verner 1988). Blue oaks and foothill pines dominate the canopy, with interior live oak (*Quercus wislizenii*), coast live oak, and valley oak often appearing as associated species. The understory may include patches of scattered shrubs in addition to annual grasses and forbs. This habitat is nearly continuous in the western foothills of the Sierra Nevada and discontinuous in the Coast Range west of the Central Valley and the Transverse Range of southern California. Coastal oak woodlands occur in coastal foothills and valleys and are variable in terms of species composition in both overstory and understory (Holland 1988). Oregon white oak (*Quercus garryana*) is common in the North Coast Range to Sonoma County, while coast live oak dominates to the south. Additional tree species occur in both more mesic and drier sites, and the understory may consist of annual grasses with scattered shrubs in open stands, dense shrubs, or a lush cover of shade-tolerant plants in closed stands. Valley oak woodlands occur in remnant patches in the Central Valley, the Sierra Nevada foothills, the Tehachapi Mountains, and valleys of the Coast Ranges (Ritter 1988b). They are dominated by valley oaks, with denser stands occurring in deep soils along river margins.

FIRE HISTORY OF CALIFORNIA OAK WOODLANDS

BURNING BY CALIFORNIA INDIANS

Humans probably learned to produce and use fire at least 20,000 yr ago, and the ancestors of American Indians probably brought this tool with them when they crossed the Bering Strait land bridge around 15,000 yr ago (Johnston 1970). Almost every tribe in the western United States deliberately set fire to vegetation (Stewart 1955), and we believe they used fire as a vegetation management tool for at least 3000 yr (Johnston 1970, Lewis 1973).

For the purpose of this paper, California Indians of oak woodlands include tribes that inhabitated the San Joaquin and Sacramento Valleys, including the foothills and western slopes of the Sierra Nevada, and the coast ranges and valleys of northern and southern California. Specific major tribes mentioned in literature cited here include but are not limited to the Yurok, Hupa, Pomo, Maidu, Miwok, Mono, Yokut, and Chumash.

While no documented accounts exist on how much burning the California Indians did, numerous ethnological and historical accounts describe how, why, and when they burned. We do not know to what extent fires ignited by California Indians modified oak woodlands (Lewis 1993), but ethno-ecological evidence indicates these fires were very common, even annual in some areas.

Anthropogenic fires were probably more common in oak woodlands than lightning-caused fires. Decades may pass in any given area between storms that bring lightning-ignited fires in oak woodlands (Griffin 1988, Lewis 1993, Stephens 1997). Natural patterns of ignition (lightning) differed significantly from California Indian patterns of burning in terms of frequency, intensity, extent, and ignition patterns (Lewis 1982, 1985). The effects of these differences are not well understood, but differences in frequency and intensity probably created different vegetation mosaics (Anderson 1993, Kay 1995).

Differences between fires ignited by California Indians and lightning include the number of simultaneous ignitions and the placement of fires. California Indians burned for specific objectives in specific locations, and the number of fires was probably small to moderate at any given time. Lightning is episodic in nature and hundreds to thousands of fires can be ignited over a single 24-hr period. Years with high lightning activity probably produced large landscape-scale fires if fuels were available for combustion. It was probably less common for large numbers of anthropogenic fires to burn simultaneously.

California Indians burned to modify plant and animal communities for their benefit (Anderson 1993, Kay 1995); more than 70 reasons are listed in the literature for why they burned (Lewis 1973, Timbrook et al. 1982). For example, burning under oaks improved the acorn crop by reducing acorn predators, removed competing conifers, kept lethal fires at bay, facilitated acorn harvests, and improved mobility and visibility both for hunting game and for increased security. Burning also moved game to favorable hunting areas and improved the quality and abundance of other food sources and materials used for cultural items. According to Anderson (1993), an important axiom in indigenous California was that conflagrations were dangerous to humans. Frequent burning kept combustible fuels down, particularly around village sites, prevented major conflagrations, and provided a defensible space.

Fire frequency is believed to have been annual in some areas (Lewis 1982, Kay 1995). The spatial extent of burning is not well understood, although both small and extensive fires did occur (Anderson and Moratto 1996, Stewart 2002). The timing of Indian burning was usually late summer or early fall (Lewis 1980, 1985, Timbrook et al. 1982), coincident with the timing of lightning storms (Lewis 1993). The probable results of frequent burning were that subsequent lightning fires behaved similarly to anthropogenic fires (Kay 1995), and that major conflagrations were relatively uncommon (Lewis 1982).

EFFECTS OF BURNING BY CALIFORNIA INDIANS

Early explorers and botanists believed the structure of the stands of oaks they saw were the result of burning by California Indians. They provided descriptions of fires set by California Indians and what they believed were the effects on the vegetation.

Due to the high frequency of burning, fires were of low intensity with little mortality of mature trees. Grass fires reduced encroachment by shrubs and conifers, which can act as fuel ladders to oak trees, and protected the oaks. Jepson (1910:11) suggested the open stands of valley oak and interior live oak he saw were the results of annual burning by California Indians. Those low-intensity frequent fires are often invoked as maintaining the open structure of presettlement valley oak woodlands (Jepson 1923:167). At Big Oak Flat in the Sierra Nevada foothills, Paden and Schlichtmann (1959:121) described the results of frequent burning by the Miwoks on the vegetation structure. The California Indians took an active role in manipulating the vegetation, and following the reduction in burning by California Indians, vegetation structure changed and the understory became more dense (Steward 1935:40–41 in Anderson 1993). The extent of burning in the foothills of the southern Sierra Nevada is discussed by a Chukchansi informant in Gayton (1948:176).

These observations are generally consistent with results of research on frequent, low-intensity fires in oak woodlands. A study of fire scars and stand ages in blue oak woodlands in the Tehachapi Mountains of southern California concluded that the woodlands were less dense during the period when California Indians occupied the area (Mensing 1992). It is likely that all sizes of trees were present and possibly abundant when European settlement began, and that recruitment of new trees was low but relatively continuous (Mensing 1992). It is important to note that the usefulness of evidence from fire-scar histories is limited. Frequent fires may have been of such low intensity that scarring was not likely, and trees harboring older fire scars may be rare (Lewis 1980, McClaran and Bartolome 1989).

We should be cautious in implying that these open conditions existed in all oak woodlands at all times. It is unlikely that California Indians would have burned all of the California oak woodlands in a given year, or in any set of years (Lewis 1993). The actual impact in an area would depend to a large extent on local population pressures. Even though the California Indian population was estimated to be among the highest in North America, the Indians probably would not have been able to burn all or even most of the vegetation on a regular basis, even if they wanted to do so (Lewis 1993). The high frequency and localized burning created a much more complex overall pattern than would have been the case with only lightning fires (Lewis 1993).

The California Indians used the resources of two or more ecosystems and their ecotones, and they were able to modify the locations of these ecotones to create a complex interface, particularly the ecotone between oak woodlands and chaparral. Authorities generally believe that, prior to suppression, chaparral was restricted to the higher slopes and ridges (Lewis 1993).

The reduction in American Indian populations resulting from disease and genocide, along with early state regulations prohibiting the setting of fires on state or federal land (Sampson 1944), greatly restricted the areas burned annually until, by the mid-nineteenth century, burning by California Indians was no longer a significant factor in the oak woodlands of California (Lewis 1993).

Euro-American Burning

Burning by Euro-American settlers is better documented than burning by California Indians. Increased fire frequency occurred in some areas following Euro-American settlement in 1848 (McClaran and Bartolome 1989). Surface fires were very common in the foothills of the Sierra Nevada in the late 1800s until the mid-1900s (Stephens 1997). Studies of fire history have revealed average fire-return intervals of 8–15 yr during this period (Sampson 1944, McClaran and Bartolome 1989, Stephens 1997).

Fires were probably of low intensity but spread extensively through the foothill communities because of high horizontal fuel continuity from grasses and forbs. The replacement of the original bunchgrass vegetation by introduced annual plants, which began with the arrival of the Spanish colonists in 1769 (Burcham 1957), may have altered fire behavior. Prior to their replacement, the clumped bunchgrasses and the bare areas surrounding them could have reduced horizontal fuel continuity perhaps affecting the spread rate and extent of fires, although the presence of native annuals growing around the bunchgrasses should not be ignored. Rancher-ignited fires were reduced drastically in the late 1950s in most of the state because of more people moving into these areas, problems with escaped fires, and state and federal opposition to privately ignited rangeland fires (Biswell 1989).

Effects of Euro-American Burning

The main objective of burning following Euro-American settlement was to increase or maintain forage production for livestock (Cooper 1922, Biswell 1989). Burning also increases the palatability, nutrition, and yield of forage (Sampson 1944). Large areas of shrublands and woodlands were converted into grasslands or savannas with the use of fire, chemicals, and mechanical methods. Fire hazards were reduced by frequent burning. Differences in California Indian and Euro-American patterns of burning are related to differing objectives—grass and cattle for ranchers and numerous plant and animal species for hunter-gatherers (Lewis 1985).

While recruitment of oaks appears to have been slow and steady during the California Indian occupation of the oak woodlands, high rates of regeneration and recruitment occurred in some areas in the mid-1800s, coincident with European settlement in the region (Mensing 1992). Pulses of blue oak regeneration may have resulted from sprouting of top-killed saplings and trees. Swiecki and Bernhardt (1998), however, believe they resulted from the release of understory seedlings, caused by cutting and burning of the overstory between the 1850s and the first decades of the twentieth century. Because Euro-American settlers burned concurrently with clearing for agriculture, fuel wood, mining, and range improvement, it is difficult to decouple the effects of fire and clearing on overall tree density. Where blue oak woodlands were entirely cleared followed by repeated disturbance, conversion to annual grassland was essentially permanent and the extent of oak woodlands was reduced (Swiecki and Bernhardt 1998). Where blue oaks persisted due to sprouting and release of understory seedlings, they clearly rebounded and the overall change was an initial decrease in oak density and canopy cover followed by even-aged stands of oaks (Holzman and Allen-Diaz 1991, Swiecki and Bernhardt 1998).

FIRE SUPPRESSION

Fire suppression began on private ranch lands in the 1940s and 1950s and came after millennia of natural ignitions and frequent anthropogenic fire. Suppression has resulted in longer fire-return intervals, increases in surface and crown fuels, changes in species composition, and changes in both vertical and horizontal structure and pattern (Kilgore 1981, Biswell 1989, Stephens 1997). The invasion of woody vegetation in the understory, including chaparral species and highly flammable young conifers, has probably been the most noticeable change (Dodge 1975, Griffin 1976, Rotenberry et al. 1995). Tree density has also increased (Byrne et al. 1991, Lewis 1993). The result is that high-severity fires are more likely (Rossi 1980).

PRESCRIBED BURNING

Although interest in prescribed burning has increased recently due to concerns about fuel accumulation, many oak woodlands in California were burned by ranchers beginning in the late 1800s up to the 1950s (Biswell 1989, Stephens 1997). Depending on the prescription, the effects of prescribed fire may be similar in many ways to those of California Indian fires. Prescribed fire can kill or thin woody vegetation (Vreeland and Tietje 1998). Lawrence (1966) found that prescribed fire significantly reduced shrub cover with a corresponding increase in grasses and forbs, and did little damage to trees, although foothill pines were largely eliminated. Fry (2002) found low tree mortality following low-intensity, prescribed fires, and little change in overall stand structure in an area with a relatively dense pre-fire canopy cover of 50% and negligible shrub cover. The species assemblage at this site varied from nearly pure stands of California black oak (*Quercus kelloggii*), blue oak, and valley oak to stands of mixed codominance. At the same site, M. Homrighausen (unpubl. data) found a substantial increase in bare ground and cover of native forbs immediately following the fire.

Widespread residential development in oak woodlands increases fire management problems and complicates both suppression and efforts to restore fire, and the fuel buildup resulting from decades of fire suppression further exacerbates this problem (Stephens 1997). Strict air-quality standards and air pollution costs also restrict the amount of prescribed burning that can be done. On the other hand, prescribed burning can reduce the risk of high-intensity wildfires and potentially restore habitat conditions similar to those under which many bird species of the oak woodlands evolved. It may take more than one application to achieve desired results—the first to remove shrubs and woody debris, the second to kill the shrub seedlings that come up after the first burn (Biswell 1989).

GENERAL EFFECTS OF FREQUENT, LOW-INTENSITY FIRE

The most obvious and agreed-upon effect of fire, regardless of its intensity, is that it reduces shrub cover (Lawrence 1966, Lewis 1973, Dodge 1975, Griffin 1976, Vreeland and Tietje 1998). Most shrub species in these habitats are nonsprouting species (e.g., wedgeleaf ceanothus [*Ceanothus cuneatus*], chaparral whitethorn [*Ceanothus leucodermis*], and Mariposa manzanita [*Arctostaphylos viscida mariposa*]) that do not completely recover for several yr after burning, and even then many openings persist (Sampson 1944).

Grass and forb cover initially decrease but generally return to prefire cover following the next rains (Lawrence 1966, Lewis 1993, Vreeland and Tietje 2002). Results of research on fire effects in grasslands demonstrate that the warmth of the blackened and unshaded soil encourages earlier foliage growth in the first postfire season, and many species of grasses and forbs flower in great profusion the first or second season after a fire (Daubenmire 1968). Herbaceous plants have higher moisture content and are more nutritious (Sampson 1944), and forbs are likely to increase relative to grasses (Bentley and Fenner 1958, Daubenmire 1968).

Foothill pines are susceptible to damage by fire due to their thin bark, high resin content, and the presence of congealed resins from wounds (Lawrence 1966, Powers 1990). Foothill pines increased in an area ungrazed since 1934 and unburned since 1929 at the San Joaquin Experimental Range (Woolfolk and Reppert 1963).

Oaks vary in their sensitivity to fire. Although the bark is thin (McDonald 1990), mature blue and valley oaks are relatively tolerant of fire (Griffin 1987, Haggerty 1994), especially low-intensity fire (Rossi 1980, Lewis 1993). Both seedlings and saplings are capable of resprouting after fire (Swiecki and Bernhardt 1998), but seedlings may be killed by frequent fire (Swiecki and Bernhardt 1998, Tietje et al. 2001). Acorn and leaf production of blue oaks increase as a result of reduced competition with understory vegetation after fire (Lewis 1993). Coast live oak is extremely fire resistant (Plumb 1980), but interior live oak is sensitive to fire due to its thin bark (Plumb 1980), although it readily resprouts (Biswell 1967). Short fire-return intervals maintain interior live oak as small, multi-stemmed trees (Plumb and Gomez 1983).

With frequent fire, mean tree size is larger (Jepson 1923, Paden and Schlichtmann 1959) as larger trees are more likely to survive following fire. While number of saplings is likely to decrease, fire may benefit oak seedling recruitment (Lathrop and Osborne 1991). Although fire topkills oak seedlings (Allen-Diaz and Bartolome 1992), they readily resprout (Tietje et al. 2001). Fire may promote sapling establishment by reducing competition from other vegetation and recycling nutrients sequestered in organic material. The overall effect is to reduce the density of trees of all sizes, resulting in decreased basal area and increased spacing of trees (Jepson 1923, Byrne et al. 1991, Lewis 1993).

While tree mortality may be quite low with low-intensity fire (Haggerty 1994, Fry 2002), fire reduces the number of snags (Gayton 1948). Trees weakened by disease or insects may be killed, perhaps partially offsetting the loss of snags. Fire scars can serve as entry points for rot and disease (Edwards 1957), which may create snags. Abundance of coarse woody debris is reduced (Gayton 1948, Vreeland and Tietje 1998, 2002), and litter is greatly reduced following a fire (Daubenmire 1968, Rotenberry et al. 1995).

EFFECTS OF FIRE ON THE LANDSCAPE

At the landscape scale, we expect frequent, low-intensity fire to create a complex mosaic of habitats, resulting in an overall structure of irregular patches and abundant edges. The fine-grained mosaics we expect resulted from high-frequency, low-intensity fires such as those ignited by California Indians differ from fragmentation of oak woodland habitat resulting from other types of disturbance.

Fragmentation in oak woodlands is a complex issue compared to forested habitats, and traditional thinking on fragmentation can be only loosely applied. Fragments in oak woodlands are not simply islands of residual, undisturbed habitat, nor does the idea of a matrix of radically modified habitat apply except perhaps in cases where nearly all trees are removed for housing subdivisions or vineyards. Habitat is generally not completely lost but rather is modified to a greater or lesser extent along a continuum. As oak woodland parcels change ownership, they can be altered in ways that can either reduce vegetation density (e.g., home construction, road building, overgrazing, and fuel treatments) or increase vegetation density (e.g., fire suppression and removal of livestock grazing), and changes may occur in only one or all of the vegetation layers. The key concepts here are that all oak woodlands were historically altered by human activities, and changes continue to occur in both directions along the continuum. Residential development, involving increased numbers of structures, roads, altered land-use patterns, and reduction in oak density and other vegetation, has been shown to affect bird species composition independently of stand structure in the surrounding landscape (Merenlender et al. 1998).

RESPONSE OF THE BIRD COMMUNITY

Fire rarely kills birds directly (Lawrence 1966, Dickson 1981, Quinn 1994); rather, fire alters bird habitat structure, food levels, and perhaps the abundance of competing species (Rotenberry et al. 1995).

We know of only one study that has directly examined the effects of fire, specifically prescribed fire, on oak woodland birds. Vreeland and Tietje (1998, 2002) censused birds at 86 50-m-radius, point-count stations from spring 1997 through spring 1999 in blue oak and mixed blue oak-coast live oak woodlands. Following a low-intensity prescribed fire in fall 1997 that burned half of their point count stations, they found reduced cover of grass and coarse woody debris, but no change in the relative abundance of breeding birds 2 yr after the burn (Table 1). Relative abundance of Dark-eyed Juncos (*Junco hyemalis*), one of the two most common species, did not change after the prescribed fire.

Tietje and Vreeland (1997) found that oak woodlands with high vertical diversity and well-developed shrub and canopy layers supported the greatest numbers of oak woodland bird species. They used

TABLE 1. SUMMARY OF LITERATURE CITED ON THE RESPONSE OF BIRDS TO FIRE IN OAK WOODLAND, SHRUBSTEPPE, AND CHAPARRAL HABITATS. STUDIES IN SHRUBSTEPPE AND CHAPARRAL ARE INCLUDED HERE BECAUSE OF THE SCARCITY OF STUDIES IN OAK WOODLAND.

Species	State	Year after fire	Size of fire (ha)	No. of sites (burned, unburned)	Response[a]	Type of fire	Reference[b]	Comments
Mourning Dove (*Zenaida macroura*)	AZ	4	1,000	56 (22, 28)[c]	+	wild	1	Mesquite grassland. Fire consumed nearly all vegetation except mesquite trunks and major branches. Response only in fall of burn year and breeding seasons up to 3 yr postfire.
Horned Lark (*Eremophila alpestris*)	WA	2	>2,000	3 (1,2)	+	wild	2	Shrubsteppe. Fire consumed nearly all shrubs. Response in year 1 postfire.
	AZ	4	1,000	56 (22, 28)[c]	+	wild	1	Mesquite grassland. Fire consumed nearly all vegetation except mesquite trunks and major branches. Response in fall of burn year and breeding seasons up to 3 yr postfire.
Brewer's Sparrow (*Spizella breweri*)	MT	2–3	220	2 (1, 1)	0	wild	3	Shrubsteppe. 100% sagebrush mortality. Ungrazed since 1891.
Lark Sparrow (*Chondestes grammacus*)	TX	0–6	not reported	7 (7, 0)	+	prescribed	4	Mesquite grassland. Measured nest density. Sites studied for only 1 yr each. Response declined as litter accumulated.
	MT	2–3	220	2 (1, 1)	0	wild	3	Shrubsteppe. 100% sagebrush mortality. Ungrazed since 1891.
	AZ	4	1,000	56 (22, 28)[c]	+	wild	1	Mesquite grassland. Fire consumed nearly all vegetation except mesquite trunks and major branches. Response in year 2 postfire, breeding season.
Sage Sparrow (*Amphispiza belli*)	WA	2	>2,000	3 (1, 2)	+	wild	2	Shrubsteppe. Fire consumed nearly all shrubs. Response in year 1 postfire.
Lark Bunting (*Calamospiza melanocorys*)	MT	2–3	220	2 (1, 1)	0	wild	3	Shrubsteppe. 100% sagebrush mortality. Ungrazed since 1891.
Dark-eyed Junco (*Junco hyemalis*)	CA	2	73, 130	3 (2, 1)	0	prescribed	5	Oak woodlands. Data from 86 point count stations: 43 burned, 43 unburned.
Western Meadowlark (*Sturnella neglecta*)	MT	2–3	220	2 (1, 1)	0	wild	3	Shrubsteppe. 100% sagebrush mortality. Ungrazed since 1891.

[a] Change in abundance: + = increase; - = decrease; 0 = no effect or study inconclusive.

[b] References: 1 = Bock and Bock 1992; 2 = Rotenberry and Wiens 1978; 3 = Bock and Bock 1987; 4 = Renwald 1977; 5 = Vreeland and Tietje 2002.

[c] Burned and unburned sites were distributed evenly between native and exotic grassland.

spot mapping to estimate densities of 23 bird species on nine 5.7-ha plots for 3 yr. Abundance of breeding birds was high in dense oak woodland characterized by high shrub cover, high canopy cover, dense mature trees and saplings, a well-developed litter layer, and more coarse woody debris compared to open stands with little shrub cover and ground cover of mostly grasses. Some species, such as Western Bluebirds (*Sialia mexicana*) and White-breasted Nuthatches (*Sitta carolinensis*), were more abundant in open, less structurally diverse areas, but more species were more abundant in well-structured vegetation that included a shrubby understory, logs and other downed woody material, and accumulated litter and duff. These results suggest that avian diversity could decline following fire if it reduces these habitat components. These authors found little effect of low-intensity prescribed fire on breeding birds (Vreeland and Tietje 2002), however, and we hypothesize that numbers and diversity of birds will increase if fire results in increased habitat complexity.

Because of the lack of studies on the effects of fire on oak woodland birds, we now examine results of studies with similar bird species and guilds and habitats with similar structural elements, such as grasslands and shrublands. Bird response to altered vegetation structure often resulted in a predictable response related to foraging and nesting habitats (Lawrence 1966, Rotenberry et al. 1995). The responses of shrubsteppe birds to fire depended on the differing relationships of individual species to the presence of shrub cover (Rotenberry and Wiens 1978, Bock and Bock 1987). A negative response of birds to fire may result from lack of cover for nest sites, especially with intense fires. Sage Sparrows (*Amphispiza belli*), a species whose density is correlated with sagebrush cover, decreased following wildfire while Horned Larks (*Eremophila alpestris*), which decrease with increasing shrub cover, increased in shrubsteppe habitat in southeastern Washington (Rotenberry and Wiens 1978). In shrubsteppe habitat in Montana, Lark Buntings (*Calamospiza melanocorys*), Lark Sparrows (*Chondestes grammacus*), and Brewer's Sparrows (*Spizella breweri*) avoided the burned area following a wildfire that caused 100% sagebrush mortality, while Western Meadowlarks (*Sturnella neglecta*) showed no preference (Bock and Bock 1987). Florida Scrub-jays (*Aphelocoma coerulescens*) require periodic fire for maintenance of the low, open oak-scrub habitat they prefer. Unburned areas of oak scrub were progressively abandoned by Florida Scrub-jays, and birds using them were less productive (Woolfenden and Fitzpatrick 1984).

Although few species nest on the ground in oak woodlands, many species forage on the ground. Early descriptive studies of fire in other habitats focusing on ground-foraging game birds found that numbers of quail, doves, and Wild Turkeys (*Meleagris gallopavo*) increased following fire (Stoddard 1931 in Johnston 1970, Lawrence 1966, Lewis 1993). Response to removal of the litter layer by fire differs among species. The absence of litter on recently burned ground makes seeds available for seed-eating birds such as Mourning Doves (*Zenaida macroura*), Horned Larks, Lark Sparrows (Renwald 1977, Bock and Bock 1992), and Northern Bobwhite (*Colinus virginianus*) (Stoddard 1946). The effect is expected to be short (Renwald 1977), as normal litter cover is generally restored in 2–6 yr in grassland systems (Daubenmire 1968).

Ground gleaners that forage beneath shrubs for cover might be expected to decrease with decreasing shrub cover (Tietje, pers. comm.). California Thrashers (*Toxostoma redivivum*) and Spotted Towhees (*Pipilo maculatus*), species that forages on the ground beneath high vegetative cover, avoided burned chaparral habitat but were found in high densities in unburned chaparral shrubs at fire boundaries (Quinn 1994).

Water often limits wildlife populations in oak woodlands, especially during the hot summer months following the breeding season when juvenile survival may be key to population health. Water is a key habitat element for many species, including California Quail (*Callipepla californica*), Mourning Doves, Greater Roadrunners (*Geococcyx californianus*), Black Phoebes (*Sayornis nigricans*), Yellow-billed Magpies (*Pica nuttalli*), and Lawrence's Goldfinches (*Carduelis lawrencei*) (Verner et al. 1980), and surface water flows may increase after fire due to reduced plant transpiration (Biswell 1967, 1989).

If fire increases horizontal habitat complexity, including the amount of edge habitat and patchiness of the habitat mosaic, we would expect that the numbers and diversity of birds should increase. This should be especially true for edge species and species associated with early seral stages.

Predicting Bird Responses from Habitat Data

Knowledge of habitat relations of oak woodland birds should enable the prediction of responses of birds to fire by examining the expected changes in vegetation structure (Rotenberry et al. 1995). At the San Joaquin Experimental Range (37º06'N, 119º44'W) in the western foothills of the Sierra

Nevada, Madera County, California, we collected habitat data in 0.04-ha circular plots at nest sites of oak woodland birds from 1988 through 1994. The experimental range occupies about 1875 ha in blue oak-foothill pine woodland and ranges in elevation from 215–520 m. Dominant tree species include blue oak, interior live oak, and foothill pine. Dominant understory shrub species include wedgeleaf ceanothus, chaparral whitethorn, and Mariposa manzanita. Ground cover consists of mostly non-native annual grasses and both native and non-native forbs. Most of the experimental range has been lightly to moderately grazed since about 1900 except for a 29-ha research natural area that has been ungrazed since 1934. The few lightning fires that have occurred over the past 70 yr have been suppressed and all were less than 4 ha in size (California Division of Forestry and Fire Suppression, unpubl. data).

To the extent that nesting habitat relates to habitat requirements for these species, we examined the responses of 17 bird species to six variables expected to be altered by fire, including two primary cavity nesters, eight secondary cavity nesters, five tree nesters, and two shrub nesters. We assumed that fire reduces shrub cover (including cover of the dominant nonsprouting wedgeleaf ceanothus), lowers tree density, and results in fewer snags, saplings, and logs. For all variables we considered, low values represent conditions expected to result from frequent, low-intensity fire and high values result from lack of fire or suppression. Therefore, the average rank for each species across the six variables can be interpreted as an index of fire response for the 17 species (note that these ranks are relative to the set of bird species examined here, and do not reflect the availability of each habitat element). Our results suggest that Western Kingbirds (*Tyrannus verticalis*), Western Bluebirds, and Violet-green Swallows (*Tachycineta thalassina*) would increase in abundance following fire, as they nest in habitat consistently similar to that expected to result from frequent, low-intensity fires and their mean ranks for fire response were between two and three for the six variables (Table 2). These three species nested in open areas with the lowest shrub cover and the lowest density of trees. Bluebird nest sites had intermediate cover of logs, but nest sites of swallows and kingbirds had less log cover than all species except Anna's Hummingbird (*Calypte anna*) (Table 2). And these same three species, along with House Finch (*Carpodacus mexacanus*), nested in areas with the lowest number of snags and saplings (Table 2). The fourth most fire-associated species was the European Starling (*Sturnus vulgarus*), followed closely by the House Finch (Table 2).

The species that nested in habitat similar to that expected to result from fire suppression were variable. Species nesting in areas with the highest shrub cover were Western Scrub-Jays, California Towhees (*Pipilo crissalis*), and Bewick's Wrens (*Thryomanes bewickii*) (Table 2). Bewick's Wrens, Nuttall's Woodpeckers (*Picoides nuttallii*), and Bushtits (*Psaltriparus minimus*) selected dense stands for nesting (Table 2). Ash-throated Flycatchers (*Myiarchus cinerascens*), Nuttall's Woodpeckers, and House Wrens (*Troglodytes aedon*) selected nesting areas with high snag densities (Table 2), and California Towhees and Nuttall's Woodpeckers nested in areas with numerous saplings (Table 2). House Wrens, Bewick's Wrens, and Acorn Woodpeckers (*Melanerpes formicivorus*) nested in areas with more logs (Table 2). In short, our results consistently predict that the same three fire-associated species will benefit from the effects of fire, while the species negatively affected vary widely among the variables examined. If fire produces a mosaic of habitat patches, rather than a homogeneous landscape, we expect that most species' habitat needs will be provided for.

Although we have examined the potential responses of only the most common species found at San Joaquin Experimental Range, species with low numbers are most likely to be of conservation and management concern. With declining shrub cover due to fire, we would expect numbers of uncommon species such as Wrentits (*Chamaea fasciata*) and California Thrashers to decline (Verner et al. 1997). These two chaparral specialists are more abundant at higher elevations in foothill oak woodlands, and the scattered shrubs present at the experimental range and in other oak woodlands are probably marginal habitat for them to begin with. As the fire regime of chaparral vegetation differs significantly from that of oak woodlands, it would be a mistake to target management practices in oak woodlands, particularly those related to fire, to conserve these species. Uncommon species characteristic of oak woodlands in California include Long-eared Owls (*Asio otus*) and Lawrence's Goldfinches (*Carduelis lawrencei*). Long-eared Owls require dense vegetation for nesting and roosting adjacent to grasslands or shrublands (Marks et al. 1994). Lawrence's Goldfinches prefer open woodlands that include brushy areas, tall annual weed fields, and a water source (Davis 1999). They do not appear to be sensitive to management activities, particularly those that increase the number of annual seed plants (Davis 1999). These two species are hypothesized to benefit from

TABLE 2. MEANS (± SE) FOR SIX FIRE-RESPONSE VEGETATION VARIABLES MEASURED AT NEST SITES OF 17 BIRD SPECIES BREEDING AT THE SAN JOAQUIN EXPERIMENTAL RANGE, MADERA COUNTY, CALIFORNIA. LOW VALUES REPRESENT CONDITIONS EXPECTED TO RESULT FROM FREQUENT, LOW-INTENSITY FIRE. INDEX SCORE IS THE AVERAGE RANK FOR EACH SPECIES ACROSS ALL SIX VARIABLES. VEGETATION VARIABLES WERE MEASURED IN 0.04-HA CIRCULAR PLOTS CENTERED ON NESTS.

Species	Index score	Nest type [a]	Wedgeleaf ceanothus [b] (% cover)	All shrubs (% cover) [c]	Live tree basal area (m^2/ha) [d]	No. of snags [e]	No. of saplings [f]	Logs [g] (% cover)
Western Kingbird	2.0	OPN	0 ± 0	0.2 ± 0.2	5.9 ± 1.0	0.2 ± 0.1	0.4 ± 0.3	0.3 ± 0.3
(*Tyrannus verticalis*)			20	20	21	20	20	20
Violet-green Swallow	2.3	SCN	0.4 ± 0.2	0.6 ± 0.3	6.3 ± 0.7	0.1 ± 0.1	0.3 ± 0.2	0.3 ± 0.1
(*Tachycineta thalassina*)			23	23	23	24	24	23
Western Bluebird	3.0	SCN	0 ± 0	0.6 ± 0.3	5.9 ± 0.6	0.3 ± 0.1	0.4 ± 0.2	0.6 ± 0.3
(*Sialia mexicana*)			32	32	34	30	30	32
European Starling	5.7	SCN	0.6 ± 0.2	1.0 ± 0.3	6.7 ± 0.5	0.5 ± 0.1	0.7 ± 0.2	0.8 ± 0.2
(*Sturnus vulgaris*)			107	107	111	81	81	81
House Finch	6.5	OPN	1.6 ± 0.8	1.7 ± 0.9	8.3 ± 0.9	0.3 ± 0.2	0.3 ± 0.2	0.6 ± 0.3
(*Carpodacus mexicanus*)			20	20	20	10	10	20
Acorn Woodpecker	8.5	PCN	0.9 ± 0.3	3.5 ± 0.7	7.3 ± 0.5	0.4 ± 0.1	1.0 ± 0.2	1.5 ± 0.2
(*Melanerpes formicivorus*)			92	92	95	80	80	92
White-breasted Nuthatch	8.7	SCN	1.1 ± 0.5	2.0 ± 0.6	9.5 ± 0.9	0.8 ± 0.2	0.9 ± 0.3	1.0 ± 0.3
(*Sitta carolinensis*)			42	42	43	33	33	42
Anna's Hummingbird	9.3	OPN	3.4 ± 1.4	4.8 ± 1.4	10.4 ± 1.1	0.8 ± 0.3	1.0 ± 0.4	0.2 ± 0.1
(*Calypte anna*)			33	33	34	20	20	33
Oak Titmouse	10.3	SCN	0.9 ± 0.2	2.9 ± 0.5	11.2 ± 0.7	1.3 ± 0.2	2.0 ± 0.4	0.7 ± 0.1
(*Baeolophus inornatus*)			112	112	113	80	80	112
House Wren	10.7	SCN	0.8 ± 0.4	2.1 ± 0.6	10.3 ± 1.1	1.6 ± 0.4	1.3 ± 0.5	1.7 ± 0.5
(*Troglodytes aedon*)			39	39	40	37	37	39
Western Scrub-Jay	10.7	OPN	12.6 ± 1.5	17.8 ± 1.6	9.2 ± 0.7	0.6 ± 0.2	1.6 ± 0.3	0.5 ± 0.1
(*Aphelocoma californica*)			118	118	125	81	81	118
Bushtit	11.7	ENC	1.7 ± 0.6	4.7 ± 0.9	12.3 ± 0.7	1.2 ± 0.2	2.1 ± 0.3	0.4 ± 0.1
(*Psaltriparus minimus*)			126	126	126	95	95	126
Mourning Dove	11.7	OPN	2.1 ± 0.9	3.6 ± 1.0	10.0 ± 0.9	0.8 ± 0.2	2.1 ± 0.5	1.1 ± 0.3
(*Zenaida macroura*)			60	60	64	45	45	60
Nuttall's Woodpecker	12.3	PCN	1.1 ± 0.8	2.3 ± 1.1	13.1 ± 1.6	1.7 ± 0.4	2.5 ± 1.0	0.7 ± 0.4
(*Picoides nuttallii*)			19	19	23	19	19	19
Ash-throated Flycatcher	12.8	SCN	1.2 ± 0.5	2.2 ± 0.7	10.9 ± 0.9	1.9 ± 0.4	2.2 ± 0.5	1.2 ± 0.3
(*Myiarchus cinerascens*)			47	47	50	44	44	47
California Towhee	12.8	OPN	9.9 ± 1.8	13.8 ± 1.8	8.4 ± 0.8	1.1 ± 0.3	2.7 ± 0.7	0.7 ± 0.2
(*Pipilo crissalis*)			73	73	87	56	56	73
Bewick's Wren	14.8	SCN	6.0 ± 3.2	9.1 ± 3.5	13.8 ± 2.5	1.3 ± 0.4	2.1 ± 0.7	1.6 ± 0.6
(*Thryomanes bewickii*)			17	17	24	17	17	17

[a] PCN = primary cavity nester, SCN = secondary cavity nester, OPN = open nester.

[b] Percent cover of wedgeleaf ceanothus (*Ceanothus cuneatus*) shrubs.

[c] Percent cover of all shrubs combined.

[d] Basal area of live trees (m^2/ha) around the nest.

[e] Number of snags >3 cm diameter at breast height (dbh).

[f] Total number of saplings (3–8 cm dbh) of blue oak (*Quercus douglasii*), interior live oak (*Quercus wislizenii*), and foothill pine (*Pinus sabiana*).

[g] Percent cover of logs (≥5 cm dia).

fire, especially if fire results in a mosaic of habitat patches with increased edge (Lewis 1980, 1993, Anderson 1993), increased flow of springs (Lewis 1993), and increased forb cover (Daubenmire 1968, Lewis 1993). We do not know of any species that might have been extirpated from foothill oak woodlands due to changes in fire regimes.

GRAZING AND FIRE

Grazing has often been considered helpful, and even necessary, to reducing the risk of wildfire. Because an increase in shrub understory has been the primary response to reduced fire frequency in California oak woodlands and our own work has shown that the most obvious result of excluding livestock from oak woodlands was increased shrub cover, the question naturally arises to what extent livestock grazing creates habitat similar to that created by historical fire. We examined data from two 30-ha plots at the San Joaquin Experimental Range that were similar in total canopy cover and general topography. One site had been grazed since at least 1900; the other had been ungrazed for more than 60 yr. Neither site had burned since 1935 to our knowledge except for a small fire, 1.6 ha in size, on the ungrazed site in 1988 that was suppressed. Therefore, the sites differed only in grazing history. Compared to the grazed site, the ungrazed site had nearly nine times the cover of wedgeleaf ceanothus, the most common shrub (Purcell and Verner 1998). Grazing and fire both reduce fuels, shrub cover, and fire hazard (Duncan and Clawson 1980), but we know little about how other aspects of grazing may differ from fire.

Grazing impacts primarily differ from fire because livestock selectively seek out shade and water, form trails, trample the ground, and eat oak seedlings, saplings, and acorns when forage is scarce (Wells 1962). The effects of soil compaction due to trampling are mostly unknown, but germination of woody plants is reduced (Wells 1962) and may alter plant species composition. These differences between fire and grazing remain unstudied.

Verner et al. (1997) mapped territories of breeding birds on an ungrazed (and unburned) plot that had significantly more shrub cover compared to a grazed plot. The grazed and ungrazed plots had similar canopy cover and tree density. Verner et al. (1997) found greater species richness of breeding birds on the ungrazed plot but no difference in the total number of territories and few differences between the abundances of individual species on the two plots. The grazed site had significantly more territories of House Wrens and the ungrazed site had significantly more territories of shrub nesters and California Towhees (Verner et al. 1997). The ungrazed site, however, was a sink habitat for California Towhees (Purcell and Verner 1998). The ungrazed sink habitat we studied was the result of both lack of grazing and fire suppression. This is the only extensive ungrazed habitat in the area we know of, and prior to fire suppression, this sink habitat may once have been fairly rare and patchy in distribution. Teasing out the varying effects of grazing and fire suppression may be key to understanding the population dynamics of California Towhees.

CONCLUSION

More fire-history research is needed to understand the fire regimes of oak woodlands in modern and historic times. Even so, it will be difficult to ascertain the extent of fires before 1800 because of the lack of old, fire-scarred trees in most oak woodlands.

Even if we had complete knowledge of the patterns of Indian burning, would we want to reproduce them? Although California Indians burned primarily to enhance hunting and gathering activities and not to create wildlife habitat, their high-frequency, low-intensity, localized fires created a complex overall pattern (Martin and Sapsis 1992, Lewis 1993) that probably supported high avian diversity, especially compared to the relative uniformity resulting from the cattle rancher’s objective of increased forage (Lewis 1985). We believe the effects of fires set by the California Indians need to be acknowledged and considered in oak woodland management.

The long-standing policy of fire suppression complicates intentions to restore fire to its historical role as an ecosystem process. Current land ownership patterns create difficulties in implementing prescribed burning plans in many areas, particularly those in urban-wildland interfaces. With careful planning and attention, however, low-intensity prescribed fires can be safely implemented and used to reestablish fire’s influence on oak woodlands. Mechanical thinning can also be used, with or without prescribed fire, to reduce fuel load and ladder fuels and preempt the danger of unplanned high-severity fires, but we should bear in mind that the effects of thinning are also unstudied in oak woodlands. Perhaps mechanical thinning is best limited to pretreatment prior to burning, in dense areas resulting from fire suppression, until the effects of thinning can be studied. The effects of prescribed fire on vegetation and the bird community clearly require more research. Perhaps most importantly, the effects of grazing and the extent to which grazing mimics fire require more study. Only with this much-needed research can we determine whether and in what ways past and current livestock grazing has helped counter the effects of fire suppression and how it differs from fire.

To conserve avian diversity, we need to monitor bird population trends in oak woodlands and to understand the conditions needed to maintain healthy populations. With so little work done on fire’s effects on birds in oak woodlands, we need tests of our hypotheses on species’ response to decreased shrub cover, lowered tree density, and decreased numbers of snags, saplings, and logs following fire. Other unstudied questions relate to response to increased surface water following fire, and responses of seed-eating, ground-foraging birds to fire, including the duration of the response. Finally, we need to test our working hypothesis that a mosaic of habitat patches will provide the habitat conditions needed to sustain high avian diversity in oak woodlands. This information is crucial to our understanding of avian diversity and habitat relations in oak woodlands, and answers to these questions will be useful to landowners and land managers and planners.

ACKNOWLEDGMENTS

We thank those who have assisted with fieldwork at the San Joaquin Experimental Range. Fig. 1 is adapted from the Cal PIF Oak Woodland Bird Conservation Plan and was prepared by D. Drynan. The manuscript benefited from reviews by J. Verner, L. de Jong, B. Block, and an anonymous reviewer.

Studies in Avian Biology No. 30:46–62

FIRE AND BIRDS IN MARITIME PACIFIC NORTHWEST

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Abstract. Resource managers face the challenge of understanding how numerous factors, including fire and fire suppression, influence habitat composition and animal communities. We summarize information on fire effects on major vegetation types and bird/fire relations within the maritime Pacific Northwest, and pose management-related questions and research considerations. Information on how fire affects birds is limited for the maritime Pacific Northwest, even though fire is an essential process within natural vegetation communities throughout the region. We describe fire regimes, vegetation succession patterns, bird communities, and fire effects on birds for 12 major vegetation types in the region. Fire regimes and fire effects vary considerably within this region due to its diverse topography and climate. Seven of the types have a low- to moderate-severity fire regime and five have a high-severity fire regime with fire-return intervals that span several centuries. Bird communities and effects of fire are best known from the western hemlock type, which has a high-severity fire regime. The postfire stand-initiation stage in this type supports a reasonably distinct avifauna compared to other successional stages, a phenomenon that has been documented for high-severity fire regimes in other regions. In general, there is a high turnover of species after high-severity fires, with a shift primarily from canopy-dwelling to ground-, shrub-, and snag-dwelling species that mostly are not associated with other successional stages. No studies exist that directly address how bird communities are affected by habitat changes from fire suppression in this region. The most likely bird communities vulnerable to these changes are in low-severity, high-frequency fire regimes that include the Douglas-fir type, drier portions of the white fir type, Oregon-oak woodlands and savannas, native grasslands and sclerophyllous shrublands. In general, prescribed fire is not being used for bird conservation in this region. Where prescribed fire is being used to restore fire as an ecological process or more often for reducing potentially hazardous fuels, bird conservation objectives can be achieved as a secondary benefit. New land management polices that will greatly accelerate fuel reduction activities throughout the Pacific Northwest, including use of prescribed fire, are currently being undertaken with limited scientific information on the ecological consequences for bird communities.

Key Words: birds, fire, fire-suppression, forest management, Pacific Northwest, succession.

EL FUEGO Y LAS AVES EN LA PORCIÓN MARÍTIMA DEL NOROESTE

Resumen. Los manejadores de recursos naturales, enfrentan el reto de entender como numerosos efectos, incluyendo incendios y supresión de estos, influyen en la composición del habitat y sus comunidades de animales. Resumimos información de los efectos del fuego en la mayoría de los tipos de vegetación y las relaciones ave-incendios alrededor del las zonas marítimas de la costa del Noroeste pacífico, y postulamos preguntas y consideraciones de investigación relacionadas al manejo. La información de cómo el fuego afecta a las aves es limitada en la región marítima del Noroeste Pacífico, a pesar de que el fuego es un proceso esencial para las comunidades vegetales naturales de dicha región. Describimos regimenes de incendios, patrones de sucesión vegetal, comunidades de aves y los efectos del fuego en las aves, en 12 tipos principales de vegetación en dicha región. Los regimenes y los efectos del fuego varían considerablemente en esta región, debido a la diversidad topográfica y climática. Siete de los tipos tienen un régimen de severidad de incendios de bajo a moderado, y cinco tienen un régimen de severidad alto, con intervalos de repetición de incendios separados por varios siglos. Las comunidades de aves y sus efectos al fuego son mejor conocidos para el tipo de bosque occidental de abeto, el cual tiene un alto régimen de severidad de incendios. El estado de iniciación post incendio de este tipo, soporta a una avifauna razonablemente distinta comparado con otros estados sucesionales, fenómeno el cual ha sido documentado por regimenes severos de incendios altos en otras regiones. En general, existe una alta recuperación de las especies después de incendios con regimenes de alta severidad, con un cambio primordialmente de especies que viven en las copas de los árboles contra las del suelo, arbustos, y tocones, las cuales principalmente no están asociadas con otro estado sucesional. No existen estudios en esta región los cuales muestren directamente cómo las comunidades de aves son afectadas por cambios en el habitat, ocasionados por supresión del fuego. Las comunidades de aves más vulnerables a estos cambios se encuentran en el tipo de baja severidad, con regimenes de incendio de alta frecuencia, los cuales incluye el tipo *Pseudotsuga menziessi*, porciones más secas del tipo de Abies blanco, bosques de encino y sabana de Oregon, en pastizales nativos y en arbustos sclerophylus. En general, las quemas prescritas no son utilizadas para la conservación de aves en esta región. Las quemas prescritas son utilizadas para restaurar, como un proceso ecológico o más a menudo, para reducir potencialmente combustibles riesgosos. Al restaurar con fuego, objetivos para la conservación de aves pueden ser alcanzados, como beneficio secundario. Nuevas políticas de manejo de la tierra en la región del Noroeste Pacífico acelerarán enormemente actividades de reducción de combustible, incluyendo el uso de quemas preescritas, las cuales son actualmente aplicadas con información científica limitada en cuanto a las consecuencias ecológicas para las comunidades de aves.

Disturbances can modify physical and biological environments and have profound effects on ecological processes, patterns, and interactions (e.g., White 1979). Primary disturbance agents include fires, wind, insect and disease outbreaks, floods, landslides, and human-related activities (Pickett and White 1985). In the Maritime Pacific Northwest, fires have been the most wide-ranging and continuous disturbance agent (Agee 1993), except for forest harvest, over the last few decades. Fire regimes and fire effects vary considerably within this region, primarily due to a diverse climate and topography that ranges from arid lands to rainforest and sea level to mountain peaks >4,300 m. Fire severities range from slight to cataclysmic, and natural fire-return intervals from almost annually to >1,000 yr (Agee 1993). In general, the north and coastal environments of western Washington and northwest Oregon have infrequent, stand-replacing fires that are part of a high-severity fire regime. In southwest Oregon and northwest California, and on the east side of the Cascade Mountains, fire occurs more frequently, a low- to moderate-severity fire regime, often with effects that are less severe, but more variable.

With effective fire suppression that began 80–100 yr ago, the natural patterns of fire have changed, especially in areas where fires burn most frequently (Agee 1993). In areas of low- to moderate-fire severity regimes, effective fire prevention may change habitat composition, shift the composition of biological communities, and lead to unnatural fuel accumulations associated with severe fires that cannot be withstood by historical ecosystems. When fire suppression increases fuel loads and the risk of severe fires, it becomes difficult to address the social and ecological concerns to protect property and lives, sensitive species and their habitat, and air and water quality, thus reinforcing widespread suppression of fires. However, consequences of continuing to suppress fires (i.e., passive management) without corrective measures also are high (Agee 2002). Shifts in fire prevention strategies are underway that propose to ameliorate potentially hazardous fuel conditions in areas of low- to moderate-fire severity regimes by steadily increasing prescribed fires (a fire ignited under known fuel conditions, weather, and topography to achieve specified objectives); thinning tree canopies to create shaded fuel breaks (Agee et al. 2000); and introducing other fuel reduction activities as part of a revised National Fire Plan (USDI et al. 2001). Such actions, however, often are planned and implemented with minimal understanding or considerations for effects on biota. Ecological objectives, if stated in planning documents, are almost always secondary to those for reducing hazardous fuels.

The purpose of this paper is to summarize information on bird-fire relations within the Maritime Pacific Northwest (hereafter Pacific Northwest), an area that encompasses the east slope of the Cascade Ranges, and the western portions of Washington, Oregon, and northern California (Fig. 1). This area is roughly equivalent to the range of the Northern Spotted Owl (*Strix occidentalis caurina*), the Northwest Forest Plan (USDA and USDI 1994b), and similar to the Southern Pacific Rainforest and Cascade Mountains physiographic stratifications used for the Breeding Bird Survey (Droege and Sauer 1989; map at http://www.mbr-pwrc.usgs.gov/bbs/physio.html [23 July 2004]). Our paper is organized into four parts: (1) a description of environmental conditions, vegetation communities, the role of fire in the major habitats and bird communities of the Pacific Northwest, and a summary of information on the effects of fire on birds; (2) a discussion of the major alterations to low- and moderate-severity fire regimes and their known or hypothesized effects on birds in this region; (3) a discussion of the role of prescribed fire in low- and moderate-severity fire regime and the implications for bird conservation; and (4) the critical management issues and research questions for this region.

ENVIRONMENTAL SETTING AND ROLE OF FIRE

FIRE REGIMES

Fire regimes have been described for the Pacific Northwest forests by Agee (1981, 1990, 1993, and 1998). Fires in high-severity fire regimes usually occurred >100 yr apart with >70% of the vegetative basal area removed; in moderate-severity fire regimes, fires were 25–100 yr apart with 20–70% basal area removed; and in low-severity fire regimes, they averaged 1–25 yr apart with <20% of the basal area removed. Grasslands and shrublands typically are part of a high severity regime, in which fires are

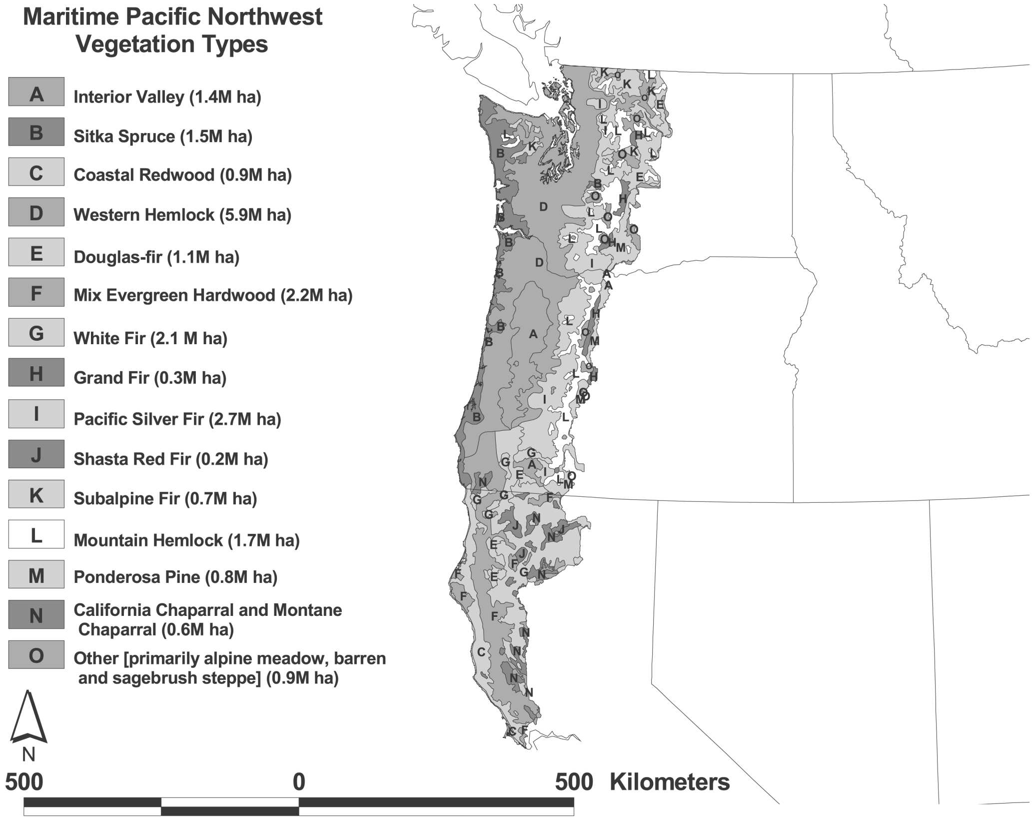

FIGURE 1. Generalized distributions of major vegetation types in the maritime Pacific Northwest (adapted from Kuchler 1964). Two types displayed on the map, ponderosa pine and chaparral (California and montane types combined), are not covered in this chapter because they have large geographic distributions primarily outside the maritime Pacific Northwest.

considerably more frequent than in most forested areas in this regime.

Vegetation patterns after fire depend on fire severity (Agee 1998). Agee found that for the low-, moderate-, and high-severity fire regimes, respectively, burn patch size created by fire tends to be small (~1 ha), medium (up to 300+ ha), and large (up to 10,000+ ha). He also found that the amount of patch edge, or contrasting conditions created by fire, tends to be low, high, and moderate, according to fire regime.

In high-severity fire regime areas of the Pacific Northwest, post fire stand-initiation can be prolonged for many decades as trees reestablish slowly after a fire (e.g., Hemstrom and Franklin 1982, Huff 1995). After burning or logging, this stage can be hastened through replanting trees and suppressing competing vegetation. Once trees establish in high-severity fire regime areas, the stem-exclusion and re-initiation of understory stages may continue for a century or two, leading to an old-growth stage that can persist for centuries depending on the natural fire rotation. Moderate-severity fire regimes sustain a highly variable forest structure by creating stands of uneven size and age trees and patchiness at landscape scales. Of the three fire regimes, low severity is most likely to create a balanced tree age-class distribution, where each fire only affects pattern and process on a small portion of a landscape (Agee 1998).

ECOLOGICAL UNITS

Geographic distribution of vegetation and fire regimes in the Pacific Northwest are closely linked to complex topographic, moisture, and temperature gradients that can change rapidly with elevation, latitude, geological formations, substrate, and proximity to the Pacific Ocean (Agee 1993). In classifying the environments of Washington, Oregon, and California, Franklin and Dyrness (1973) and Barbour and Major

(1977) divided the states into broad ecological units using two approaches: (1) physiographic provinces based on geography, geology, and soils, and (2) vegetation zones (hereafter types) based on associations of natural plant communities.

In this paper, we use the physiographic area delineated in the Northwest Forest Plan (Forest Ecosystem Management Team 1993, USDA and USDI 1994a, 1994b, 2000) (Fig. 1) to describe distributions of broad vegetation types, fire regimes, and avifauna (Table 1). We aggregated vegetation types into five major ecosystems: lowlands and foothills, coastal forests, lower montane, upper montane, and subalpine. We describe the distribution of 12 vegetation types (Fig. 1), fire regimes, and establishment patterns after fire, using Franklin and Dyrness (1973, 1988) (vegetation of Washington and Oregon), Barbour and Major (1977) (vegetation of California), and Agee (1993) (fire regimes and effects) as our initial source. About 59% of the Pacific Northwest is covered by a high-severity fire regime and about 41% by a low- or moderate-severity fire regime based on vegetation types and fire regimes in Table 1 and Fig. 1. Below we describe the major vegetation types within the five ecosystems.

Lowlands and Foothills Ecosystem

This ecosystem occurs in a relatively dry environment within and near interior valley bottomlands. The diverse vegetation within the lowlands and foothills is aggregated into one vegetation type, interior valley. It is a mosaic of grasslands (e.g., Johannessen et al. 1971, Franklin and Dyrness 1973) and oak savannas, oak woodlands, mixed oak-conifer forests (e.g., Habeck 1961, Thilenius 1968, Smith 1985, Riegel et al. 1992); and sclerophyllous shrublands (i.e., chaparral) dispersed sporadically across southwestern Oregon and northern California (Whittaker 1954, Barbour and Major 1977). Generally, fire history has not been well documented in the lowlands and foothills because fires carried by grass and herbs are short duration, low intensity, and high-severity in which most vegetation is consumed and because much of the vegetation has been converted to other uses, such as urban and suburban, cropland, pasture, and forestry.

Oak woodlands and savannas are dominated by Oregon white oak (*Quercus garryana*) in Oregon; California black oak (*Quercus kellogii*) is an important species in the southern portion of the lowlands and foothills. At present, the ground flora has been so altered in these communities, especially through livestock grazing, that benefits of using fire for restoration are uncertain. Sprouting appears to be the primary process for recruitment. The role fire plays in perpetuating these communities by stimulating sprouts or influencing acorn germination and seedling survival is not well understood (Harrington and Kallas 2002). Sclerophyllous shrublands,

TABLE 1. FOREST VEGETATION TYPES OF THE MARITIME PACIFIC NORTHWEST BY FIVE ECOSYSTEM TYPES AND BY MOISTURE AND FIRE REGIMES.

	Forest vegetation types	
Ecosystem type	Wet to mesic environments/ high-severity fire regime	Dry to mesic environments/ low- to moderate-severity fire regime
Lowlands and foothills		Interior valley—a mosaic of oak woodlands and savannas; oak-conifer; grasslands[a], and sclerophyllous shrublands[a].
Coastal forests	Sitka spruce	Coast redwoods.
Lower montane	Western hemlock	Douglas-fir. Mix evergreen hardwood. White fir. Grand fir. (Ponderosa pine[b]). (California and montane chaparral[a,b]).
Upper montane	Pacific silver fir	Shasta red fir.
Subalpine	Subalpine fir Mountain hemlock	

[a] Occurs in dry to mesic environments and has a high-severity fire regime.

[b] Ponderosa pine and California and montane chaparral types were not covered in this chapter because they have large geographic distributions primarily outside the maritime Pacific Northwest.

established near grasslands and oak communities in valley bottoms and serpentine soils, are maintained by fire, and dominated mostly by shrubs, such as *Ceanothus* spp., *Arcostaphyllus* spp, and *Baccharis* spp. High-severity fires are common, and burned areas are readily re-colonized by these shrub species when they resprout and their long-lived seeds quickly respond to scarification from burning. These shrublands appear to be declining in the Pacific Northwest because human development and fire suppression favor tree establishment (Chappell and Kagan 2000).

Coastal Forests Ecosystem

Two major vegetation types occur within the coastal forests, Sitka spruce (*Picea sitchensis*) and coast redwood (*Sequoia sempervirens*), hug the coastline and extend up major river valleys inland where summer fog lingers. Important tree species found in the Sitka spruce type are Sitka spruce western hemlock (*Tsuga heterophylla*) and western red cedar (*Thuja plicata*); grand fir (*Abies grandis*) and Douglas-fir (*Pseudotsuga menziesii*) are minor components (Fonda 1974, Henderson et al. 1989). Fire history has not been documented for this type (Agee 1993). The climatic conditions and the extent of older age classes indicate that it burned infrequently (likely even less often than the wettest areas of the western hemlock type), and belongs to a high-severity fire regime. Fire is more likely to spread into the coastal Sitka spruce type from nearby areas within the lower montane western hemlock type by the occasional dry east winds during rare climatic conditions, than from fires that originate from within the type (Agee 1993). Because fire occurs so infrequently, wind is probably a more important disturbance agent in this type.

Coast redwood, the tallest tree the world, is the principal species of the coast redwood type (Waring and Major 1964, Zinke 1977, Noss 1999). Other important trees within the type's broad moisture gradient include western hemlock, western red cedar, Sitka spruce, tan oak (*Lithocarpus densiflorus*), and Douglas-fir. The type's fire regime is moderate severity, with fires mostly occurring as low-to-moderate severity with infrequent high-severity events (Veirs 1982; Jacobs et al. 1985; Stuart 1987; Finney and Martin 1989, 1992). Fire-return intervals may exceed 500 yr in moist areas, and be as low as 20–50 yr at drier inland locations. Structurally diverse, multi-aged forests maintained by fires are characteristic of the type.

Lower Montane Ecosystem

This is the most diverse ecosystem type and covers the largest geographic area. We recognize five major vegetation types within the lower montane ecosystem: western hemlock; Douglas-fir; mixed evergreen hardwood; white fir; and grand fir. In the western hemlock type, which encompasses the largest area, western hemlock and Douglas-fir commonly co-occur, with the hemlock more prevalent at the wet end and the fir at the dry end of the moisture gradient (Franklin and Dyrness 1973, Zobel et al. 1976, Topik et al. 1987, Topik 1989, Henderson et al. 1989, Hemstrom and Logan 1986, Ruggiero et al. 1991, Atzet et al. 1996). Other important species are Sitka spruce in the coastal areas and Pacific silver fir (*Abies amabilis*) within a wide band of vegetation that transitions into the upper montane. Fire frequency is variable across the type, reflecting diverse moisture and temperatures conditions found within the type. In the areas of high moisture fires burn very infrequently, with 250 to >500-yr return intervals (Hemstrom and Franklin 1982, Agee and Flewelling 1983, Agee and Huff 1987, Henderson et al. 1989, Agee 1991a, Huff 1995, Impara 1997, Agee and Krusemark 2001). A high-severity fire regime predominates throughout much of the type. Fires often create large patches of killed trees with a few very widely scattered Douglas-firs that survived, as well as, an occasional small island of trees that was spared. Trees may reestablish slowly in these burned patches, and may remain a forest opening for many decades. In the drier southern portion of the type, average fire-return interval drops quickly from about 200 yr down to 100–30 yr as the fire regime grades into a moderate severity (Means 1982, Teensma 1987, Morrison and Swanson 1990, Cissel et al.1998, Weisberg 1998, Van Norman 1998, Olson 2000, Weisberg and Swanson 2003). In these more fire-prone areas, overlapping fires of varying severities create a complex age-class structure. Western hemlock (in wetter environments), Douglas-fir, and western red cedar are early seral species that attain great sizes, dominate for centuries, and, in late-successional conditions, show substantial structural diversity. In mesic and drier environments, Douglas-fir dominates after fire, sometimes in pure stands.

The Douglas-fir type usually occupies the warmest and driest environments in the lower montane (Franklin and Dyrness 1973; Atzet et al. 1992, 1996). It is often found upslope and adjacent to types dominated by ponderosa pine (*Pinus ponderosa*) or oaks. Douglas-fir is commonly an early and late-successional species throughout the Douglas-fir type, with ponderosa pine distributed widely in dry and warm environments. Other locally important species are lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), Jeffrey pine (*Pinus jeffreyi*), and incense-cedar (*Libocedrus decurrens*). A low-severity fire regime is common throughout the type; characteristics of a moderate-severity regime emerge as moisture increases (Agee 1990, 1991b; Chang 1996; Skinner and Chang 1996; Taylor and Skinner 1997; Everett et al. 2000). Historically, fires probably burned often over relatively small areas and were confined mostly to the understory. Infrequent, larger fires that burned with varied severity eclipsed effects of these smaller fires. Fire history studies from across the region indicate that frequencies in dry locations averaged <10 yr but ranged up to 50 yr with increasing moisture. In this type, fire severity varied considerably by topographic position. Here, the most severe fires occur on upper slopes, ridge tops, and south- and west-facing slopes. These fires resulted in simple forest structures, whereas lower slope positions and riparian areas with less severe fires created complex forest structures, including the largest trees (e.g., Taylor and Skinner 1998).

The mixed evergreen hardwood type has the most restricted distribution in the lower montane ecosystem, but the most diverse tree composition (Whittaker 1960, 1961; Sawyer et al. 1977; Atzet et al. 1992, 1996). The type is most prominent in the coastal mountains and at mid slope and elevation, and moderate aspects. Important tree species are Douglas-fir, usually an overstory dominant, and tan oak. Tan oak has increased its density and cover throughout the type, presumably a result of fire suppression (Atzet et al. 1992). Other major species are Pacific madrone (*Arbutus menziesii*) and ponderosa pine.

The few fire-related studies in the mixed evergreen hardwood type show a wide range of fire severities, frequencies, and sizes (Thornburgh 1982, Wills and Stuart 1994, Agee 1991b), indicating that the type largely belongs in a moderate-severity fire regime. The mean fire-return intervals in pre-settlement times cluster around 15–35 yr, but range from 3 to >70, and the size of some fires have been quite large. Complex successional patterns have developed that parallel the variable nature of fire in this type. In general, after low- to moderate-severity fires, tanoak regenerates beneath a canopy of Douglas-fir. After more severe fires, Douglas-fir regenerates beneath a canopy of tanoak, a species that can sprout profusely after fire and have rapid early growth. Older forests usually have one to three age classes resulting from past fires, with Douglas-fir as an emergent canopy above various hardwoods, mostly evergreen.

The white fir type occurs in a range of environments wider than all other types in the Lower Montane except western hemlock (Rundel et al. 1977; Sawyer et al. 1977; McNeil and Zobel 1980; Atzet et al. 1992, 1996). White fir (*Abies concolor*), the most dominant tree species, can form pure stands in the coolest environments. The importance of Douglas-fir, relative to white fir, increases with increasing dryness and temperature. Ponderosa pine becomes a major species in drier environments. The white fir type typically exhibits a diverse and lush understory; yet, the fire regime likely fits a moderate or moderate-to-low severity. Documented mean fire-return intervals of ~10–65 yr and up to 160 yr (McNeil and Zobel 1980, Bork 1985, Agee 1991b, Stuart and Salazar 2000), broadly overlap other lower montane vegetation types in southwest Oregon and northwestern California, yet the type has not been studied extensively considering its breadth of environments. Fires are less frequent at higher elevations where white fir forms pure or nearly-pure stands. White fir has increased in cover and density with decades of fire suppression. In the white fir type, fires typically overlap to create a patchy mosaic of multiple structures and age classes, providing conditions for white fir to persist.

The grand fir type is found at mid-slopes in eastern Washington and Oregon on moist to dry sites (Hopkins 1979, Topik et al. 1988, Topik 1989, Lillybridge et al. 1995). In addition to grand fir, major tree species include ponderosa pine in warm and dry locations, lodgepole pine in cool and dry, Douglas-fir in environments broadly across the type, and western larch in the northern reaches of the type. Information on fire frequency and effects is scarce from this type (Agee 1993). Behavior of natural fires can be quite unpredictable, varying quickly from intense crown fires to surface fires. Higher severity fires may be an important part of forest development in the grand fir type, but to what degree is unclear. Preliminary indications are that a moderate-severity fire regime might be more likely than a low- or high-severity fire regime. Forest succession after fire should reflect fire-severity patterns and species present at the time of the fire: frequent low-to-moderate severities would favor, if present, Douglas-fir, ponderosa pine, and western larch survival and regeneration, while high severities would favor establishment of lodgepole pine in areas that are cool and dry. Grand fir can establish in open to partially shaded environments with moderate moisture, probably over a wide range of fire severities with low to moderate frequencies (Hall 1983).

Upper Montane Ecosystem

The vegetation types of the upper montane are found upslope from the lower montane, as conditions become cooler and wetter at higher elevations. There are two major upper montane vegetation types in the Pacific Northwest, Shasta red fir (*Abies magnifica*) and Pacific silver fir. The Shasta red fir type occupies a narrow ~500 m elevation band, typically above the white fir type and below the mountain hemlock type where Shasta red fir is common in the overstory and understory in a broad range of environments (Rundel et al. 1977; Sawyer et al. 1977; Atzet et al. 1992, 1996). Other important tree species include lodgepole pine and western white pine (*Pinus monticola*). Studies from Shasta red fir type and California red fir type (adjacent to the Pacific Northwest region), indicate that mean fire-return intervals are about 20–50 yr, with ranges of ~5–65 yr and fire-free periods spanning ~150 yr (McNeil and Zobel 1980, Pitcher 1987, Taylor and Halpern 1991, Agee 1993, Taylor 1993, Chappell and Agee 1996, Bekker and Taylor 2001, Taylor and Solem 2001). The type has a moderate-severity fire regime that creates a very patchy environment of diverse patch sizes and stand structures in close proximity that range from closed- and open-canopied late-successional forests to young, regenerating stands and open meadows.

In the Pacific silver fir type, Pacific silver fir is the dominant species; western and mountain hemlocks (*Tsuga mertensiana*) co-dominate at the lower and upper limits of the type, respectively (Fonda and Bliss 1969, Franklin and Dyrness 1973, Hemstrom et al. 1982, Packee et al. 1983, Brockway et al. 1983, Franklin et al. 1988, Henderson et al. 1989). Other important tree species are Douglas-fir and noble fir (*Abies procera*) in relatively dry and warm climates, Alaska-cedar (*Chamaecyparis nootkatensis*) in cooler and wetter sites, and western white pine in moderate environments. Subalpine fir (*Abies lasiocarpa*) is an important species in the eastern Cascades where the Pacific silver fir type transitions into a subalpine ecosystem. The type has a high-severity fire regime, in which fires burn infrequently (Agee 1993). Although fire history data are scant for this type, known fire-return intervals were about 100–200 yr along the drier eastern edge of the type that is influenced by a continental climate (Agee et al. 1990), and about 300–550 yr in the moister westside of the Cascades (Hemstrom and Franklin 1982). Pre-settlement fires in this type were usually associated with large fires that swept through adjacent types, creating large patches where most of the vegetation in the Pacific silver fir type was killed. This type, however, can act as a barrier to fire spread, unless extreme conditions associated with prolonged drought and dry east winds are met. Pacific silver fir, a fire-sensitive species, rarely survives where fires have burned and postfire conditions are often too harsh for it to establish, except in very cool and wet locations. Stand establishment after fire can last for decades, and be very prolonged if seed sources are absent for species that function as pioneers, such as Douglas-fir, western white pine, noble fir, subalpine fir, and lodgepole pine. Pacific silver fir is more prominent as forests mature.

Subalpine Ecosystem

Two major vegetation types occur in subalpine ecosystems: subalpine fir and mountain hemlock. Subalpine fir dominates throughout the subalpine fir type and forms nearly pure stands (Franklin and Mitchell 1967; Fonda and Bliss 1969; Henderson 1973, 1982; Agee and Kertis 1987; Franklin et al. 1988; Henderson et al. 1989; Lillybridge et al. 1995). Other species that typically co-occur with subalpine fir are Pacific silver fir in transition upslope into the type; whitebark pine (*Pinus albicaulis*) at higher elevations; Engelmann spruce (*Picea engelmanii*) as the type transitions to the east and lodgepole pine in harsh environments and locations with higher fire frequencies. A high-severity fire regime characterizes the subalpine fir type (Fahnestock 1977, Agee and Smith 1984, Agee et al. 1990, Taylor and Fonda 1990, Huff and Agee 1991, Agee 1993). Fires in this type typically burn infrequently, though more often than in the mountain hemlock type because precipitation and snow pack are lower and summer months are warmer. The fire-return interval ranges about 100–250 yr from relatively dry to wet environments. Tree reestablishment can be slow and inconsistent (except where lodgepole pine is prevalent) due to severe climatic and site conditions for establishment and insufficient distribution of seed, leaving the postfire environment in a park-like setting for decades.

In the mountain hemlock type, mountain hemlock tends to occur in mixed stands with Pacific silver fir as a co-dominant, and with subalpine fir, lodgepole pine, and Alaska-cedar (Fonda and Bliss 1969; Henderson 1973, 1982; Sawyer et al. 1977; Agee and Kertis 1987; Franklin et al. 1988; Henderson et al. 1989; Atzet et al. 1992, 1996). Fire history is poorly understood in the mountain hemlock type; however, it is likely that fires burn very infrequently, suggesting a high-severity fire regime (Agee 1993, Dickman and Cook 1989). Fire-return interval for similar mountain hemlock forests in nearby Canada were found to be >1,000 yr (Lertzman and Krebs 1991). All major tree species in this type are easily killed by fire, although older mountain hemlocks can survive with fire scars where fires burned at lower intensities. Stand establishment after fire is slow, inhibited by harsh climatic conditions and seeds that are poorly dispersed (Agee and Smith 1984).

FIRE AND BIRD COMMUNITIES IN THE PACIFIC NORTHWEST

Computer simulations of Pacific Northwest forests have demonstrated that over the last 3,000 yr, historical fire regimes maintained highly variable forest age-class distributions. Wimberly et al. (2000) estimated that the proportion of older forest age classes varied from 25–75% at various times during this period. Such fire-related fluctuations in habitat availability have important implications for understanding the dynamics of bird populations across the Pacific Northwest. We took a two-step approach to describe interactions between fire and birds. First, we identified bird species that were common and indicative of each vegetation type. When literature was not available for a specific vegetation type, we used general sources that synthesize bird distribution and habitat relations in the Pacific Northwest (e.g., Johnson and O'Neil 2001). Second, we characterized the responses of birds to short- and long-term effects of fire using existing literature from the Pacific Northwest; however bird-related information was not available for many of the vegetation types.

Lowlands and Foothills Ecosystem

Bird communities of the interior valley vegetation type are difficult to characterize because vegetation prior to European settlement has been dramatically altered over the last 150 yr. Contemporary species' habitat relations in natural dry grasslands or prairies and oak savannahs are based on reports from agriculturally dominated landscapes, where only small, scattered remnants of original habitat remain. Using natural history information and historical accounts, Altman et al. (2000) developed a list of bird species historically associated with dry grassland and oak savannah in this region. They list six species as highly associated (abundance is likely to be significantly higher in this habitat during the breeding season than elsewhere in the Pacific Northwest) with dry grasslands and oak savannas, including the: Burrowing Owl (*Athene cunicularia*) (probably extirpated from the region), Western Meadowlark (Sturnella neglecta), Vesper (*Pooecetes gramineus*) and Grasshopper Sparrows (*Ammodramus savannarum*), Horned Lark (*Eremophila alpestris*), and Western Bluebird (*Sialia mexicana*). Most of these species are not widely distributed elsewhere within the Pacific Northwest. No information was available regarding fire effects on birds inhabiting native grassland and savannah habitats.

To document possible long-term changes in oak woodland bird communities where fire was excluded, Hagar and Stern (2001) re-sampled three of Anderson's (1970) oak woodland bird study sites about three decades later. Results of both studies were expressed in terms of density (birds 100 acres^{-1}). Hagar and Stern (2001) found 14 species that were rare or absent in 1967–1968 but more abundant in 1994–1996, and three species detected in 1967–1968 that were absent in 1994–1996. These authors hypothesized that fire suppression had allowed more coniferous trees and a thicker understory to develop, favoring birds that the authors characterized as forest-dwelling species (e.g., Swainson's Thrush [*Catharus ustulatus*], Purple Finch [*Carpodacus purpureus*], House Wren [*Troglodytes aedon*], and Pacific-slope Flycatcher [*Empidonax difficilis*]) over birds favoring partially open habitat (e.g., Chipping Sparrow [*Spizella passerina*], Bushtit [*Psaltriparus minimus*], and Yellow Warbler [*Dendroica petechia*]).

Bird populations closely linked to oaks could be in jeopardy if fire exclusion continues. Oak-dominated woodlands of the Pacific Northwest are maintained by fire (Agee 1993), which has been controlled tenaciously because oaks are in close proximity to rural communities. Because fire exclusion in this vegetation has caused major structural and compositional changes (e.g., a shift to dominance by conifers) (Tveten and Fonda 1999), thus potentially jeopardizing bird populations closely linked to oaks. Bird species most likely to be affected by declining oak habitat resulting from fire suppression are White-breasted Nuthatch (*Sitta carolinensis*), Western Scrub-Jay (*Aphelocoma californica*), and Acorn Woodpecker (*Melanerpes formicivorus*), and in southern Oregon and northern California the Ash-throated Flycatcher (*Myiarchus cinerascens*) and Oak Titmouse (*Baeolophus inornatus*; Altman et al. 2000).

Western Scrub-Jay, California Towhee (*Pipilo crissalis*), and Lesser Goldfinch (*Carduelis psaltria*) appear to be the most common species in fire-dependent sclerophyllous shrublands of the interior valley type, based on informal field observations (Altman et al. 2000). These shrublands support a unique assemblage of bird species that seldom breed elsewhere in the Pacific Northwest, including Wrentit (*Chamaea fasciata*), Green-tailed Towhee (*Pipilo chlorurus*), and Fox Sparrow (*Passerella iliaca*). The effects of fire on this vegetation type probably are similar to other high-severity fire regimes where most of the aboveground vegetation is killed, although the amount and distribution of mortality can vary considerably within and among fires. Studies from burned and unburned shrublands suggest that after fire, bird occupancy shifts to species that appear to favor open environments, and that shrub-dwelling species persist at moderately to substantially lower populations or leave and re-colonize later when the shrub cover is suitable (e.g., Moriarty et al. 1985).

Coastal Forests Ecosystem

The bird community of coastal forest types are similar, and include: Olive-sided Flycatcher in early seral with residual trees; Hutton's Vireo in shrub with small tree regeneration; Winter Wren (*Troglodytes troglodytes*), Wilson's Warbler (*Wilsonia pusilla*), Pacific-slope Flycatcher, and Hermit Warbler (*Dendroica occidentalis*) in young and mature forest; Varied Thrush (*Ixoreus naevius*)and Pileated Woodpecker (*Dryocopus pileatus*) in mature forest; Red Crossbill (*Loxia curvirostra*) in mature and old-growth forest; and Vaux's Swift (*Chaetura vauxi*) in old-growth forests with snags (Oregon-Washington Partners in Flight (PIF) http://community.gorge.net/natres/pif.html). Also, the federally listed Northern Spotted Owl breed in these types, as well as federal species of concern including Olive-sided Flycatcher (USDI Fish and Wildlife Service 2002).

Historically, fire played an important role in maintaining a mosaic of seral stages or habitat structures (e.g., snags) that have facilitated the persistence of these species. The Sitka spruce and wetter portions of the western hemlock types have high-severity fires and birds probably respond to fire similarly in these types (see section on *Lower Montane Ecosystem*). Fire suppression probably has had little effect on bird communities in the Sitka spruce type because the fire-return interval is so long. The direct effects of fire on coast redwood forest bird communities are not well documented. Where fires are infrequent in the redwoods, fire is probably less important than other disturbances, such as wind-throw. In areas with frequent low to moderate severity fires, such as drier coastal forest sites, fire played a role in maintaining forest structure by limiting the amount of downed woody debris, or reducing understory vegetation.

Lower Montane Ecosystem

Bird communities have been studied extensively in the western hemlock type (e.g., Morrison and Meslow 1983a and 1983b, Manuwal and Huff 1987, Carey et al. 1991, Gilbert and Allwine 1991, Huff and Raley 1991, Manuwal 1991, McGarigal and McComb 1995, Bettinger 1996, Chambers et al. 1999). The most widespread and abundant bird species of older forests (>200 yr after fire) are Chestnut-backed Chickadee (*Poecile rufescens*), Pacific-slope Flycatcher, Winter Wren, Hermit Warbler, and Golden-crowned Kinglet (*Regulus satrapa*). Other important species are Varied Thrush (wet environments), Wilson's Warbler (with increasing importance of deciduous trees and shrubs), Red-breasted Nuthatch (*Sitta canadensis*; drier environments), and Northern Spotted Owl—for which a large proportion of its habitat lies within the western hemlock type (Bart et al. 1992).

In the wet Olympic Mountains where fires are rare, breeding bird communities were examined at two sites covering a long stand initiation stage, 1–3 and 19 yr after fire, and compared to surveys from the other successional stages (Huff 1984, Huff et al. 1985). Winter Wren and Dark-eyed Junco (*Junco hyemalis*) were the most abundant species during the first three years after fire. At year 19 after fire, Winter Wren abundance was 3–4 times below the three most abundant species, Dark-eyed Junco, Rufous Hummingbird (*Selasphorus rufus*), and American Robin (*Turdus migratorius*). Year 19 had the highest species richness and diversity, including the highest amount of woodpecker species. In general, the stand initiation stage was most favorable for ground- and brush-foraging species, while unfavorable for canopy-feeding species. A high proportion of species bred only in the stand initiation stage after fire (30%), as observed in other regions (e.g., Taylor and Barmore 1980). Pacific-slope Flycatcher, abundant in older forests, was negatively affected by fire during the stand initiation stage; more so than any other species (Huff et al. 1985).

In a high severity fire regime, wildfires and timber harvest followed by site preparation with fire have a few similar effects on bird habitat: loss of live tree overstory followed by re-colonization of herbs, shrubs, and trees. After logging followed by broadcast burning in the western hemlock type in Oregon, the most common birds in open managed stands (<15 yr-old and planted with conifer regeneration) were mostly ground- and brush-foraging species that included White-crowned Sparrow (*Zonotrichia leucophrys*) and Song Sparrow (*Melospiza melodia*), Swainson's

Thrush, Rufous Hummingbird, Spotted Towhee (*Pipilo maculates)*, American Goldfinch (*Carduelis tristis*), Dark-eyed Junco, and MacGillivray's (*Oporornis tolmiei*) and Orange-crowned Warbler (*Vermivora celata*; Morrison and Meslow 1983b, Bettinger 1996). In contrast to the stand initiation stage after a fire (e.g., Wyoming, Taylor and Barmore 1980; Washington, Huff 1984), primary and secondary cavity nesting birds were nearly absent in logged areas because past practices in this region typically removed most or all standing dead trees. Hermit Warbler, Chestnut-backed Chickadee, Golden-crowned Kinglet, Swainson's Thrush and Dark-eyed Junco that are common in young-tree thickets of rapidly maturing managed forests ~15–35 yr old (Bettinger 1996), are probably associated with similar conditions after wildfires but take longer to develop. About 80 yr after wildfires, bird species composition in the western hemlock type tends to stabilize, (i.e., Huff and Raley 1991), that is, generally not changing until the next wildfire, which could be centuries. During this extended period between fires, relative abundance among species appears to be regionally distinct and varies as forests grow older (Huff and Raley 1991). Bark foragers, such as Brown Creeper (*Certhia americana*), Hairy Woodpecker (*Picoides villosus*), Pileated Woodpecker, and Red-breasted Nuthatch tend to increase overtime as forests develop old-growth characteristics.

Relative to other lower montane forest types, the bird community of mixed evergreen hardwood type had more insectivorous species, foliage gleaning species, and snag nesting species (Alexander 1999). The mixed evergreen hardwood type also provides habitat for the federally listed Northern Spotted Owl and federal species of concern such as Olive-sided Flycatcher (USDI Fish and Wildlife Service 2002).

No studies have directly measured the response of mixed evergreen hardwood type bird communities to fire. Like the coastal forests, bird communities in this type vary among forest age classes (Raphael et al. 1988, Ralph et al. 1991). However, unlike the coastal forests, fire was probably far more widespread than any other disturbance. As a result, most authors agree that the historical fire regime has created and maintained high spatial and biological heterogeneity of vegetation in this type (Wills and Stuart 1994, Agee 1991b, 1993). Therefore, fire likely played an important role in maintaining the richness and diversity of these bird communities. Specifically, fires may influence communities by maintaining a heterogeneous seral composition, creating snags for foraging and nesting, and increasing availability of limiting food resources. The relative importance of these mechanisms is likely to be highly variable among species.

Upper Montane and Subalpine Ecosystems

The bird community of upper montane Shasta red Fir type is less species rich than those in Lower Montane Ecosystem types (Alexander 1999). The federally listed Northern Spotted Owl use this type, as do species of concern such as Olive-sided Flycatcher (USDI Fish and Wildlife Service 2002).

In the Shasta red fir type, the relatively mixed effects of fire may be important for understanding the composition of the bird community. Red-breasted Nuthatch and Golden-crowned Kinglet, both strongly associated with this vegetation type, decrease in response to fire (Kreisel and Stein 1999) and management practices that reduce canopy cover (Chambers et al. 1999). However, Alexander (1999) also documented a high proportion (relative to lower montane conifer forests) of canopy seed-eating, ground-foraging, and ground-nesting species in this type. The persistence of both canopy dependent and shrub-dependent species may be facilitated by landscape-scale patchiness created by fire.

Bird communities of the Pacific silver fir and mountain hemlock types of the Pacific Northwest are likely comparable to those in the same vegetation types in nearby areas of southern British Columbia, Canada, studied by Waterhouse et al. (2002). The most common species found at >900 m were Red Crossbill and Pine Siskin (*Carduelis pinus*); other relatively common species were Dark-eyed Junco, Winter Wren, Golden-crowned Kinglet, Chestnut-backed Chickadee, Townsend's Warbler(*Dendroica townsendi*), and Varied Thrush, which also were important species at lower elevations. Birds characteristic of the subalpine fir type in Washington include Pine Siskin, Mountain Chickadee (*Poecile gambeli*), Yellow-rumped Warbler (*Dendroica coronata*), and Clark's Nutcracker (*Nucifraga columbiana*; Manuwal et al. 1987).

Bird response to fire in the high-severity regime of the mountain hemlock, Pacific silver, and subalpine fir types probably parallels high-severity regimes of the western hemlock type. After fire, forest reestablishment is slower in these types than the western hemlock type due to short growing seasons, favoring ground- and brush-dwelling species over canopy feeder for up to a century or more. In subalpine environments, species that use edges and forest openings, such as Olive-sided Flycatcher, may benefit from fires (Altman and Sallabanks 2000, but see Meehan and George 2003).

ALTERATIONS TO FIRE REGIMES

Southwest Oregon and northwest California have a long history of anthropogenic influence on fire regimes (Frost and Sweeney 2000). This influence began with burning by American Indians (Boyd 1999), continued with fires set by Euro-American settlers, and then shifted to policies of fire suppression during the 20th century. However, establishing how and to what extent these activities have changed the natural fire regime is difficult. Such alterations in fire regimes can influence the local and landscape patterns of vegetation structure and community composition that determine habitat availability and quality for many forest birds.

The use of fire by American Indians in low- to moderate-severity fire regimes of the Pacific Northwest is accepted (Frost and Sweeney 2000), but the extent of these fires is not well known. Most burning by Indians probably occurred in oak woodland and pine forests (LaLande and Pullen 1999), possibly leading to a pattern where ignition of fires by American Indians was greatest at low elevations and decreased at higher elevations; there is little evidence that coniferous forests at higher elevations were significantly affected by aboriginal burning (Frost and Sweeney 2000).

Although burning by American Indians declined after the initiation of European settlement in the early 1800s (Frost and Sweeney 2000), a number of anecdotal accounts suggest that Euro-American settlement lead to large and severe fires throughout many areas of the West (Biswell 1989). Although more frequent fires may have been the case in some areas, quantitative evidence has not shown this effect to be ubiquitous. In Douglas-fir dominated forests of the California Klamath Mountains, Taylor and Skinner (1998) found no difference between pre-settlement (1626–1849) and post-settlement (1850–1904) fire-return intervals. Similarly, at Kinney Creek in the eastern Oregon Klamath Mountains, Agee (1991b) documented a pre-settlement (1760–1860) fire frequency of 16 yr that was not substantially different from a nearby post-settlement (1850–1920) estimate of 12 yr.

As in most of the West, fire suppression became the policy towards forest fires in the Pacific Northwest in the early 1900s (Atzet and Wheeler 1982, Biswell 1989, Agee 1993). However, most evidence suggests that this policy did not become highly effective until after World War II, when fire fighting became more mechanized (Pyne 1982). Additionally, increases in cattle and sheep grazing in the California and Oregon Klamath Moutains (Atzet and Wheeler 1982) may have facilitated effective fire suppression if it reduced fuels that carried fires (Biswell 1989).

Given the inherent variability within and among the different forest types, drawing generalizations about the effects of fire suppression on low- to moderate-severity fire regimes is difficult. At Oregon Caves National Monument in the Oregon Klamath Mountains, Agee (1991b) found that the fire-free period between 1920 and 1989 was the longest in over 300 yr. Perhaps more convincingly, in mixed conifer forests of the California Klamath Mountains, fire-return intervals increased from 12.5 yr during 1850–1904 (during the pre-suppression period) to 21.8 yr from 1905–1992 (during suppression) (Taylor and Skinner 1998), and fire rotation (the time required for the entire study area to burn) increased 10 fold from 20–238 yr (Taylor and Skinner 2003). Although increases in fire severity are often ascribed to policies of suppression (Biswell 1989), the evidence to support this hypothesis is limited and requires more information. Because fire suppression has reduced fire frequency, fuel levels are likely to be greater than they were historically. In areas where fire-return intervals were short, such build-ups may result in fires that are more severe and larger than they would have been historically (Agee 1993). However, in an analysis of fires in the Klamath Mountains between 1909 and 1997, Frost and Sweeney (2000) determined that although high severity fires were more common than they were prior to 1950, there was no conclusive evidence that this trend was outside of the historical range. More data are needed before we understand how fire suppression has affected fire severity in low- and moderate-severity fire regimes.

Effects of 20th century fire suppression may be responsible for changes in forest structure and landscape composition at several spatial scales in the Pacific Northwest (Kauffmann 1990). Generally, such effects can be more pronounced in forest types where historical fire-return intervals were shorter, low- and moderate-severity fire regimes, than where they were longer (Agee 1993). Fire suppression can alter the habitat potential for species associated with the composition and structure maintained by recurring fires by, for example, creating dense canopy layers that can substantially reduce herbaceous ground cover (e.g., Thilenius 1968, Hall 1977) and altering important roost characteristics used by birds of prey (e.g., Dellasala et al. 1998). At larger spatial scales, the effect of fire suppression on landscape composition may be more pronounced (Agee 1993). It has been hypothesized that in the mixed-conifer forests types with low- and (to a lesser extent) moderate-severity fire regimes in the Pacific Northwest, fire suppression has decreased stand heterogeneity and promoted a forest landscape that is more even-aged than was historically present (Agee 1993). In the Klamath Mountains and California Cascade Range, this hypothesis is supported by a comparison of forest openings measured in 1945 and again in 1985 (Skinner 1995). He found that during this time period, the median distance from random points to the nearest opening doubled, suggesting that the spatial diversity of forest structure has declined since 1945. Such changes are likely to reduce variation in fire severity, an important source of structural diversity among stands in forested landscapes (Taylor and Skinner 2003), and may decrease biological richness.

In forest types that have experienced fire-return intervals >40 yr, structural and biological changes may be relatively minor because the period of fire suppression has been shorter than the typical fire-free intervals (Chappell and Agee 1996), though this is difficult to validate. Because large areas of Sitka spruce, western hemlock, subalpine fir, and mountain hemlock forest types have fire-return intervals that greatly exceed fire-free intervals fire suppression effects to date are probably minimal. In the Shasta red fir type, Chappell and Agee (1996) found little evidence that fuel loads or vegetation structure of stands were outside of the range of natural variation at the stand scale. They suggested, however, that at larger spatial scales fire suppression has allowed more stands to develop late-successional characteristics, and thus creating more structural homogeneity across the landscape.

EFFECTS OF FIRE SUPPRESSION ON BIRDS

No studies have directly addressed effects of fire suppression on bird abundance in the Pacific Northwest. However, we do know that many bird species vary in abundance across successional vegetation gradients (Marcot 1984, Raphael et al. 1988, Huff and Raley 1991, Ralph et al. 1991). Thus, if fire suppression has changed forest composition, regional patterns of bird abundance may have also changed (e.g., Raphael et al. 1988). If subtle demographic mechanisms are important in the birds and operate even in the absence of successional changes, then the effects of fire suppression may be more complex and difficult to quantify.

Fire suppression may be one factor contributing to changes in bird community composition in the interior valley type. In the absence of fire, coniferous trees and non-native shrubs encroach upon these habitats (Tveten and Fonda 1999). Such changes have been implicated in changes in bird community composition between the late 1960s and early 1990s in oak woodlands (Hagar and Stern 2001). Fire has also been suppressed in sclerophyllous shrublands enabling trees to establish (Altman et al. 2000). Although the addition of trees to sclerophyllous shrublands could increase bird species diversity, converting the shrublands to forest is likely detrimental to shrubland bird populations.

Identifying general mechanisms by which fire suppression may influence changes in bird abundance may be difficult in coniferous forests. Information from nearby regions suggests that changes in forest structure caused by fire have important consequences for bird abundance. Studies in the Sierra Nevada and northeastern Washington reported canopy-dwelling and foraging species, including Golden-crowned Kinglet, Red-breasted Nuthatch, and Brown Creeper are consistently less abundant in burned areas (Bock and Lynch 1970, Kreisel and Stein 1999). These results are supported by similar responses of these species to commercial thinning (Chambers et al. 1999) or stand age (Marcot 1984, Raphael et al. 1988) that were studied in our region. To the extent that fire suppression has allowed denser forest canopies to develop over broad areas within the low-severity fire regime, species that use dense canopy characteristics should increase, while species strongly associated with fire-maintained vegetation composition and structure (e.g., canopy openings or diverse herb and shrub layers) should decrease. Olive-sided Flycatchers, for example, which typically increase in response to forest openings and open understory conditions created by fire (Hutto 1995; Altman, unpublished data) or commercial thinning (Chambers et al. 1999), declined broadly throughout the western North America from 1966 to 1996 (Altman, unpubl. data). These declines may be associated with habitat loss from fire suppression, but such an effect is difficult to verify over broad areas. Furthermore, changes in abundance may not be the best measure of habitat quality. In a study of Olive-sided Flycatchers in northern California, Meehan and George (2003) showed that although burned sites were more likely to be occupied than unburned sites, nest success was greater on the unburned sites.

ROLE OF PRESCRIBED FIRE AND FIRE MANAGEMENT

PRESCRIBED BURNING FOR HABITAT RESTORATION AND MAINTENANCE

Prescribed fire is increasingly recognized as a tool for restoring and maintaining forest health and reducing fuels (Biswell 1989), yet the risks of escape and smoke production have limited its application. Estimates of how much area to should be treated with fuel reduction activities were made during revisions to the Northwest Forest Plan (USDA and USDI 2000). The estimated area burned historically in this region (~190,000 ha yr^{-1}) was used as a starting point, and this was reduced by the average area currently burned by wildland fire and what is feasible to treat considering budget constraints to arrive at a goal of treating 76,000 ha annually.

In areas that burn frequently, fire may play an important role in maintaining species composition of some unique vegetation communities. Fire has been reintroduced to grasslands within the Pacific Northwest, for example, to maintain endangered plant species (Pendergrass et. al. 1999) and to restore prairie-like conditions (Clark and Wilson 2001). Such applications of fire are considered experimental because so little is known about the natural fire regime and the desired results have not necessarily been achieved. Using prescribed fire to mimic natural fire regimes in these habitats has the potential to restore and maintain vegetation communities at watershed scales (e.g., Taylor and Skinner 2003) and associated bird communities.

BIRD CONSERVATION STRATEGIES USING PRESCRIBED FIRE

Bird conservation plans developed by Oregon-Washington Partners in Flight (2000) recommend prescribed burning in oak woodlands and savannas of the interior valley type in western Oregon and Washington. Burning in oak woodlands is being used as a conservation strategy for birds by reducing encroachment of Douglas-fir, stimulating oak seedling recruitment, and creating multi-aged stands. Prescribed fire is also being used to restore oak woodlands in other regions of the United States (e.g., Abrams 1992). Although prescribed fire may restore forest plant communities, the effects on bird communities are not well documented. Potential declines may occur as a result of changes in vegetation structure or in response to fires that take place during the breeding season (e.g., Artman et al. 2001). Although the timing of prescribed fire relative to the breeding season should be considered, these relatively short-term disturbances should not outweigh the long-term conservation benefits of restoring oak woodlands (Oregon-Washington Partners in Flight 2000).

Although the effects of prescribed burning on bird abundance in the Pacific Northwest have not been documented, observations from the Sierra Nevada (e.g., Kilgore 1971) have been incorporated into the Oregon-Washington PIF conservation strategy for coniferous forests on the east slope of the Cascade Range (Oregon-Washington Partners in Flight 2000). This strategy recommends use of prescribed fire to reduce fuel loads and accelerate development of late-seral conditions. Such conditions are hypothesized to enhance habitat for Olive-sided Flycatchers as well as Cassin's Finch (*Carpodacus cassinii*), Western Wood-Pewee (*Contopus sordidulus*), Mountain Bluebird (*Sialia currucoides*), Northern Flicker (*Colaptes auratus*), American Kestrel (*Falco sparverius*), and American Robin (Oregon-Washington Partners in Flight 2000). Similarly, the California Partners in Flight conservation strategy for coniferous forests has identified the restoration of fire cycles as potential conservation measures for Black-backed Woodpeckers (*Picoides arcticus*), Fox Sparrows, and Olive-sided Flycatcher (California Partners in Flight 2002a).

Awareness is growing that prescribed fire and other forest management activities need to be considered within the context of natural wildfire on the landscape. The ability of birds to recruit to a site after fire depends on management activities that occur before and after fires. In particular, snag-nesting species, which typically increase following fire, are affected by postfire snag availability (e.g., Haggard and Gaines 2001). Snag-nesting bird communities were compared among three salvage-logged treatments (high, moderate, and low amounts of snags), 4–5 yr after a high-severity fire in the Douglas-fir type of the east-central Washington Cascades (Haggard and Gaines 2001). Distribution patterns of snags (e.g, clustering) and snag size affected cavity-nesting species response. Intermediate densities (15–35 snags ha^{-1}) of snags >25 cm diameter at breast height (dbh) were associated with the highest abundance, species richness, and nesting densities of cavity nesters.

Another example of the interaction between fire and forest management is the potential effect of fire and fire management on habitat for endangered species. This is illustrated by the habitat requirements of the Northern Spotted Owl in areas of moderate-severity fire regimes throughout the Pacific Northwest. Historically, much of the habitat in this fire regime was spatially and temporally dynamic because of fires. More recently, decades of fire suppression and selective harvest of large, fire-resistant trees have created multi-canopied forests with thick understories of fire-intolerant species, which possibly has accelerated a shift towards larger and more severe fires (Agee and Edmonds 1992). As a result, the amount of suitable Northern Spotted Owl habitat (USDI 1992, Agee 1993) may have increased in some forest types, particularly the grand fir type. Because these areas provide high quality owl habitat, they have been protected as late successional reserves designed to sustain owl populations. Consequently, high-severity fires are expected to burn a greater portion of the landscape than they did historically, increasing the probability that Northern Spotted Owl habitat will be altered for longer periods and at larger spatial scales. Some level of low-severity fire that maintains high canopy cover may have modest, or even beneficial effects for Northern Spotted Owls (Bond et al. 2002). The owl is more likely to be present and persist in areas of mixed successional stages and forest structures in northern California where fire is likely a major contributing factor to the mosaic of conditions that are favorable (Thome et al. 1999, Zabel et al. 2003). Severely-burned areas, however, are avoided and may reduce owl productivity (Bevis et al. 1997, Gaines et al. 1997, cf. Bond et al. 2002). If the extent of severely burn area increases substantially, the amount of Northern Spotted Owl habitat in reserves and managed areas may not be sufficient to sustain owl populations.

MANAGEMENT QUESTIONS AND FUTURE RESEARCH CONSIDERATIONS

Managing fire and fuels to meet the ecological, economic, and public safety concerns of society is challenging. From an ecological perspective, the ability to apply effective management is mostly limited by lack of relevant information to make informed decisions. In the Pacific Northwest, where fire has undoubtedly had a profound effect on bird communities, few studies have addressed how fire affects birds (Table 2), and basic information about bird species composition and relative abundance patterns was lacking for most vegetation types in this region. To effectively manage fire and fuels in this region while considering short- and long-term bird conservation will require substantial investments to accurately portray potentially affected bird communities across vegetation types, monitor response to varied management actions, and develop models to predict related bird response. Monitoring within the context of adaptive management (Holling 1978, Walters and Holling 1990) will be critical to assure that ecological goals of fire management are met (Tiedemann et al. 2000). In some cases, monitoring programs may be designed in such a way to contribute information to important research questions, and vice-versa. With this potential in mind, we have outlined ten questions that, if answered, will, at least, provide critical information for the application of fire management toward effective bird conservation.

What Were Characteristics of Natural Fire Regimes in the Pacific Northwest?

Clearly one of the most crucial steps to understanding the relationships between fire and bird abundance is to understand their interactions at a large spatial scale. This requires understanding, not just of the central tendency of fire regimes, but also their variability (Gill and McCarthy 1998). Given the complex nature of fire regimes in the Pacific Northwest, more data on the frequency, severity, and spatial distribution of fires is needed, especially in regions with low- to moderate-severity fire regimes.

How Do Bird Populations Change in Response to Fire?

Even relatively basic information on the response of birds to fire is still lacking. Few studies have distinguished between changes in behavior (e.g., habitat use or nest-site selection) versus larger-scale changes in population density. Studies that measure behavioral responses to fire (e.g., foraging activity [Kreisel and Stein 1999]), and nesting density and demographics (e.g., Saab and Dudley 1998, Saab et al. 2002) could provide these data. Using geographic information system (GIS) data to link these patterns with landscape level patterns may provide useful insights (Dettmers and Bart 1999, Saab et al. 2002). If fire affects important demographic patterns (e.g., Saab and Vierling 2001), then we should consider how source/sink dynamics might be influenced at large spatial scales.

When Bird Populations Change in Response to Fire, What Are the Driving Factors?

With a better understanding of how bird abundance changes in response to fire, it will be important to determine causal explanations. A number of mechanisms have been hypothesized to influence postfire changes in bird communities, including food availability (Apfelbaum and Haney 1981), nest-site availability (Hutto 1995), predator abundance (Altman and Sallabanks 2000, Saab and Vierling 2001), and vegetation structure (Bock and Lynch 1970). An evaluation of the relative importance of these factors

TABLE 2. SUMMARY OF BIRD RESPONSES TO FIRE BY SPECIES.

Species	State	Year after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments[c]
Blue Grouse (*Dendragapus obscurus*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Spotted Owl (*Strix occidentalis*)	CA, AZ, NM	1	>540 (1)	11 territories	0	2	2, Postfire estimates not outside range of unburned estimates.
Rufous Hummingbird (*Selasphorus rufus*)	WA	1–515	no data (7)	7 plots	m	3	3, Most abundant 19 yr postfire.
Downy Woodpecker (*Picoides pubescens*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Hairy Woodpecker (*Picoides villosus*)	WA	4	4000 (2)	13 burned, 9 unburned	+	1	1
American Three-toed Woodpecker (*Picoides dorsalis*)	WA	4	4000 (2)	13 burned, 9 unburned	+	1	1
Black-backed Woodpecker (*Picoides arcticus*)	WA	4	4000 (2)	13 burned, 9 unburned	+	1	1
Pileated Woodpecker (*Dryocopus pileatus*)	WA	4	4000 (2)	13 burned, 9 unburned stations	0	1	1
Pacific-slope Flycatcher (*Empidonax difficilis*)	WA	1–515	np (7)	7 plots	–	3	3
Gray Jay (*Perisoreus canadensis*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Steller's Jay (*Cyanocitta stelleri*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Clark's Nutcracker (*Nucifraga columbiana*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Black-billed Magpie (*Pica hudsonia*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Common Raven (*Corvus corax*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Black-capped Chickadee (*Poecile atricapilla*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Mountain Chickadee (*Poecile gambeli*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Chestnut-backed Chickadee (*Poecile rufescens*)	WA	1–515	np (7)	7 plots	–	3	3
Red-breasted Nuthatch (*Sitta canadensis*)	WA	4	4000 (2)	13 burned, 9 unburned	–	1	1
White-breasted Nuthatch (*Sitta carolinensis*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Brown Creeper (*Certhia Americana*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Brown Creeper	WA	1–515	np (7)	7 plots	m	3	3
Winter Wren (*Troglodytes troglodytes*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Winter Wren	WA	1–515	np (7)	7 plots	+	3	3
Golden-crowned Kinglet (*Regulus satrapa*)	WA	4	4000 (2)	13 burned, 9 unburned	–	1	1
Golden-crowned Kinglet	WA	1–515	np (7)	7 plots	–	3	3
American Robin (*Turdus migratorius*)	WA	1–515	np (7)	7 plots	m	3	Most abundant 3–19 yr postfire.
Varied Thrush (*Ixoreus naevius*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1
Townsend's Warbler (*Dendroica townsendi*)	WA	1–515	np (7)	7 plots	m	3	3
Dark-eyed Junco (*Junco hyemalis*)	WA	1–515	np (7)	7 plots	+	3	3
Red Crossbill (*Loxia curvirostra*)	WA	4	4000 (2)	13 burned, 9 unburned	0	1	1

[a] Only wildland fires are reported in this table.

[b] + = increase; – = decrease; 0 = no effect or study inconclusive; m = mixed response.

[c] References: 1 = Kreisel and Stein 1999, compared 13 stations in two 80-ha stand replacement burns with nine unburned stations; 2 = Bond et al. 2002, compared survival, site fidelity, and reproductive success for owls 1 yr postfire to unburned estimates; 3 = Huff et al. 1985, chronosequence comparing seven sites ranging from 1–515 yr postfire, positive fire response if birds more abundant in years immediately after fire.

for different nesting and foraging guilds is needed. An effective evaluation of these hypotheses could include experimental manipulations or large sample sizes in many treatments. Understanding the mechanisms responsible for these changes will provide a better understanding of the unique ecological effects of fire-mediated habitat change.

How Do Fire Regimes Influence the Bird Community Structure at Local and Landscape Levels?

With data on the response of bird populations to fire, researchers and managers will be in a better position to understand how fire regimes structure bird communities. To date, most studies of bird communities and fires have been performed at the scale of single forest stands (Bock and Lynch 1970, Kreisel and Stein 2000, but see Saab et al. 2002). In order to understand the relationship of fires and birds, it is important not only to measure the effect of fire at burned and unburned points, but to quantify the effect of fire, and different spatial patterns of fire, at larger spatial scales, such as watersheds or regions. Fire likely influences abundance and distribution of birds throughout entire regions, not simply within the immediate area of disturbance.

How Do Changes to Fire-return Intervals Affect Bird Populations?

It is clear that fire suppression has lengthened fire-return intervals in the low- and to some degree moderate-severity fire regimes, and may have altered patterns of fire severity. The ecological effects of these changes are not well understood (Chappell and Agee 1996, Frost and Sweeney 2000), but changes in composition and spatial distribution of large-scale habitat characteristics are probably important (Skinner 1995). Effects of reducing fire frequencies on bird abundance and demographics should be evaluated if a policy of suppression continues, and at least outside of wilderness areas it probably will. Such evaluations should be conducted at multiple spatial scales by expanding analyses beyond comparisons of burned and unburned points to consider how spatial distribution of landscape characteristics (e.g., edge/patch ratios or habitat composition around points). Inferences drawn from microhabitat and landscape-scale characteristics may be substantially different and vary depending on life-history characteristics (e.g., migration strategy) of the birds in question (Mitchell et al. 2001).

Have the Effects of Wildfires on Bird Populations Changed?

Fire suppression may have created fires that are less frequent, larger, and more severe than those occurring previously. The potential shift to large and more severe fires may affect bird abundance and community composition. Little is known about potential changes in bird populations as a result of changing fire regimes. Comparing long-term data on bird abundance (e.g., Breeding Bird Survey data) with demographic models that can evaluate the effect of landscape composition on bird populations may be one way to evaluate the effect of changes created by fire suppression. Such an approach may be especially useful in evaluating the degree to which long-term declines of species that respond positively to fire may be a result of fire suppression policies.

How Does Prescribed Fire Change Conditions for Birds?

A return to more natural fire regimes is often advocated, but given the constraints imposed by concerns of public safety, economics, and air quality, it is more likely that this will be achieved through the application of prescribed fire in combination with manual and mechanical treatments (e.g., thinning of trees and removal of invasive shrubs). The application of these management tools may occur during seasons when fires did not normally burn. In the Pacific Northwest, fires burned naturally from June through September, with most occurring in late summer or early fall (Taylor and Skinner 1998, Brown et al. 1999). To maximize fire control, however, late winter or early spring is usually a better time to apply prescribed burns (Biswell 1989) to prevent escape. Effects of such burning schedules on bird abundance may be immediate, especially for ground- and shrub-nesting species, when they conflict with the breeding season. Such effects may be relatively short-lived and must be considered within the context of long-term benefits of prescribed fire (California Partners in Flight 2002). These changes are poorly understood in the Pacific Northwest, but are presumed to include vegetation changes that lead to longer-lasting changes in bird abundance (Kilgore 1971) or nest success (Jones et al. 2002). Prescribed fire can be applied in many different ways and have many different effects on vegetation and fuel and are most likely to be applied to the low- and moderate-severity fire regime vegetation types. Use and effects of prescribed fire in these types, which include Douglas-fir, grand fir, mixed evergreen hardwood, white fir, Shasta red fir, and coast redwood, is complex and generalizations are not easily drawn from one type that can be applied easily to birds in another type.

How Do Fire Surrogates (Fuels Treatments) Affect Bird Populations?

An alternative to prescribed fire is the use of fire surrogates (usually mechanical methods) to reduce fuels and mimic other structural and possibly ecological effects of fire. Such management activities vary widely in intensity, from collection and removal of fuels by hand to large-scale mechanical processes that have high amounts of incidental disturbance. Evidence suggests that these activities do not create the same structural or ecological conditions as a natural or prescribed fire (Imbeau et al. 1999, and see Hannon and Drapeau, this volume). For example, when reproductive success was examined for Olive-sided Flycatchers associated with recent burns and logged areas in the western Oregon Cascade Mountains (Altman and Sallabanks 2000), nest success at burned sites was nearly twice that in logged area, suggesting that openings created by fire are better habitat for the flycatcher than logged areas. In contrast, a similar study by Meehan and George (2003) showed that the probability of nest-loss was greater in burned than unburned areas. Clearly even the effect of fire on bird reproduction, let alone the ability of mechanical fuels reduction to mimic these effects, is poorly understood. Mechanical methods reduce fuels and are certainly likely to reduce fire risk. After fire, however, standing dead trees remain. Trees removed by mechanical methods create habitat that is structurally and ecologically different from postfire conditions. These activities should be monitored with respect to their effect on bird populations in order to evaluate their ecological effects.

What Are Effects of Postfire Salvage?

Postfire salvage logging is a controversial practice that removes some amount of dead and at least apparently damaged live trees from burned areas. After fire, snags provide important nest sites and foraging opportunities for many cavity-nesting and bark-foraging birds (Hutto 1995, Kreisel and Stein 1999). Salvage logging has negative consequences for some bird species (Hutto 1995, Wales 2001). Studies from the Washington Cascades (Haggard and Gaines 2001) and ponderosa pine forests of southwestern Idaho (Saab and Dudley 1998) have both suggested that snag density and distribution are important factors influencing the abundance of cavity-nesting birds. As in many other situations, the effects of such treatments may interact with burn severity. Removing structure from severely burned areas may have different effects than the same level of extraction from less severely burned areas (Kotliar et al. 2002). Investigations of the effects of salvage should consider these types of interactions.

If Climate Change Alters Fire Regimes, What Is the Effect on Bird Communities?

The possibility that climate change may alter local fire regimes should be considered (Johnson and Larsen 1991). Such changes may affect bird abundance, community composition, distribution, and diversity. Predicting the effects of climate change on fire regimes and bird communities may provide us with the opportunity to test hypotheses about the relative importance of deterministic and stochastic processes in community assembly.

ACKNOWLEGMENTS

We thank Rich Young for assistance on developing the map figure. Portions of this paper benefited from our discussions with Danny Lee and Steve Norman. Bob Altman, Vicki Saab, Hugh Powell, and two anonymous reviewers provided helpful editorial comments.

Studies in Avian Biology No. 30:63–75

THE ROLE OF FIRE IN STRUCTURING SAGEBRUSH HABITATS AND BIRD COMMUNITIES

Steven T. Knick, Aaron L. Holmes, and Richard F. Miller

Abstract. Fire is a dominant and highly visible disturbance in sagebrush (*Artemisia* spp.) ecosystems. In lower elevation, xeric sagebrush communities, the role of fire has changed in recent decades from an infrequent disturbance maintaining a landscape mosaic and facilitating community processes to frequent events that alter sagebrush communities to exotic vegetation, from which restoration is unlikely. Because of cheatgrass invasion, fire-return intervals in these sagebrush ecosystems have decreased from an historical pattern (pre-European settlement) of 30 to >100 yr to 5–15 yr. In other sagebrush communities, primarily higher elevation ecosystems, the lack of fire has allowed transitions to greater dominance by sagebrush, loss of herbaceous understory, and expansion of juniper-pinyon woodlands. Response by birds living in sagebrush habitats to fire was related to the frequency, size, complexity (or patchiness), and severity of the burns. Small-scale fires that left patchy distributions of sagebrush did not influence bird populations. However, large-scale fires that resulted in large grassland expanses and isolated existing sagebrush patches reduced the probability of occupancy by sagebrush-obligate species. Populations of birds also declined in sagebrush ecosystems with increasing dominance by juniper (*Juniperus* spp.) and pinyon (*Pinus* spp.) woodlands. Our understanding of the effects of fire on sagebrush habitats and birds in these systems is limited. Almost all studies of fire effects on birds have been opportunistic, correlative, and lacking controls. We recommend using the large number of prescribed burns to develop strong inferences about cause-and-effect relationships. Prescribed burning is complicated and highly contentious, particularly in low-elevation, xeric sagebrush communities. Therefore, we need to use the unique opportunities provided by planned burns to understand the spatial and temporal influence of fire on sagebrush landscapes and birds. In particular, we need to develop larger-scale and longer-term research to identify the underlying mechanisms that produce the patterns of bird responses to fire in sagebrush ecosystems.

Key Words: *Amphispiza belli*, *Bromus tectorum*, *Centrocercus urophasianus*, disturbance, exotic annual, fire regime, *Oreoscoptes montanus*, sagebrush ecosystems, *Spizella breweri.*

EL PAPEL DEL FUEGO EN LA ESTRUCTURA DE HABITATS DE ARTEMISIA Y COMUNIDADES DE AVES

Resumen. El fuego es una perturbación dominante y evidente en ecosistemas de artemisia (*Artemisia* spp.). En elevaciones bajas, en comunidades de artemisia xérica, el papel del fuego ha cambiado en las últimas décadas de una perturbación infrecuente que mantiene el mosaico del ecosistema y facilita los procesos de las comunidades, a eventos frecuentes que alternan las comunidades de artemisia a vegetación exótica, por lo cual la restauración no es muy prometedora. Debido a la invasión del zacate bromo, los intervalos de repetición de incendios en los ecosistemas de artemisia han disminuido de su patrón histórico (asentamiento pre-Europeo) de 30> a >100 años a 5–15. En otras comunidades de artemisia, principalmente en elevaciones más altas, la ausencia de fuego ha permitido transiciones tales como el incremento en dominancia de artemisia, la pérdida de la primera capa de vegetación de herbáceas y la expansión de bosques de juníperos-piñón. La respuesta al fuego de las aves que habitan en habitats de artemisia estaba relacionada a la frecuencia, tamaño, complejidad (o diversidad de parches), y a la severidad de los incendios. Incendios de pequeña escala que produjeron parches distribuidos de artemisia, no afectaron a las poblaciones de aves. Sin embargo, incendios de larga escala que resultaron en la expansión de largos pastizales y aislaron parches de artemisia existentes, redujeron la probabilidad de ser ocupadas por especies obligadas de artemisia. Las poblaciones de aves también disminuyeron en ecosistemas de artemisia, con el incremento en la dominancia de bosques de junípero (*Juniperus* spp.) y de piñón (*Pinus* spp.). Nuestro entendimiento de los efectos del fuego en habitats de artemisia y aves en este sistema es limitado. La mayoría de los estudios de los efectos del fuego en aves han sido oportunistas, correlativos y con falta de control. Recomendamos utilizar un gran número de quemas prescritas para desarrollar fuertes inferencias de las relaciones causa efecto. Las quemas prescritas son complicadas y altamente contenciosas, particularmente en comunidades de artemisia xérica de baja elevación. Es por esto que para entender la influencia espacial y temporal del fuego en paisajes y aves de artemisia, necesitamos utilizar la oportunidad única que nos dan los incendios planeados. En particular, necesitamos desarrollar investigación de amplia escala y de largo plazo, para identificar los mecanismos que producen los patrones de las respuestas de las aves hacia el fuego en ecosistemas de artemisia.

Fire is one of the dominant and most visible disturbances influencing sagebrush (*Artemisia* spp.) ecosystems in the Intermountain region of western North America. A disturbance is any relatively discrete event in time that disrupts ecosystem, community, or population structure and changes resources, substrate availability, or the physical environment (Pickett and White 1985:8). Fire is an important disturbance that maintains forb and grass components, facilitates nutrient cycling, and regulates other ecosystem processes within the sagebrush community. Because of variation in location, size, frequency, severity (level of biological and physical impact), and complexity of fires, the effects of fire on sagebrush habitats and bird communities are expressed at multiple scales in space from individual plants to landscapes and across time scales from immediately postfire to decades or longer.

Sagebrush habitats dominate >43,000,000 ha across western North America (Fig. 1) (McArthur 1994, McArthur 2000). Despite this wide distribution, sagebrush habitats are highly imperiled because of extensive degradation and loss across much of their distribution (Knick et al. 2003). Consequently, conservation of sagebrush habitats and birds is a primary management concern (Paige and Ritter 1999).

The historical fire regime and role of fire in sagebrush ecosystems has changed during the past century. Prior to the late 1800s, recurrent fires that varied in frequency and severity across a landscape resulted in a mosaic of sagebrush and interspersed grassland communities in different stages of community succession (Young et al. 1979). Landscapes now dominated by exotic annual grasses have drastically increased fire frequency in landscapes (Whisenant 1990, Billings 1994, Peters and Bunting 1994). In contrast, reduced fine fuel biomass because of livestock grazing or fire suppression has decreased fire frequencies in other regions (Miller and Wigand 1994, Miller and Rose 1999). In the interior Columbia Basin, the departure from pre-settlement patterns was greatest in sagebrush communities compared to other habitats (Hann et al. 1997, Hann et al. 2002).

In this review, we discuss the role of fire in influencing the composition and configuration of sagebrush systems and subsequent effects on birds living in these communities. We summarize information on the historical role of fire and the mechanisms by which land use and management practices have altered the fire regime. We then describe the effects of fire on bird communities caused by changes in the local vegetation and surrounding landscape. Because more fire-related research has been conducted on Greater Sage-Grouse (*Centrocercus urophasianus*) than nongame species, we present findings separately. Finally, we identify the critical management needs and research issues.

HISTORICAL PATTERNS OF VEGETATION DYNAMICS AND BIRD COMMUNITIES

Vegetation Dynamics

Sagebrush often is the dominant shrub on salt-free soils at elevations between 150 and 3,300 m where precipitation exceeds 178 cm (West 1983, Miller and Eddleman 2001). We distinguish, when possible, three subspecies of big sagebrush, which have different growth and foliage characteristics and occupy different ecological sites (Shumar and Anderson 1986, Jensen 1990). Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), and mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) vary along climate, elevation, and soil gradients. The landscapes occupied by each subspecies differ in their susceptibility to invasion by exotic plant species, the disturbance regime, and subsequent pattern of community succession and community response. Most studies of bird communities in sagebrush ecosystems have failed to recognize these differences (with the exception of recent research on Greater Sage-grouse). We also present ancillary information on dwarf sagebrush (low sagebrush [*Artemisia arbuscula*], black sagebrush [*Artemisia nova*]), and salt desert shrub communities which often intergrade with big sagebrush communities.

Sagebrush is highly sensitive to fire; fire kills individual sagebrush shrubs and none of the primary species of *Artemisia* or subspecies can resprout from root crowns (West and Young 2000). Historically, native herbaceous species of annuals and perennials would increase in the absence of shrubs following fire. Recovery following burns to sagebrush-dominated landscapes is a function of shrub regeneration from existing seed sources. Seed production must come from remaining sagebrush plants that survive the fire or from pre-existing seed pools. Although sagebrush seeds present in the soils rarely germinate after 0.5–1 yr (Young and Evans 1978, Hassan and West 1986), recruitment of mountain big sagebrush following complete burns occurred from seeds produced 3 yr previously (R. F. Miller, personal observation). Seed dispersal is limited to the immediate area surrounding the mother plant (Young and

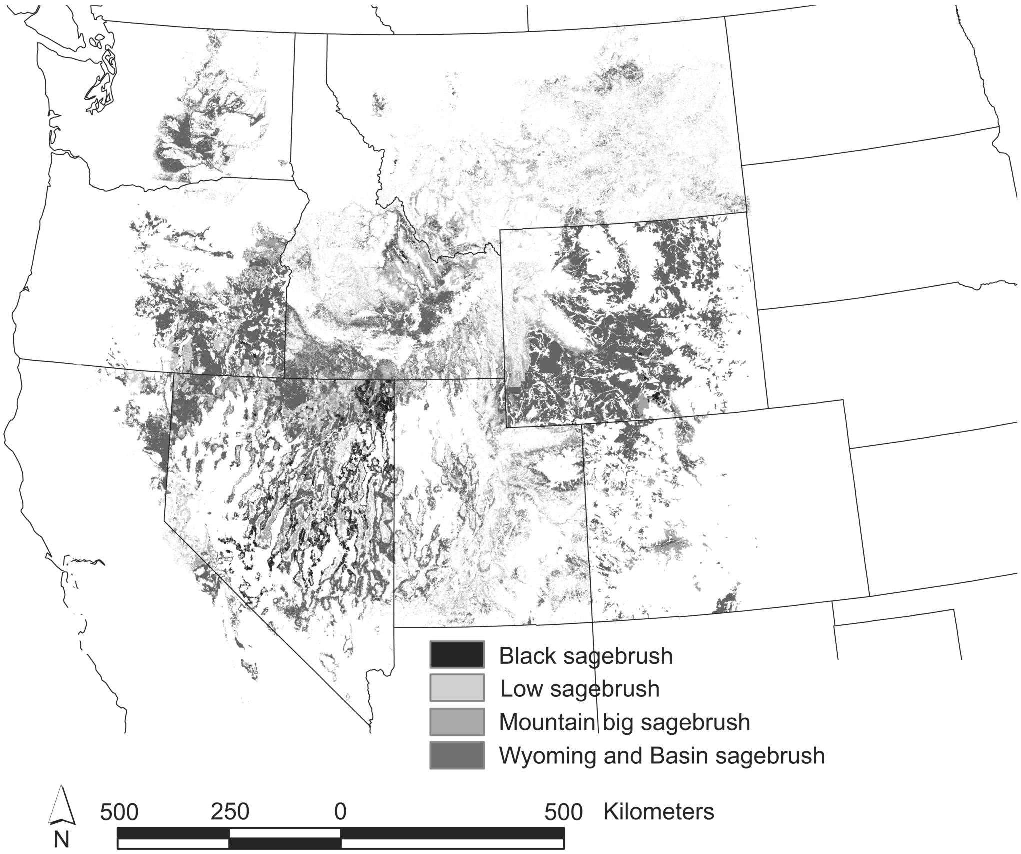

FIGURE 1. Sagebrush habitats cover approximately 43,000,000 ha in western North America. The map depicts the current distribution of the primary species of dwarf and tall sagebrush species (Comer et al. 2002). Sagebrush areas are not shown for states and provinces having limited geographic distribution of sagebrush or for which reliable maps were not available.

Evans 1989, Meyer 1994) and recovery of large expanses devoid of sagebrush following burns may require >100 yr (USDI 1996, Hemstrom et al. 2002). Therefore, completeness of the burn in destroying individual plants is the most important factor in determining the recovery dynamics of burned sagebrush landscapes.

Pre-settlement fire regimes have been described for a few communities of big and dwarf sagebrush systems bordering forested areas (summarized in Miller and Tausch 2001). However, the lack of large trees that bear fire history through scarring limits our ability to date pre-settlement fires and to determine return intervals for most sagebrush landscapes (Miller and Tausch 2001). Therefore, proxy information on geographic location and topography, plant life history and fire adaptations, fuel characteristics, and climate and weather patterns has been used to supplement the limited direct information.

Pre-settlement fire regimes in the sagebrush biome were highly variable both temporally and spatially. Severity and frequency of occurrence varied among different plant associations and site characteristics with mean fire-return intervals ranging from as little as 10 yr in higher elevation sites to greater than 200 yr in lower elevation, xeric regions (Fig. 2) (Miller and Tausch 2001). Severe fires that completely burned large areas likely were rare.

BASIN BIG SAGEBRUSH

Basin big sagebrush is the tallest form of big sagebrush (120–180 cm) and may reach 240 cm in height (Winward and Tisdale 1977). Basin big sagebrush occupies areas of deep, loamy soils in annual precipitation zones from 32–36 cm. Because these soils are highly fertile, most areas previously dominated by basin big sagebrush have been converted to

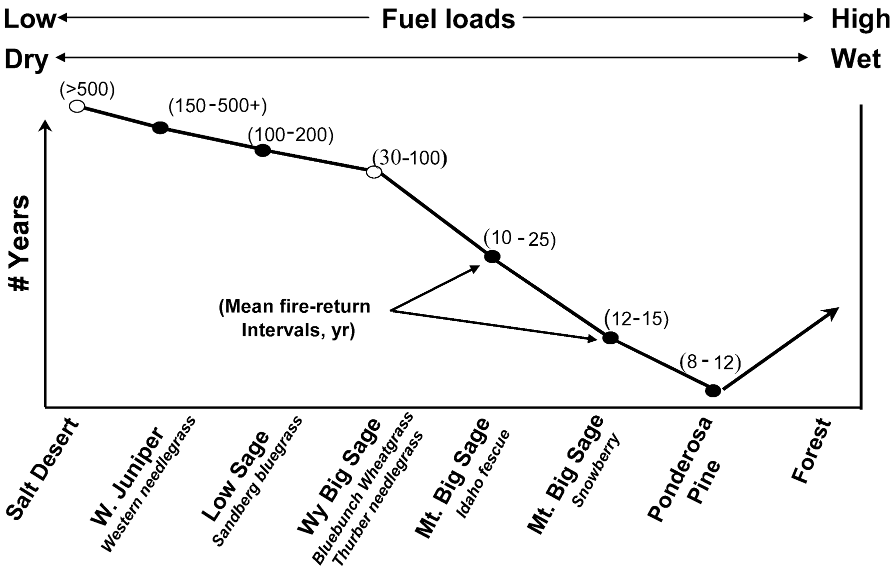

FIGURE 2. Presettlement mean fire-return intervals (MFRI) for salt desert, old growth western juniper-western needlegrass (*Stipa occidentalis*), low sagebrush (*Artemisia arbuscula* Nutt.)-Sandberg bluegrass (*Poa sandbergii* Vasey), Wyoming big sagebrush (*A. tridentata.* ssp. *wyomingensis* Welsh.)-bluebunch wheatgrass (*Agropyron spicatum* Pursh)-Thurber needlegrass (*Stipa thurberiana* Piper), mountain big sagebrush (*A. t.* ssp. *vaseyana* Rydb.)-Idaho fescue (*Festuca idahoensis* Elmer), mountain big sagebrush-snowberry (*Symphoricarpos spp.*), and ponderosa pine (*Pinus ponderosa* Laws.) communities. Solid circles are MFRI estimates supported by data, and open circles are estimates with little to no information (derived from Miller and Tausch 2001).

agriculture in Washington (Dobler et al. 1996) and an estimated 99% of lands once covered by basin big sagebrush now is absent from the Snake River Plains in Idaho (Noss et al. 1995). Basin big sagebrush is less resilient to disturbance than mountain big sagebrush but is more resilient than Wyoming big sagebrush. Historical fire-return intervals probably were >50 yr between fire events but fires may have been more frequent (10–20 yr) on productive sites containing greater amounts of basin wildrye grass (*Leymus cinereus*).

WYOMING BIG SAGEBRUSH

Wyoming big sagebrush is widely distributed through the Intermountain West of the United States (McArthur 1994). Wyoming big sagebrush grows in shallower soils and more xeric conditions (20–30 cm yr^{-1} annual precipitation) compared to basin big sagebrush. The average size of Wyoming big sagebrush is 45–100 cm (Winward and Tisdale 1977). Very little direct information exists to document pre-settlement fire regimes in regions dominated by Wyoming big sagebrush; estimated fire-return intervals range from 50 to >100 yr (Wright and Bailey 1982). Fire occurrence, severity, size, and complexity were probably highly variable in space and time. Due to limited fuels, most fires in the pre-settlement landscape probably were patchy, uneven burns that left islands of sagebrush within the burn that provided seed sources to initiate recovery to a shrubland landscape. However, occasional fires with limited spatial complexity probably occurred under severe weather conditions and in years following above average moisture resulting in the build up of fine fuels.

MOUNTAIN BIG SAGEBRUSH

Mountain big sagebrush grows at higher elevations (usually >1,600 m) than basin or Wyoming big sagebrush. Mountain big sagebrush communities generally are more resilient to disturbance and recovers more rapidly than either basin or Wyoming big sagebrush because of greater precipitation (>30 cm yr^{-1}) and possibly longer seed viability. Mountain big sagebrush sites also are less susceptible to invasion by alien weeds than the other subspecies of big sagebrush. Historical fire-return intervals are thought to be relatively frequent (10–25 yr) in the more productive communities (Miller and Rose 1999, Miller et al. 2000). However, drier sites with reduced fuel loadings may have had less frequent returns with moderate severity fires occurring between 30–70 yr. The fire regime for mountain big sagebrush associations in arid locations on pumice influenced soils was characterized by infrequent but high severity, stand replacement fires that occurred only under severe weather conditions and may have been >150 yr (Miller and Tausch 2001).

DWARF SAGEBRUSH

Dwarf sagebrush communities dominated by low sagebrush or black sagebrush often intergrade with big sagebrushes. Historic fire-return intervals of low sagebrush communities are perhaps more variable than big sagebrush species. The average fire-return interval in low sagebrush-bluebunch wheatgrass (*Pseudoroegneria spicata*) probably ranged between 20–50 yr. For low sagebrush-Sandberg's bluegrass, the average fire-return interval probably was >100 yr (Young and Evans 1981, Miller and Rose 1999).

SALT DESERT SHRUB

Salt desert shrublands, dominated by members of the Chenopodiaceae, cover approximately 16,000,000 ha of western North America (Blaisdell and Holmgren 1984). Individual shrubs are widely spaced and total vegetative cover often is sparse. Invasion by exotic annuals generally is not a problem except in localized regions and northern parts of the range. Historical fire returns may have been as long as 500 yr or greater in salt desert shrub communities. Fire disturbance in these communities generally was not a significant factor in community dynamics. However, fire frequency has increased in recent decades concurrent with increases in biomass and continuity of fine fuels and biomass as a consequence of invasion by exotic plants (West and Young 2000, Brooks and Pyke 2001).

BIRD COMMUNITIES IN SAGEBRUSH ECOSYSTEMS

Bird species whose distribution is closely tied to sagebrush habitats during at least part of the year are considered sagebrush obligates (Braun et al. 1976, Paige and Ritter 1999). These include Greater Sage-grouse, Gunnison Sage-Grouse (*Centrocercus minimus*), Sage Thrasher (*Oreoscoptes montanus*), Sage Sparrow (*Amphispiza belli*), and Brewer's Sparrow (*Spizella breweri*) although these species also may use other shrubland habitats. Gray Flycatcher (*Empidonax wrightii*) relies heavily, although not exclusively, on sagebrush habitats (Sterling 1999). The above species place their nests in or beneath big sagebrush shrubs and occur in a wide spectrum of structural conditions. Other widespread species that use sagebrush habitats include Lark Sparrow (*Chondestes grammacus*) and Black-throated Sparrow (*Amphispiza bilineata*). Green-tailed Towhee (*Pipilo chlorurus*) is common in mesic sagebrush communities and the Loggerhead Shrike (*Lanius ludovicianus*) occurs throughout most of the sagebrush biome, with the highest densities associated with the taller shrub communities (Yosef 1996). Species primarily associated with grasslands adjacent to sagebrush habitats include Burrowing Owl (*Athene cunicularia*), Western Meadowlark (*Sturnella neglecta*), Horned Lark (*Eremophila alpestris*), Vesper Sparrow (*Pooecetes gramineus*), Grasshopper Sparrow (*Ammodramus savannarum*), and Long-billed Curlew (*Numenius americanus*) (Knick and Rotenberry 2002). Grasshopper and Vesper sparrows are associated with perennial bunchgrass cover (Janes 1983, Vander Haegen et al. 2000). Long-billed Curlews and Burrowing Owls are generally associated with shorter stature grasslands in open habitats (Green and Anthony 1989, Pampush and Anthony 1993).

Patterns of distribution and bird diversity are dictated in part by structural and floristic characteristics of vegetation at a local scale (Rotenberry 1985) and sagebrush habitats generally support fewer bird species than other more diverse habitats (Rotenberry 1998). Species diversity increases when sagebrush habitats form a shrub-grassland mosaic. Avian diversity further increases when tree components, such as pinyon-juniper woodlands, form part of the mosaic (Medin et al. 2000). However, as dominance by trees increases, the shrub layer and often the herbaceous components decrease (Miller et al. 2000) and result in a decrease in avian abundance and diversity (Medin et al. 2000).

Bird assemblages in presettlement sagebrush-dominated sites near the end of a fire cycle likely were dominated by the sagebrush obligate species. Grassland species, such as Vesper and Grasshopper sparrows, Western Meadowlarks, and Horned Larks would increase following a fire as a function of shrub removal. Songbird species obligate to sagebrush habitats may not respond immediately to landscapes in which <50% of original shrub canopy cover is reduced (Petersen and Best 1987). However, larger, high severity burns like those in Wyoming big sagebrush-bunchgrass communities in which shrub removal is more complete likely resulted in reductions in these birds that use sagebrush, and even rendered blocks of habitat unsuitable for years until shrubs reestablished. In relatively mesic plant communities in the mountain big sagebrush cover type where mean fire-return intervals were <20 yr, burns also probably were spatially complex due to their low severity. Increased fire occurrence in this cover type usually resulted in more but smaller fires (Miller and Rose 1999).

Recent large-scale conversion of shrublands to expanses of annual grasslands is contributing to a reduced structural complexity in the plant community and a corresponding decrease in bird community diversity. At the other extreme, high densities of sagebrush or pinyon and juniper and depleted herbaceous understories caused by livestock grazing and fire suppression have simplified these systems and do not provide suitable habitat for grassland species. Thus, the relatively low diversity in native shrubsteppe systems has been reduced and habitats and avian communities further homogenized.

DISRUPTIONS TO NATURAL FIRE REGIMES IN SAGEBRUSH COMMUNITIES

Livestock Grazing

Livestock grazing over the past 140 yr is the single most important influence that has changed sagebrush habitats and influenced fire regimes throughout the Intermountain West (Robertson 1954, Bock et al. 1993, West and Young 2000). Livestock grazing can increase the frequency of fires by disturbing soils and reducing competition from native grasses to facilitate spread of the highly flammable cheatgrass (Shaw et al. 1999). In mesic sagebrush communities not favorable to cheatgrass, grazing by livestock on perennial grasses and forbs reduced the fine fuels available to spread fires across a landscape and increased the interval between fires (Miller and Rose 1999, Miller and Tausch 2001). Excessive grazing of herbaceous components in these systems increases shrub density and cover. In south central Oregon, the role of fire was greatly reduced after 1870, just after the introduction of large numbers of livestock, but 46 yr before organized fire suppression (Miller and Rose 1999). Active fire suppression (especially after the 1940s) and a reduction in human ignition furthered the reduction in fires (Miller and Rose 1999). Finally, management of sagebrush landscapes has been directed primarily toward increasing forage biomass and conditions for livestock grazing. Prescribed fires have been used to eradicate sagebrush (Vale 1974, Braun et al. 1976) and large areas replanted to nonnative perennial grasses, such as crested wheatgrass (*Agropyron cristatum*) (Hull 1974, Evans and Young 1978, Young 1994). However, shrub eradication also may increase the susceptibility of the area to weed invasions and increased risk to subsequent fires.

ENCROACHMENT BY JUNIPER AND PINYON PINE WOODLANDS

Communities dominated by juniper (*Juniperus* sp.) and pinyon (*Pinus* sp.) woodlands further disrupt natural fire regimes because they become essentially fire-proofed and lengthen the time between fires (Miller and Tausch 2001). Sites that have transitioned from shrubsteppe to woodland may now burn only with severe weather conditions that create crown fires in tree-dominated communities. The consequences of burns also are much different than in historic times because those communities now may be converted to habitat sinks dominated by annual grasslands.

Juniper and pinyon species currently occupy over 30,000,000 ha in the Intermountain West. Prior to European settlement, pinyon-juniper woodlands were estimated to have occupied less than 3,000,000 ha (Gedney et al. 1999). While these woodlands have fluctuated historically in extent (Tausch 1999), the post-settlement expansion is unprecedented compared to those during the Holocene (Miller and Wigand 1994). The increase in juniper and pinyon woodlands are primarily a result of livestock grazing that reduced the grass and forb fuels coupled with a corresponding decrease in historical fire frequencies that killed fire-prone woodlands (Savage and Swetnam 1990, Miller and Rose 1999, Miller and Tausch 2001). Approximately 45 yr are required for a tree to reach 3 m in height; trees <3 m are easily killed by fires (Miller and Tausch 2001). Climate shifts also have played a role in the expansion of juniper and pinyon woodlands and increased atmospheric carbon dioxide may be accelerating rates of canopy expansion (Miller and Rose 1999, Miller and Tausch 2001).

NON-NATIVE PLANT INVASIONS

Cheatgrass

The introduction of cheatgrass to the arid portions of the sagebrush biome has fundamentally and perhaps irreversibly altered the natural fire regime by increasing the frequency and severity of fires (West 1979). Consequently, wildfires have caused extreme rates of fragmentation and loss of shrublands and now maintain the vast expanses of exotic annual grasslands by short fire-return intervals (Young and Evans 1973, Peters and Bunting 1994). Fire frequencies reduced from 30 to >100 yr between fire events to as low as 5–15 yr in parts of the Snake River Plains (Whisenant 1990) have altered significantly not only current habitats but also the future dynamics of these systems (Knick and Rotenberry 1997, Knick 1999). Many Wyoming big sagebrush communities in more arid regions at low elevations now exist in an grassland state from which recovery to a shrubland landscape may not be possible (Westoby 1981, Laycock 1991, Allen-Diaz and Bartolome 1998, West and Young 2000).

Cheatgrass was well established throughout much of its current distribution in the Intermountain West by 1930 (Stewart and Hull 1949, Piemeisel 1951, Klemmedson and Smith 1964, Mack 1981). However, cheatgrass has rapidly increased its dominance in native plant communities in the past 30 yr (Monsen 1994). Although cheatgrass can colonize regions in the absence of fire (d'Antonio 2000), the combination of fire, livestock grazing, habitat management practices, other disturbances, and climate conditions have most rapidly facilitated the heavy dominance by cheatgrass in sagebrush systems (d'Antonio and Vitousek 1992, Young 1994). Cheatgrass now dominates the understory in many sagebrush ecosystems and an estimated 25% of the original sagebrush steppe has been converted to annual grasslands (West 2000).

Cheatgrass colonizes and dominates a system through a variety of mechanisms by which it out competes native plants for resources and promotes a self-sustaining fire disturbance (Pyke and Novak 1994, Pyke 2000). Cheatgrass out competes native plants by germinating in the autumn, remaining dormant through winter, and putting on new growth during early spring. The shallow rooting system is especially adapted to capture available soil water and nutrients. Cheatgrass sets abundant seed annually and senesces earlier than native grasses which advances the onset of the fire season. The dense, continuous cover of cheatgrass compared to intermittent fuels provided by native bunchgrasses promotes fire spread resulting in the increase in fire frequency and larger, more complete, and less complex fire patterns.

OTHER NON-NATIVE PLANT INVADERS

We have focused on cheatgrass in this review because of its ability to change the form and function of entire landscapes. Other exotic plants that may invade independently of or subsequent to cheatgrass domination (Shaw et al. 1999) include medusahead wildrye (*Taeniatherum asperum*), yellow star-thistle (*Centaurea solstitialis*) and other species of the genus *Centaurea*, halogeton (*Halogeton glomeratus*), rush skeleton-weed (*Chondrilla juncea*), and barbwire Russian thistle (*Salsola paulsenii*). The unfortunate reality is that we may not yet be at the bottom of the ecological barrel in the succession of sagebrush landscapes. Removing or controlling cheatgrass, such as by use of herbicides (Ogg 1994, Shaw and Monsen 2000), may only open the landscape to an increasingly undesirable plant community that is incompatible with birds dependent on sagebrush ecosystems.

USE OF PRESCRIBED FIRE IN SAGEBRUSH ECOSYSTEMS

The use of prescribed fire to manipulate habitats is one of the most common yet most contentious issues in management of sagebrush ecosystems (Miller and Eddleman 2001, U.S. Department of Interior 2002, Wambolt et al. 2002). Total area of prescribed burning by the U.S. Bureau of Land Management increased from 56,000 ha in 1995 to 861,094 ha in 2001 (National Interagency Fire Center 2003). Cost to conduct prescribed burns increased from $1,200,000 in 1996 to $10,600,000 in 1999. Objectives for prescribed burning include (1) control of annual grasses, (2) reduction of cover density of sagebrush, (3) promotion of grass and forb growth, and (4) control expansion of juniper and pinyon woodlands. Despite the increased amount of areas treated by prescribed fire, its use should be considered cautiously because subsequent restoration of sagebrush communities after burning is extremely difficult due to low and variable precipitation, competition for resources by exotic vegetation, disruption of nutrient cycles, and continued disturbance by grazing domestic livestock (Allen 1988, Meyer 1994, Roundy et al. 1995, McIver and Starr 2001). Therefore, use of prescribed burning to reduce density of sagebrush and promote grass and forb growth should be considered only in those sagebrush types, such as mountain big sagebrush landscapes, that have favorable precipitation and consequent resilience to disturbance. Although individual small burns (<10 ha) are recommended (USDI 2002), the high cost of conducting small projects may be prohibitive.

Prescribed burning may reduce cheatgrass on a short-term basis but original densities can return within 2 yr from seeds remaining in the seed bank (Pyke 1994). Timing of prescribed burns to control cheatgrass is critical. Prescribed fires during the period of seed maturation can reduce the densities of cheatgrass. However, fires conducted after seed dispersal have little effect and may increase future dominance of exotic plants because of nitrogen released during the burn (Stubbs 2000, Brooks and Pyke 2001). Prescribed burning also may facilitate invasion by an additional suite of noxious weeds. We conclude that fires, including prescribed burns in more xeric landscapes dominated by Wyoming and basin big sagebrush, likely will have the unintended consequence of stimulating cheatgrass production and dominance (Bunting et al. 1987).

THE EFFECT OF FIRE ON BIRDS IN SAGEBRUSH HABITATS

Very little information has been published on bird response to fire in sagebrush environments. Our search of the primary literature revealed few published papers that examined direct effects of a particular fire event, although several additional papers evaluated the longer-term effect of fires at a landscape scale (Table 1). With few exceptions, studies of a particular fire event examined short-term responses in abundance, as opposed to the response of demographic parameters such as productivity and survival. Few studies used before and after treatment designs with controls (Petersen and Best 1999). Such studies examining short-term responses to fire have serious limitations (Rotenberry et al. 1995, Petersen and Best 1999). Chief among them is that shrubsteppe songbirds may respond slowly to environmental disturbances (Best 1972, Castrale 1982, Wiens and Rotenberry 1985, Wiens et al. 1986) and the observed short-term response may not accurately portray long-term effects (Petersen and Best 1999, Knick and Rotenberry 2000).

Effects of Fire

Birds that use sagebrush as their primary habitat declined dramatically in landscapes where shrub removal was complete and at large scales (Bock and Bock 1987, Knick and Rotenberry 1995, Knick and Rotenberry 1999). Loggerhead Shrikes, which also rely on shrublands for nesting habitat, were reduced by approximately 50% following a large mosaic burn in a basin and Wyoming sagebrush community (Humple and Holmes, unpubl. data). Because extensive, high-severity fires are increasing in frequency in lower elevation xeric communities, substantial expanses of habitat unsuitable for shrub dependent species are created until shrubs reinvade and establish appropriate cover. In unaltered systems this process can take decades (Hemstrom et al. 2002). When sagebrush re-establishment is precluded either by recurring wildfire or by lack of seed sources within the burned area, habitat loss for birds depending on sagebrush habitats may be permanent.

Numbers of songbird species obligate to sagebrush ecosystems were not greatly reduced over the short term with partial removal (<50%) of sagebrush (Best 1972, Petersen and Best 1987, Petersen and Best 1999). Although approximately 50% of the sagebrush cover was removed, a patchy distribution of sagebrush remained at a larger scale in the landscape and continued to provide the habitat structure and components used by nesting birds.

Numbers of Horned Larks and Vesper Sparrows increased or remained unchanged following fire (Table 1). Similar responses by these species (as well as decreases in one or more sagebrush obligate species) have resulted when shrubs were removed through mechanical clearing or herbicide (Best 1972, Schroeder and Sturges 1975, Wiens and Rotenberry 1985).

Abundance of Western Meadowlarks or Grasshopper Sparrows did not change in response to burns (Table 1), although their habitat associations suggest that they should benefit from increases in the cover of grasses. Western Meadowlarks had greater probabilities of occurrence in regions where landscape measures of shrub cover were lower because of frequent and recurring wildfires (Knick and Rotenberry 1999).

Burning could improve habitat for Long-billed Curlews by removing shrubs and creating a more open habitat (Pampush and Anthony 1993). In the year following a fall range fire, breeding density of Long-billed Curlews increased 30% at a site in western Idaho (Redmond and Jenni 1986). Burrowing Owls have colonized recently burned areas (Green and Anthony 1989), but this may have been due to combined changes in habitat structure and prey populations. Long-term population increases for Long-billed Curlews and Burrowing Owls, determined from Breeding Bird Surveys (Sauer et al. 2001), suggest populations of these species may be benefiting from conversion of sagebrush habitats to more open annual grasslands in the Columbia Plateau.

Only one study (Petersen and Best 1987) examined how fire influenced reproductive success of songbirds. Nestling growth or reproductive output for either Sage Sparrow or Brewer's Sparrow was unchanged in 3 yr following a fire that removed approximately 45% of the shrubs (Petersen and Best 1987). The lack of measurable short-term responses in this and other studies of the effects of disturbance

TABLE 1. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSE OF BREEDING BIRDS TO FIRE IN SAGEBRUSH HABITATS OF NORTH AMERICA. LITERATURE ON THE RESPONSE OF GREATER SAGE-GROUSE IS SUMMARIZED IN TABLE 2. NP INDICATES THAT THE INFORMATION WAS NOT PROVIDED.

Species	State	Years after fire	Size (ha) and No. of fires[a]	Fire Type[b]	No. of replicate sites	Response[c]	Reference[d]	Comments
Long-billed Curlew (*Numenius americanus*)	ID	1	142	w	1	+	1	
Mourning Dove (*Zenaida macroura*)	OR, ID, UT, WY, MT	np	np	np	13	–	2	Occurred on 8% of burned transects; 69% of adjacent unburned transects.
Gray Flycatcher (*Empidonax wrightii*)	NV	1–2	15,000	w	12	–	3	
Horned Lark (*Eremophila alpestris*)	ID	1–3	np	p	4	+	4	About 45% burned in mosaic.
	UT	3–4	np	p	2	+	5	Compared one burned to one unburned seeding.
	NV	1–2	15,000	w	12	+	3	
	OR, ID, UT, WY, MT	np	np	np	13	0	2	Greater numbers of detections on burned transects; not statistically significant.
	OR	<5	np	np	8	0	6	Higher density in unburned; not statistically significant.
Sage Thrasher (*Oreoscoptes montanus*)	ID	1–7	np	p	4	+	4	Densities higher 2–7 yr postfire; significant in year 4; 45% of treatment plots burned.
	UT	3–4	np	p	2	0	5	Compared one burned to one unburned seeding.
	NV	1–2	15,000	w	12	–	3	
	OR, ID, UT, WY, MT	np	np	np	13	–	2	Not detected on burned transects and 54% of adjacent unburned transects.
Green-tailed Towhee (*Pipilo chlorurus*)	NV	1–2	15,000	w	12	0	3	
Brewer's Sparrow (*Spizella breweri*)	ID	1–7	np	p	4	m	4	Reduction in density 1–2 yr postfire; pre-fire densities in 3–7 yr; 45% of treatment plots burned.
	MT	2–3	220	w	2	–	7	One burned and one unburned site; 100% sagebrush mortality.
	UT	3–4	np	p	2	–	5	One burned and one unburned seeding.
	NV	1–2	15,000	w	12	–	3	
	OR, ID, UT, WY, MT	np	np	np	13	–	2	Not detected on burned transects; occurred on 92% of adjacent unburned transects.
	OR	<5	np	np	8	–	6	Density 75% lower at burned sites.
	ID	>5	np	w	119	–	8	Probability of occurrence reduced in landscapes with shrub loss due to wildfire.
Vesper Sparrow (*Pooecetes gramineus*)	ID	1–7	np	p	4	+	4	Colonized burned plots 3 yr postfire; 45% of treatment plots burned.
	UT	3–4	np	p	2	0	5	One burned and one unburned seeding.

TABLE 1. CONTINUED.

Species	State	Years after fire	Size (ha) and No. of fires[a]	Fire Type[b]	No. of replicate sites	Response[c]	Reference[d]	Comments
Vesper Sparrow	NV	1–2	15,000	w	12	+	3	
(*Pooecetes gramineus*)	OR, ID, UT, WY, MT	np	np	np	13	0	2	Greater numbers of detections in unburned; not statistically significant.
	OR	<5	np	np	8	+	6	
Lark Sparrow (*Chondestes grammacus*)	MT	2–3	220	w	2	–	7	One burned and one unburned site; 100% sagebrush mortality.
	OR, ID, UT, WY, MT	np	np	np	13	0	2	Not detected on burned transects; occurred on 15% of adjacent unburned transects.
Sage Sparrow	ID	1–7	np	p	4	0	4	45% of treatment plots burned.
(*Amphispiza belli*)	ID	3–21	np	w	164	–	8	Examined cumulative effect of multiple wildfires.
	NV	1–2	15,000	w	12	–	3	
	OR, ID, UT, WY, MT	np	np	np	13	–	2	Absent on burned transects; occurred on 85% of adjacent unburned transects.
	OR	<5	np	np	8	–	6	Density 90% lower in burns.
Grasshopper Sparrow (*Ammodramus savannarum*)	MT	2–3	220	w	2	–	7	
Western Meadowlark	MT	2–3	220	w	2	0	7	
(*Sturnella neglecta*)	UT	3–4	np	p	2	0	5	One burned and one unburned seeding.
	NV	1–2	15,000	w	12	m	3	Difference observed only year one postfire.
	ID	1–7	np	p	4	0	4	45% of treatment plots burned.
	OR	<5	np	np	8	+	6	
	ID	>5	np	w	119	+	8	Probability of occurrence greater in landscapes with less shrub cover due to recurring wildfire.
	OR, ID, UT, WY, MT	np	np	np	13	–	2	Mean number of detections on burned less than half that of unburned.

[a] Number of fires reported for each study = 1.

[b] + = increase; - = decrease; 0 = no effect or study inconclusive; m = mixed response.

[c] w = wildland fire; p = prescribed fire; np = type of fire not provided in source.

[d] References: 1 = Redmond and Jenni 1986; 2 = Welch 2002; 3 = McIntyre 2002; 4 = Petersen and Best 1987; 5 = Castrale 1982; 6 = Reinkensmeyer 2000; 7 = Bock and Bock 1987; 8 = Knick and Rotenberry 1999.

on shrubland birds may be in part attributable to time lags on individual and population responses stemming at least in part from site tenacity by breeding adults (Wiens et al. 1986, Knick and Rotenberry 2000).

Effects of Fire Suppression

The expansion of juniper and pinyon woodlands in regions where fire has been suppressed has changed habitat structure and composition of associated bird assemblages. Woodland species, including Ash-throated Flycatcher (*Myiarchus cinerascens*), Pinyon Jay (*Gymnorhinus cyanocephalus*), American Robin (*Turdus migratorius*), Mountain Bluebird (*Sialia currocoides*), Juniper Titmouse (*Baeolophus ridgwayi*), and Western Kingbird (*Tyrannus verticalis*), among others, colonize shrubsteppe habitat once sufficient woodland structure is provided (Medin et al. 2000). Brown-headed cowbirds (*Molothrus ater*) also increased in communities having juniper woodlands (Rienkensmeyer 2000, Noson 2002). Shrub cover consistently declined in big sagebrush communities when juniper increased (Tausch and West 1995, Miller et al. 2000). Herbaceous vegetation also declined where restrictive soil layers were present (Miller et al. 2000). Loss of structural complexity in the shrub and herbaceous layers as a result of woodland development negatively affects many wildlife species. Shrub and ground nesting birds declined as a function of increasing western juniper density (Fig. 3). Brewer's Sparrows had lower nest survival in areas of increased tree density (Welstead 2002) and abundance decreased as a function of proximity to woodland edge (Sedgewick 1987). Thus, reduced use of habitat in or near woodlands may stem in part from avoidance of nest predators.

SAGE-GROUSE AND FIRE

Fire has been promoted widely as a tool to improve habitat quality for nesting and brood-rearing in sage-grouse (Wambolt et al. 2002). The primary management objective by using fire is to achieve or maintain a balance of shrubs, forbs, and grasses, at various scales throughout the landscape. In mountain big sagebrush, burns may be conducted to limit the expansion of fire-prone juniper and pinyon to reduce potential perches for raptors and to limit the conversion of shrub steppe habitats. The outcomes of fire on sage-grouse habitat may be a function of site potential, site condition, functional plant groups, and pattern and size of burn (Miller and Eddleman 2001).

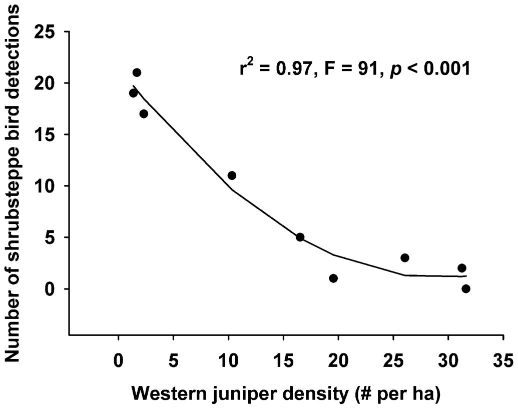

FIGURE 3. Abundance of ground and shrub nesting bird species in relation to density of western juniper trees >8 cm diameter at breast height in Lassen County, California 2002 (Point Reyes Bird Observatory, unpubl. data). Data points represent total number of observations within 100 m at four point count stations, sampled twice each year, within each study area.

Direct evidence that prescribed fires have benefited sage-grouse is virtually non-existent (Table 2). A short-term increase in forb production occurs after some fires (Harniss and Murray 1973; Martin 1990; Pyle and Crawford 1996) but not others (Fischer et al. 1996; Nelle et al. 2000). Forb response following a fire is a function not only of pre-burn site condition but also precipitation patterns. Because recovery of sagebrush canopy cover to pre-burn levels may require 20 yr or longer, short-term benefits of increased forb production may not balance the loss of sagebrush canopy requisite for nesting by sage-grouse (Fischer et al. 1996, Nelle et al. 2000).

Declines in lek attendance by Greater Sage-Grouse and rates of lek extinction during the 5 yr after a fire were greater in a Wyoming big sagebrush community where 57% of the habitat was affected by a prescribed fire compared to the surrounding regions (Connelly et al. 2000). Dramatic declines in populations of Greater Sage-Grouse were correlated with habitat losses from a 2,000% increase in fire incidence in Idaho and subsequent conversion of Wyoming big sagebrush communities to cheatgrass habitats (Crowley and Connelly 1996). Therefore, the usefulness of prescribed fire for sage-grouse in arid sagebrush communities probably is very limited.

Negative impacts from fire exist even in the more resilient mountain big sagebrush communities. For both nesting and brood rearing, Greater Sage-Grouse avoided burns that were <20 yr old and lacked

TABLE 2. RESPONSE BY SAGE GROUSE AND IMPORTANT BROOD REARING HABITAT FEATURES TO FIRE IN SAGEBRUSH HABITATS.

Response variable	State	Dominant sagebrush type	Years post burn	Response[a]	Reference
Rate of lek loss	ID	Wyoming	1–5	–	Connelly et al. 2000
Lek attendance	ID	Wyoming	1–5	–	Connely et al. 2000
Nesting use	ID	Wyoming	1–2	0	Martin 1990
	OR	Various	1–60	–	Byrne 2002
Brood rearing use	OR	Various	1–60	–	Byrne 2002
Movement patterns	ID	Wyoming	1–3	0	Fischer et al. 1997
Forb cover	ID	Wyoming	1–3	0	Fischer et al. 1996
	ID	Mountain	>10	0	Nelle et al. 2000
	ID	Mountain	1–2	+	Martin 1990
	OR	Mountain	1–2	+	Pyle and Crawford 1996
Insect abundance	OR	Mountain	1–2	0	Pyle and Crawford 1996
	ID	Wyoming	1–3	–	Fischer et al. 1996
	ID	Mountain	>10	0	Nelle et al. 2000

[a] + = increase; – = decrease; 0 = no effect or study inconclusive

sagebrush cover (Byrne 2002). In landscapes with a short fire-return interval, unburned areas played an important role in population maintenance.

Although sage-grouse evolved in an ecosystem where fire was an important disturbance factor, fire-return intervals have been lengthened in mountain big sagebrush and shortened in Wyoming sagebrush. Decisions to use or suppress fire for managing habitat for sage-grouse must be made with extreme caution and on a site-by-site basis.

CRITICAL MANAGEMENT QUESTIONS AND RESEARCH ISSUES

Successional dynamics in sagebrush ecosystems are described by state-and-transition models of alternative pathways and thresholds (Westoby 1981, Laycock 1991, Allen-Diaz and Bartolome 1998, West and Young 2000). We need to identify environmental factors, such as plant association, current condition, soil type, elevation, and climate that facilitate transition into undesirable states following fire disturbance. We then need to map those regions that have a high risk of displacement of sagebrush by cheatgrass or that are at risk of pinyon-juniper expansion. Identification of those environmental factors and corresponding maps of risk assessment would greatly assist land managers in understanding the potential effect of fire in sagebrush communities. This information could be used by agencies to prioritize areas for prescribed burning, fire suppression, and rehabilitation activities.

Sagebrush is one of the few habitats in which large areas of planned burning occurs every year, thus presenting an opportunity to conduct experiments absent in most other areas of North America. Therefore, planned burns provide an opportunity to determine the influence of fire disturbance on sagebrush ecosystems. Study designs that include control sites can be used to identify pre- and postfire dynamics and to determine causal relationships between birds and habitats. Although most prescribed fires are site-specific, larger-scale objectives also are possible because managers use multiple burns to manipulate landscapes at the large spatial extents used by birds such as sage-grouse (Hann and Bunnell 2001, Morgan et al. 2001). Because distribution and abundance of birds in sagebrush communities is based on a complex process of selection for habitat features (Wiens et al. 1987, Rotenberry and Knick 1999, Knick and Rotenberry 2002), we recommend large-scale (>100,000 ha) and long-term (>10 yr) designs to adequately understand the mechanisms by which birds respond to fire and plant community succession in sagebrush habitats.

We emphasize that demographic parameters such as productivity and survival are a critical component in elucidating the mechanisms by which populations respond to habitat changes due to fire. Except for measures of nest success, no studies have determined the effects of fire on productivity per unit area or age-structured survivorship of birds in sagebrush habitats. Development of demographic models (Caswell 2001) can provide the mechanisms of population response to habitat disturbance but requires the commitment of large-scale and long-term research and funding.

SUMMARY

Fire was a spatially and temporally complex disturbance in the sagebrush biome ranging from 10 to

>200-yr return intervals with varying severities in communities dominated by sagebrush and may have been >500 yr in some salt-desert shrub communities. The frequency of fires that completely burn large areas has increased dramatically in some regions, particularly in Wyoming big sagebrush communities at low elevations containing a cheatgrass understory. In other regions, widespread reductions in fire frequency and extent followed the introduction of livestock to western rangelands and resulted in increased shrub cover, loss of herbaceous understory, and increasing rates of woodland encroachment. Populations of bird species that use sagebrush as their primary habitat declined either from conversion of sagebrush landscapes to cheatgrass dominated grasslands or to increases in woodland cover. We expect that populations of grassland birds, including Long-billed Curlews, Horned Larks, and Burrowing Owls, will increase with greater proportions of grasslands in the landscape. Similarly, increases in pinyon and juniper should benefit populations of bird species associated woodlands.

ACKNOWLEDGMENTS

Cara Meinke created the GIS map. We thank Diana Humple and Dan Barton for data collected in 2002. This is Point Reyes Bird Observatory contribution number 1149.

Studies in Avian Biology No. 30:76–96

VARIATION IN FIRE REGIMES OF THE ROCKY MOUNTAINS: IMPLICATIONS FOR AVIAN COMMUNITIES AND FIRE MANAGEMENT

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Abstract. Information about avian responses to fire in the U.S. Rocky Mountains is based solely on studies of crown fires. However, fire management in this region is based primarily on studies of low-elevation ponderosa pine (*Pinus ponderosa*) forests maintained largely by frequent understory fires. In contrast to both of these trends, most Rocky Mountain forests are subject to mixed severity fire regimes. As a result, our knowledge of bird responses to fire in the region is incomplete and skewed toward ponderosa pine forests. Research in recent large wildfires across the Rocky Mountains indicates that large burns support diverse avifauna. In the absence of controlled studies of bird responses to fire, we compared reproductive success for six cavity-nesting species using results from studies in burned and unburned habitats. Birds in ponderosa pine forests burned by stand-replacement fire tended to have higher nest success than individuals of the same species in unburned habitats, but unburned areas are needed to serve species dependent upon live woody vegetation, especially foliage gleaners. Over the last century, fire suppression, livestock grazing, and logging altered the structure and composition of many low-elevation forests, leading to larger and more severe burns. In higher elevation forests, changes have been less marked. Traditional low-severity prescribed fire is not likely to replicate historical conditions in these mixed or high-severity fire regimes, which include many mixed coniferous forests and all lodgepole pine (*Pinus contorta*) and spruce-fir (*Picea-Abies*) forests. We suggest four research priorities: (1) the effects of fire severity and patch size on species' responses to fire, (2) the possibility that postfire forests are ephemeral sources for some bird species, (3) the effect of salvage logging prescriptions on bird communities, and (4) experiments that illustrate bird responses to prescribed fire and other forest restoration methods. This research is urgent if we are to develop fire management strategies that reduce fire risk and maintain habitat for avifauna and other wildlife of the Rocky Mountains.

Key Words: coniferous forests, fire management, fire regimes, passerine birds, U.S. Rocky Mountains, woodpeckers.

VARIACIÓN EN REGÍMENES DEL FUEGO EN LAS ROCALLOSAS: IMPLICACIONES PARA COMUNIDADES DE AVES Y MANEJO DEL FUEGO

Resumen. La información respecto a las respuestas de las aves al fuego en las Rocallosas de los Estados Unidos, está basado únicamente en estudios de incendios de copa. Sin embargo, el manejo de incendios en esta región esta basada primordialmente en estudios de bosques de pino ponderosa (*Pinus ponderosa*) de baja elevación, los cuales se mantienen primordialmente con incendios en la primera capa vegetativa. En contraste a ambas tendencias, la mayoría de los bosques de las Rocallosas están sujetas a regimenes mixtos de severidad de incendios. Como resultado, nuestro conocimiento de las respuestas de las aves a los incendios en la región es incompleta y dirigida hacia los bosques de pino ponderosa. Recientes investigaciones de grandes incendios en las Rocallosas, indican que grandes incendios ayudan a la avifauna. En la ausencia de estudios controlados en las respuestas de las aves al fuego, utilizando resultados de estudios en habitats incendiados y sin incendiar, comparamos el éxito reproductivo de seis especies que anidan en cavidades. Aves en bosques de pino ponderosa quemado por incendios de reemplazo, tienden a obtener un mayor éxito de anidación que los individuos de la misma especie en habitats sin quemar, pero se necesitan áreas sin quemar, que sirvan a especies dependientes de vegetación forestal viva, especialmente de follaje espigado. Desde el último siglo, la supresión de incendios, el pastoreo y los aprovechamientos forestales han alterado la estructura y composición de varios bosques de baja elevación, llevándolos a incendios mayores y severos. En bosques con mayor elevación, los cambios han sido menos marcados. Es muy poco probable replicar condiciones históricas en estos regimenes mixtos y de alta severidad con quemas prescritas tradicionales de baja severidad , las cuales incluyen varios bosques de coníferas y todos los bosques de pino (*Pinus contorta*) y de abeto (*Picea-Abies*). Sugerimos cuatro prioridades de investigación: (1) efectos de la severidad del incendio y tamaño del parche, en las respuestas de la especie al fuego, (2) la posibilidad de que bosques después de un incendio sean fuentes efímeras para algunas especies de aves, (3) los efectos de incendios prescritos en aprovechamientos forestales de salvamento en comunidades de aves, y (4) experimentos que ilustren respuestas de aves a incendios preescritos y otros métodos de restauración forestal. Esta investigación es urgente si queremos desarrollar estrategias de manejo del fuego, las cuales reduzcan el riesgo de incendios y mantengan el habitat para la avifauna y otras especies silvestres de las Rocallosas.

Forest landscapes of the U.S. Rocky Mountains are structured by a complex interplay of climate, topography, soils, and disturbance (Peet 2000, Schoennagel et al. 2004). They are shifting mosaics whose vegetation reflects variation in disturbance frequency, severity, and time since disturbance, which ranges from years to centuries (Peet 2000). Many of these fire regimes have been altered since Euro-American settlement due to fire suppression, logging, livestock grazing, and, in some cases, climate change (Veblen 2000, Allen et al. 2002, Schoennagel et al. 2004). After decades of fire suppression, elevated fuel loads in many forests have increased the likelihood of unusually large and severe fires (Arno and Brown 1991, Covington and Moore 1994), and the yearly area burned has increased (Grissino-Mayer and Swetnam 2000, Keane et al. 2002).

Severe wildfire seasons in 2000 and 2002 (collectively, 6,800,000 ha burned) focused public attention on the risks posed by fuel accumulations (Graham et al. 2004), and served as an impetus for the National Fire Plan (USDA 2000) and the Healthy Forests Initiative (White House 2002). This initiative was passed into law as HR1904, the Healthy Forests Restoration Act of 2003. A primary goal of these federal programs is to diminish the risk of severe wildland fire by reducing fuel loads and restoring historical forest structure and fire regimes. Prescribed fire and mechanical treatments are increasingly being used to meet this goal.

An assumption driving the recent fire management initiatives is that by reproducing the range of forest conditions and fire regimes that characterized a specific location and time period, we will provide the myriad ecological conditions that a diverse array of species require (e.g., Covington et al. 1997, Keane et al. 2002, Graham et al. 2004). However, the ecological paradigm underlying recent fire management policies in many Rocky Mountain forests, namely frequent understory fires and open forest structures (Covington and Moore 1994, Swetnam et al. 1999, Allen et al. 2002), was developed primarily from experience in ponderosa pine forests of the American Southwest (see Ehle and Baker 2003, Schoennagel et al. 2004). Recent evidence, however, suggests that historical fire regimes and forest structures of ponderosa pine forests were considerably more variable than suggested by the southwest paradigm (Brown and Sieg 1996, Shinneman and Baker 1997, Brown et al. 1999, Veblen et al. 2000). Thus, Rocky Mountain species associated with crown-burned forests, such as Lewis's Woodpeckers (*Melanerpes lewis*) and Black-backed Woodpeckers (*Picoides arcticus*), may be negatively affected by the southwest paradigm's emphasis on understory fire (Dixon and Saab 2000, Saab and Vierling 2001).

Managers who oversee Rocky Mountain forests require a fuller understanding of the variability inherent in the region's fire regimes, as well as the responses of its avifauna along such range of variation. In this paper, we summarize these topics. First, we review current knowledge about historical fire regimes for five dominant forest types. We discuss the degree to which fire regimes have been altered since Euro-American settlement. For each forest type, we summarize studies that have investigated the response of birds to wildfires and fire exclusion. Finally, we discuss the implications of forest restoration and fire management programs for avian communities of the Rocky Mountains.

ROCKY MOUNTAIN FORESTS

For purposes of this review, we define the U.S. Rocky Mountain region as the area from northern Montana and Idaho southward across the interior West, through Wyoming and Colorado to northern New Mexico (Fig. 1). Our definitions and descriptions of major vegetation types of the Rocky Mountains are taken largely from Peet (2000) and Arno (2000).

We describe five major vegetation types in this review: (1) pinyon-juniper (*Pinus-Juniperus*) woodland, (2) ponderosa pine forest, (3) mixed-coniferous forest, (4) lodgepole pine forest, and (5) spruce-fir forest. These vegetation classifications are derived from gradients in elevation, moisture, substrate, and disturbance regime (Peet 2000).

For each vegetation type we describe the distribution, elevation, dominant plant species, and characteristic birds, including those identified as priority species by Partners in Flight (2004). We also describe fire regimes for each vegetation type prior to and after European settlement, alterations to fire regimes, and probable effects on birds.

Floristically, the Rocky Mountains can be divided into several regions, two within our area of interest: the southern Rocky Mountains, from southern Colorado to central Wyoming, and the central Rocky Mountains of central Wyoming to Jasper National Park, Canada (Peet 2000). Across these regions, forest vegetation ranges from low elevation, dry forests to high elevation, mesic forests with various fire regimes (Fig. 1, 2; Peet 2000, Schmidt et al. 2002). Forest cover types occur from 1,100–3,500 m (limits vary geographically), and annual precipitation ranges from 12–245 cm. We used current cover types

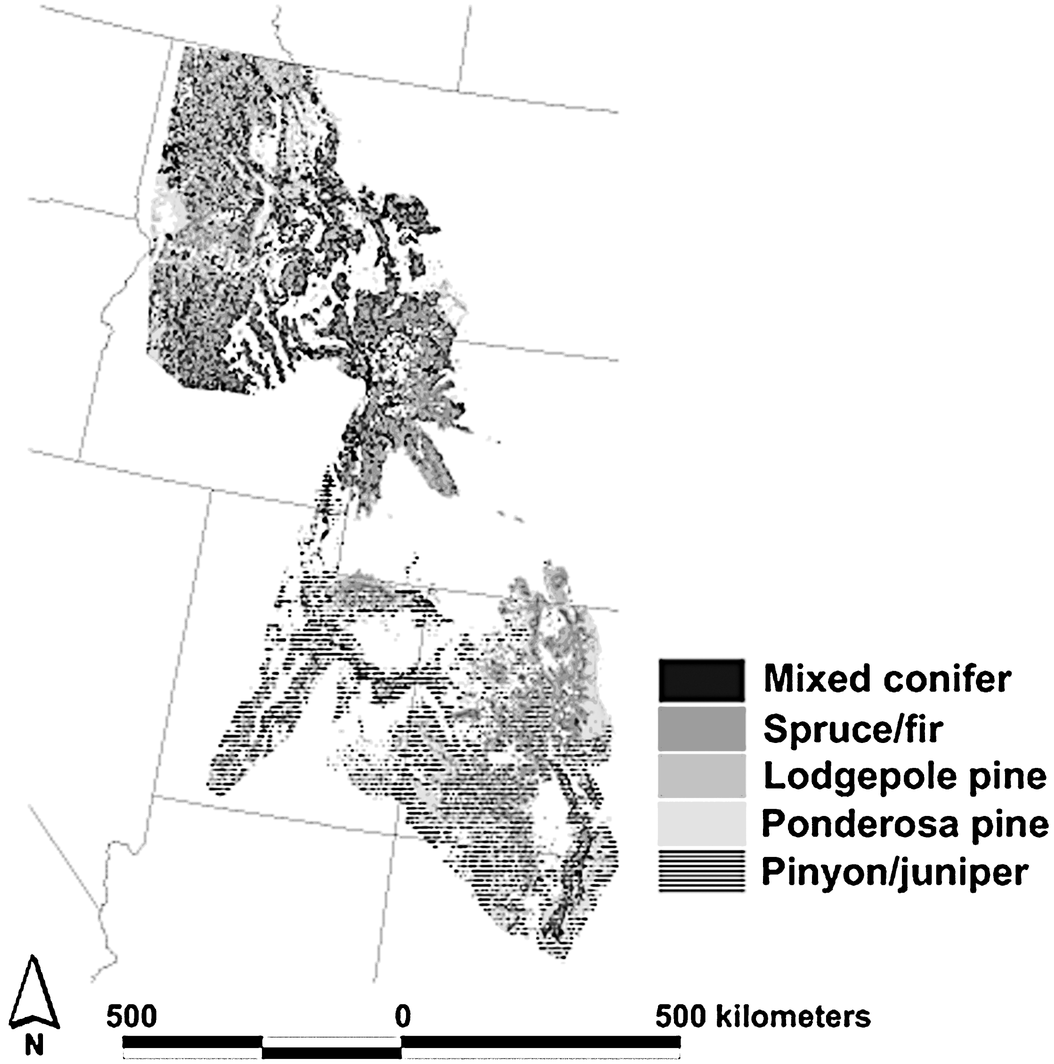

FIGURE 1. Map of current forest cover types in the U.S. Rocky Mountains (taken from Schmidt et al. 2002).

mapped by Schmidt et al. (2002) to estimate the area (in million ha) occupied by each of five major vegetation types within the U.S. Rocky Mountains: (1) pinyon-juniper woodland, 5.0; (2) ponderosa pine forest, 5.6; (3) mixed-coniferous forest, 8.7; (4) lodgepole pine forest, 9.7; and (5) spruce-fir forest, 5.0.

PINYON-JUNIPER WOODLANDS

Pinyon-juniper (pygmy) woodlands are most prevalent in the Madrean and southern Rocky Mountains (Peet 2000). West of the continental divide, pinyon-juniper woodlands extend northward into Idaho (Daubenmire 1943). Pinyon pine (*Pinus edulis*) occurs throughout the range; oneseed juniper (*Juniperus monosperma*) occurs on the eastern slope, whereas singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus. osteosperma*) share dominance with pinyon pine on the western slope (Daubenmire 1943). Rocky Mountain juniper (*Juniperus scopulorum*) is co-dominant with Utah juniper over much of the southern Rocky Mountains, and is frequent in the pinyon zone and adjacent lower reaches of ponderosa pine woodlands (Peet 2000). Stand densities tend to increase with moisture and elevation (Paysen et al. 2000).

The role of fire in these habitats remains poorly understood (Baker and Shinneman 2004). Frequent

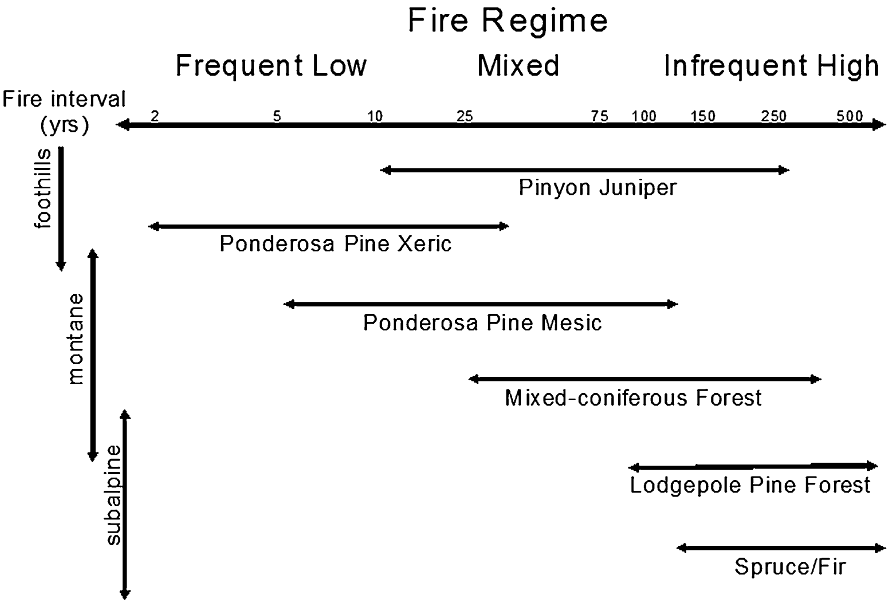

FIGURE 2. Range of variation in historical fire regimes for dominant forest types of the U.S. Rocky Mountains. Information for this graph was based largely on Arno (2000) and Schoennagel et al. (2004), and other sources referenced in the text by dominant forest type.

surface fires at intervals from 10 to <35 yr were considered prevalent in pinyon-juniper woodlands of the Rocky Mountains (e.g., Paysen et al. 2000). Recent evidence, however, suggests that natural fires in dense stands were infrequent and severe, occurring at intervals of 200–300 yr or longer (Floyd et al. 2000, Romme et al. 2003, Baker and Shinneman 2004). Frequent, low-severity fires were probably more common in the upper ecotone than in the closed woodland zone of pinyon-juniper forests (Baker and Shinneman 2004). A clear understanding of historical fire regimes at both local and landscape scales is sorely needed.

BIRDS OF PINYON-JUNIPER WOODLANDS

Characteristic birds of pinyon-juniper woodlands include Ferruginous Hawk (*Buteo regalis*), Gray Flycatcher (*Empidonax wrightii*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Gray Vireo (*Vireo vicinior*), Western Scrub-Jay (*Aphelocoma californica*), Pinyon Jay (*Gymnorhinus cyanocephalus*), Juniper Titmouse (*Baeolophus ridgwayi*), Bushtit (*Psaltriparus minimus*), Blue-gray Gnatcatcher (*Polioptila caerulea*), Black-throated Gray Warbler (*Dendroica nigrescens*), and Virginia's Warbler (*Vermivora virginiae*) (Balda and Masters 1980). Partners in Flight (2004) priority bird species for this habitat include Gray Flycatcher, Gray Vireo, Pinyon Jay, and Juniper Titmouse. Many of these species are pinyon-juniper obligates (e.g., Juniper Titmouse), and all of these species rely on pinyon-juniper as their primary breeding habitat.

BIRD RESPONSE TO FIRE IN PINYON-JUNIPER WOODLANDS

To our knowledge, no detailed information is available on avian response to fire in pinyon-juniper woodlands in the Rocky Mountains. Response of vegetation and birds to fire will likely depend upon prefire plant composition and successional stage (Miller and Tausch 2001). Depending on fire severity, the loss of cover for shrub and tree-nesting species such as Bushtit, Gray Flycatcher, and Black-throated Gray Warbler may initially result in a negative response by these species. Residual snags would likely provide nest sites for cavity-nesting species such as Western (*Sialia mexicana*) and Mountain Bluebirds (*Sialia currucoides*). Site-specific studies are needed to evaluate these possibilities given the range of variability in fire regimes that likely exists in this habitat.

National assessments suggest that many pinyon-juniper woodlands have missed one or more low-severity surface fires since Euro-American settlement (Baker and Shinneman 2004). For these reasons, low-severity, prescribed fire has been the focus of fire management in pinyon-juniper woodlands. This management emphasis may not be appropriate throughout these woodlands, and many of the pinyon-juniper forests were likely maintained by infrequent, high-severity fire (Baker and Shinneman 2004).

Disproportionate attention on low-severity surface fire, or treatments that create like conditions, could adversely affect avian species associated with mature pinyon-juniper woodlands (cf. Horton 1987, Sedgwick 1987). Nesting numbers of Virginia's Warblers declined after applications of prescribed fire in ponderosa pine woodlands, possibly due to removal of nesting sites in low shrubs and understory trees (Horton 1987). Prescribed fire treatments in pinyon-juniper woodlands could affect Virginia's Warblers in a similar manner. Abundance of Black-throated Gray Warblers decreased after mechanical chaining was used to reduce tree densities in pinyon-juniper woodlands (Sedgwick 1987). Treatments, including prescribed fire, that reduce tree densities and other fuels potentially decrease foraging opportunities for some bird species by removing litter and understory forbs.

PONDEROSA PINE FORESTS

Ponderosa pine spans the full extent of the Rocky Mountains, but considerable variation in stand structure and dynamics occurs across latitudes and elevations (Peet 2000, Schoennagel et al. 2004). Xeric ponderosa pine woodlands dominate montane forests of the southern Rocky Mountains and the lower montane zone of the central and northern Rocky Mountains (Peet 1981). Stand density is relatively low but is often higher in mesic areas with finely textured soils (Peet 1981, Arno 2000). In the upper montane zone and at more northern latitudes, mixed ponderosa pine and Douglas-fir (*Pseudotsuga menziesii*) forests are dominant; we treat these associations as mixed-coniferous forests (Schoennagel et al. 2004). Associated species include aspen (*Populus tremuloides*) in more mesic areas and limber pine (*Pinus flexilis*) along rocky outcrops (Daubenmire 1943, Peet 1981).

Frequent surfaces fires are characteristic of dry, warm woodlands and open-canopy forests, including low-elevation ponderosa pine (Schoennagel et al. 2004). Abundant grasses and forbs contribute to fire initiation and spread, allowing frequent fires. Crown fires are usually rare and small. Short fire intervals, generally 1–50 yr, help to maintain the open structure by killing understory trees and small patches of mature trees (Allen et al. 2002). Fire intervals tend to be shorter in southwestern ponderosa pine than along the Colorado Front Range and Black Hills of Wyoming (Shinneman and Baker 1997, Brown and Sieg 1999, Veblen et al. 2000, Ehle and Baker 2003).

Fire frequency tends to decrease, and severity increase, with increasing altitude and latitude (Veblen et al. 2000, Brown 2004). The most comprehensive fire histories in ponderosa pine are from the American Southwest and southern Rocky Mountains where prior to Euro-American settlement, frequent surface fires predominated (but see Baker and Ehle 2001 for alternative interpretation) and mean fire intervals were short (e.g., 4–36 yr; Swetnam and Baisan 1996). Much longer fire-free periods also have been observed (e.g., 76 yr; Swetnam and Baisan 1996). Longer mean fire-return intervals and fire-free periods are frequently reported in the central and northern Rocky Mountains (Arno et al. 1995, Brown and Sieg 1996, Shinneman and Baker 1997), although stands at grassland ecotones and at lower elevations typically burn more frequently (Barrett and Arno 1982, Brown and Sieg 1999, Veblen et al. 2000).

The historical fire regime in dry, low-elevation ponderosa pine forests has been altered substantially as a result of fire suppression, livestock grazing, and logging and their effects on historical fuel structure (Arno and Gruell 1983, Covington and Moore 1994, Swetnam and Baisan 1996, Veblen et al. 2000, Schoennagel et al. 2004). With reductions in grass fuel, fire intervals have lengthened, and dense stands have developed in which fine fuels are less abundant and ladder fuels carry fire to the canopy (Allen et al. 1998, Schoennagel et al. 2004). Consequently, high-severity fires can strike dry ponderosa pine forests, where historically they were rare. This pattern is well documented for ponderosa pine forests throughout the Rocky Mountain region, including Arizona and New Mexico (e.g., Allen et al. 1998, Moore et al. 1999), some sites in Colorado (e.g., Veblen and Lorenz 1991, Brown et al. 1999, Kaufmann et al. 2000), and portions of Montana (Gruell 1983, Arno et al. 1995).

Evidence of natural, mixed-severity fire regimes is found in some ponderosa pine forests (Mast et al. 1999, Kaufmann et al. 2000, Ehle and Baker 2003). Both surface and crown fires occurred historically in pure or nearly pure ponderosa pine forests of Montana (Arno and Petersen 1983, Arno et al. 1995), the Black Hills of South Dakota (Brown and Sieg

1996, Shinneman and Baker 1997, Brown 2004), and other locations in the Rocky Mountains (e.g., Gruell 1983, Mast et al. 1999, Brown et al. 1999, Ehle and Baker 2003). The relative importance of surface versus crown fires and the size of postfire patches in configuring forests of mixed-severity fire regimes remain uncertain and have likely varied spatially and temporally (Schoennagel et al. 2004).

BIRDS OF PONDEROSA PINE FORESTS

Over 100 bird species use ponderosa pine forests for some portion of their life history (Diem and Zeveloff 1980). Some characteristic species include Flammulated Owl (*Otus flammeolus*), Lewis's Woodpecker, White-headed Woodpecker (*Picoides albolarvatus*), Pygmy Nuthatch (*Sitta pygmaea*), Western Bluebird, and Cassin's Finch (*Carpodacus cassinii*). Partners in Flight priority bird species for ponderosa pine forests of the Rocky Mountains include Flammulated Owl, Lewis's Woodpecker, White-headed Woodpecker, Pygmy Nuthatch, and Cassin's Finch (Partners in Flight 2004). These species require large trees and snags or open canopy provided by this habitat.

BIRD RESPONSE TO FIRE IN PONDEROSA PINE FORESTS

Although avian responses to burned ponderosa pine forests have been studied in the southwestern U.S. (Bock and Block, *this volume*), no studies have examined the effect of fire on avian reproductive success by directly comparing burned and unburned ponderosa pine forests in the Rocky Mountains. To overcome the lack of controlled comparisons, we found reproductive success data for six cavity-nesting species studied in burned ponderosa pine forests in Idaho (2–5 yr postfire; Table 1): Lewis's, Hairy (*Picoides villosus*), Black-backed, and White-headed Woodpeckers, Northern Flicker (*Colaptes auratus*), and Western Bluebird. We then searched the literature for data on the same species nesting in natural cavities in unburned coniferous forests of the West, for comparison. Although many uncontrolled variables occur among these studies, we present the following summary as an exploratory effort in describing patterns of cavity-nesting bird response to fire in ponderosa pine forests.

The nest success values cited in Table 1 were calculated with the Mayfield method (Mayfield 1961) except where we note that apparent nest success was used. The method of apparent nest success contains a known positive bias (Jehle et al. 2004).

Overall, nest success appeared higher for the six species in burned habitats (median nest success = 81.5%, range 70–100%) than in unburned habitats (median = 69%, range 29–100%). Nest success was higher in burned than unburned habitats in 11 of the 14 possible species-by-species comparisons in Table 1, although in two of these 11 the differences were small (< 3%).

We found three interesting exceptions to the general trend of higher nest success in unburned forests. First, Hairy Woodpeckers and Northern Flickers in unburned mixed coniferous-aspen of the Mogollon Rim, Arizona, had essentially the same or greater nest success as individuals in burned ponderosa pine of Idaho (Table 1). The same species nesting in unburned ponderosa pine of Idaho had lower nest success by >20%. In Arizona, these two species nested extensively in aspen (Martin and Li 1992). Many cavity excavators select aspen trees at remarkably high rates compared to their availability (Hutto 1995, Martin et al. 2004); perhaps this tendency is related to high nest success in aspen.

Second, White-headed Woodpeckers had consistently high nest success (>80%) in both burned and unburned ponderosa pine forests of Idaho and Oregon. This species frequently nests in large dead trees but forages in live trees for pine seeds (Dixon 1995, Garrett et al. 1996). White-headed Woodpeckers may benefit from the mosaic of live and dead trees created by low and mixed severity fires.

Third, Western Bluebirds nesting in thinned (i.e., partial tree harvest) or prescribe-burned plots in ponderosa pine forests of Arizona nested with slightly higher success than in the stand-replacement-burned forests in Idaho (75% vs. 70%, respectively). Bluebirds nesting in unburned, untreated ponderosa pine in Arizona had success rates nearly half that recorded in burned ponderosa pine of Idaho (39% vs. 70%, respectively, Table 1). Most nest failures in the Arizona study were due to predation, and fewer potential nest predators were observed in the treated forests (Germaine and Germaine 2002). This comparison gives tentative evidence that prescribed burning and stand-replacement burns in ponderosa pine may result in similar conditions for Western Bluebirds.

A final observation from the nest success values in Table 1 concerns the relative effects of two disturbance types. Black-backed Woodpeckers in burned ponderosa pine had higher nest success than in unburned mixed coniferous forest undergoing a mountain pine beetle (*Dendroctonus ponderosae*) outbreak (87% vs. 69%, respectively, Table 1). This beetle outbreak killed most of the lodgepole pines on the study area and presumably resulted in

TABLE 1. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSES OF BREEDING BIRDS (CHANGE IN ABUNDANCE) TO WILDFIRE IN FORESTS OF THE ROCKY MOUNTAINS.

Species[a]	State	Year after fire	Size of fires (ha)	No. replicate sites[b]	Response[c]	Habitat/Reference[e]	Comments
Red-tailed Hawk	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Buteo jamaicensis*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	Density not estimated; observed in one burned site.
Osprey	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Pandion haliaetus*)	WY	2–5	235, 648	2 b, 2 u	0	Lodgepole and spruce-fir[3]	In burned/unburned forest edge at one site.
American Kestrel	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Falco sparverius*)	MT	1–4	120, 480	2 b, 3 u	+	Mixed coniferous[2]	
	MT	2–6	15,000	2 b, 1 u[g]	+	Lodgepole[4]	Both nest and bird abundance.
Blue Grouse	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Dendragapus obscurus*)	WY	2–5	235, 648	2 b, 2 u	0[d]	Lodgepole and spruce-fir[3]	
	WY	5–10	6, 83	2 b, 6 u	0[d]	Lodgepole[5]	In both burned and unburned sites.
Ruffed Grouse	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Bonasa umbellus*)	MT	1–4	120, 480	2 b, 3 u	0[d]	Mixed coniferous[2]	In both burned and unburned sites.
	WY	2–5	235, 648	2 b, 2 u	–	Lodgepole and spruce-fir[3]	
	WY	1–29[f]	40–1,414	6 b, 6 u	–[d]	Lodgepole and spruce-fir[6]	
Mourning Dove	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Zenaida macroura*)	MT	1–4	120, 480	2 b, 3 u	+	Mixed coniferous[2]	
	WY	5–10	6, 83	2 b, 6 u	0	Lodgepole[5]	In both burned and unburned clearcut forest.
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
Common Nighthawk	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Chordeiles minor*)	MT	1–4	120, 480	2 b, 3 u	+[d]	Mixed coniferous[2]	
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole[5]	1 yr postfire.
	WY	1–29[f]	40–1,414	6 b, 6 u	0[d]	Lodgepole and spruce-fir[6]	In 7 and 25 yr old burns.
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
Calliope Hummingbird	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Stellula calliope*)	MT	1–4	120, 480	2 b, 3 u	+[d]	Mixed coniferous[2]	
Rufous Hummingbird	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Selasphorus rufus*)	WY	2–5	235, 648	2 b, 2 u	0[d]	Lodgepole and spruce-fir[3]	In burned/unburned forest edge at one site.
Lewis's Woodpecker	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	In one burned site.
(*Melanerpes lewis*)	ID, CO	1–5	89,159; 12,467	2 b, 2 u	+	Ponderosa pine and cottonwood[8]	Comparison of reproductive success in burned coniferous vs. unburned cottonwood forests.
Williamson's Sapsucker	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Sphyrapicus thyroideus*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	In burned/unburned forest edge at one site.
	WY	2–5	235, 648	2 b, 2 u	–	Lodgepole and spruce-fir[3]	1 yr postfire.
	WY	1–29[f]	40–1,414	6 b, 6 u	0	Lodgepole and spruce-fir[6]	High densities recorded in 13 yr old burn.
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous[7]	

TABLE 1. CONTINUED.

Species[a]	State	Year after fire	Size of fires (ha)	No. replicate sites[b]	Response[c]	Habitat/Reference[e]	Comments
Red-naped Sapsucker	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Sphyrapicus nuchalis*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	Reported as Yellow-bellied Sapsucker (*Sphyrapicus varius*); in burned/unburned forest edge at one site.
	MT	2–6	15,000	2 b, 1 u[g]	–	Lodgepole[4]	Both nest and bird abundance.
	WY	1–29[f]	40–1,414	6 b, 6 u	0[d]	Lodgepole and spruce-fir[6]	Reported as Yellow-bellied Sapsucker (*Sphyrapicus varius*); in 43 yr old burn.
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
Downy Woodpecker	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Picoides pubescens*)	MT	1–4	120, 480	2 b, 3 u	0[d]	Mixed coniferous[2]	
	MT	2–6	15,000	2 b, 1 u[g]	+	Lodgepole[4]	Both nest and bird abundance.
Hairy Woodpecker	MT	1–2	25–277,880	33 b	C	Mixed coniferous[1]	
(*Picoides villosus*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	m	Lodgepole and spruce-fir[3]	
	MT	2–6	15,000	2 b, 1 u[g]	+	Lodgepole[4]	Both nest and bird abundance.
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole[5]	
	WY	1–29[f]	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
	WY, ID	1–2	3400[h]	1 b, 2 u	+	Lodgepole[9]	Highest nest densities in burned forests.
Three-toed Woodpecker	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Picoides tridactylus*)	MT	1–4	120, 480	2 b, 3 u	+	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir[3]	
	MT	2–6	15,000	2 b, 1 u[g]	+ and 0	Lodgepole[4]	Positive for nest abundance; no significant difference observed in bird abundance.
	WY	1–29[f]	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
	WY, ID	1–2	3,400[h]	1 b, 2 u	+	Lodgepole[9]	
Black-backed Woodpecker	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Picoides arcticus*)	MT	1–4	120, 480	2 b, 3 u	+	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir[3]	1 yr postfire.
	MT	2–6	15,000	2 b, 1 u[g]	+	Lodgepole[4]	Both nest and bird abundance.
	WY	5–10	6, 83	2 b, 6 u	–	Lodgepole[5]	1 yr postfire.
	WY	1–29[f]	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir[6]	
	WY, ID	1–2	3,400[h]	1 b, 2 u	+	Lodgepole[9]	

TABLE 1. CONTINUED.

Species[a]	State	Year after fire	Size of fires (ha)	No. replicate sites[b]	Response[c]	Habitat/Reference[e]	Comments
Northern Flicker	MT	1–2	25–277,880	33 b	C	Mixed coniferous[1]	
(*Colaptes auratus*)	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir[3]	
	MT	2–6	15,000	2 b, 1 u[g]	+ and 0	Lodgepole[4]	Positive for nest abundance; no significant difference observed in bird abundance.
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole[5]	Densities highest 1 yr postfire.
	WY	1–29[f]	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous[7]	
Pileated Woodpecker	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Dryocopus pileatus*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	In burned/unburned forest edge at one site.
	MT	2–6	15,000	2 b, 1 u[g]	–	Lodgepole[4]	
Olive-sided Flycatcher	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Contopus cooperi*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	0	Lodgepole and spruce-fir[3]	In both burned forest and unburned forest edge.
	WY	5–10	6, 83	2 b, 6 u	m	Lodgepole[5]	
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
Western Wood-Pewee	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Contopus sordidulus*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	High densities at one site 4 yr after fire.
	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir[3]	
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole[5]	
	WY	1–29[f]	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
Hammond's Flycatcher	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Empidonax hammondii*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous[2]	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous[7]	
Dusky Flycatcher (*Empidonax oberholseri*)	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
Warbling Vireo	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Vireo gilvus*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous[7]	
Plumbeous/Cassin's Vireo (*V. plumbeus/V. cassinii*)	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	Reported as Solitary Vireo (*V. solitarius*).
	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	Present as Solitary Vireo (*V. solitarius*); in burned/unburned forest edge at one site.
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous[7]	

TABLE 1. CONTINUED.

Species[a]	State	Year after fire	Size of fires (ha)	No. replicate sites[b]	Response[c]	Habitat/Reference[e]	Comments
Gray Jay	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Perisoreus canadensis*)	WY	2–5	235, 648	2 b, 2 u	–	Lodgepole and spruce-fir[3]	
	WY	5–10	6, 83	2 b, 6 u	m	Lodgepole[5]	
	WY	1–29[f]	40–1,414	6 b, 6 u	m	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous[7]	
Steller's Jay	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Cyanocitta stelleri*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	In one burned site.
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous[7]	
Clark's Nutcracker	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Nucifraga columbiana*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	–	Lodgepole and spruce-fir[3]	
	WY	5–10	6, 83	2 b, 6 u	0	Lodgepole[5]	Low numbers at both burned and unburned sites.
	WY	1–29[f]	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir[6]	>4 yr postfire.
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
Common Raven	MT	1–2	25–77,880	33 b	F	Mixed coniferous[1]	
(*Corvus corax*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	0	Lodgepole and spruce-fir[3]	Low numbers in burned and burned/unburned forest edge.
Tree Swallow	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Tachycineta bicolor*)	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir[3]	
	MT	2–6	15,000	2 b, 1 u[g]	+	Lodgepole[4]	For both nest and bird abundance.
	WY	5–10	6, 83	2 b, 6 u	0	Lodgepole[5]	
	WY	1–29[f]	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir[6]	>4 yr postfire.
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	
Black-capped Chickadee	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Poecile atricapilla*)	WY	2–5	235, 648	2 b, 2 u	0	Lodgepole and spruce-fir[3]	Low numbers in burned/unburned forest edge.
Mountain Chickadee	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Poecile gambeli*)	WY	2–5	235, 648	2 b, 2 u	–	Lodgepole and spruce-fir[3]	
	WY	1–29[f]	40–1,414	6 b, 6 u	–	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous[7]	
Chickadee (*Poecile* spp.)	MT	2–6	15,000	2 b, 1 u[g]	–	Lodgepole[4]	Includes *P. atricapilla*, *gambeli*, and *rufescens*; negative for both nest and bird abundance.
Chickadee (*Poecile* spp.)	MT	1–4	120, 480	2 b, 3 u	–	Mixed coniferous[2]	No distinction made between *P. atricapilla* and *gambeli.*

TABLE 1. CONTINUED.

Species^{a}	State	Year after fire	Size of fires (ha)	No. replicate sites^{b}	Response^{c}	Habitat/Reference^{e}	Comments
Red-breasted Nuthatch	MT	1–2	25–277,880	33 b	F	Mixed coniferous^{1}	
(*Sitta canadensis*)	MT	1–4	120, 480	2 b, 3 u	–	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	0	Lodgepole and spruce-fir^{3}	Low numbers on both burned and unburned sites.
	MT	2–6	15,000	2 b, 1 u^{g}	–	Lodgepole^{4}	For both nest and bird abundance.
	WY	1–29^{f}	40–1,414	6 b, 6 u	–	Lodgepole and spruce-fir^{6}	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous^{7}	
Pygmy Nuthatch	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous^{7}	
(*Sitta pygmaea*)							
Brown Creeper	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Certhia americana*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous^{2}	Low numbers in unburned forest adjacent to forest burn.
	WY	2–5	235, 648	2 b, 2 u	–	Lodgepole and spruce-fir^{3}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	m	Lodgepole and spruce-fir^{6}	Moderate severity portions of burn.
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous^{7}	
House Wren	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Troglodytes aedon*)	MT	1–4	120, 480	2 b, 3 u	+	Mixed coniferous^{2}	
	MT	2–6	15,000	2 b, 1 u^{g}	+	Lodgepole^{4}	For both nest and bird abundance.
	WY	1–29^{f}	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir^{6}	Moderate severity or >6 yr postfire.
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous^{7}	
Rock Wren	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Salpinctes obsoletus*)	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous^{7}	
Golden-crowned Kinglet	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Regulus satrapa*)	MT	1–4	120, 480	2 b, 3 u	–	Mixed coniferous^{2}	
	WY	5–10	6, 83	2 b, 6 u	0	Lodgepole^{5}	In one unburned site.
	WY	1–29^{f}	40–1,414	6 b, 6 u	–	Lodgepole and spruce-fir^{6}	
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous^{7}	
Ruby-crowned Kinglet	MT	1–2	25–277,880	33 b	F	Mixed coniferous^{1}	
(*Regulus calendula*)	MT	1–4	120, 480	2 b, 3 u	–	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	m^{d}	Lodgepole and spruce-fir^{3}	
	WY	5–10	6, 83	2 b, 6 u	0	Lodgepole^{5}	Low numbers in one burned and one unburned site.
	WY	1–29^{f}	40–1,414	6 b, 6 u	–	Lodgepole and spruce-fir^{6}	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous^{7}	
Swainson's Thrush	MT	1–2	25–277,880	33 b	F	Mixed coniferous^{1}	
(*Catharus ustulatus*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous^{2}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	m	Lodgepole and spruce-fir^{6}	

TABLE 1. CONTINUED.

Species^{a}	State	Year after fire	Size of fires (ha)	No. replicate sites^{b}	Response^{c}	Habitat/Reference^{e}	Comments
Hermit Thrush	MT	1–2	25–277,880	33 b	F	Mixed coniferous^{1}	
(*Catharus guttatus*)	WY	2–5	235, 648	2 b, 2 u	–	Lodgepole and spruce-fir^{3}	
	WY	5–10	6, 83	2 b, 6 u	m	Lodgepole^{5}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	–	Lodgepole and spruce-fir^{6}	
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous^{7}	
American Robin	MT	1–2	25–277,880	33 b	C	Mixed coniferous^{1}	
(*Turdus migratorius*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	m	Lodgepole and spruce-fir^{3}	
	WY	5–10	6, 83	2 b, 6 u	m	Lodgepole^{5}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir^{6}	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous^{7}	
Varied Thrush	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Ixoreus naevius*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous^{2}	
Townsend's Solitaire	MT	1–2	25–277,880	33 b	C	Mixed coniferous^{1}	
(*Myadestes townsendi*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous^{2}	
	WY	5–10	6, 83	2 b, 6 u	m	Lodgepole^{5}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	m	Lodgepole and spruce-fir^{6}	In 7 yr old burn.
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous^{7}	
Mountain Bluebird	MT	1–2	25–277,880	33 b	F	Mixed coniferous^{1}	
(*Siala currucoides*)	MT	1–4	120, 480	2 b, 3 u	+	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir^{3}	
	MT	2–6	15,000	2 b, 1 u^{g}	+	Lodgepole^{4}	For both nest and bird abundance.
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole^{5}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir^{6}	
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous^{7}	
Western Bluebird	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Siala mexicana*)	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous^{7}	
European Starling	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Sturnus vulgaris*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous^{2}	
Yellow-rumped Warbler	MT	1–2	25–277,880	33 b	C	Mixed coniferous^{1}	
(*Dendroica coronata*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	m	Lodgepole and spruce-fir^{3}	
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole^{5}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	–	Lodgepole and spruce-fir^{6}	
	CO	0–8	43–7,337	8 b, 8 u	–	Mixed coniferous^{7}	

TABLE 1. CONTINUED.

Species[a]	State	Year after fire	Size of fires (ha)	No. replicate sites[b]	Response[c]	Habitat/Reference[e]	Comments
Townsend's Warbler	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Dendroica townsendi*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	0	Lodgepole and spruce-fir[3]	In one burned site.
Orange-crowned Warbler	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Vermivora celata*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	
MacGillivray's Warbler	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Oporornis tolmiei*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous[2]	
Wilson's Warbler	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Wilsonia pusilla*)	WY	2–5	235, 648	2 b, 2 u	0	Lodgepole and spruce-fir[3]	In burned/unburned forest edge.
Western Tanager	MT	1–2	25–277,880	33 b	C	Mixed coniferous[1]	
(*Piranga ludoviciana*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	m[d]	Lodgepole and spruce-fir[3]	
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole[5]	
	WY	1–29[f]	40–1,414	6 b, 6 u	–	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous[7]	
Lazuli Bunting	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Passerina amoena*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous[2]	
Chipping Sparrow	MT	1–2	25–277,880	33 b	C	Mixed coniferous[1]	
(*Spizella passerina*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous[2]	
	WY	2–5	235, 648	2 b, 2 u	m	Lodgepole and spruce-fir[3]	
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole[5]	
	WY	1–29[f]	40–1,414	6 b, 6 u	m	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous[7]	
Fox Sparrow	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Passerella iliaca*)	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole[5]	
Song Sparrow	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Melospiza melodia*)	WY	1–29[f]	40–1,414	6 b, 6 u	0	Lodgepole and spruce-fir[6]	
Lincoln's Sparrow	MT	1–2	25–277,880	33 b	F	Mixed coniferous[1]	
(*Melospiza lincolnii*)	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir[3]	
White-crowned Sparrow	MT	1–2	25–277,880	33 b	U	Mixed coniferous[1]	
(*Zonotrichia leucophrys*)	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir[3]	
	WY	5–10	6, 83	2 b, 6 u	0	Lodgepole[5]	
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous[7]	

TABLE 1. CONTINUED.

Species^{a}	State	Year after fire	Size of fires (ha)	No. replicate sites^{b}	Response^{c}	Habitat/Reference^{e}	Comments
Dark-eyed Junco	MT	1–2	25–277,880	33 b	C	Mixed coniferous^{1}	
(*Junco hyemalis*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir^{3}	Highest densities in burned forest but present in high densities in unburned forest.
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole^{5}	Listed as Gray-headed Junco (*Junco caniceps*); highest densities in burned forest but present in high densities in unburned forest.
	WY	1–29^{f}	40–1,414	6 b, 6 u	m	Lodgepole and spruce-fir^{6}	Listed as Oregon Junco (*J. hyemalis oreganos*).
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous^{7}	
Brown-headed Cowbird	MT	1–2	25–277,880	33 b	F	Mixed coniferous^{1}	
(*Molothrus ater*)	WY	2–5	235, 648	2 b, 2 u	0	Lodgepole and spruce-fir^{3}	
Brewer's Blackbird	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Euphagus cyanocephalus*)	MT	1–4	120, 480	2 b, 3 u	0	Mixed coniferous^{2}	
Evening Grosbeak	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Coccothraustes vespertinus*)	MT	1–4	120, 480	2 b, 3 u	–	Mixed coniferous^{2}	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous^{7}	
Pine Grosbeak	MT	1–2	25–277,880	33 b	U	Mixed coniferous^{1}	
(*Pinicola enucleator*)	WY	2–5	235, 648	2 b, 2 u	–	Lodgepole and spruce-fir^{3}	
	WY	5–10	6, 83	2 b, 6 u	0	Lodgepole5	
	WY	1–29^{f}	40–1,414	6 b, 6 u	–^{d}	Lodgepole and spruce-fir^{6}	
Cassin's Finch	MT	1–2	25–277,880	33 b	F	Mixed coniferous^{1}	
(*Carpodacus cassinii*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir^{3}	
	WY	5–10	6, 83	2 b, 6 u	+	Lodgepole^{5}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	+	Lodgepole and spruce-fir^{6}	>2 yr postfire.
	CO	0–8	43–7,337	8 b, 8 u	+	Mixed coniferous^{7}	
Red Crossbill	MT	1–2	25–277,880	33 b	F	Mixed coniferous^{1}	
(*Loxia curvirostra*)	MT	1–4	120, 480	2 b, 3 u	–	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	0^{d}	Lodgepole and spruce-fir^{3}	
	WY	1–29^{f}	40–1,414	6 b, 6 u	0^{d}	Lodgepole and spruce-fir^{6}	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous^{7}	
Pine Siskin	MT	1–2	25–277,880	33 b	C	Mixed coniferous^{1}	
(*Carduelis pinus*)	MT	1–4	120, 480	2 b, 3 u	m	Mixed coniferous^{2}	
	WY	2–5	235, 648	2 b, 2 u	+	Lodgepole and spruce-fir^{3}	

TABLE 1. CONTINUED.

Species[a]	State	Year after fire	Size of fires (ha)	No. replicate sites[b]	Response[c]	Habitat/Reference[e]	Comments
Pine Siskin (*continued*)	WY	5–10	6, 83	2 b, 6 u	m	Lodgepole[5]	
(*Carduelis pinus*)	WY	1–29[f]	40–1,414	6 b, 6 u	m[d]	Lodgepole and spruce-fir[6]	
	CO	0–8	43–7,337	8 b, 8 u	m	Mixed coniferous[7]	

[a] Species not included in the table proper were those reported by only one study and recorded as uncommon by Hutto (1995) or as + by other references listed in footnote e, including Northern Goshawk (*Accipiter gentilis*), Ferruginous Hawk (*Buteo regalis*), Band-tailed Pigeon (*Patagioenas fasciata*), Flammulated Owl (*Otus flammeolus*), Black-chinned Hummingbird (*Archilochus alexandri*), White-headed Woodpecker (*Picoides albolarvatus*), Western Scrub-Jay (*Aphelocoma californica*), Pinyon Jay (*Gymnorhinus cyanocephalus*), Gray Flycatcher (*Empidonax wrightii*), Cassin's Kingbird (*Tyrannus vociferans*), Gray Vireo (*Vireo vicinior*), Bushtit (*Psaltriparus minimus*), Juniper Titmouse (*Baeolophus ridgwayi*), Virginia's Warbler (*Vermivora virginiae*), Scott's Oriole (*Icterus parisorum*), Evening Grosbeak (*Coccothraustes vespertinus*).

[b] All studies were of wildfire; b = number of burned sites; u = number of unburned sites.

[c] + = increase; – = decrease; 0 = no effect or study inconclusive; m = mixed response; for responses without a comparison to unburned forests (i.e., Hutto 1995), frequency of occurrence was classified as U = uncommon (< 25% of burns), F = frequently observed (25–75% of burns) and C= common (> 75% of burns).

[d] Low detections, < 0.05 birds/ha.

[e] References: 1 = Hutto 1995; 2 = Harris 1982; 3 = Pfister 1980; 4 = Caton 1996; 5 = Davis 1976; 6 = Taylor and Barmore 1980; 7 = Kotliar et al. 2002; 8 = Saab and Vierling 2001; 9 = Hoffman 1997.

[f] Sites censused > 29 yr after fire were considered unburned.

[g] Number of unburned replicates not reported.

[h] Area surveyed within burned forest; size of fire not reported.

a flush of beetle larvae available as food for Black-backed Woodpeckers (Goggans et al. 1988). Such an increase in woodpecker prey is qualitatively similar to the increase in wood-boring beetle larvae that accompanies stand-replacing fire, inviting the suggestion that fire and bark beetle outbreaks create similar habitat conditions for woodpeckers. However, bark and wood-boring beetles have marked ecological differences that affect their value as woodpecker prey (Mitton and Sturgeon 1982, Powell 2000). Bark beetle outbreaks almost certainly offer more woodpecker prey than unburned forests without outbreaks, but they are not necessarily as abundant in prey as burned forests (Powell 2000).

One study in Table 1 measured a reproductive success variable other than nest success for Lewis's Woodpecker (Saab and Vierling 2001), a species well known to strongly favor burned forests (e.g., Tobalske 1997, Linder and Anderson 1998). Saab and Vierling (2001) compared productivity of Lewis's Woodpeckers between burned ponderosa pine of Idaho and unburned cottonwood (*Populus fremontii*) riparian forests of Colorado. Nests in burned ponderosa pine had nearly double the productivity of nests in unburned cottonwood riparian (0.69 vs. 0.38 female fledglings per female per year, respectively), leading the authors to suggest that burned ponderosa pine forest may be a source habitat for Lewis's Woodpeckers.

The cavity-nesting birds reviewed here breed with relatively high success in stand-replacement burns of ponderosa pine forest. High reproductive success and increased productivity in recently burned forests might be explained in part by a reduction or elimination of nest predators following stand-replacement fires (Saab and Vierling 2001). Fire management of ponderosa pine forests in the Rocky Mountains has emphasized prescribed, understory fire to restore ecosystem function (e.g., Arno 2000). Stand-replacement fire may be equally important in maintaining some ponderosa pine forests (Veblen et al. 2000, Baker and Ehle 2001, Ehle and Baker 2003), and for the long-term persistence of cavity-nesting birds that thrive in these habitats. We found no published studies that investigated the effects of prescribed fire on birds in the southern and central Rocky Mountains. Such studies are needed to understand the ecological consequences of managing forests with prescribed fire, fire exclusion, or wildland fire.

MIXED CONIFEROUS FORESTS

Mixed coniferous (mesic montane) forests occur predominantly at mid-elevations, where the topographic variation creates a mosaic of tree species and densities (Peet 2000). In the central Rocky Mountains, Douglas-fir often occurs with white fir (*Abies concolor*), blue spruce (*Picea pungens*), ponderosa pine, limber pine, and quaking aspen; in the northern Rocky Mountains, Douglas-fir, grand fir (*Abies grandis*), ponderosa pine, and western larch (*Larix occidentalis*) are associated species (Daubenmire 1943).

On the west slope of the northern Rocky Mountains, mesic cedar-hemlock (*Thuja-Tsuga*; Cascadian) forests occur as a result of the Pacific maritime influence (Daubenmire 1943, Peet 2000). Dominant species include western hemlock (*Tsuga heterophylla*), western redcedar (*Thuja plicata*), grand fir, and Pacific yew (*Taxus brevifolia*) (Daubenmire 1943). These forests resemble those found in the western Cascade Mountains (Peet 2000).

Mixed-severity fire regimes are characteristic of mixed coniferous forests (Schoennagel et al. 2004). For example, mixed coniferous forest in western Montana burned in stand-replacement fires at long intervals of 150 to >400 yr, while low severity, understory fires burned at short intervals (20–30 yr averages) (see Arno 2000).

In mixed-severity regimes, the extent of postfire tree mortality varies from sparse to complete, depending on the severity of the surface fire. The variation in fire behavior inherent in mixed-severity regimes results in complex forest age structures within burns (Agee 1998). Upper-montane ponderosa pine forests, especially those with a greater component of Douglas-fir, typically experienced both frequent surface fires and infrequent crown fires (i.e., a mixed-severity regime).

Reductions of fire activity in mixed coniferous forests began in the early twentieth century as a result of livestock grazing (removing fine fuels), fire exclusion, and logging (Arno 2000). The densities of relatively fire intolerant and shade tolerant species, such as Douglas-fir and grand fir, have increased in response (Arno et al. 1995, Kaufmann et al. 2000). This is particularly evident within the mixed coniferous zone at lower elevations, on drier aspects, and adjacent to grasslands where fires historically were more frequent (Schoennagel et al. 2004). In some areas, removal of overstory trees in more than a century of logging has contributed to thickets of relatively small trees (Kaufmann et al. 2000). An increase in forest disturbance (e.g., logging, fires) in many areas of the Rocky Mountains during early Euro-American settlement probably synchronized large areas of the landscape and increased aspen coverage, which subsequently diminished by the late twentieth century in many areas due to senescence and encroachment by conifers (Veblen 2000).

BIRDS OF MIXED CONIFEROUS FORESTS

Sanderson et al. (1980) list 96 species that use mixed coniferous forests. Of 166 bird species detected during point count visits conducted across a variety of habitats in the northern Rocky Mountains, 75 were detected in mixed coniferous forests (Hutto and Young 1999). Some characteristic species include Northern Goshawk (*Accipiter gentilis*), Blue Grouse (*Dendragapus obscurus*), Williamson's Sapsucker (*Sphyrapicus thyroideus*), Hairy Woodpecker, Hammond's Flycatcher (*E. hammondii*), Mountain Chickadee (*Poecile gambeli*), Brown Creeper (*Certhia americana*), Golden-crowned Kinglet (*Regulus satrapa*), Ruby-crowned Kinglet (*R. calendula*), Hermit Thrush (*Catharus guttatus*), Yellow-rumped Warbler (*Dendroica coronata*), Western Tanager (*Piranga ludoviciana*), Evening Grosbeak (*Coccothraustes vespertinus*), and Pine Siskin (*Carduelis pinus*). Partners in Flight priority bird species for mixed coniferous forests of the Rocky Mountains include Northern Goshawk, Williamson's Sapsucker, and Brown Creeper due to their need for high canopy closure and high densities of large diameter trees (Partners in Flight 2004).

BIRD RESPONSE TO FIRE IN MIXED CONIFEROUS FORESTS

Generalizations regarding bird response to fire in mixed coniferous forests are difficult due to variation in topography, stand densities, forest structure, fire history, and tree and understory species composition. Most data available on avian response to fire in mixed coniferous forests come from a handful of studies (Harris 1982, Hutto 1995, Hitchcox 1996, Kotliar et al. 2002).

Of these studies, only Harris (1982) and Kotliar et al. (2002) directly compared bird response in burned and unburned mixed coniferous forests (Table 2). Although Hutto (1995) did not compare abundance between burned and unburned forests, he did report the relative occurrence of 87 species within 33 burned forests. Hutto (1995) and Kotliar et al. (2002) did not distinguish between different types of burned forest, so we include them in this section only. Species responses were based on frequency of occurrence (Hutto 1995), abundance estimates from point counts (Kotliar et al. 2002), and fixed-width transect surveys (Harris 1982). These techniques

TABLE 2. COMPARISON OF REPRODUCTIVE SUCCESS FOR SIX BIRD SPECIES IN BURNED AND UNBURNED HABITATS. NUMBERS ARE MAYFIELD-CORRECTED PERCENT SUCCESS EXCEPT WHERE OTHERWISE INDICATED[a].

	Burned forest			Unburned forest		
Species	N	Nest success (%)	Habitat	N	Nest success (%)	Habitat
Lewis's Woodpecker	283	78	Ponderosa pine, Idaho[b]	65	46	Cottonwood riparian, Colorado[b]
		0.69[c]			0.38[c]	
Hairy Woodpecker	91	75	Ponderosa pine, Idaho[d]	8	74	Mixed coniferous-aspen, Arizona[e]
				29	48	Ponderosa pine, Idaho[f]
Black-backed Woodpecker	33	87	Ponderosa pine, Idaho[d]	19	69[a]	Mixed coniferous, beetle-killed, Oregon [g]
	14	100[a]	Lodgepole pine, Wyoming[h]			
White-headed Woodpecker	6	100	Ponderosa pine, Idaho[d]	41	83[a]	Ponderosa pine, Oregon[i]
	20	85	Ponderosa pine, Oregon[f]	16	88	Ponderosa pine, Oregon[i]
Northern Flicker	97	70	Ponderosa pine, Idaho[d]	34	100	Mixed coniferous-aspen, Arizona[e]
				48	49	Ponderosa pine, Idaho[f]
Western Bluebird	100	70	Ponderosa pine, Idaho[d]	41	39	Ponderosa pine, untreated, Arizona[j]
				56	75	Ponderosa pine, thinned or prescribe-burned, Arizona[j]
				39	29	Oak-pine, California[k]

[a] Values are apparent nest success.
[b] Saab and Vierling 2001.
[c] Variable is productivity, in number of female fledglings per female per year.
[d] Saab and Dudley 1998.
[e] Martin and Li 1992.
[f] Saab et al., unpubl. data.
[g] Goggans et al. 1988. Values are apparent nest success.
[h] Dixon and Saab 2000. Values are apparent nest success.
[i] Garrett et al. 1996 (two regions reported separately). Values are apparent nest success.
[j] Germaine and Germaine 2002 (two treatments reported separately).
[k] Purcell et al. 1997.

are best for estimating abundances of songbirds but usually underestimate those species that do not sing consistently and those with large home ranges (e.g., woodpeckers and raptors) (cf. Martin and Eadie 1999). Results for the groups that may be under estimated should be treated with caution and are likely biased toward non-detection.

While considerable differences exist among these three studies, some patterns do emerge. Several species were consistently present in recently burned forests (e.g., Three-toed Woodpecker [*Picoides tridactylus*], Black-backed Woodpecker, Olive-sided Flycatcher [*Contopus cooperi*], Mountain Bluebird), whereas others were consistently more abundant in unburned forests (e.g., Golden-crowned Kinglet, Mountain Chickadee, Hermit Thrush). The majority of species showed mixed or no response across studies. These species are likely affected by fire-related factors including burn severity, time since fire, and total burn area (Kotliar et al. 2002). Typical survey techniques (i.e., point counts) likely cannot detect such effects without more comprehensive study design and replication.

No studies followed bird responses from early to late postfire stages. Results from Hutto (1995) and Harris (1982) are snapshots of bird species composition in early postfire years (1–4 yr postfire). Kotliar et al. (2002) examined forests for 8 yr postfire but did not estimate abundance or density of species encountered, so changes in species responses during the study are unknown. Regrowth of understory vegetation and associated increases of free-flying arthropods, loss of residual snags, and decline of bark and wood-boring beetles can dramatically change bird species composition of burned forests in later successional stages (e.g., >5–10 yr postfire). Long-term studies that follow burned forests through these successional stages are needed (e.g., Saab et al. 2004).

Several studies have noted an increase in cavity-nesting bird densities up to 3–5 yr postfire (Taylor and Barmore 1980, Caton 1996, Hitchcox 1996, Saab and Dudley 1998). Harris (1982) noted an increase in secondary cavity-nesting bird species but a decline in woodpecker densities 3 yr postfire. Such declines may be a response to decreases in bark and wood-boring beetles with increasing year postfire (Harris 1982, Dixon and Saab 2000, Powell 2000).

Abundance may not reflect population status without corresponding information on reproductive success (Brawn and Robinson 1996, Bock and Jones 2004). We know of only one study that examined nest success in burned mixed coniferous forests of the Rocky Mountains. Hitchcox (1996) compared nesting densities and success of cavity-nesting birds in salvage-logged and unlogged burned forests of northwestern Montana 2–4 yr postfire. Hitchcox selected seven salvage-logged plots 7–34 ha in size, in which most large trees (>15 cm diameter, >4.5 m tall) were removed. Densities of cavity nests were two to three times higher in unlogged (18 nesting species) compared to salvage-logged plots (eight nesting species). Mayfield nest success for the three most abundant species was higher in unlogged than salvage-logged treatments for Northern Flicker (95% vs. 67%, respectively, both N = 24 nests) and Mountain Bluebird (67%, N = 25 vs. 34%, N = 15) and similar between treatments for House Wren (*Troglodytes aedon*) (73%, N = 34 vs. 80%, N = 9; Hitchcox 1996).

The varied responses to fire by birds associated with mixed coniferous forests reflects the mixed fire regimes characteristic of these forests, and indicates a need for both understory and stand-replacement fires (Schoennagel et al. 2004). A return to frequent understory fire in lower elevations and rare stand-replacement fire at higher elevations would provide habitat for the diverse bird communities using mixed coniferous forests. Fire exclusion or management using only prescribed fire would not provide the mosaic of habitat conditions necessary to maintain the variation in avian communities associated with these forests.

LODGEPOLE PINE FORESTS

Lodgepole pine forests of the Rocky Mountains occur at middle to high elevations in the subalpine zone. These forests typically burn infrequently and at high severity (Schoennagel et al. 2004), although at lower elevations, small surface fires occasionally burn (Kipfmueller and Baker 2000).

Lodgepole pine is shade intolerant with few lateral branches, but tends to grow in very dense stands. Over time the dense stands naturally thin, contributing to abundant dead ladder fuels (Schoennagel et al. 2004). These abundant fuels, the low crown height, and the sparse surface fuels all promote high-severity crown fires. Severe drought and strong winds are necessary for fire to spread through the wetter fuels of subalpine forests. Typically, it takes decades or centuries for appropriate fuel accumulation and climatic conditions to coincide (Romme and Knight 1981). The lower fire-return intervals probably average from 60–80 yr (Agee 1993) and the upper return intervals from 100 to >500 yr (Romme and Knight 1981).

No evidence suggests that fire suppression has changed lodgepole stand structures in recent decades (Schoennagel et al. 2004). Fire histories demonstrate that long fire-free periods (as long as or longer than the fire exclusion period during the twentieth century) characterized the fire regimes of these forests prior to European settlement (e.g., Romme 1982, Veblen 2000).

BIRDS OF LODGEPOLE PINE FORESTS

No bird species are restricted to lodgepole pine forests, yet many use this habitat for some portion of their life history. Some species that use lodgepole pine forests include Spruce Grouse (*Falcipennis canadensis*), Three-toed Woodpecker, Clark's Nutcracker (*Nucifraga columbiana*), Ruby-crowned Kinglet, and Pine Siskin (Hein 1980, Hutto and Young 1999). Partners in Flight lists no priority species for this habitat, although several species that use lodgepole forests are priority species in other habitats (Partners in Flight 2004).

BIRD RESPONSE TO FIRE IN LODGEPOLE PINE FORESTS

Several studies have examined bird response to fire in lodgepole pine forests by comparing burned and unburned habitats (Davis 1976, Pfister 1980, Taylor and Barmore 1980, Caton 1996, Hoffman 1997). Most of these studies measured bird response as abundance or density estimates based on strip transect surveys (Davis 1976, Taylor and Barmore 1980), a combination of line transect surveys and spot-mapping (Pfister 1980), or fixed-radius point counts (Caton 1996). Caton (1996) and Hoffman (1997) also compared cavity-nest abundances or densities in burned and unburned forests (Table 2).

While considerable differences in study design, habitat, and survey methods exist among these studies, some patterns emerged. As in mixed coniferous forests, certain species were always more abundant in burned forests (Black-backed Woodpecker, Three-toed Woodpecker, and Mountain Bluebird), whereas other species were more abundant in unburned forests (Mountain Chickadee, Golden-crowned Kinglet, and Hermit Thrush).

In lodgepole pine forests of south central Wyoming, Davis (1976) compared breeding bird densities and species richness in three treatments: (1) clearcut, (2) burned, and (3) unlogged, unburned, considered the control plots. Richness and density estimates of most species were highest in burned plots surveyed 5–10 yr postfire than in either clearcut or control plots. Pfister (1980) compared breeding bird densities in burned and unburned lodgepole pine and spruce-fir forests in Yellowstone National Park. In lodgepole forests, burned plots had higher species richness than unburned plots, and most species occurred at their highest densities at 4–5 yr postfire. Taylor and Barmore (1980) examined breeding bird densities in moderate-to-high severity burns of lodgepole pine forests 1–29 yr postfire and in mature forests that had not burned for at least 43 yr. Breeding bird densities were highest in forests 5–29 yr postfire. The authors suggested the closed canopy of lodgepole pine forests >40 yr old resulted in declines of bird densities. Wood-boring beetles were present within the first year postfire, followed by Three-toed and Black-backed Woodpeckers during the second year postfire. Densities of woodpeckers declined with declining numbers of wood borers. Cavities created by these species as well as Hairy Woodpecker coincided with an increase of secondary cavity nesters up to 5 yr postfire, when non-excavators reached their highest densities.

Caton (1996) estimated abundances of cavity nests in burned forests 2–6 yr after fire and compared these abundances to those reported for the same study area before it burned (McClelland 1977). Overall abundances were higher in burned forests, although nests for some species (Red-naped Sapsucker [*Sphyrapicus nuchalis*], Red-breasted Nuthatch [*Sitta canadensis*], and chickadees) were more abundant in unburned forests. Bird abundance data obtained from point counts showed a positive response to fire by wood drillers, aerial insectivores, and ground foragers, whereas foliage and bark gleaners were less abundant in burned forests. Caton (1996) also found lower densities of cavity nests in salvage-logged compared to unlogged burned forests. Relative abundance of tree-foraging species was significantly lower in salvage-logged plots, whereas non-tree foraging species showed mixed responses.

Hoffman (1997) compared nest distributions of Three-toed, Black-backed, and Hairy Woodpeckers among three forest conditions: (1) burned, unlogged forest (2) unburned, clearcut forest and (3) unburned, mature lodgepole pine forest, termed undisturbed forest. Nests of all three species were over five times more likely to be found in 1-yr-old burned forests than in undisturbed forests. Nests of all three species were over 17 times more likely to be found in burned forests 2 yr postfire than in clearcuts.

Birds of lodgepole pine forests need little in the way of new fire management practices because fire regimes in these forests have seen little alteration since European settlement. Large stand-replacement fires are necessary for biological diversity in lodgepole pine forests (Agee 1993, Arno 2000). Infrequent, stand-replacement fires in this forest type clearly favor many bird species, especially cavity-nesting birds and flycatchers (Table 2). Stand-replacement fire regimes can be controlled by creating fuel breaks near property boundaries to protect resorts and other private facilities (see Arno 2000). This practice is likely to have few impacts on lodgepole pine bird communities if conducted on small spatial scales.

SPRUCE-FIR FORESTS

Spruce-fir forests occur at the highest forested elevations in the Rocky Mountains. Engelmann spruce (*Picea engelmannii*) and subalpine fir (*Abies lasiocarpa*) are the dominant trees. Whitebark pine (*Pinus albicaulis*) grows in drier regions. Infrequent, high-severity crown fires generally occur at intervals of 100 to >500 yr (Romme and Knight 1981). Successive seasons of drought can initiate large, stand-replacing fires in these typically moist forests (Balling et al. 1992). Drought-induced large fires are very rare but account for the greatest area burned in subalpine forests (Bessie and Johnson 1995). Similar to lodgepole pine, the spruce-fir forest floor lacks fine fuels, which propagate understory fires, on the forest floor. Rather, these dense forests have abundant ladder fuels that carry fire into tree crowns (Schoennagel et al 2004).

Efforts to suppress fires in systems with long-fire-return intervals have had limited success (Romme and Despain 1989, Schoennagel et al. 2004). Variation in climate rather than fuels appears to have the greatest influence on the size, timing, and severity of fires in spruce-fir and other subalpine forests (Romme and Despain 1989, Rollins et al. 2002, Schoennagel et al. 2004).

BIRDS OF SPRUCE-FIR FORESTS

Many species that occur in mixed coniferous and lodgepole pine forests also occur in spruce-fir forests. Some species that are consistently found in spruce-fir forests throughout the Rocky Mountains include Clark's Nutcracker, Ruby-crowned Kinglet, Hermit Thrush, Yellow-rumped Warbler, Pine Grosbeak, Red Crossbill (*Loxia curvirostra*), and Pine Siskin (Smith 1980). Partners in Flight lists no priority species specifically for this habitat, although several species that use spruce-fir forests are priority species in other habitats (Partners in Flight 2004).

BIRD RESPONSE TO FIRE IN SPRUCE-FIR FORESTS

We know of two studies that measured bird responses to wildland fire in spruce-fir forests (Pfister 1980, Taylor and Barmore 1980). In both studies, species richness and composition were similar between stand-replacement burns and unburned spruce-fir forests. Breeding bird densities, however, were higher in 2–3 yr old burned forests compared to unburned forests (Pfister 1980). Although Taylor and Barmore (1980) reported similar breeding bird densities between burned forests (1–3 yr after fire) and unburned forests, densities of Three-toed, Black-backed, and Hairy woodpeckers were higher in moderately burned forests.

Studies of burned and unburned spruce-fir forests report relatively minor differences in bird communities. Still, there is a clear pattern for some woodpecker species to favor burned habitats. Similar to lodgepole pine forests, alterations in historical fire regimes have been inconsequential for spruce-fir forests. Habitats created by rare, stand-replacing fire are characteristic of these high-elevation forests and necessary for the long-term persistence of the associated bird communities. Fire suppression is generally difficult and likely does not threaten the natural fire regimes or associated bird communities due to the remote nature of this habitat.

MANAGEMENT IMPLICATIONS AND RESEARCH QUESTIONS

After reviewing the literature on birds and fire in the Rocky Mountains, we suggest that the following six areas are highly deserving of management and research attention.

1. Future research should focus on the influence of burn severity and patch size to refine our understanding of how birds respond to fires. Severity and patch size could be incorporated into the response classes of Kotliar et al. (2002). We believe that groups of bird species can be identified that respond similarly to fires of certain severities or sizes. First approaches might be best aimed at distinguishing responses to low vs. high severity and large vs. small patches. Eventually this research could greatly improve our understanding of the mixed severity fires that govern many of the forests in the Rocky Mountains.
2. Long-term studies (at least 10 yr) are needed to explain postfire changes in habitats and avifauna. Most studies of postfire bird communities end less than 5 yr postfire, even though descriptive accounts suggest that there is a characteristic avifauna of middle-successional forests (Hutto 1995). A few long-term studies are ongoing (i.e., Saab et al. 2004), but more are urgently needed to capture the variability that we know exists among forest types and fire regimes.

3. Avian responses to fire vary not only with severity, patch size, and time since fire, but also with landscape context of burns, and postfire salvage logging. Over the last two decades, postfire salvage logging has become increasingly prevalent and is often implemented with little regard for wildlife (e.g., Caton 1996, Saab et al. 2002). Many cavity-nesting birds are associated with burned forests, including woodpeckers designated as sensitive species by state and federal agencies. These woodpecker species respond variably to postfire salvage logging (Saab and Dudley 1998). Litigation on management of these species has impeded the implementation of postfire management activities. Thus, design criteria for postfire salvage logging that maintains nesting habitat for woodpeckers is needed for planning and implementation of postfire management actions (Saab et al. 2002).
4. Studies of bird relationships to fire have focused on species composition and abundance in stand-replacing wildfires. For an improved understanding of the ecological consequences of fire management for birds, more research is needed to examine reproductive success and other demographic parameters to evaluate the habitat quality and source/sink status of fire-created (prescribed and wildfire) and fire-excluded habitats.
5. Recently burned forests potentially function as ephemeral source habitats for several avian species, particularly cavity-nesting birds. Early postfire habitats provide increases in snags that offer greater opportunities for nesting and foraging (e.g., Hutto 1995), and a reduced risk of nest predation compared to unburned forests (Saab and Vierling 2001). In this summary, data reported for selected woodpecker species suggest a pattern of higher nest survival in burned than in unburned forests. High reproductive success and increased productivity in recently burned forests might be explained in part by a reduction or elimination of nest predators following stand-replacement fires (Saab and Vierling 2001). Recolonization of small mammalian and reptilian nest predators into forests affected by wildfire may take several years, thus predation rates are expected to be lower in the years immediately following fire (Saab and Vierling 2001, Saab et al. 2004). The predator-release benefit of burns is still hypothetical and needs to be tested.
6. Perhaps the most difficult question facing managers in this region is how to burn higher elevation forests that did not evolve with low-severity fire. Traditional low-severity prescribed fire is not likely to replicate historic stand conditions or avifauna in these forests, which include higher-elevation mixed coniferous forests and all lodgepole pine and spruce-fir forests (i.e., the majority of forest types in the Rocky Mountains). Research in recent large fires across the Rocky Mountains indicates that large burns support diverse and productive avifauna (Saab et al. 2004). Clearly, management of the disparate forests of this region requires both prescribed fire and wildland fire.

Managers are increasingly using prescribed fire and thinning to reduce fire severity. Birds will likely respond differently depending on cover types and size and severity of treatments. Therefore, managers should consider targeting a variety of stand densities that reflect historic variation (e.g., Ehle and Baker 2003). This approach calls for cooperation between managers and researchers to implement replicated experiments done at appropriate scales that rigorously assess the effects of different prescriptions on habitats and populations of birds. Strategies for fire management should not only reduce fire risk but also maintain habitat for avifauna and other components of biodiversity in the Rocky Mountains.

The limited applicability of the Southwest ponderosa pine paradigm, coupled with our limited understanding of fire history and fire effects on natural resources other than trees, suggests that large-scale forest restoration could pose significant ecological risks unless it is carefully targeted to move the structure, function, and disturbance of a system back to historical conditions suitable for that system. Prudent study and application of locally appropriate fire regimes will be key to maintaining diverse ecosystems (Landres et al. 1999, Allen et al. 2002). If we do not soften the pervasive view of forests as static and perpetually green, ecosystem restoration cannot be successful. Management that targets the full range of natural variability (up to and including crown fires) will be more successful and more cost effective than aiming for conditions inappropriate to local systems (Landres et al. 1999).

ACKNOWLEDGMENTS

We thank two anonymous reviewers for their comments on an earlier version of this manuscript. Scott Story and Robin Russell helped with the assembly of the manuscript.

Studies in Avian Biology No. 30:97–115

BIRD RESPONSES TO BURNING AND LOGGING IN THE BOREAL FOREST OF CANADA

Susan J. Hannon and Pierre Drapeau

Abstract. We compared how bird communities differed between burned and logged stands in black spruce (*Picea mariana)* forests of the boreal shield in Quebec and mixed-wood forests on the boreal plain in Alberta and Saskatchewan. Bird community composition was quite different in burns and clearcuts shortly after disturbance. In burns, cavity nesters and species that forage on beetles in dead trees predominated, whereas clearcuts were dominated by open-country species. Generally, snag-dependent species decreased and shrub-breeding species increased by 25 yr postfire. Species that forage and nest in canopy trees were more common 25 yr post-logging because of the retention of live residual trees. The bird communities tended to converge over time as the vegetation in burns and logged areas became more similar. Black-backed Woodpeckers (*Picoides arcticus*) and Three-toed Woodpeckers (*Picoides tridactylus*) exploit recently burned coniferous forest to forage on wood-boring insect larvae (Cerambycidae and Buprestidae) and bark beetle larvae (Scolytidae) for a short period after fire and then decline. Black-backs were absent from mature forests and found at low density in old-growth forest. Over the long term, burns may be temporary sources for fire specialists. The major conservation issue for fire- associated species is salvage logging, because woodpecker foraging and nesting trees are removed. Maintenance of suitable amounts of postfire forests spared from salvage logging is essential for sustainable forest management. Climate change is predicted to alter fire cycles: they will be shorter in the prairies leading to a shortage of old-growth forest and will be longer in Quebec leading to a shortage of younger forest.

Key Words: bird communities, Black-backed Woodpeckers, boreal forest, burns, clearcutting, even-age forest management, forest fire, logging, *Picoides arcticus*.

RESPUESTAS DE LAS AVES HACIA LOS INCENDIOS Y APROVECHAMIENTOS FORESTALES EN EL BOSQUE BOREAL DE CANADÁ

Resumen. Comparamos como difieren las comunidades de aves en áreas incendiadas y áreas con aprovechamientos forestales, en bosques de abeto negro (*Picea mariana*), en coberturas de bosque boreal en Québec y en bosques mixtos en tierras boreales de Alberta y Saskatchewan. La composición de las comunidades de aves era algo distinta poco después del disturbio en áreas con incendios y aprovechamientos forestales de tala-rasa. En áreas incendiadas, las especies que anidan en cavidades y las que buscan insectos para alimentarse predominan en los árboles muertos, mientras las áreas con aprovechamiento forestal a tala-rasa eran dominadas por especies de áreas abiertas. Generalmente las especies dependientes de los tocones disminuyeron, y las especies que se reproducen en arbustos aumentaron después de 25 años del incendio. Aquellas especies que se alimentan y anidan en las copas de los árboles eran más comunes, después de 25 años del aprovechamiento forestal, debido a la retención de árboles residuales vivos. A través del tiempo, las comunidades de aves tendían a converger, conforme la vegetación en incendios y aprovechamientos forestales era más similar. Los pájaros carpinteros (*Picoides arcticus*) y (*Picoides tridactylus*) aprovecharon por un período corto, después del incendio, los bosques de coníferas incendiados, para alimentarse de larvas (Cerambycidae and Buprestidae) y de larvas de escarabajo descortezador (Scolytidae), disminuyendo después de un tiempo. Los pájaros carpinteros (*Picoides arcticus*)eran ausentes en bosques maduros y se encontraron bajas densidades en bosques de viejos. En el largo plazo, los incendios probablemente serán una fuente temporal para especialistas en incendios. El aspecto de mayor relevancia para la conservación de contrariamente a los aprovechamientos forestales de salvamento , es esencial para un manejo forestal sustentable apropiado. Predicen que el cambio climático alterará los ciclos del fuego, los cuales serán menores en las praderas, provocando una deficiencia en los bosques viejos, y serán mayores en Québec, provocando deficiencia en bosques más jóvenes.

Unlike several ecosystems in North America, the boreal forest in Canada still retains a relatively intact natural fire regime. However, the increasing impact of industrial forestry and other land uses is changing this natural dynamic and its related bird communities. Hence, discovering the ecological differences between postfire and post-harvest forests is a key issue in the conservation of boreal forest birds. Although even-aged management practices, like stand-replacing fires, restart forest succession, they do not necessarily provide the same habitat conditions for birds. In this paper, we summarize results of studies conducted in the boreal plain and boreal shield regions of Canada that compared bird assemblages in logged and burned boreal forest and studies that focused on bird species associated with recently burned forest. We then evaluate how a natural-disturbance-based management approach in the boreal forest can develop strategies to maintain burn-associated species on harvested landscapes and highlight key research questions that remain to be answered.

THE BOREAL FOREST ECOSYSTEM

The boreal forest is the most extensive ecosystem in Canada encompassing >581,000,000 ha. Here we describe two major ecozones that occupy extensive areas in the boreal forest of Canada—the boreal plain ecozone and the boreal shield ecozone. Within each ecozone we describe the ecoregions where bird communities or species associated with burns have been studied. Decriptions of these zones and regions were taken from Environment Canada website (http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/default.cfm).

The Boreal Plains

The Boreal Plains ecozone extends southeast from northeastern British Columbia through north-central Alberta and Saskatchewan to southwestern Manitoba, an area of 74,000,000 ha (Fig. 1). The area is strongly influenced by continental climatic conditions: cold winters and moderately warm summers. The studies we summarize in this paper were conducted in the mid-boreal uplands and Wabasca lowland ecoregions of the boreal plain in Alberta and Saskatchewan. The boreal uplands stretch from northcentral Alberta to southwestern Manitoba. Mean summer temperature ranges from 13–5.5 C and mean winter temperature ranges from -13.5 to -16 C. A mean of 400–550 mm of precipitation falls annually and elevations range from 400–800 m above sea level (ASL). In upland mesic habitats, the dominant tree species are trembling aspen (*Populus tremuloides*) and white spruce (*Picea glauca*) occurring most commonly as mixed stands, but also as pure stands. Black spruce (*Picea mariana*), balsam poplar (*Populus balsamifera)*, paper birch (*Betula papyrifera*), and tamarack (*Larix laricina*) dominate wetter sites. Jack pine (*Pinus banksiana*) is found primarily in xeric sites; balsam fir (*Abies balsamea*) is relatively less common. The Wabasca lowland is a low relief area within the mid-boreal upland, where about half the area is covered with peatlands.

The Boreal Shield

At 195,000,000 ha, the boreal shield is the largest ecozone in Canada (Fig. 1). It extends from northern Saskatchewan east to Newfoundland, passing north of Lake Winnipeg, the Great Lakes, and the St. Lawrence River. Climate is strongly continental with long, cold winters and short, warm summers, but conditions are more maritime in Atlantic Canada. The studies we summarize here were conducted in the Abitibi Plains, central Laurentians and southern Laurentians ecoregions of the boreal shield in western and southern Quebec. In these ecoregions mean summer temperatures range from 12.5–14 C and mean winter temperatures from -11 to -12.5 C. Annual mean precipitation varies from 725–1600 mm. Elevation in the Abitibi Plain varies from 121–617 m ASL and in the central and southern Laurentians from 0–1100 m ASL. The southern fringe of the ecoregion is dominated by boreal mixed wood forests (white birch, trembling aspen and balsam poplar together with white (*Pinus strobus*), red (*Pinus resinosa*) and jack pine), the eastern portion by balsam fir and the central and western portions are boreal mixed woodland with an understory component of balsam fir. The northern sections of these ecoregions are dominated by pure black spruce stands with a small proportion of jack pine forests and scattered trembling aspen stands. Spruce stands (mostly black spruce) cover roughly 64% of the productive forest area, mixed stands of spruce and deciduous species 15%, aspen 11%, jack pine 4%, and balsam fir and birch 3%, whereas other species account for less than 1% (Lefort 2003). The studies reported here were conducted primarily in black spruce forest.

NATURAL DISTURBANCES

Disturbances such as fire and insect outbreaks have been major historical forces promoting the mosaic found in the boreal forest. Forest tent caterpillar (*Malacosoma disstria*) is the main herbivore of deciduous trees in western boreal, mixed woodlands, but rarely destroys entire stands (Peterson and Peterson 1992). The impact of insect herbivory on conifers in the mixed woodlands appears to be minimal compared to defoliation by spruce budworm (*Choristoneura fumiferana*) on balsam fir- and black spruce-dominated forests on the boreal shield. Here spruce budworm damage has affected far greater areas than fire or logging combined (MacLean 1980; Bergeron and Leduc 1998, Bergeron 2000). In both systems, blow downs caused by windstorms are locally important.

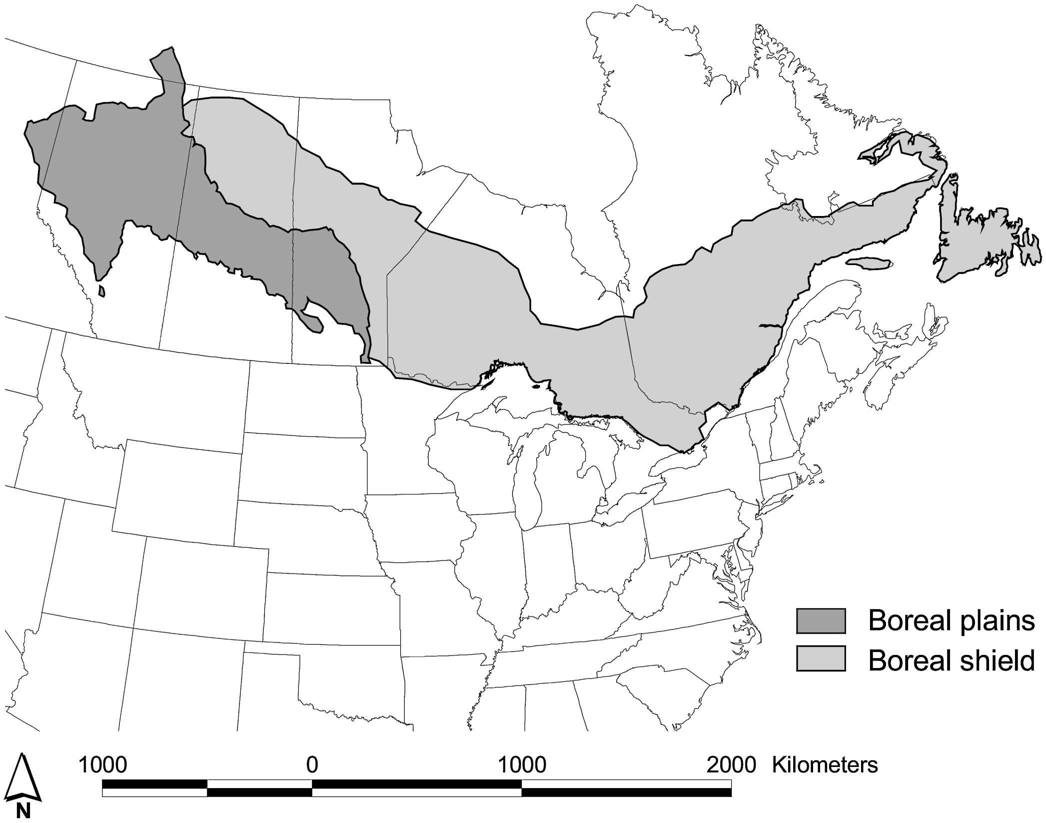

FIGURE 1. The extent of the boreal plains and the boreal shield ecozones (outlined in black) in Canada showing the ecoregions where the studies were conducted. Map taken from Environment Canada website. (http://www.ec.gc.ca/soer-ree/English/Framework/Nardesc/default.cfm.)

The major natural disturbance agent in the boreal, mixed-woodland forest is fire (Johnson 1992). Over centuries, fire frequencies have been dynamic and changes in frequency are related to climate changes, such as the Little Ice Age (Weir et al. 2000). The recent (past 200 yr) fire frequency in the mixed woodland forest on the boreal plain averaged 50–100 yr (Larsen 1997, Weir et al. 2000). Fire frequency showed a downturn between 1920 and1960 with a subsequent increase after 1970 (Johnson 1992), possibly related to climate cooling and then warming (Weber and Stocks 1998).

Fire-return intervals are longer in eastern boreal shield forests (Bergeron et al. 2001); in the Quebec North Shore and Labrador, fire-return intervals can reach 500 yr (Foster 1983). In a reconstruction of the past 300 yr of fire history on the boreal shield, Bergeron et al. (2001) noted a dramatic decrease in fire frequency from the mid-19th century throughout the 20th century, also corresponding to the end of the Little Ice Age. Although all areas showed a similar temporal decrease in area burned, Bergeron et al. (2001) observed that deciduous stands burn at the lowest frequency and black spruce stands burn at the highest frequency.

The distribution of fire sizes in both study regions follows a negative exponential distribution, with most fires burning <1,000 ha, accounting for less than 10% of the total area burned (Bergeron et al. 2002). Consequently, the large fires (>1,000 ha) are primarily responsible for the natural regeneration of the forest, resulting in large areas covered by a relatively uniform seral stage. Fires in the boreal forest are usually severe, killing most of the trees within their perimeter, but there is high variability in fire severity among fires related to climate conditions (Bergeron et al. 2002). Fire skips (unburned islands of trees) represent around 5% of the land base.

ANTHROPOGENIC DISTURBANCES

The forest on the boreal plain has been increasingly affected by anthropogenic disturbance, although fire is still the major disturbance factor (Lee and Bradbury 2002). Clearing for agriculture is prevalent along the southern fringe and in the Peace River area. Transportation routes, pipelines, and seismic lines have bisected many areas. Fire suppression, changes in land use practices and increases in forest fragmentation have altered the natural frequency and intensity of insect outbreaks and fire frequency (e.g., Murphy 1985, Roland 1993, Weir and Johnson 1998). Small-scale harvesting of white spruce for saw logs is common in some areas. Large-scale harvest of aspen dates back only to 1992. As recently as a decade ago, aspen was considered a weed tree by foresters and considerable effort and expense was used to eradicate it. Now, however, aspen has become economically important as a species used in the production of pulp and paper. The pure aspen and aspen-dominated mixed woodland forest are coming under increasing pressure from logging companies.

The province of Alberta has leased >75% of its mixed woodland area to forestry companies under Forestry Management Agreements. Mature (50–100 yr) and old (>100 yr) aspen forests are slated to be cut first. The rotation period will be 40–70 yr, so that few stands of aspen will reach the old-growth stage. Most stands are clear-cut in a checkerboard pattern, with an average cut-block size of 40 ha (maximum 60 ha). The intervening uncut blocks are harvested when trees on the original cut-blocks are about 3 m tall. If this harvesting pattern continues, it will result in high fragmentation of the forest, high edge/area ratios in the remaining uncut portions of the forest, and a lack of large continuous stands of older aspen and mixed woodland. Old aspen and mixed woodland forests are structurally unique compared to younger stands (Stelfox 1995).

The southern, mixed-wood, boreal forest on the boreal shield in Quebec has a longer forest management history than forests on the boreal plain. In the last 30 yr, commercial timber harvesting has moved farther north into coniferous black spruce forests. While the cutting rotation is longer (70–100 yr) in these black spruce forests than in aspen forests, so is the fire cycle. In forests of northeastern Ontario and northwestern Quebec almost 50% of the natural mosaic contains old forests (Bergeron et al. 2001). The prevalent management system is clearcutting that produces patchworks of even-aged stands. Foresters justify the use of clearcutting by the presence of frequent and severe fires that produce even-aged stands. However, even-aged forest regulation will not spare any forest that exceeds rotation age whereas fire can maintain a high proportion of the forest in older age classes (Bergeron et al. 2001). Hence, if we continue harvesting in the same way, the high proportion of mature and old forests in eastern boreal shield forests will be drastically reduced.

In Quebec's black spruce forests, regulations limit the size of clearcuts in any continuous block to <150 ha. However, while individual cut blocks are clearly smaller than the mean size of natural burns, they are harvested in a continuous progression. This clustering of cut-blocks creates thousands of square kilometers of regeneration containing fragments of mature forest in the form of cut-block separators, riparian buffer strips and unproductive or inaccessible forest. More recently, the Quebec government proposed a harvesting pattern that is similar to the one used in Alberta, where stands are harvested in two passes leaving a landscape with a checkerboard appearance of different aged stands. However, this harvesting pattern will not solve the problems linked to highly fragmented forests at large scales. While large areas of the boreal shield are still under natural disturbance regimes, forest management is progressing quickly and there is urgency for developing alternative forestry practices that are aimed at maintaining existing biodiversity.

ECOSYSTEM MANAGEMENT AND THE NATURAL DISTURBANCE PARADIGM

Increasingly the forest industry is embracing the concept of ecosystem management to ensure that harvesting is conducted in an ecologically sustainable manner. A recent focus has been to attempt to pattern forest harvesting (patch size, shape, frequency of cut, spatial pattern of cut, retention of trees in cut-blocks) to resemble that created by natural disturbance, predominantly fire (e.g., Hunter 1993). A critical prerequisite for implementing such a management scheme is a thorough understanding, at the stand and landscape scale, of the effects of natural disturbances on wildlife communities and how these compare with the effects of logging. Many recent studies in the boreal forest have focused on the loss of old forests and its potential effects on old forest dependent species. However, differences in forest conditions in early postfire and post-logged seral stages have often been neglected. These differences must be addressed if we intend to maintain biodiversity in managed forest landscapes.

BIRD ASSEMBLAGES IN BURNED AND LOGGED STANDS

We summarize four studies conducted on bird assemblages in burned and logged forest. Hobson and Schieck (1999) and Morissette et al. (2002) compared vegetation structure and composition and bird communities in burned and logged stands on the boreal plain in Alberta and Saskatchewan, respectively. Imbeau et al. (1999) and Drapeau et al. (2002) compared bird communities in logged and burned black spruce forest on the boreal shield in Quebec.

Hobson and Schieck (1999) and Lee (2002) studied aspen-spruce mixed woodland stands 1, 14, and 28 yr after either a stand-replacing fire or clear-cut logging. They found that the early post-disturbance vegetation structure of burned and logged stands differed markedly. Right after a stand-replacing fire, the stand was dominated by large burned snags and the ground cover was dominated by herbs, whereas after clear-cutting a few live residual canopy trees remained singly or in clumps and the ground cover was dominated by grasses such as *Calamagrostis canadensis* (Fig 2). The early post-disturbance bird communities were also quite different (Hobson and Schieck 1999). In burns, the community was dominated by cavity nesters and species that foraged on beetle infestations in dead trees, whereas clear-cuts were dominated by open country species (Fig 2). Over time, the vegetation structure and composition of burns and clear-cuts converged (Hobson and Schieck 1999, Lee 2002). By about 28 yr post-disturbance, many of the snags fell in burns and the shrubby understory was well developed. Conversely, on clear-cuts, some of the residual live trees died, increasing snag density to levels similar to burns and the shrub layer was more developed. Relative to immediately postfire, snag-dependent bird species decreased in 28-yr burns and shrub-breeding species increased (Fig 2). Species that foraged and nested in canopy trees were more prevalent in 28-yr-old regenerated cut-blocks than burns, because of the retention of live residuals in the cut-blocks (Fig. 2; Hobson and Schieck 1999; Schieck and Song 2002). No research in the mixed woodland system has compared burns and logging beyond 28 yr, but the assumption is that the both the vegetation structure and bird communities become more and more similar over time.

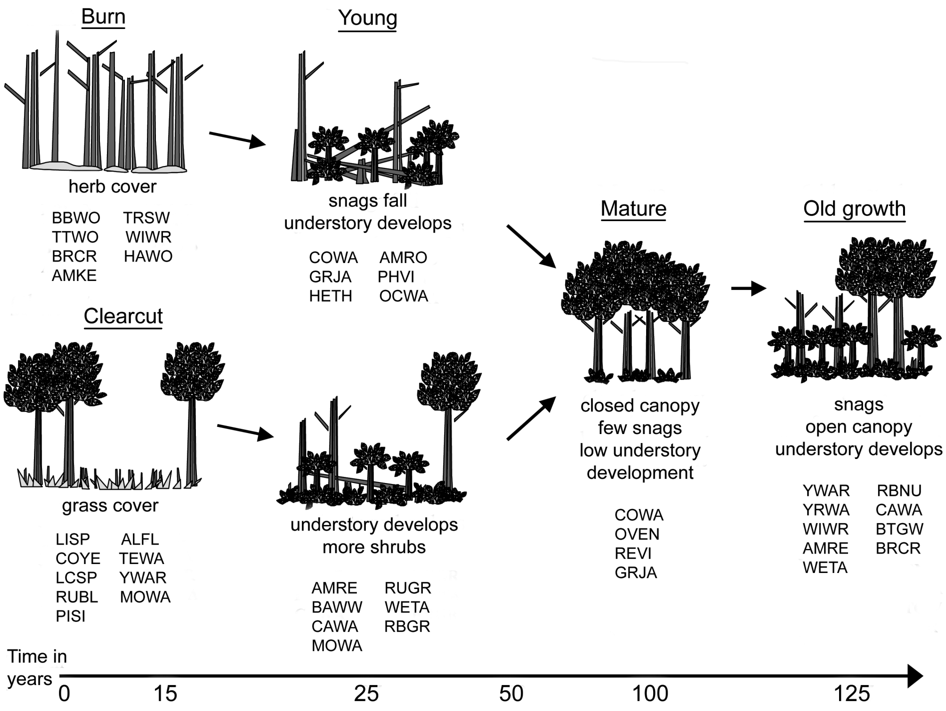

FIGURE 2. Changes in vegetation structure and bird communities after fire and logging in the boreal mixed woodland on the boreal plain of Alberta. Adapted from Hobson and Schieck (1999) and Schieck et al. (1995). Acronyms are defined in Table 1.

Morissette et al. (2002) focussed on unburned, burned and postfire salvage-logged sites three years after a stand-replacing fire in aspen-spruce mixed woodland, jack pine, and aspen stands near Meadow Lake, Saskatchewan. Burned sites had lower canopy cover, more regenerating trees, denser understory, lower litter and moss cover, higher herb and forb cover, and, in jack pine, lower lichen, and higher grass cover than unburned sites. Salvage-logged sites had no canopy cover, highest amount of grass cover and downed woody material, but were similar to burned sites in herb and litter cover and density of regenerating trees. In jack pine, salvage sites had lower moss cover than unsalvaged burns.

Bird communities reflected these differences in vegetation (Morissette et al. 2002). Most species in unburned sites were those associated with older forest: Northern Waterthrush (*Seiurus noveboracensis)* (mixed woodland), Blue-headed (*Vireo solitarius*) and Red-eyed Vireos *(V. olivaceus)* (jack pine), and Ovenbirds (*Seiurus aurocapillus)* (aspen) were most abundant in unburned stands. Burned sites were characterized by generalists, early successional species, mature forest species, and insectivores. Olive-sided Flycatcher (*Contopus cooperi)* and Western Wood-pewee (*Contopus sordidulus*) occurred most frequently in burned, un-salvaged jack pine, and aspen, and American Robin (*Turdus migratorius*) and Dark-eyed Junco (*Junco hyemalis*) were most common in jack pine burns, and Brown Creeper (*Certhia americana*) was most abundant in burned aspen. Black-backed and Three-toed woodpeckers and Black-capped Chickadees (*Poecile atricapilla*) were only encountered in burned sites. Salvage-logged sites were characterized by generalist or early successional species, cavity nesters were absent (except for House Wren (*Troglodytes aedon*), Tree Swallows (*Tachycineta bicolor*), and resident species were sparse (Boreal Chickadee [*Poecile hudsonica*], Red-breasted Nuthatch [*Sitta Canadensis*], and Brown Creeper). LeConte's Sparrow (*Ammodramus leconteii*), Song Sparrow (*Melospiza melodia*), Sharp-tailed Sparrow (*Ammodramus caudacutus*), Vesper Sparrow (*Pooecetes gramineus*), and Lincoln's Sparrow (*Melospiza lincolnii*) were only found in salvage-logged areas, and White-throated Sparrow (*Zonotrichia albicollis*), Clay-colored Sparrow (*Spizella pallida*) and Alder Flycatchers (*Empidonax alnorum*) reached their highest abundances in salvaged areas.

Imbeau et al. (1999) compared bird assemblages in black spruce forests of the boreal shield originating from fire and logging. Bird assemblages show similar responses as those on the boreal plain (Fig. 3). Bird community composition was most different between burns and logged areas immediately after fire or harvest (Imbeau et al. 1999)—species that foraged and nested in snags in recent burns were absent in harvested stands. However, these differences became less pronounced as disturbed stands reached the young forest successional stage. This emphasises the importance of standing dead wood, a key habitat feature of stand-replacement fires. Drapeau et al. (2002) studied black spruce stands after either a stand-replacing fire or logging. Comparisons in postfire and post-logged stands 20 yr after disturbance show that the mean basal area of standing snags remained significantly higher in postfire stands than in old regenerated cut-blocks, although many snags had fallen since the fire. Snag-dependent species, particularly secondary cavity nesters, also decreased in 20-yr-old burns but their abundance was significantly higher than in old cut-blocks.

FIRE ASSOCIATES

We define fire associates as species whose abundances are higher in burned stands than in older unburned stands. In Table 1 we summarized the responses of species to fire in the boreal forest in Canada. The following species appear to be associated with fire in the following stand types (i.e., they reached significantly higher abundance in burns when compared with unburned stands of the same forest type) (1) aspen-spruce mixed woodland—American Kestrel (*Falco sparverius*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Black-backed Woodpecker, Northern Flicker (*Colaptes auratus*), Gray Jay *(Perisoreus canadensis*), Tree Swallow, Brown Creeper, Winter Wren (*Troglodytes troglodytes*), Hermit Thrush (*Catharus guttatus*), American Robin, Connecticut Warbler (*Oporornis agilis*), and Yellow-rumped Warbler (*Dendroica coronata*); (2) aspen—White-throated Sparrow, Brown Creeper, House Wren, Chestnut-sided Warbler (*Dendroica pensylvanica*), Chipping Sparrow (*Spizella passerina*), Olive-sided Flycatcher, and Least Flycatcher (*Empidonax minimus*); (3) jack pine—Black-backed Woodpecker, Three-toed Woodpecker, Dark-eyed Junco, Olive-sided Flycatcher, American Robin, Western Wood Pewee, and Winter Wren; and (4) black spruce—Black-backed Woodpecker, American Kestrel, Tree Swallow, Eastern Bluebird (*Siala sialis*), American Robin, Hermit Thrush, and Cedar Waxwing (*Bombycilla cedrorum*). Note that these studies used point counts as survey methods

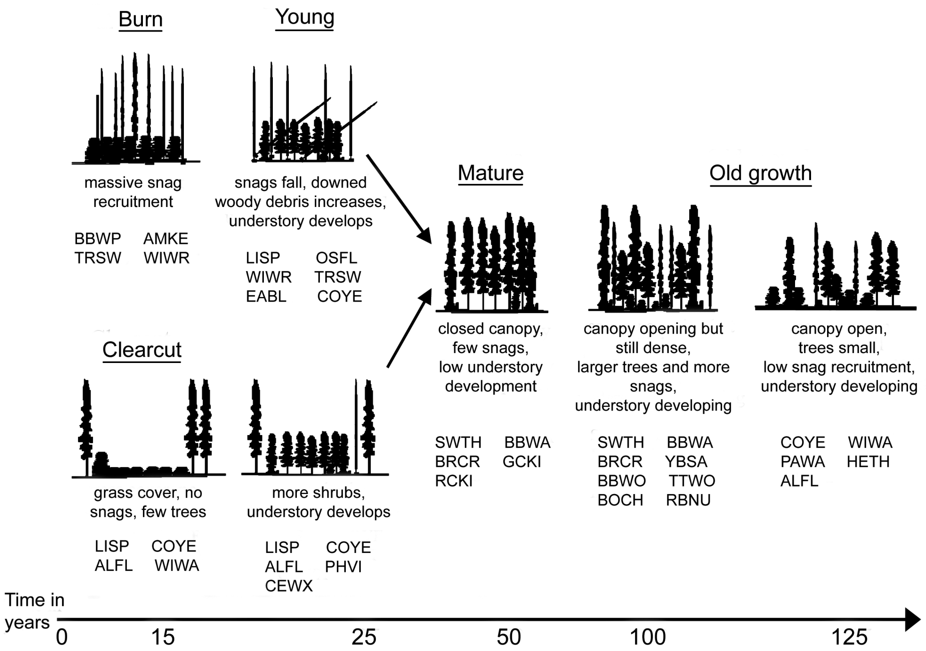

FIGURE 3. Changes in vegetation structure and bird communities after fire and logging in boreal black spruce forests on the boreal shield of Quebec. Adapted from Imbeau et al. (1999) and Drapeau et al. (2002). Acronyms are defined in Table 1, except for GCKI (Golden-crowned Kinglet, [*Regulus satrapa*]); PAWA (Palm Warbler, [*Dendroica palmarum*]); WIWA (Wilson's Warbler, [*Wilsonia Canadensis*]).

and hence did not adequately sample some taxa such as raptors, shorebirds or grouse.

Two species, Black-backed Woodpeckers and Three-toed Woodpeckers, appear to be consistent in their positive response to fire across their range, and the Black-backed Woodpecker appears to be a specialist of recently burned forests (Hutto 1995, Murphy and Lehnhausen 1998, Dixon and Saab 2000, Leonard 2001). These woodpeckers detect burns of coniferous forest and invade them rapidly after fire (Villard and Schieck 1996, Dixon and Saab 2000, Leonard 2001) to forage on insects that colonize burned trees. Black-backed Woodpeckers generally forage on moderately to heavily burned trees and excavate in the sapwood for wood-boring insect larvae (Cerambycidae and Buprestidae), whereas Three-toed Woodpeckers commonly select lightly to moderately burned trees and flake off the bark to access bark beetle larvae (Scolytidae) (Murphy and Lehnhausen 1998). The woodpeckers typically remain at high densities for 2–4 yr after fire, then decline as insect abundance declines (Niemi 1978, Murphy and Lehnhausen 1998).

On the boreal plain, Hoyt and Hannon (2002) found Three-toed Woodpeckers and Black-backed woodpeckers in burned stands of jack pine and white and black spruce (50–140 yr of age prior to burn); however, both species were absent from mature (50–100 yr) forests and were at low density in old growth (>110 yr) forest. Three-toed Woodpeckers were most abundant in sites with large diameter lightly burned spruce and persisted up to 3 yr after fire. This is probably because bark beetles were most prevalent in this type of tree (jack pine has thick bark and is more resistant to insect attack and heavily burned spruce trees are not infested at a high rate). Black-backed Woodpeckers persisted at high levels in burned stands up to 8 yr after fires, possibly because these stands contained jack pine, a species that is more fire-resistant than spruce (Hoyt and Hannon 2002). The thick bark of jack pine retards dessication, making dead and dying trees more suitable habitat for wood boring insects. Black-backed Woodpeckers in a 3-yr old patch of burned black spruce and jack pine foraged preferentially on moderately burned (100% burned, but 80–100% of the bark intact), large diameter (>15 cm diameter at breast height [dbh]) standing jack pine trees, although standing and downed spruce were also used (Hoyt 2000).

TABLE 1. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSES OF BREEDING BIRDS (CHANGE IN ABUNDANCE) TO BURNED VERSUS UNBURNED STANDS IN BOREAL FOREST HABITATS OF ALBERTA (AB), SASKATCHEWAN (SK) AND QUEBEC (QC). SPECIES CODE ACRONYMS GIVEN FOR SPECIES IN FIGS. 2 AND 3.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
American Kestrel AMKE (*Falco sparverius*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 1-yr-old burns.
American Kestrel	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. within 12-yr-burn	+	2	
Ruffed Grouse RUGR (*Bonasa umbellus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 14, 28 yr clearcuts.
Common Snipe (*Gallinago gallinago*) (three fires)	AB	1, 14, 28	Stands 50–200 ha; fire size not given	18 (three/age class of fire, three/age class of harvest)	0	1	
Yellow-bellied Sapsucker (YBSA) (*Sphyrapicus varius*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (3 fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Downy Woodpecker DOWO (*Picoides pubescens*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 14-yr-old burns.
Hairy Woodpecker HAWO (*Picoides villosus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 1-yr burns.
Three-toed Woodpecker TTWO (*Picoides tridactylus*)	AB	2–17	2-yr fire: 135,000 ha; area of older fires not given	6	+	3	Highest in 2-3-yr old burns.
Three-toed Woodpecker	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	
Three-toed Woodpecker	QC	1, 20	12,540 ha 59,720 ha (two fires)	56 stands sampled within 1-yr burn and 49 stands within 20-yr-old burn	0	5	
Three-toed Woodpecker	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled within 12-yr-old burn	0	2	
Black-backed Woodpecker BBWO (*Picoides arcticus*)	AB	1	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	
Black-backed Woodpecker	AB	2–17	2-yr fire: 135,000 ha; area of older fires not given	6	+	3	Highest in 4-8-yr old burns.
Black-backed Woodpecker	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Black-backed Woodpecker	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Black-backed Woodpecker	QC	1, 20	12,540 ha 59,720 ha (two fires)	56 stands sampled within 1-yr burn and 49 stands within 20-yr-old burn	+	5	
Northern Flicker (*Colaptes auratus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 14-yr burns.
Northern Flicker	QC	1, 20	12,540 ha, 59,720 ha (two fires)	56 stands sampled within 1-yr burn and 49 stands within 20-yr-old burn)	+	5	Highest abundance in 20-yr-old burns.
Pileated Woodpecker (*Dryocopus pileatus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Olive-sided Flycatcher OSFL (*Contopus cooperi*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned jack pine and aspen.
Western Wood-Pewee (*Contopus sordidulus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned jack pine and aspen.
Yellow-bellied Flycatcher (*Empidonax flaviventris*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Alder Flycatcher ALFL (*Empidonax alnorum*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Alder Flycatcher	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested stands.
Least Flycatcher (*Empidonax minimus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Least Flycatcher	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Eastern Phoebe (*Sayornis phoebe*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Eastern Kingbird (*Tyrannus tyrannus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Blue-headed Vireo (*Vireo solitarius*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in unburned jack pine.
Warbling Vireo (*Vireo gilvus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Philadelphia Vireo PHVI (*Vireo philadelphicus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Philadelphia Vireo	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Red-eyed Vireo REVI (*Vireo olivaceus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in unburned stands.
Red-eyed Vireo	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Gray Jay GRAJ (*Perisoreus canadensis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Gray Jay	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Most abundant in 14-yr burned forest.
Blue Jay (*Cyanocitta cristata*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Most abundant in 14/28 yr harvested forest.
Blue Jay	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Common Raven (*Corvus corax*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Tree Swallow TRSW (*Tachycineta bicolor*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Tree Swallow	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	
Tree Swallow	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Black-capped Chickadee (*Poecile atricapilla*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Black-capped Chickadee	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Boreal Chickadee BOCH (*Poecile hudsonica*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Boreal Chickadee	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	–	2	
Red-breasted Nuthatch RBNU (*Sitta canadensis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Red-breasted Nuthatch	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	

Table 1. Continued.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Brown Creeper BRCR (*Certhia americana*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Brown Creeper	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest 1 yr after fire.
Brown Creeper	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	–	2	
House Wren HOWR (*Troglodytes aedon*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Winter Wren WIWR (*Troglodytes troglodytes*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	
Winter Wren	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned jack pine.
Winter Wren	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	–	2	
Ruby-crowned Kinglet RCKI (*Regulus calendula*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	Similar abundance in burned and unburned mixed woodland.
Ruby-crowned Kinglet	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	–	2	
Swainson's Thrush SWTH (*Catharus ustulatus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Swainson's Thrush	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	Similar abundance in burned and unburned aspen.
Hermit Thrush HETH (*Catharus guttatus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest 14 yr after fire.
Hermit Thrush	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Hermit Thrush	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
American Robin AMRO (*Turdus migratorius*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
American Robin	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned jack pine.
American Robin	QC	Not specified	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Eastern Bluebird EABL (*Siala sialis*)	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Cedar Waxwing CEWX (*Bombycilla cedrorum*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.
Cedar Waxwing	QC	4, 12	42,000 ha 44,750 ha (two fires)	10 stands sampled within 4-yr-old burn and 10 stands. sampled with 12-yr-old burn	+	2	
Tennessee Warbler TEWA (*Vermivora peregrina*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 14-yr-old harvested.
Tennessee Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in unburned aspen.
Orange-crowned Warbler OCWA (*Vermivora celata*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Yellow Warbler YWAR (*Dendroica petechia*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.
Yellow Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Chestnut-sided Warbler (*Dendroica pensylvanica*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Magnolia Warbler (*Dendroica magnolia*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Magnolia Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Cape May Warbler (*Dendroica tigrina*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Yellow-rumped Warbler YRWA (*Dendroica coronata*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Yellow-rumped Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Black-throated Green Warbler BTGW (*Dendroica virens*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Bay-breasted Warbler BBWA (*Dendroica castanea*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Black-and-white Warbler BAWW (*Mniotilta varia*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 28 yr harvested.
Black-and-white Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
American Redstart AMRE (*Setophaga ruticilla*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 28 yr harvested.
American Redstart	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Ovenbird OVEN (*Seiurus aurocapillus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 28 yr harvested.
Ovenbird	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest unburned aspen.
Northern Waterthrush (*Seiurus noveboracensis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest unburned mixed woodland.
Connecticut Warbler COWA (*Oporornis agilis*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	+	1	Highest in 28 yr burn.
Connecticut Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Mourning Warbler MOWA (*Oporornis philadelphia*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.
Mourning Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged mixed woodland.
Common Yellowthroat COYE (*Geothlypis trichas*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.
Common Yellowthroat	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Canada Warbler CAWA (*Wilsonia canadensis*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 28 yr harvested.
Canada Warbler	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Western Tanager WETA (*Piranga ludoviciana*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Western Tanager	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Chipping Sparrow (*Spizella passerina*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 1 yr harvested.
Chipping Sparrow	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	+	4	Highest in burned aspen.
Clay-colored Sparrow (*Spizella pallida*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged mixed woodland, jack pine.
Vesper Sparrow (*Pooecetes gramineus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged jack pine.
Sharp-tailed Sparrow (*Ammodramus caudacutus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Le Conte's Sparrow LCSP (*Ammodramus leconteii*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 1 yr harvested.
Le Conte's Sparrow	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Fox Sparrow (*Passerella iliaca*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Song Sparrow (*Melospiza melodia*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged jack pine.
Lincoln's Sparrow LISP (*Melospiza lincolnii*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 1 yr harvested.
Lincoln's Sparrow	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	–	4	Highest in salvaged jack pine.
Swamp Sparrow (*Melospiza georgiana*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
White-throated Sparrow (*Zonotrichia albicollis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	m	4	Highest in salvaged mixed woodland and jack pine, high in burned aspen.
White-throated Sparrow	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	

TABLE 1. CONTINUED.

Species/species code	State or province	Years after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Dark-eyed Junco (*Junco hyemalis*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	m	4	Highest in salvaged mixed woodland and burned jack pine.
Dark-eyed Junco	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	0	1	
Rose-breasted Grosbeak RBGR (*Pheucticus ludovicianus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Rose-breasted Grosbeak	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 14 yr harvested.
Rusty Blackbird RUBL (*Euphagus carolinus*)	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in 1 yr harvested.
Pine Siskin (PISI) (*Carduelis pinus*)	SK	3	Stands 6–70 ha; fire 40,000 ha (one fire)	79 stands sampled within burn	0	4	
Pine Siskin	AB	1, 14, 28	Stands 50–200 ha; fire size not given (three fires)	18 (three/age class of fire, three/age class of harvest)	–	1	Highest in harvested.

[a] Only wildland fires are reported in this table.

[b] + = increase; – = decrease; 0 = no effect or study inconclusive, m = mixed response.

[c] References: 1 = Hobson and Schieck (1999), we inferred a negative response when highest abundance was in clearcuts, no response when there was no significant difference between burns and clearcuts, and a positive response if abundance was highest in burns, no stands over 28 yr were compared; 2 = Imbeau et al. (1999); we inferred a positive or negative response for significant differences in abundance between burns and other stand types (harvested or burned) and no response when there was no significant difference; 3 = Hoyt and Hannon (2002); 4 = Morissette et al. (2002); we inferred no response if there was no significant difference among treatments. Note that some species were uncommon and hence the inference of no response could be incorrect; 5 = Nappi (2000); occurrence patterns in 1-yr- and 20-yr-old burns were compared to mature and old forests that all originate from natural disturbances.

On the boreal shield, Nappi (2000) found that the Black-backed Woodpecker reached its highest densities in early postfire black spruce forests. Its occurrence in burns was close to ten times higher than in the early stages of old forest types (>100 yr). The Three-toed Woodpecker was, however, much less abundant in burns than the Black-backed Woodpecker. Its occurrence was similar in burns and in the early stages of old growth development. Nappi et al. (2003) noted that Black-backed Woodpeckers in a 1-yr-old burned, black spruce/jack pine stand preferred to forage on large diameter pine and spruce snags that were lightly burned and still had most of their branches. They also measured the density of wood-boring beetle larvae holes on snags of different size and deterioration classes to assess the relationship between food availability and snag characteristics. Larger snags that were less deteriorated by fire contained higher prey densities (wood-boring beetle holes) than smaller and more deteriorated snags. Hence, they concluded that snag selection was not random—woodpeckers selected snags and portions of snags that contained higher densities of wood-boring insects.

Over the long-term, burns may be temporal habitat sources for fire specialists (Hutto 1995, Murphy and Lehnhausen 1998, Hoyt and Hannon 2002). Secondary cavity nesters such as Eastern Bluebird and Tree Swallow used Black-backed Woodpecker nesting cavities the second and third year following fire (Drapeau, unpubl. data). In addition, species such as Northern Hawk-Owls (*Surnia ulula*) appeared to be abundant in postfire stands (Kotliar et al. 2002). Use of burned stands by fire associates relates to a number of factors affecting insect colonization including tree species composition, age of stand prior to fire and fire severity (Hutto 1995, Murphy and Lehnhausen 1998, Morissette et al. 2002).

CRITICAL MANAGEMENT AND RESEARCH ISSUES

Fire Suppression

Provincial governments in Canada are trying to eliminate fire from boreal forest landscapes, despite the fact that several species have been lost in highly managed forests where fire has been removed (e.g., in Fennoscandia [Östlund et al. 1997, Angelstam 1998]), and that in other regions of North America fire is being reintroduced (e.g., for management of the Red-cockaded Woodpecker (*Picoides borealis*; James et al. 1997)). In Alberta, plans exist to fireproof forested landscapes by cutting fire-breaks through the forest at large scales (Cumming 2001). Another important disruptor of natural fire spread in the boreal plain is the increase in land clearing for agriculture at the fringe of the boreal forest, which might prevent the spread of large fires into forested areas (Weir and Johnson 1998).

Given the size of the boreal forest and the limited access, attempts at active fire suppression in this biome appear to have had limited effect, although this is controversial (Murphy 1985, Johnson 1992). In Québec, for example, most of the forest fires <1,000 ha (90% of the fires since 1940) are suppressed by the Fire Control Agency. Fires >1,000 ha are less likely to be controlled and these large fires are responsible for the regeneration of most of the forest cover of the boreal forest in Québec (Bergeron et al. 2002). Fire suppression has not had a real impact on these fire events. In fact, mean fire size has been greater for the period following the beginning of fire suppression activities than the previous period without intervention (Chabot et al. 1997, Johnson et al. 2001).

Salvage Logging

The most important current threat for birds associated with recently burned forests is salvage logging (e.g., Saab and Dudley 1998, Kotliar et al. 2002). Given the major contribution of recently burned forests both as a key habitat for primary cavity-nesting birds and as the main source of recruitment for dead wood, the intensification of salvage cutting in the boreal forest raises serious concerns. It may not only compromise the maintenance of viable populations for burn-dependent species such as Black-backed Woodpeckers, but it may also greatly reduce the overall availability of dead wood to wildlife across current and future landscapes. In Alberta and Québec, stands that have been recently disturbed by fire and insect outbreaks are salvage logged. All burned trees of commercial timber value are logged and the remainder are knocked down for safety reasons, although patches of live trees >4 ha are left unharvested. Harvesting is not currently conducted with guidelines that incorporate biodiversity concerns, however in both provinces new guidelines are being developed that specify retention of groups of burned trees. While large areas of forest are still inaccessible by road, timber harvesting is expanding to the north and the road network will increase considerably in next 20 yr. Burned areas will thus become increasingly accessible and salvage logging will increase and pose a problem to species that show some dependency on stand-replacement fires.

Trees that are salvaged are in the same diameter classes that woodpeckers use for foraging and nesting (i.e., >20 cm dbh) (Hoyt 2000, Nappi 2000, Nappi et al. 2003). In a study of burned, boreal mixed woodlands (*Populus* and white spruce) where the majority of trees were either harvested or knocked down (<100 standing trees/100 ha), densities of Three-toed Woodpeckers, Black-backed Woodpeckers, Downy Woodpeckers, and Hairy Woodpeckers were lower than in un-salvaged burns (Schmiegelow et al. 2001). In addition, secondary cavity nesters such as House Wrens, American Kestrels, and Brown Creepers were more abundant in un-salvaged versus salvaged-logged burns (Schmiegelow et al. 2001). Similar results were obtained in black spruce forests. Nappi et al. (2003) found that Black-backed Woodpeckers were concentrated in the un-salvaged portions of a burned forest where salvage logging covered 64% of the burned area, and where no snags were left within harvested blocks. Species vary in their responses to salvage logging; however, species tied to recently burned forests are most sensitive (Kotliar et al. 2002).

Hutto (1995) and Murphy and Lehnhausen (1998) also noted the conflict between salvage logging in recently burned or insect-infested old forest and the maintenance of suitable habitat for Black-backed Woodpeckers and other burn associates. Delaying salvage logging in burns for up to 3 yr post-harvest would allow woodpeckers to reproduce, but this conflicts with forestry management practices. Damage to trees from beetle infestations and desiccation usually restricts salvage logging operations to 2 yr postfire. While, for economic reasons, the increase in salvage logging may be unavoidable, there is a crucial need to provide science-based guidelines about how recently burned forests may be managed to provide appropriate habitat conditions to maintain biodiversity. For example, Powell (2000) found that rates of insect colonization differed considerably depending on tree species and degree of burn, hence some tree species could be salvage logged without reducing food supplies for burn-dependent birds. Maintenance of suitable amounts of postfire forests that are spared from commercial salvage logging should be considered as a prerequisite condition for sustainable forest management of early seral stages. The question, however, is how much is enough? A better understanding of the ecology of fire-dependent species in recently burned forests could help us determine the size of un-salvaged burned areas, their spatial arrangement and the quality of standing dead trees that should be left in these areas. Saab et al. (2002) provides useful guidelines for nesting Black-backed Woodpeckers in Ponderosa pine (*Pinus ponderosa*) forests of western Idaho.

Ecosystem Management: Replacing Fire with Logging

The natural disturbance paradigm suggests that the negative impacts of timber extraction on biodiversity can be mitigated by harvesting to emulate natural disturbance patterns, however it remains to be tested. Indeed, the application of ecosystem-management concepts is still not well developed (Simberloff 1998, 2001) and few studies suggest silvicultural treatments and management strategies that allow practical application of these concepts (but see Bergeron et al. 1999, 2002). A major concern for sustainable forest management has been the truncation of the age-class distribution of managed forest landscapes, with a reduction in the abundance of old forests. How forest practices should be modified to maintain structural and compositional characteristics of early postfire stages has been less of an issue. At the stand level, some forest companies have attempted to emulate fire by leaving residual patches of standing dead trees to increase the supply of snags and improve structural heterogeneity. These structured blocks have higher avian-species diversity than traditional clear-cut patches and patches of residual trees are occupied by some species usually found in older forests (Norton and Hannon 1997, Imbeau et al. 1999, Schieck and Hobson 2000, Schieck et al. 2000, Tittler et al. 2001, Schieck and Song 2002). However, they do not provide the abundance of standing dead trees that are found after natural disturbance events and that are key elements of early post-burned stands. Perhaps some form of prescribed burning after harvesting could provide the conditions for insect colonization of the burned residual trees and hence habitat for burn specialists. Wikars (2002), however, found that prescribed burning of residual trees after logging did not provide sufficient habitat for birds that require burned habitats instead of single burned trees. In addition, burn-associated species vary widely in their preferences for foraging and nesting sites (Kotliar et al. 2002). Hence, it is unlikely that modifying forest harvest practices will produce forest conditions similar to those found after natural disturbance events. Thus, a key challenge to ecosystem management is to maintain large tracts of burnt, uncut forest habitat in the landscape.

CLIMATE CHANGE AND HABITAT SUPPLY FOR BURN-DEPENDENT BIRDS

Historical reconstruction of fire dynamics in the Canadian boreal forest has revealed that fire regimes vary regionally and temporally, and future climate change will maintain this variability (Flannigan et al. 1998). In the boreal forest of western Canada, short fire cycles (50–75 yr) (Johnson et al. 1998) could persist because the central boreal plains and western shield and taiga are predicted to have longer, warmer, drier summers, and more fires. For species associated with stand replacement fires this would mean increased habitat supply. However, a coincident increase in areas logged and burned by fire would result in a landscape dominated by young forest stands and concomitant reduction in old-growth habitat. Old-growth forests have experienced an increase in the area burned by fire since the 1970s and a coincident increase in unburned area logged, suggesting that logging is not replacing fire but is adding to it (Lee and Bradbury 2002).

In contrast, in the mixed or coniferous forest regions of northeastern Ontario and Quebec, summers are predicted to be wetter and cooler and the historical intermediate fire-return interval (around 150 yr) (Bergeron et al. 2001) should persist or lengthen. Hence, habitat supply of recent burns might decrease for fire-associated birds. Secondary disturbances such as insect outbreaks and windthrows, that occur in the absence of fire as in the Quebec North Shore or Labrador, are likely to become more important in northwestern Quebec. While these disturbances could provide some suitable habitat for Black-backed Woodpeckers (Goggans et al. 1989, Thompson et al. 1999, Setterington et al. 2000), it is not clear whether viable populations of this species could be maintained in the absence of fire.

KEY RESEARCH QUESTIONS FOR THE FUTURE

Kotliar et al. (2002) outlined a number of important research questions that address avian responses to fire. We agree with these questions and feel that for the boreal forest in Canada the most important questions are:

1. How do bird communities on burns vary with severity of the fire, season of burn, size of burn, age of burn, and stand age and composition prior to the fire? Most studies in boreal forests have focussed on comparing burns to logging and have not investigated the variation in bird responses to severity of burn, either within a single burn or across several burns. Different tree species vary in their susceptibility to fire, hold their bark, fall down, and dessicate at different rates after fires. Also many cavity nesting birds require trees of a certain diameter for nesting and foraging, hence stand composition before burns is likely to be a determinant of species composition after fire (Saab et al. 2002). In addition, some birds may be more likely to detect larger than smaller burns. Bird communities are expected to change over time after fire as bark beetles and wood boring insects decline, trees fall, and cavities are created by primary excavators.
2. How do fire-associated species find recent burns? How large should burns be to attract birds? Are isolated burns detected by fire-associates? It is unclear whether burn-associates move into burns from adjacent unburned stands or whether they can detect burns from further away. If, for example, they find burns by following smoke plumes, how far away can these be detected and how large does the fire have to be to create detectable smoke? The answers to these questions will inform decisions about which burned stands to leave unsalvaged and where one might conduct prescribed burns.
3. How can we change silvicultural prescriptions to leave habitat for burn-associated birds? If forest managers wish to leave some trees on burned stands during salvage logging, they need guidelines on how many trees to leave, their spatial arrangement, what species to leave, and the physical condition of retained trees in order to attract insects and birds. In addition, more work should be done to determine whether prescribed burning can create suitable habitat for burn-associates. Researchers should work with forest managers to set up adaptive management experiments in burned areas to test assumptions about how birds respond to burned habitats.
4. How does the spatial distribution and size of burns and old-growth forest affect the population dynamics of burn-associated birds? For fire specialists, such as the Black-backed Woodpecker, long-term population persistence may depend on a supply of burned habitat over time (Hutto 1995, Murphy and Lehnhausen 1998). In order to determine whether the population dynamics of this species is a temporal source-sink system, we need to conduct detailed demographic studies (reproductive success, survival, and dispersal) in old growth forest and recently burned forest.
5. How will the supply of burned and old-growth habitats change under various climate warming scenarios, predicted levels of forestry development,

and other land uses? Models should be developed to predict habitat supply for burn-associated birds into the future to determine whether fires will become rarer and if so, whether logging activities will further deplete the supply of burned habitats. This would allow managers to introduce prescribed burns to ensure habitat for these species.

ACKNOWLEDGMENTS

We thank C. McCallum for drawing the figures and S. Song for providing an unpublished summary document. V. Saab, H. Powell and E. C. Murphy reviewed the manuscript.

Studies in Avian Biology No. 30:116–126

FIRE REGIMES AND AVIAN RESPONSES IN THE CENTRAL TALLGRASS PRAIRIE

Dan L. Reinking

Abstract. Grasslands make up the largest vegetative province in North America, and one that has been significantly altered over the past two centuries. The tallgrass prairie of the eastern Great Plains and Midwest has declined to a greater extent than any other ecosystem, primarily due to plowing for cereal grain production. Grassland bird populations have declined at a greater rate and over a wider area than any other group of species. Past fire regimes shaped and maintained the tallgrass prairie ecosystem. Fires set by American Indians and caused by lighting were common and probably differed in timing, frequency, and scale from contemporary fire regimes, although historical regimes are not well understood. Fire affects both the composition and the structure of vegetation, and can affect birds in a variety of ways. Direct effects of fire on birds include destruction of nests, while indirect effects may involve changes to vegetation, which favor some bird species over others. Greater-Prairie Chickens (*Tympanuchus cupido*), Henslow's Sparrows (*Ammodramus henslowii*), and Dickcissels (*Spiza americana*) respond negatively to annual fire. Grasshopper Sparrows (*Ammodramus savannarum*) and meadowlarks (*Sturnella* spp.) appear unaffected or respond positively to annual fire. Fire management across the largest remaining portions of tallgrass prairie frequently overemphasizes or de-emphasizes fire over large areas, creating homogenous habitat that does not support the full compliment of tallgrass prairie birds. Availability of adequately sized grasslands in a variety of seral stages is needed to ensure long-term population stability for the suite of bird species inhabiting tallgrass prairie.

Key Words: fire, grassland birds, habitat loss, habitat management, nest success, prairie ecology, tallgrass prairie, vegetation response.

RESPUESTAS DE REGÍMENES DEL FUEGO Y AVES EN LA PRADERA CENTRAL DE ZACATES ALTOS

Resumen. Los pastizales conforman el mayor tipo vegetativo de Norte América, los cuales han sido significativamente alterados en los últimos dos siglos. Los pastizales de zacate alto de las Grandes Planicies del este y del Medio oeste, han decaído mucho más que cualquier otro ecosistema, principalmente debido al arado de la tierra para la producción de granos para cereal. Las poblaciones de aves de pastizales han disminuido en un alto grado y sobre un área mayor, que cualquier otro grupo de especies. Los regimenes anteriores de incendios daban forma y mantenían los ecosistemas de zacates altos en pastizales. Los incendios provocados por los Indios Americanos y por relámpagos eran comunes y probablemente difieren de los contemporáneos en tiempo, frecuencia y escala, sin embargo, los regimenes históricos aún no son del todo comprendidos. El fuego afecta tanto a la composición como a la estructura de la vegetación, y puede afectar a las aves de varias maneras. Los efectos directos del fuego en las aves, incluyen la destrucción de los nidos, mientras que los efectos indirectos quizás involucre cambios en la vegetación, los cuales favorezcan a ciertas especies sobre otras. Los polluelos (*Tympanuchus cupido*), (*Ammodramus henslowii*), y (*Spiza americana*), responden negativamente a los incendios recurrentes. El saltamontes (*Ammodramus savannarum*) y *Sturnella* spp., parece que no son afectados, o responden positivamente a los incendios recurrentes. El manejo del fuego a lo largo de las porciones más grandes que quedan de praderas de zacates altos, frecuentemente sobre enfatiza o minimiza la importancia del fuego sobre grandes áreas, creando habitats homogéneos, los cuales no cumplen completamente con los requerimientos de las aves de las praderas de zacates altos. La disponibilidad del tamaño adecuado de los pastizales con variedad de estados serales es requerido para asegurar la estabilidad a largo plazo de las poblaciones de aves que habitan las praderas de altos pastos.

Grasslands as a whole make up the largest vegetative province in North America, once covering some 17% of the continent (Knopf 1988). Among the varied grasslands of North America, those of the Great Plains are by far the largest. The shortgrass prairie lies west of the mixed grass prairie, and both shortgrass and mixed grass prairies are more arid than the productive tallgrass prairie. I restrict my discussion of fire ecology here to the tallgrass prairie (Fig. 1) where annual precipitation varies from 60–100 cm occurring mostly during the growing season, but late summer droughts are common (Steinauer and Collins 1996, but also see Bock and Bock 1998). Seasonal temperatures range from -35–45 C. Dominant plants include warm-

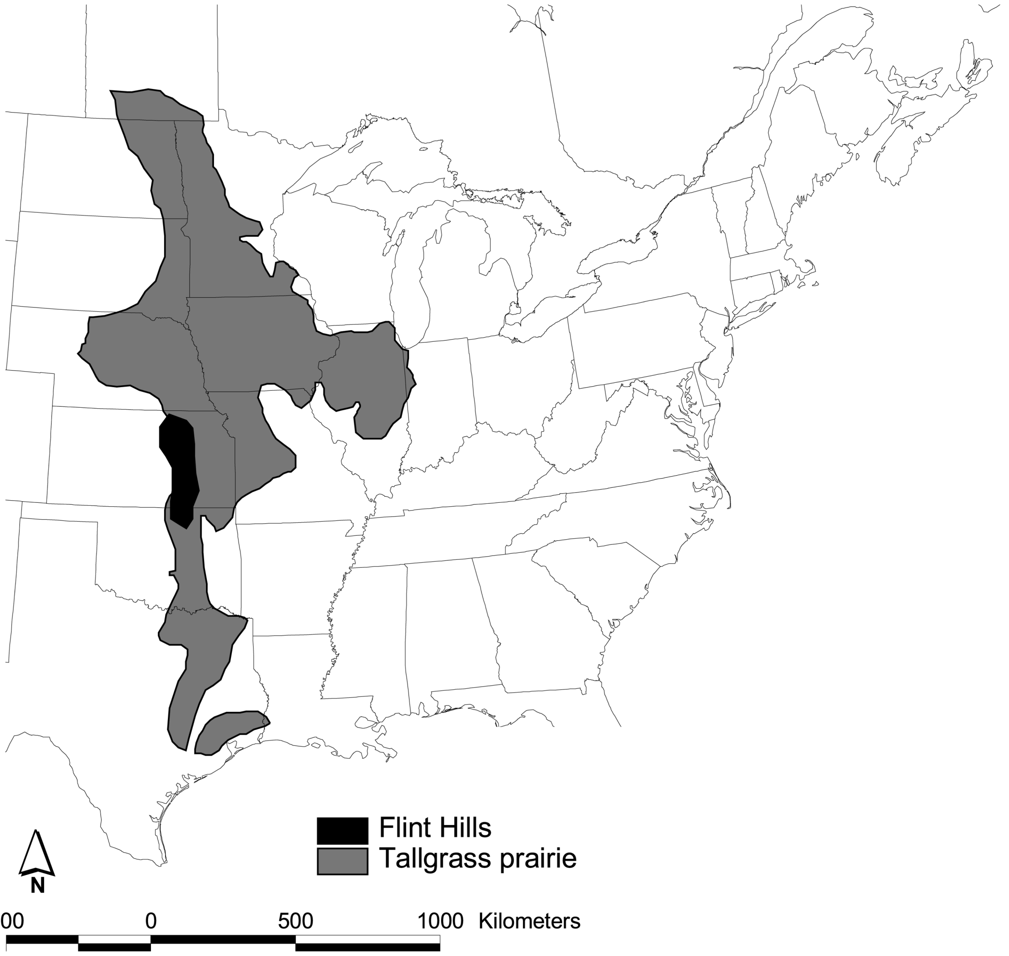

FIGURE 1. Original extent of tallgrass prairie in North America (shaded area), and location of the Flint Hills (darkly shaded area). Adapted from Steinauer and Collins (1996) and Reichman (1987).

season grasses such as big bluestem (*Andropogon gerardi*), Indiangrass (*Sorghastrum nutans*), switchgrass (*Panicum virgatum*), and little bluestem (*Schizachrium scoparius*). The tallgrass prairie once covered some 577,500 km^2 in central North America (Knopf 1988), but its level, fertile soils are ideal for cereal grain production and it has been largely plowed and converted to agricultural uses. An estimated 88–99% of the native tallgrass prairie has been lost, a decline greater than any other North American ecosystem has sustained (Vickery et al. 2000; Table 1). These landscape changes are reflected in grassland bird populations, which have shown steeper and more widespread declines than any other guild of North American species (Knopf 1994).

The tallgrass prairie is of relatively recent origin, as evidenced by its shared taxa with adjoining habitats and the scarcity of endemism (Axelrod 1985). For example, no vascular plants are known to be endemic to Kansas (Wells 1970). Despite the once extensive area of grasslands in the North American landscape, only 5% of North American bird species apparently evolved in the Great Plains (Udvardy 1958, Mengel 1970, Knopf 1994). Mengel (1970) lists 12 bird species as endemic to grasslands, most of which are found west of the tallgrass prairie region in mixed or shortgrass plains. Another 25 species are considered secondarily associated with grasslands, but occur within a larger geographic area, including habitats with trees or shrubs at the periphery of the plains (Knopf 1994). Many of these were later defined as obligate grassland species

TABLE 1. ESTIMATED ORIGINAL AND CURRENT AREA AND PERCENT OF ORIGINAL AREA OF TALLGRASS PRAIRIE. ADAPTED FROM SAMSON AND KNOPF (1994) AND STEINAUER AND COLLINS (1996).

State/Province	Historic area (ha)	Current area (ha)	Decline (%)
Manitoba	600,000	300	99.9
Illinois	8,900,000	930	99.9
Indiana	2,800,000	404	99.9
Iowa	12,500,000	12,140	99.9
Kansas	6,900,000	1,200,000	82.6
Minnesota	7,300,000	30,350	99.9
Missouri	5,700,000	30,350	99.9
Nebraska	6,100,000	123,000	98.0
North Dakota	1,200,000	1,200	99.9
Oklahoma	5,200,000	N/A	N/A
South Dakota	3,000,000	449,000	85.0
Texas	7,200,000	720,000	90.0
Wisconsin	971,000	4,000	99.9

(Vickery et al. 1999b). Among this latter group are several species commonly found in tallgrass prairie, including Greater Prairie-Chicken (*Tympanuchus cupido*), Upland Sandpiper (*Bartramia longicauda*), Eastern Meadowlark (*Sturnella magna*), Dickcissel (*Spiza americana*), Grasshopper Sparrow (*Ammodramus savannarum*), and Henslow's Sparrow (*Ammodramus henslowii*). All but the Upland Sandpiper have shown substantial population declines since Breeding Bird Survey monitoring efforts were initiated in 1966 (Sauer et al. 2001).

Loss and conversion of native grasslands are not the only factors affecting tallgrass prairie birds. Shaped by the forces of drought, grazing, and fire, grasslands are dynamic ecosystems (Axelrod 1985, Gibson and Hulbert 1987, Collins 1990, Coppedge et al. 1998a). These forces have dramatic effects on vegetation composition and structure, as well as on animal life. Axelrod (1985) argued that fire is a key element in the formation and maintenance of the central prairies, and Steuter (1991) emphasized the role of aboriginal peoples in shaping fire regimes. Given that historical fire regimes helped create and maintain the tallgrass prairie, existing tallgrass prairie vegetation and birds are well adapted to conditions in the Great Plains, including periodic fire. Contemporary fire regimes, however, are often very different from these in terms of timing, frequency, and scale (Howe 1994; Engle and Bidwell 2001).

HISTORICAL AND CONTEMPORARY FIRE REGIMES IN THE TALLGRASS PRAIRIE

At the outset, it must be said that our understanding of historical (i.e., pre-European settlement) fire regimes in the central grasslands is incomplete. Few interpretable biological data exist from which to elucidate historical fire regimes. The largely treeless plains offer few scarred tree rings for examination, nor extensive, long-lived woody vegetation (trees) from which to evaluate age structures of vegetation over wide areas (Higgins 1986). The mean fire interval in gallery forests in tallgrass prairie of northeastern Kansas, as determined from fire scars on trees, was estimated to be about 11–20 yr during the period 1858–1983. Because of a limited sample size, Abrams (1985) believed the actual interval to be smaller. In one innovative study, Umbanhowar (1996) tested core samples from four lakes in the northern Great Plains for charcoal concentrations which indicate fire activity, including one in South Dakota at the western edge of the tallgrass prairie. He concluded that charcoal deposition was much lower in the years following European settlement than in the years prior to it, suggesting a decrease in fire activity post-settlement.

Beyond the scanty physical evidence, our understanding of fire regimes is largely based on accounts of early explorers. This written historical record is geographically spotty, biased toward frequently traveled routes, and relies more on anecdotal comments than on observations systematic in terms of geography, timing, or observer. After considering these problems and reviewing a large number of historical accounts, Higgins (1986) concluded that for the northern Great Plains, Fires started by American Indians were mentioned much more often than lightning-caused fires in historical accounts. Indian-set fires occurred in every month except January, with peak frequency of occurrence in the months of April and October. Lightning-caused fires sharply peaked in July and August, with lesser numbers from April through June and in September. Indians used fire as a means of directing movements of bison (*Bos bison*) herds, setting relatively frequent but smaller fires for this purpose. Accidental fires were also common near Indian campgrounds. Most of the really large fires were probably lightning-caused, occurred less frequently, and may have caused hardships for tribes.

Reichman (1987, p. 106) indicates a likely fire interval of 3–4 yr, with a maximum interval of 10 yr, noting that Kansas tallgrass prairie vegetation is most productive in terms of biomass with a fire interval of 2–4 yr. Moore (1972) suggests that the highest frequency of fires in the southern plains region occurred in late summer and fall, coinciding with the peak lightning season.

The effects of fire on tallgrass prairie vegetation have been summarized by Reichman (1987, pp. 107–111). The most obvious and direct effect of fire is to remove standing dead vegetation and litter, reducing the aboveground biomass and exposing the soil to the sun. This allows the soil to warm dramatically faster in the spring, encouraging seed germination. New leaves are able to undergo photosynthesis and push upward much more easily. Fires also recycle small amounts of nutrients, such as nitrogen, which are retained in dead vegetation. Removal of the dead vegetation also allows more rainfall to reach the soil instead of being trapped above ground on vegetation where it can be lost to evaporation. Lightning changes some of the plentiful atmospheric nitrogen to a form that can be used by plants, which falls in rain. Significant amounts of the available nitrogen in tallgrass prairie result from this process, and a host of nitrogen-consuming microbes exist on dead vegetation and in litter, so their removal by fire allows more nitrogen to reach the soil where plants can use it, although frequent fires actually reduce available nitrogen. Fire also kills plants such as forbs and woody vegetation, whose growing tissues are at the top rather that at the base of the plant as in the fire-adapted grasses. All of these factors together favor biomass increases in grasses in the years immediately following a burn.

Public opinion and resulting management of tallgrass prairie has changed over time. Early ecological studies in the drought years of the 1930s resulted in the belief that fire was harmful and should be suppressed (Collins 1990). Over the subsequent decades, research began to show some of the now well-understood positive effects of burning. One study in Kansas tallgrass prairie showed a 34% increase in tree and shrub cover from 1937–1969 on unburned sites, while burned sites showed a mere 1% increase (Bragg and Hulbert 1976). Similarly, Briggs and Gibson (1992) documented a 60% increase in the number of trees in a northeastern Kansas prairie over a 5-yr period without fire, while the number of trees decreased in an annually burned area. This gives a strong indication of the importance of fire in maintaining tallgrass prairie, because woody vegetation encroached rather rapidly without fire. The rate of woody invasion in the absence of fire varies depending on topography and soil type, but such invasion seems characteristic of tallgrass prairie, which does contain trees in moist riparian areas and steep valleys. This change in relative dominance between grasses versus forbs and woody vegetation makes tallgrass prairie an example of a non-equilibrium ecological system (Knapp and Seastedt 1998). It is also important to note that the effects of disturbances such as fire and grazing on tallgrass prairie vegetation may be interactive. Collins (1987) showed that burning significantly reduced plant species diversity on ungrazed plots, while grazing significantly increased diversity on burned plots.

The vast majority of original, native tallgrass prairie has been converted to row-crop agriculture (Table 1) and no longer functions ecologically as a grassland. Virtually all of the prairie peninsula extension of the tallgrass prairie through Iowa and Illinois has yielded to the plow. What little remains of the northern and eastern portions of the original tallgrass prairie exists mostly in small areas of South Dakota, Minnesota, Missouri, and Nebraska, with additional areas in Texas (Knopf 1994, Steinauer and Collins 1996; Table 1). The decline of the tallgrass prairie has one notable exception within a relatively large landscape of eastern Kansas and northeastern Oklahoma. This region, known as the Flint Hills, consists of from 1.6–2,000,000 ha of native tallgrass prairie, and is the largest remaining such area in North America. Its existence today is a result of the region's topography and geology, with hills and shallow, rocky soils making cultivation impractical. Grazing of livestock is instead the major economic use of this area.

During recent decades, the burning of tallgrass prairie has been increasingly used as a management tool for promoting productivity of vegetation utilized by grazers, as well as for management of ungrazed areas. The percentage of cover of warm season grasses declines with time since last burning, while forbs and woody plants increase (Gibson and Hulbert 1987). The total herbage production increases with regular fire treatment, with early spring burns producing the greatest effect (Towne and Owensby 1984), provided that adequate moisture is available after the burn. In the Flint Hills, this understanding of the relationship between burning and herbage production has led to the development of a grazing system known as intensive early stocking, (hereafter IES) (Launchbaugh and Owensby 1978, Smith and Owensby 1978, Vermeire and Bidwell 1998). Under this system, prairie is burned annually or biennially in the spring, which promotes growth of warm season grasses such as big bluestem and Indiangrass. The lush re-growth of palatable, nutritious grass resulting from the burn enables managers to graze twice as many cattle (*Bos*) per unit area as would be done under a year-round, continuous grazing system. Yearling steers are allowed to graze for about 100 d before being removed in July. This allows the grass to recover from grazing pressure, rebuild fuel loads, and go to seed before winter. This system is profitable for ranchers, but results in a high percentage of land in this region receiving fire treatment nearly every year, an interval shorter than that believed to be the historical fire interval of 3–4 yr (Robbins and Ortega-Huerta 2002). The spring timing of these burns also differs from the historical timing of lightning-set fires, which were usually ignited in late summer.

Gibson (1988) evaluated the effects of a 4-yr burning interval (burning in early April) on tallgrass prairie vegetation. Total live biomass of vegetation was lowest after the fire in the year of the burn (called year 0), while biomass was significantly higher in years one, two, and three. Grass biomass, however, was highest in year 0 and 1 and declined thereafter. Biomass of forbs was lowest in year 0, and increased during the following 3 yr. A recent review of vegetation responses to fire in tallgrass prairie indicates that the conventional belief that all fires except those taking place late spring act to decrease desirable forage grasses and increase weedy forbs may not be accurate (Engle and Bidwell 2001). Burning date is just one of many factors influencing vegetation response to fire; other factors include fire frequency, grazing history, and topographic and edaphic factors. Several studies indicate some positive (from a grazing manager's perspective) responses of vegetation to early dormant-season burns (Hulbert 1988; Mitchell et al. 1996, Coppedge et al. 1998b.). Furthermore, Engle and Bidwell's review (2001) also suggests that the assumed or perceived increase in weedy forbs following an early dormant-season fire is often nonexistent or much less than believed.

Engle and Bidwell also point out the irony in the scarcity of studies evaluating the effects of late growing season fires on tallgrass vegetation, given that a high proportion of pre-settlement fires in this habitat occurred at this season. Ewing and Engle (1988) found that the effects of late summer fire on tallgrass vegetation in Oklahoma were influenced by the intensity of the fire, something that is partially dependent on fuel loads at the time of the burn. Intense late summer fires in areas with high fuel loads changed community composition by reducing warm season grasses and increasing non-matrix ruderals, though total biomass production remained consistent and matrix grasses recovered by the end of the following growing season. Engle et al. (1993, 1998) further addressed the issue of late summer fire and concluded that its effects on vegetation were variable, especially with regard to little bluestem, forbs, and cool-season, annual grasses. Such burns did not severely reduce herbage production nor drastically alter community composition for more than 1 yr. Tallgrasses tolerated growing-season fire, a result valuable to document but not too surprising, given the evolutionary history of repetitive fires in this habitat and the resulting dominance of warm-season tallgrasses.

While contemporary range management in large portions of the Flint Hills overemphasizes fire within an historical context, fire suppression in other portions of the Flint Hills and wider tallgrass prairie ecosystem has induced biologically important changes as well. As discussed above, fire acts to reduce woody vegetation and encourages dominance of warm season grasses. Fire suppression therefore allows encroachment of woody vegetation into tallgrass prairie. Among the most significant examples of this process is the invasion of eastern red cedar (*Juniperus virginiana*) and ashe juniper (*Juniperus ashei*) into western rangelands. By 1950 these two species had invaded 607,000 ha in Oklahoma; by 1985 the total was nearly 1,500,000 ha, and by 1994 almost 2,500,000 ha were occupied by these species (Engle et al. 1996). The extent of this problem goes beyond tallgrass prairie into more western grasslands, but significant portions of tallgrass prairie in Oklahoma and other states have been affected. Briggs et al. (2002) demonstrated that Kansas tallgrass prairie can be converted to closed-canopy, red cedar forest in as little as 40 yr. Junipers are well suited to colonization of prairie given their rapid growth rate, high reproductive output, and dispersal ability (Holthuizjen and Sharik 1985, Briggs et al. 2002). Housing developments in tallgrass prairie regions result in fire suppression, and residential planting of junipers for landscaping purposes exacerbates the spread of these species (Briggs et al. 2002). The effectiveness of burning as a control measure for red cedar is primarily a function of tree height (Engle and Kulbeth 1992). Red cedar trees in

Oklahoma tallgrass prairie grow faster than those located farther west in the state in more arid grasslands, and therefore fire frequency must be greater in tallgrass prairie to constrain cedar expansion (Engle and Kulbeth 1992). Juniper invasion reduces available herbaceous forage in tallgrass prairie, and therefore reduces the sustainable stocking rates for livestock (Engle et al. 1987, 1996). Annual grazing of livestock can reduce the above-ground fuel load to a point where even annual fires are not effective in controlling red cedars because the fires are of insufficient intensity to cause tree mortality (Briggs et al. 2002). This relationship between grazing, fire, and red cedar control warrants further study, and managers need to be vigilant for indications that this process may be occurring on their lands. The prompt reintroduction of fire (and/or mechanical methods of tree removal) into areas that have been burned too infrequently is needed if the widespread and rapid succession of tallgrass prairie to red cedar forest is to be halted or reversed (Engle et al. 1996).

EFFECTS OF FIRE REGIMES ON BIRDS

Too Much Fire or Not Enough?

Fire is required for the maintenance of tallgrass prairie and its associated birds. As defined by Vickery et al. (1999b), obligate grassland birds are "species that are exclusively adapted to and entirely dependent on grassland habitats and make little or no use of other habitat types... Obligate grassland birds would almost certainly become extinct without the appropriate grassland habitat." The non-equilibrium tallgrass prairie ecosystem shifts to a state of dominance by woody vegetation in the absence of fire, at the expense of the appropriate grassland habitat needed by grassland birds. As an example, the ongoing rapid invasion of tallgrass prairie by junipers, occurring largely as a result of fire suppression, has consequences for a range of tallgrass prairie species. Given known habitat preferences of Greater Prairie-Chickens (Schroeder and Robb 1993), Grasshopper Sparrows (Vickery 1996), Henslow's Sparrows (Herkert et al. 2002), and Dickcissels (Temple 2002), just to name a few, it is clear that expanding areas of red cedar forest are unlikely to support most tallgrass prairie bird species. Increased use of fire as a habitat maintenance tool is required in portions of the tallgrass prairie.

How then are birds affected by fire in the tallgrass prairie? As illustrated by the preceding section, the effects of fire on tallgrass prairie vegetation are highly variable and are dependent upon a host of factors. The effects of fire on tallgrass prairie birds are varied as well, ranging from direct effects such as nest mortality to less direct but still obvious effects on vegetation structure and subsequent habitat suitability. In some cases, fire effects on one bird species may be opposite those on another species, so management objectives must be clear to understand the relative value or harm of a tallgrass prairie fire. Several examples may help illustrate the variable nature of avian responses to tallgrass prairie fire.

Because most bird species are highly mobile, fires generally create little in the way of direct adult mortality (Reichman 1987). However, a fire occurring during a vulnerable time in the life cycle of a bird, such as the nesting season, may result in mortality of nests or recently fledged young. Early nesting species such as Greater Prairie-Chickens may be harmed by frequent spring burning of tallgrass prairie for IES grazing operations (Zimmerman 1997, Robbins and Ortega-Huerta 2002). In contrast, the use of late summer fires after the nesting season which at one time were the most frequent seasonal fires, would minimize effects on most bird species. While it is true that many species (including prairie-chickens) will re-nest after the loss of a first nest, presumably some species that may have had the opportunity to rear more than one brood in a season may be unable to do so as a result of losing a first brood.

Short-term effects of fire depend upon several factors, such as precipitation in the months following a fire. As indicated earlier, vegetative productivity of tallgrass prairie often increases following a fire, but in years of below-average rainfall, productivity in burned prairie is lower than that of unburned prairie (Hulbert 1988; Briggs et al. 1989). Zimmerman (1992) found reduced bird abundances in burned Kansas prairie during drought years for a large group of species as a whole, with striking differences for a number of individual species including Northern Bobwhite (*Colinus virginianus*), Brown Thrasher (*Toxostoma rufum*), Bell's Vireo (*Vireo belli*), Common Yellowthroat (*Geothlypis trichas*), Field Sparrow (*Spizella pusilla*), and Henslow's Sparrow.

Grassland birds are known to respond to habitat structure (Wiens 1973, Rotenberry and Wiens 1980, Bock and Webb 1984, Patterson and Best 1996, Zimmerman 1997). Frequent fires in tallgrass prairie have been shown to reduce avian diversity in part by removing woody vegetation required by many bird species (Zimmerman 1992, 1997). Frequently burned grasslands are structurally simpler than unburned grasslands, and as a result support fewer species. From studies in Kansas, Zimmerman (1992) stated "Fire has a direct structural impact on the community and eliminates certain species by affecting critical dimensions of their niches, not as a result of competitive resource partitioning, but rather by obliterating species-appropriate resource space." Henslow's Sparrows (*Ammodramus henslowii*) and Common Yellowthroats were particularly affected this way by burning in Zimmerman's study. This reduction in structural complexity of vegetation through the use of frequent fires, and the resulting reduction in avian diversity, is biologically significant given current widespread use of IES as a grazing regime. Significant portions of the Flint Hills landscape are burned annually or near-annually, creating structurally homogenous grasslands rather than the naturally occurring patchy mosaic of varying structure that once existed.

Herkert et al. (1999) monitored Northern Harrier (*Circus cyaneus*) and Short-eared Owl (*Asio flammeus*) nests in Illinois grasslands. Areas that had been mowed, burned, hayed, or grazed (all of which reduce the height or density of vegetation) during the preceding 12 mo were managed grasslands, while those that had not received any management treatment were unmanaged grasslands. Northern Harriers showed strong selection for unmanaged grasslands for nesting, while Short-eared Owls nested only in managed grasslands. These divergent habitat preferences are related to the height of vegetation in the different treatments, and possibly to the amount of standing dead vegetation as well. Harriers in the Great Plains generally nest in areas with vegetation >55 cm tall and where dead vegetation makes up at least 12% of total cover (Duebbert and Lokemoen 1977, Kantrud and Higgins 1992). In contrast, Short-eared Owls usually nest in grasslands with vegetation <50 cm tall (Duebbert and Lokemoen 1977, Kantrud and Higgins 1992).

Such contrasting responses to changes in vegetation structure are apparent in passerines as well. At The Nature Conservancy's Tallgrass Prairie Preserve in northeastern Oklahoma, study plots were monitored for nesting birds and habitat changes in response to land management from 1992–1996. Avian relative abundance data and vegetation structure data were collected on plots with differing fire and grazing histories. Relative abundance of Grasshopper Sparrows following a burn was highest and essentially stable in year 0 and one, but declined with each passing year in the absence of fire through year six, the longest interval measured (G. M. Sutton Avian Research Center, unpubl. data). No Henslow's Sparrows were detected in areas which were 0 and 1 yr after burning, while areas 2, 3, and >3 yr after burning all contained similar numbers of birds (Reinking et al. 2000). Vegetation height and structure are dramatically different in areas recently burned versus areas that have not been burned for several years. Results from this and other studies indicate that Grasshopper Sparrows prefer areas with sparser vegetation (at least in tallgrass prairie), while Henslow's Sparrows require areas with tall, dense, vegetation (also see Dechant et al. 2001, Herkert 2001; Table 2). Annual burning therefore seems either to benefit or at least pose little threat to Grasshopper Sparrows in tallgrass prairie, while effectively eliminating suitable habitat for Henslow's Sparrows (Table 2).

Avian abundance in response to habitat manipulation is usually apparent and relatively easy to measure by point counts or other survey methods. Other potential effects of fire on birds, such as nest success, may be more subtle or harder to measure, or may interact with other factors such as grazing, complicating our interpretation of observed responses to fire. Nest success is a critical demographic parameter for managing bird populations and may not be correlated with relative abundance, which is easier to measure (Van Horne 1983, Maurer 1986, Vickery et al. 1992). Fire may affect nest success through changes in vegetation height and density, potentially providing nest predators with either easier or harder access to nests. Johnson and Temple (1990) found several grassland birds in Minnesota to have higher nest success in areas that had been recently burned. They attributed this response to the tall, dense re-growth following a fire providing better nest concealment, along with increased seed and insect production, allowing more time to be spent in nest defense and less time in foraging.

Fires have varied effects on insect diversity and abundance (Swengel 2001), with grasshoppers and predaceous ground beetles becoming much more abundant in the months following a fire. Zimmerman (1997) found no increase in either nest success or in fledging weights of young from successful nests for a number of species including Dickcissels, Eastern Meadowlarks, Red-winged Blackbirds (*Agelaius phoeniceus*), or Mourning Doves (*Zenaida macroura*) in burned versus unburned Kansas prairie and concluded that food was not a limiting resource, even in unburned prairie.

In the largest remaining area of tallgrass prairie, the Flint Hills, it is often difficult to separate the effects of fire from those of grazing, given the near-ubiquitous and closely associated burning and grazing of grasslands in this region. Both Zimmerman (1997) and Rohrbaugh et al. (1999) found reduced

Table 2. Short-term responses to prescribed fire in tallgrass prairie for selected species. All studies took place during the breeding season. Year 0 represents the nesting season following a spring fire. N/A means not applicable or not reported.

Species	State	Year after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Northern Harrier	Kansas	0–1	variable	several	m	1	Nested in unburned; foraged in burned.
(*Circus cyaneus*)	Illinois	0–1	8–120	17	–	2	Mowing used more than burning.
Greater Prairie-Chicken	Kansas	0	N/A	N/A	–	3	Spring fires cause direct mortality of early nesters.
(*Tympanuchus cupido*)	Kansas	0	variable	many	–	4	No population declines where rangeland is not burned annually.
Upland Sandpiper	Wisconsin	0–1?	N/A	several	–	5	No nesting in year with burning.
(*Bartramia longicauda*)	Kansas	N/A	N/A	N/A	0	6	
	Kansas	0	varied	several	m	1	No nesting in burned areas during year of fire; foraged in burned areas.
Short-eared Owl (*Asio flammeus*)	Illinois	0–1	8–120	17	+	2	Mowing used more than burning.
Grasshopper Sparrow (*Ammodramus savannarum*)	Minnesota	0–3	16–486	8	+	7	Nest success declined with ≥4 yr since burning in larger fragments.
	Kansas	0	varied	2 burned; 7 unburned	0	1, 3, 8	Relative abundance similar in burned and unburned areas.
	Illinois	1–3	0.4–650	11	+	9	More abundant in recently burned areas.
	Missouri	varied	6–571	42	+	10	Declined with increasing time since last disturbance.
	Kansas	0	9.3–13.8	10	+	11	More abundant in burned tallgrass than in burned CRP fields.
	Kansas	0–4	9.7–16.8	12	0	12	Abundance non-significantly greater in burned areas.
	Missouri	0–2	31–1084	13	0	13	Abundance not affected by burning.
	Oklahoma	0–3+	>16	6	0	14	Nest success, clutch size and number fledged per successful nest did not differ in burned vs. unburned. Nesting densities declined with time since last burn.
Henslow's Sparrow	Kansas	0	varied	4	–	3, 15	
(*Ammodramus henslowii*)	Oklahoma	0	varied	20	–	16	Nests only in areas not recently burned.
	Kansas	0	9.8–39.1	14	–	17	Absent in spring burns.
	Illinois	0–2	0.5–650	24	–	9, 18	Absent in year 0, present in year 1, more abundant in year 2 after fire.
	Missouri	0–3	6–571	42	–	10	More abundant in yr 1–3 after a fire than in year 0.
	Missouri	0–2	31–1084	13	–	13	Reduced abundance in year 0 of fire; numbers increased by yr 1 and 2 after fire.
	Illinois	0–4	125–300	3	–	19	Nearly absent in year 0 after a burn; present in similar numbers in yr 1, 2, 3, and 4 after fire.

TABLE 2. CONTINUED.

Species	State	Year after fire	Size (ha) and No. of fires[a]	No. of replicate sites	Response[b]	Reference[c]	Comments
Henslow's Sparrow (*continued*)	Kansas	0–2	N/A	N/A	–	20	Mostly absent in yr 0 and 1 following a burn; present in yr 2 and 3 after fire.
	Oklahoma	0–3+	varied	5	–	21	Absent in yr 0 and 1 after burn; similar numbers in yr 2, 3 and >3 after fire.
Dickcissel (*Spiza americana*)	Illinois	0–5+	1.5–48.2	139	–	22	Peak nest density in year 2 after burn.
	Kansas	0	varied	2 burned, 7 unburned	0	1, 8	Abundance unaffected by burning.
	Missouri	0–3	6–571	42	0	10	Abundance unaffected by burning.
	Kansas	0	varied	2 burned, 7 unburned	–	3	When combined with grazing, burning reduced abundance and nest success.
	Kansas	0–4	9.7–16.8	12	–	12	Abundance and nest success lower in year 0 after a burn.
	Missouri	0–2	31–1084	13	0	13	
	Oklahoma	0–3+	>16	6	–	14	Nest success lower in burned and grazed areas; nest numbers, clutch size, and number fledged per successful nest did not differ.
Eastern Meadowlark (*Sturnella magna*)	Illinois	0–5+	1.5–48.2	139	0	22	Nest density similar in burned and unburned areas.
	Kansas	0	varied	2 burned, 7 unburned	0	1, 3, 8	
	Illinois	0–2	0.5–650	24	0	9	
	Missouri	0–2	31–1084	13	0	13	Abundance slightly lower in year 0 after burn than in later yr.
	Oklahoma	0–3+	>16	6	0	14	Nest success, clutch size, and number fledged per successful nest did not differ in burned and grazed areas vs. unburned/ungrazed areas; nest numbers declined in unburned areas over time.
(*Sturnella* spp.)	Kansas	0–4	9.7–16.8	12	+	12	Abundance increased in year 0 after burn.

[a] All reported fires were prescribed.

[b] + = positive; – = negative; 0 = no effect or study inconclusive; m = mixed response.

[c] References: 1 = Zimmerman (1993); 2 = Herkert et al. (1999); 3 = Zimmerman (1997); 4 = Robbins and Ortega-Huerta (2002); 5 = Buss and Hawkins (1939); 6 = Bowen (1976); 7 = Johnson and Temple (1990); 8 = Zimmerman (1992); 9 = Herkert 1994a; 10 = Swengel (1996); 11 = Klute et al. (1997); 12 = Robel et al. (1998); 13 = Winter (1998); 14 = Rohrbaugh et al. 1999; 15 = Zimmerman (1988); 16 = Reinking and Hendricks (1993); 17 = Schulenberg et al. (1994); 18 = Herkert (1994b); 19 = Herkert and Glass (1999); 20 = Cully and Michaels (2000); 21 = Reinking et al. (2000); 22 = Westemeier and Buhnerkampe 1983.

nest success rates for Dickcissels in burned and grazed tallgrass prairie of Kansas and Oklahoma, respectively. Zimmerman's study did not indicate reduced nest survival in grazed but unburned prairie, nor in burned but ungrazed prairie. These studies provide examples about bird responses to factors that interact with fire, which are potentially different from conditions produced by fire alone. Rohrbaugh et al. (1999) found no difference in clutch size or in the number of young fledged per successful nest for Dickcissel, Grasshopper Sparrow, or Eastern Meadowlark between burned/grazed plots versus unburned/ ungrazed plots. Zimmerman (1997) also noted no differences in fledging weights of birds in burned versus unburned areas.

Mechanisms behind observed nest success differences in burned/grazed versus unburned/ungrazed prairie are not well understood. The close association between burning and subsequent grazing in this region makes separation of the effects of fire from those of grazing difficult to interpret, but both disturbances act to reduce vegetation density. Fretwell (1977) argued that density of Dickcissels was significantly related to nest predation rates. Zimmerman (1984), however, demonstrated that there was no density-dependent effect on nest predation rates in this species. Askins (2000) suggested that the succulence and nutrition of new vegetation growth resulting from a fire provides increased foraging opportunities for grazers (such as insects), and consequently such areas also offer better foraging for insect predators, including birds and other vertebrates. By inference, this suggests that potential nest predators could also benefit from increased prey biomass in recently burned areas.

Relatively little research has been conducted on the winter ecology of tallgrass prairie birds. Zimmerman (1993) reported a mean species richness of 7.7 and 1.2 during winter in unburned prairie and annually burned prairie, respectively. American Tree Sparrows (*Spizella arborea*) and Northern Harriers were the only species regularly found in annually burned areas and both were more abundant in unburned areas.

PERSPECTIVES IN MANAGING AND UNDERSTANDING THE CENTRAL TALLGRASS PRAIRIE

Tallgrass prairie habitat continues to be lost (Warner 1994), making effective management of remaining prairie critical to sustaining grassland bird populations. In portions of remaining tallgrass prairie, fire is under utilized (Engle et al. 1996, Briggs et al. 2002), a trend that if not halted and reversed will have increasingly severe consequences for grassland birds. Understanding the consequences of different fire-return intervals is necessary for maintaining the long-term floristic and faunal diversity of the tallgrass prairie. When fire is applied at a shorter return interval than is considered natural for this ecosystem (Robbins and Ortega-Huerta 2002), the objective is usually to promote dominance of a few livestock forage species (Fuhlendorf and Engle 2001). This leads to reduced structural diversity in vegetation, which then results in reduced bird species diversity owing to exclusion of some species, and may reduce nest success in others (Table 2).

Patch burning involves burning roughly one-third of a given area in each year (Fuhlendorf and Engle 2001). This creates focal points of intense herbivory, results in a fire-return interval of 3 yr, leads to increased structural heterogeneity, and, at least initially, appears to be productive in terms of herbivore response. This management regime is probably closer to the natural patterns and processes of tallgrass prairie (Howe 1994). Burning annually (IES) or taking no action to reduce encroachment of red cedar both create large areas of homogenous habitat that do not support the full complement of grassland bird species. Results of several studies have demonstrated area sensitivity in a number of grassland bird species (Johnson and Temple 1986; Herkert 1994a, 1994c; Vickery et al. 1994; Winter 1998). Species-specific area requirements reported by Herkert (1994c) for Illinois include 5 ha for Eastern Meadowlark, 30 ha for Grasshopper Sparrow, and 55 ha for Henslow's Sparrow. In Missouri, Upland Sandpipers occurred only in grasslands larger than 75 ha, and while Dickcissel density was not correlated with fragment size, nest success in this species was positively correlated with fragment size (Winter 1998). This underscores the importance of collecting and using demographic population measures in addition to population density when evaluating the effects of fragment size. Samson (1980) indicated that >100 ha were needed for Greater Prairie-Chickens, though a total of 4,000–8,000 ha has recently been suggested as a necessary land area for sustaining a healthy population of this species (Bidwell 2003).

Historical evidence suggests that pre-settlement tallgrass prairie fires took place at irregular intervals of perhaps 3–10 yr in any given area. Fires were ignited by both American Indians and by lightning at various times of the year but especially in late summer. Contemporary use of fire in tallgrass prairie is a necessary and powerful management tool that can yield dramatic results in terms of the response of both vegetation and birds. Fire and grazing today rarely operate at the same frequency or with the same seasonality as they did historically, and certainly not at the same scale. Contemporary fire regimes have been altered for a variety of reasons, including agriculture, development to accommodate expanding human populations, profitability of ranching, and changes in our understanding of the importance and consequences of fire in the tallgrass prairie ecosystem. In Oklahoma, areas of low human population density favor Neotropical migrants, ground and shrub-nesting species, and three obligate grassland species (Greater Prairie-Chicken, Grasshopper Sparrow and Dickcissel), whereas areas of high human population density favored habitat generalist species (e.g., European Starling [*Sturnus vulgaris*], Common Grackle [*Quiscalus quiscula*], and House Sparrow [*Passer domesticus*]; Boren et al.1999). As human populations and land development increase, effective management of remaining tallgrass prairie becomes increasingly important.

Long-term research on the interactions of fire, vegetation, and bison grazing has been conducted at both the 3,500-ha Konza Prairie near Manhattan, Kansas, and at the Tallgrass Prairie Preserve, a 15,700-ha property managed by The Nature Conservancy in northeastern Oklahoma (Vinton et al. 1993, Hamilton 1996, Hartnett et al. 1996, Coppedge et al. 1998a; Knapp and Seastedt 1998). Monitoring is ongoing to understand avian responses to the developing mosaic of habitats created by dynamic applications of fire and grazing (i.e., patch burning). Studies examining the relationships among vegetative, invertebrate, and vertebrate responses to varying applications of fire and grazing will help our understanding of land management activities to sustain tallgrass prairie systems. Additional research into the mechanisms behind nest success differences among disturbance regimes will help managers in sustaining bird populations. Perhaps most useful would be intensive nest monitoring using cameras or other technology to determine the identity of the significant nest predators, together with measures of predator abundance in areas subjected to differing fire applications. The reported reduction in nest success for several bird species in burned and grazed prairie suggests that this relationship between disturbances and nest predation rates is important for prairie management. Predator species and key factors (vegetation structure, food availability, or others alone or in combination) influencing the abundance of these birds remain unclear. More evaluation on the economics (from a ranching perspective) of patch burning in tallgrass prairie will help in deciding the extent to which such management techniques can be implemented. Finally, further investigation of the winter ecology of tallgrass prairie birds is also needed to determine the effects of prairie burning on birds during this understudied but critical period of the avian life cycle.

Current widespread use of annual or near-annual burning in the spring, together with widespread lack of burning in other areas, promotes a single type of grassland habitat available to birds. Such uniformity of management does not provide adequate habitat for the suite of tallgrass prairie bird species. A shift to more varied fire regimes, which still maintain the profitability of ranching, would allow for greater avian species diversity and potentially higher nest success as well.

ACKNOWLEDGMENTS

Hugh Powell, Vicki Saab, and two anonymous reviewers provided thoughtful, constructive comments that resulted in many improvements to this manuscript. Michael Patten and Don Wolfe provided helpful information.

Studies in Avian Biology No. 30:127–138

FIRE ECOLOGY AND BIRD POPULATIONS IN EASTERN DECIDUOUS FORESTS

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Abstract. Eastern deciduous forests are located across the central portion of eastern North America and provide habitat for a wide diversity of bird species. The occurrence of fire in the region has been associated with the presence of humans for over 10,000 yr. While pre-European fire regimes are poorly understood, fire is widely thought to have promoted and maintained large expanses of oak forest, woodland, and savanna documented in original land surveys. Forest composition is gradually shifting from fire-tolerant oaks (*Quercus* spp.) to other species (e.g., maples [*Acer* spp.]) and suppression of fire has been implicated as a primary cause. Prescribed fire has been used successfully to restore and maintain oak savannas and has been advocated to improve the sustainability of oak forests. Fire ecology research has addressed short-term effects of prescribed fire on habitat structure, breeding bird populations, and nesting productivity. In the short term, prescribed fire reduces habitat suitability for forest-interior birds that nest on the ground and in low shrubs but provides more favorable conditions for disturbance-dependent birds associated with savannas, woodlands, and early-successional forest. The use of prescribed burning requires tradeoffs in terms of management and conservation because some bird species benefit while others are negatively affected, depending on the degree to which fire changes habitat features. There is a critical need for long-term studies to better understand the effects of different fire regimes on bird populations in the eastern deciduous forest region.

Key Words: eastern deciduous forest, fire history, fire suppression, forest-interior birds, maple, oak, prescribed fire, savanna.

ECOLOGÍA DEL FUEGO Y POBLACIONES DE AVES EN BOSQUES DECIDUOS DEL ESTE

Resumen. Los bosques deciduos del este, se encuentran en la porción central del este de Norte América, y proveen de habitat a un gran número de especies de aves. La ocurrencia de incendios en la región ha sido asociada con la presencia de humanos de hace 10,000 años. Aunque los regimenes del fuego pre-Europeos son pobremente comprendidos, se piensa que el fuego ha promovido y mantenido grandes extensiones de bosque de encino, bosques y sabanas, esto documentado en inspecciones originales de campo. La composición del bosque cambia gradualmente de encinos (*Quercus* spp.) a otras especies (ej. maples [*Acer* spp.]) siendo la supresión del fuego la principal causa. Las quemas prescritas han sido utilizadas exitosamente para restaurar y mantener sabanas de encinos y han sido soportadas, para mejorar las sustentabilidad de los bosques de encino. La investigación en ecología del fuego ha resultado en efectos de corto plazo en quemas prescritas, como en la estructura del habitat., en poblaciones de aves reproductoras y en la productividad de anidamiento. En el corto plazo, las quemas prescritas reducen los requerimientos del habitat apropiados para aves del interior del bosque, las cuales anidan en el suelo y en los arbustos bajos, pero provee condiciones más favorables para las aves dependientes de los disturbios, asociadas con sabanas, bosques, y bosques de sucesión temprana. El uso de quemas preescritas requiere intercambios en términos de manejo y conservación, ya que algunas especies de aves se benefician, mientras que otras son afectadas negativamente, dependiendo el grado en el cual el incendio cambie las características del habitat. Existe una necesidad crítica de estudios de largo plazo, para entender mejor los efectos de diferentes regimenes del fuego en poblaciones de aves en la región de bosques deciduos del este.

Eastern deciduous forests provide habitat for a wide diversity of bird species. Specific habitat requirements for resident, breeding, and migratory bird species in the region include closed-canopy forests, open woodlands, savannas, and early-successional forests (DeGraaf 1991). Bird populations in eastern deciduous forests have been the subject of increasing conservation concern as long-term declines have been detected for many species, particularly forest-interior species (Robbins et al. 1989, Sauer et al. 2001). Declines are also occurring for many bird species associated with disturbance-mediated habitats, such as savannas, woodlands, and early-successional habitats (Askins 2000, Brawn et al. 2001, Hunter et al. 2001, Sauer et al. 2001). Conservation priorities in the region should be balanced to provide a mix of habitat for both forest-interior and disturbance-dependent bird species (Askins 2000, Hunter et al. 2001). Fire was historically an important disturbance factor in some ecosystems, such as oak-dominated forests, savannas, and woodlands, providing habitat for a variety of disturbance-dependent bird species. Fire frequency declined during the period of active fire suppression, but is now increasing through experimental use of prescribed burning. Reintroduction of fire is considered to be necessary to maintain the health and sustainability of ecosystems and to provide habitat for disturbance-dependent bird species. Tradeoffs in the use of prescribed burning may be apparent, however, because some forest-interior bird species may be negatively affected by burning treatments.

Here we review the structure and composition of eastern deciduous forests, the historical and current occurrence of fire, and the effects of fire on bird populations. We focus on ecosystems in which oaks (*Quercus* spp.) are a dominant component because fire was an important process historically and prescribed fire is being advocated and used to restore and maintain these systems (Anderson et al. 1999, Brose et al. 2001, Healy and McShea 2002). Fire is much less frequent in maple-beech-birch and mixed mesophytic forests; fire regimes and effects of fire for these and other ecosystems within the region were reviewed by Wade et al. (2000).

EASTERN DECIDUOUS FORESTS: COMPOSITION AND STRUCTURE

Eastern deciduous forests as defined by Braun (1950) are located across the central portion of eastern North America (Fig. 1), currently covering 155,000,000 ha (Smith et al. 2001). The eastern deciduous forests are bounded to the north and south by coniferous forest and to the west by prairies. The boundaries between vegetation types are based on climatic conditions (Delcourt and Delcourt 2000). The northern boundary where northern hardwood forests blend into boreal forests is defined by average minimum temperatures of -40 C; the southern boundary where oak-pine forests blend into southern pine forests is defined by average minimum temperatures of 0 to -15 C; and the western boundary where oak-hickory forests and savannas make the transition into prairies is defined by annual precipitation of 60–100 cm.

Within the eastern deciduous forest region, forest types are classified based on location and dominant tree species. Oak-hickory is the dominant forest type within the region, covering 52,000,000 ha (Smith et al. 2001). This forest type, also referred to as the central hardwoods covers expansive areas in the central and southern portions of the region (Fig. 1). Oak-pine forests, forming the transition zone between oak-hickory and southern pine forests, cover 14,000,000 ha. Maple-beech and birch-aspen forests, also referred to as the northern hardwoods cover 29,000,000 ha, and are located in northern portions of the region, between oak-hickory and boreal forests. Elm-ash-cottonwood forests (not shown in Fig. 1), located along northern river and stream bottoms, cover 5,000,000 ha. Oak-gum cypress forests (also not shown in Fig. 1), located along southern river and stream bottoms, cover 12,000,000 ha.

Closed-canopy forests (>70% canopy closure) have been a predominant component of the landscape throughout the region, although the total area of such forests has changed over time due to shifts in land-use practices (Smith et al. 2001). As European settlers replaced American Indians, nearly all forests were harvested for homesteading and agriculture (e.g., crops, livestock, buildings, and firewood) or industrial uses (e.g., lumber, charcoal, and transportation). Most forest clearing was confined to the Atlantic coast prior to 1790 (Delcourt and Delcourt 2000), but a dramatic influx of settlers into the Ohio River valley occurred after 1790, resulting in widespread forest harvesting, which continued into the 20th century (Williams 1989). Since 1940, forest cover has increased in the north following abandonment of agricultural land and remained relatively stable in the south (Smith et al. 2001).

Savannas and woodlands are distinguished from forests by a more open structure, generally 10–70% canopy closure (Anderson et al. 1999). Savannas and woodlands were a significant component of the landscape in the transitional zone between eastern forests and midwestern prairies. Savannas covered some 11–13,000,000 ha at the time of European settlement (Nuzzo 1986). However, following conversion to agricultural use and succession to forest, savannas now occupy less than 1% of their former range (Nuzzo 1986, Anderson and Bowles 1999).

FIRES AND FOREST ECOLOGY

Oak-dominated forests in the region have been maintained, in part, by the recurrence of fire both before and after European settlement. Most species of oaks possess a suite of morphological and physiological traits that promote resistance to fire. These traits include thick bark, effective wound compartmentalization, high root-to-shoot ratios, the ability to sprout repeatedly after being top-killed, and drought tolerance (Crow 1988, Reich et al. 1990, Hengst and Dawson 1994, Huddle and Pallardy 1996, Smith and Sutherland 1999). Fire also creates favorable

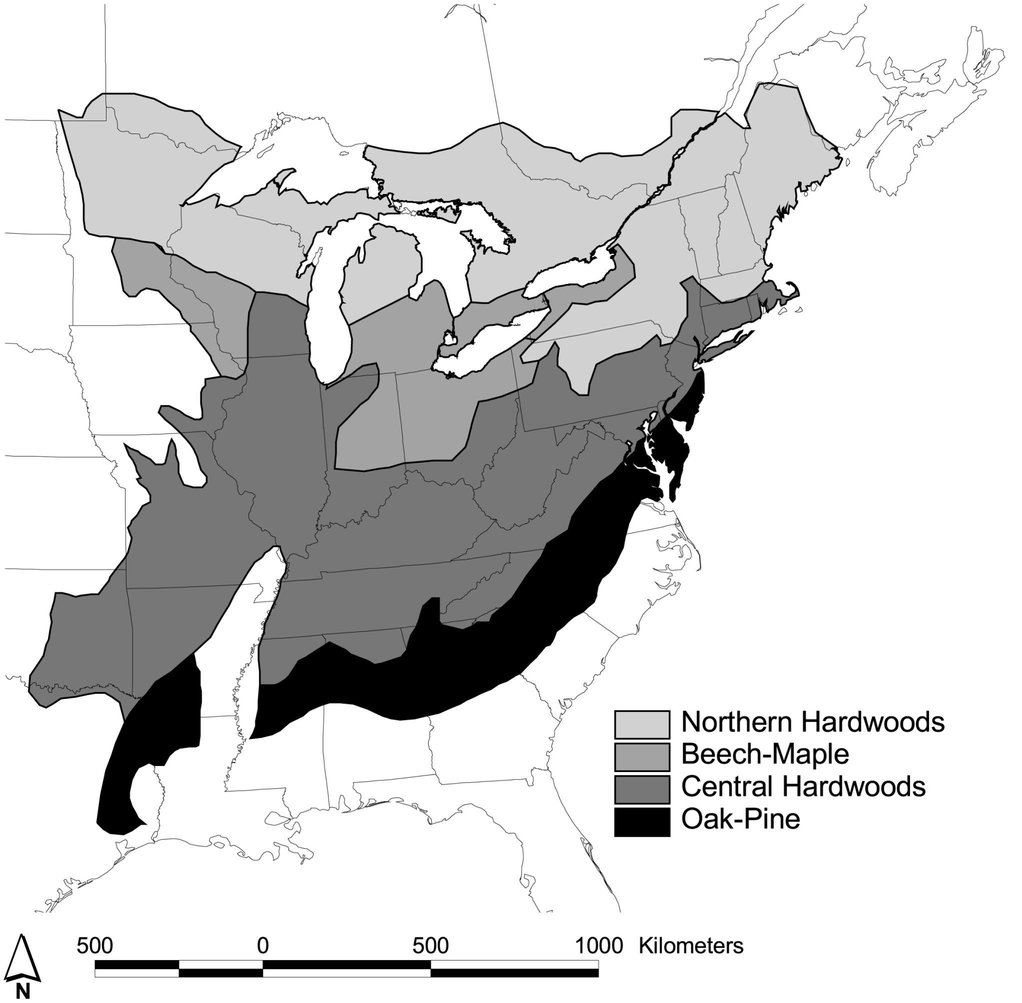

FIGURE 1. Distribution of forest land in the eastern United States by forest type (Smith et al. 2001).

conditions for oak regeneration by creating a suitable seedbed for burial and germination of acorns and reducing competition from fire-intolerant tree species (Lorimer 1985).

Fires have also been important in maintaining oak savannas and woodlands in the transitional region between eastern deciduous forests and central prairies. Frequent low-intensity surface fires control invading woody species and maintain the open structure of savannas and woodlands (White 1983, Faber-Langendoen and Davis 1995, Peterson and Reich 2001). Without recurring fire, savannas rapidly convert to closed-canopy forests, with eastern red cedar (*Juniperus virginiana*) being one of the most aggressive woody invaders (Wade et al. 2000).

Fires have been relatively unimportant in the ecology of the northern hardwood forests (Wade et al. 2000). Forests in these areas, dominated by a mix of maples (*Acer* spp.), beech (*Fagus grandifolia*), and birch (*Betula* spp.), have been called asbestos forests because fires are so uncommon (Bormann and Likens 1979). The lack of fires has been attributed to a rapid turnover of litter from high decomposition rates and minimal amounts of dead wood on the forest floor, thus limiting fuel loads (Bormann and Likens 1979). Fires in these areas occur occasionally as catastrophic, stand-replacing burns, following major windfalls such as hurricanes or tornadoes (Stearns 1949, Bormann and Likens 1979, Wade et al. 2000).

HISTORY OF FIRE

PRE- AND POST-EUROPEAN SETTLEMENT

The history of fire in the region has been dictated by a combination of human activity, climatic conditions, and vegetation types (Wade et al. 2000). Fire regimes varied from low-intensity surface fires in the central hardwoods to high-severity stand-replacement fires in the northern hardwoods and savannas (Wade et al. 2000). Humans have been and continue to be the primary source of ignition (Leete 1938, Wade et al. 2000), although lightning-caused fires occur rarely, particularly during drought years (Ruffner and Abrams 1988). Humans have been present in the region throughout its postglacial development, and American Indian populations were large prior to European contact (Denevan 1992). Although precise fire regimes are unknown, evidence from several sources suggests that fire has been a recurring disturbance in parts of the region prior to and after European settlement, and that fire played an important role in shaping the structure and composition of vegetation.

Written accounts of the landscape by early European explorers provide evidence that Americans Indians used fire to manage the landscape for hunting, gathering, agriculture, and travel (Day 1953, Pyne 1982, Williams 1989, Whitney 1994, Bonnickson 2000). Direct observations of fire and burned-over landscapes were numerous, and indirect evidence of fire was provided by descriptions of open park-like forests. While most reviews conclude that human use of fire was frequent and widespread, Russell (1983) argued that fire was only frequent around settlements, at least in New England. However, Denevan (1992) argued that much of the landscape had recovered from intensive American Indian land use practices by the time of early European exploration and description. Bonnickson (2000) summarized early accounts of presettlement forests as consisting of "a mosaic of young, middle-aged and old pioneer forests, and dense old transitional forests and self-replacing forests." Variation in topography and human disturbance thus interacted to maintain "a dynamic and diverse landscape of people and forests" (Bonnickson 2000).

Analyses of fire scars on tree rings and fossil pollen and charcoal in peat deposits have shown that fire frequency and extent have been highly variable throughout the region (Table 1). Most variation in fire frequency has been attributed to changes in human activity, population levels, and cultural values. Fire regimes have also been affected by local topography, with the spread of fire inhibited by rugged terrain and barriers such as steep bluffs, streams, lakes, and rock outcrops (Dey and Guyette 2000, Guyette et al. 2002, Guyette et al. 2003). Weather patterns have been unimportant in influencing local fire regimes with no correspondence between fire and drought (Cutter and Guyette 1994, Sutherland 1997, Guyette et al. 2003), possibly because insufficient fuel was available to sustain fires during drought years (Cutter and Guyette 1994).

Before European settlement, fire frequency was directly correlated with population levels of American Indians. Fire frequency increased during periods of American Indian occupation and declined when American Indians moved away from specific geographic areas (Guyette and Cutter 1991, Clark and Royall 1995, Dey and Guyette 2000, Guyette et al. 2003). In southern Ontario, for example, the highest charcoal accumulation rates in sediments occurred during Iroquois occupation, from 1350–1650 (Clark and Royall 1995). Low fire frequencies at sites in Missouri, Indiana, and southcentral Ontario were attributed to movement of American Indians away from the sites (Guyette and Cutter 1991, Dey and Guyette 2000, Guyette et al. 2003).

Frequent fires associated with American Indians contributed to major changes in forest composition. Clark and Royall (1995) reported that a change in forest composition occurred 600 yr ago in southern Ontario, with oaks replacing beech and maple. The timing of this transition was substantiated by the co-occurrence of charcoal deposits, changes in abundance of oak, maple, and beech pollen, and archaeological evidence of Indian occupation. After Indian occupation ended, oaks were replaced by the more typical northern hardwood forest (Clark and Royall 1995). Similarly, Delcourt and Delcourt (1998) observed the co-occurrence of charcoal deposits and abundant oak pollen in pond and bog sediments from Kentucky, Tennessee, and North Carolina. The timing of increases in charcoal deposits and oak pollen at these sites also coincided with evidence of Indian settlement (Delcourt and Delcourt 1998).

Fires continued to occur after European settlement but the frequency varied spatially and temporally based on factors such as fuel loads, land use changes, and cultural values. Guyette et al. (2002) identified distinct stages in the history of fire regimes after European settlement, based on tree-ring analyses in Missouri: (1) from 1850–1890, greater numbers of ignitions caused frequent fires but limited the accumulation of fuels; (2) from 1890–1940, land use changes such as agricultural and rural development caused fragmentation of fuels, limiting the spread,

TABLE 1. SUMMARY OF LITERATURE ON THE FREQUENCY OF FIRE IN EASTERN DECIDUOUS FORESTS OF NORTH AMERICA.

Reference	Time	Location, habitat	Number of samples	Mean fire-return interval
Tree-ring analyses				
Guyette and Cutter 1991	1656–1989	southern Missouri, oak savanna	43	pre-1810—4.3 yr
				post-1810—6.4 yr
Cutter and Guyette 1994	1734–1991	Missouri, oak-hickory forest	24	pre-1850—2.8 yr
				post-1850—24 yr
Sutherland 1997	1856–1995	southern Ohio, mixed-oak forest	14	5.4 yr for all fires; 11.3 yr for major fires
Dey and Guyette 2000	1636–1994	southcentral Ontario, oak forest	7	Range—6–29 yr
Shumway et al. 2001	1615–1958	western Maryland, oak forest	20	7.6 yr; no fires after 1959
Guyette et al. 2002	1680–1990	southeastern Missouri, oak-pine forests	257	pre-1850—10 yr (range 2.3–45 yr)
				1851–1890—3.5 yr (range 1.5–6.8 yr)
				1891–1940—5.8 yr (range 1.7–19 yr)
				post-1940—>20 yr (range 6.8–50 yr)
Guyette et al. 2003	1650–1999	southern Indiana, barren-forest mosaic	27	Overall—8.4 yr (range 1–129 yr)
				pre-1820—23.0 yr (range 4–129 yr)
				post-1820—5.3 yr (range 1–40 yr)
Fossil pollen and charcoal analysis				
Clark and Royall 1995	pre-1360 to present	Crawford Lake, Ontario		pre-1350—low accumulation
				1350–1650—accumulation with two major fires
				1650–1900— low accumulation
				post-1900—high accumulation with no major fires

frequency, and size of fires; and (3) from 1940–1996, active fire suppression, motivated in part by increased economic value of timber, resulted in significant reductions in fire frequency. Not all evidence supports these general characterizations, however. Fire frequency was higher before than after European settlement at two sites in Missouri (Guyette and Cutter 1991, Cutter and Guyette 1994). In contrast fires occurred more frequently after European settlement at a site in southern Indiana, with burning occurring on almost an annual basis from 1896–1908 (Guyette et al. 2003). Overall, a significant heterogeneity in fire regimes occurred at the landscape scale throughout the history of the region.

Fire-suppression legislation was passed in the early 20th century in response to destructive fires that hampered reforestation efforts. The Weeks Act of 1911 provided federal funds to state forestry bureaus for fire protection on state and private lands. Funding increased in 1924 with the Clarke-McNary Act which, over time, produced an effective fire detection and suppression infrastructure (Pyne 1982). Analyses of fire scars showed that fire frequency was much lower after 1930 at sites in southern Ohio (Sutherland 1997) and western Maryland (Shumway et al. 2001). Wildfire statistics for southern Ohio (1912–2001) provide an example of the dramatic decline in the annual area burned since organized fire suppression began (Fig. 2).

As forest succession and fire suppression have proceeded in many areas, early-successional habitats have been reduced and oak-dominated forests are gradually being replaced by forests dominated by a mix of maples and beech (Griffith et al. 1993, Abrams 1998, Askins 2000, Hunter et al. 2001). In an old-growth forest in western Maryland, the overstory is currently dominated by oaks, but the recruitment layer has shifted from oaks to maple and birch, with the timing of this shift corresponding with a lack of major fires since 1930 (Shumway et al. 2001).

Current Use of Prescribed Fire

In the last 10 yr, concern has increased regarding the long-term sustainability of oak-dominated forests as has interest in the history and ecological effects of fire in the region. Prescribed fire, alone or in combination with silvicultural treatments, has been widely advocated to restore the historic fire regime, particularly in savannas and oak-dominated forests (Lorimer 1993, Van Lear and Watt 1993, Brose et al. 2001, Healy and McShea 2002). The actual use of prescribed fire, however, has been limited. Prescribed burning has been used in national

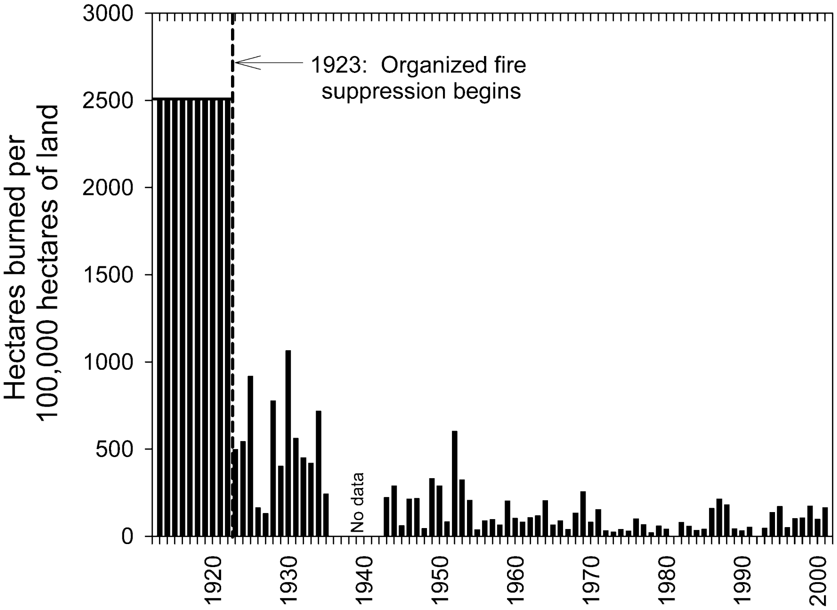

FIGURE 2. Annual area burned per 40,000 ha of land for 10 counties in southern Ohio, 1912–2001. The 1913–1922 annual value is based on an estimate that 133,418 ha (of 520,000 total forest ha) were burned within the previous 10 yr, from a 1931 Ohio Division of Forestry report titled "Forest fire control plan for Ohio." Data from 1923–1935 are from Leete (1938). Other data (1943–2001) are from Ohio Division of Forestry records.

forests to improve sustainability of oak-dominated forests, improve wildlife habitat, restore savannas, and reduce fuel loads, but the spatial extent of burning has been relatively small on most forests. Nearly 70% of forest land in the region is owned by non-industrial private landowners (Smith et al. 2001) where prescribed fire is seldom used. Several states (Ohio, Virginia, and North Carolina) have initiated programs to certify public land managers and private citizens in the use of prescribed burns. Prescribed burning thus may be used more frequently on private lands in the future.

Most prescribed fires in the region are low- to moderate-intensity surface fires, occurring during early spring prior to the greening of vegetation or in autumn following senescence. Fewer fires occur during summer, when the canopy is closed, understory vegetation is lush, and humidity levels are high. The primary fuel is unconsolidated leaf litter. Single low-severity fires cause little mortality to overstory trees (Barnes and Van Lear 1998, Brose and Van Lear 1999, Elliott et al. 1999), but repeated fires can result in reduced tree survival (Huddle and Pallardy 1996). In contrast to the overstory, single and repeated fires result in high mortality of small trees and saplings (Barnes and Van Lear 1998, Blake and Schuette 2000). On the forest floor, the cover and richness of herbaceous plants increases and shrub cover decreases following fire (Hutchinson and Sutherland 2000). A single fire may consume 30–80% of the leaf litter and repeated fires expose mineral soil as the duff layer is also reduced (Barnes and Van Lear 1998, Boerner et al. 2000).

Although prescribed fire has been widely advocated to improve oak regeneration, short-term studies have shown mixed results. Use of prescribed fire alone (or understory removal to simulate fire) has been shown to either improve the competitive status of oaks (Lorimer et al. 1994, Barnes and Van Lear 1998) or have a neutral effect (McGee et al. 1995, Elliott et al. 1999, Kuddes-Fisher and Arthur 2002). Use of prescribed fire in combination with overstory thinning has shown positive and negative effects on the competitive status of oaks (Wendel and Smith 1986, Kruger and Reich 1997, Brose and Van Lear 1998). In part, there must be a long enough fire-free interval for oak seedlings to attain a sufficient degree of fire resistance (Johnson 1993). For example, no oak recruitment occurred from 1750–1810 in Missouri when the mean fire-return interval was only 4.3 yr (Guyette and Cutter 1991). Variation in fire frequency, with some long fire-free intervals, thus appears to be critical to oak regeneration.

BIRDS AND FIRE ECOLOGY

Prescribed Fire in Closed-canopy Forests

Little information has been published on bird responses to fire in eastern deciduous forests (Table 2). Research was conducted to assess short-term effects of prescribed fire on bird populations in closed-canopy forests in southern Ohio (Artman et al. 2001, Artman and Downhower 2003) and southern Indiana (Aquilani et al. 2000). In southern Ohio, prescribed burns were applied as a repeated series of low-intensity, surface fires with treatments occurring over a 4-yr period. Frequent sites were burned 4 yr in a row and infrequent sites were burned twice during a 4-yr period (Artman et al. 2001, Sutherland et al. 2003). All fires occurred during early spring, before leaf-out and before arrival of most migratory bird species. Bird populations were monitored 1 yr before burning, during each of the 4 yr after burning, and at control (unburned) sites for comparison. The size of burned and unburned sites ranged from 20–30 ha, and the experimental design included four replicates for each treatment. In southern Indiana, prescribed burns were applied twice during a 3-yr period (Aquilani et al. 2000). These fires also occurred during early spring. Bird populations were monitored in the burned site for 2 yr after the fires and at an adjacent unburned site for comparison. The size of each site was approximately 140 ha.

The low-intensity surface fires in both Ohio and Indiana resulted in significant reductions in population levels of several species of ground- and low-shrub-nesting bird species. Among the affected bird species were the Ovenbird (*Seiurus aurocapillus*) Worm-eating Warbler (*Helmitheros vermivorus*), Hooded Warbler (*Wilsonia citrina*), Northern Cardinal (*Cardinalis cardinalis*), and Black-and-white Warbler (*Mniotilta varia*) (Aquilani et al. 2000, Artman et al. 2001). Four years of repeated fires in southern Ohio resulted in incremental population declines, with no recovery within one year after the fires, as shown for the Hooded Warbler and Ovenbird in Fig. 3a and 3b (Artman et al. 2001). Populations of ground- and low-shrub nesting bird species continued to occur at low population levels even after the four successive years of fires (Artman et al. 2001). However, nesting success rates for ground- and low-shrub-nesting bird species were lower in burned than unburned areas in both Ohio and Indiana, possibly because nests were more exposed to predators in burned areas (Aquilani et al. 2000, Artman, unpubl. data). If prescribed fire is applied on a frequent basis or across large spatial scales in closed-canopy forests,

TABLE 2. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSE OF BIRD SPECIES (CHANGE IN ABUNDANCE) TO PRESCRIBED FIRE IN EASTERN DECIDUOUS FORESTS OF NORTH AMERICA.

Species by nest site position	State	Years after fire	Size of fire (ha)	No. replicate sites [a]	Response [b]	Reference[c]
Ground						
Black-and-white Warbler	IN	2–3	140	1 b, 1 u	–	1
(*Mniotilta varia*)	OH	1–2	20–30	8 b, 4 u	0	2
Carolina Wren	OH	1–2	20–30	8 b, 4 u	0	2
(*Thryothorus ludovicianus*)						
Field Sparrow	MN	1	8–18	5 b, 2 u	+	3
(*Spizella pusilla*)						
Kentucky Warbler	IN	2–3	140	1 b, 1 u	0	1
(*Oporornis formosus*)	OH	1–2	20–30	8 b, 4 u	0	2
Lark Sparrow	MN	1	8–18	5 b, 2 u	+	3
(*Chondestes grammacus*)						
Louisiana Waterthrush	OH	1–2	20–30	8 b, 4 u	0	2
(*Seiurus motacilla*)						
Ovenbird	IN	2–3	140	1 b, 1 u	–	1
(*Seiurus aurocapillus*)	OH	1–2	20–30	8 b, 4 u	–	2
	MN	1	8–18	5 b, 2 u	–	3
Ruffed Grouse	WV	1–2	3	10 b	+	4
(*Bonasa umbellus*)						
Vesper Sparrow	MN	1	8–18	5 b, 2 u	+	3
(*Pooecetes gramineus*)						
Wild Turkey	MS	1–5	400	26 b	+	5
(*Meleagris gallopavo*)						
Worm-eating Warbler	IN	2–3	140	5 b, 2 u	0	1
(*Helmitheros vermivorus*)	OH	1–2	20–30	8 b, 4 u	–	2
Low shrub						
Gray Catbird	MN	1	8–18	5 b, 2 u	–	3
(*Dumetella carolinensis*)						
Chestnut-sided Warbler	MN	1	8–18	5 b, 2 u	–	3
(*Dendroica pensylvanica*)						
Indigo Bunting	OH	1–2	20–30	8 b, 4 u	0	2
(*Passerina cyanea*)						
Hooded Warbler	IN	2–3	140	1 b, 1 u	0	1
(*Wilsonia citrina*)	OH	1–2	20–30	8 b, 4 u	–	2
Brown Thrasher	MN	1	8–18	5 b, 2 u	+	3
(*Toxostoma rufum*)						
Mid-story						
Acadian Flycatcher	OH	1–2	20–30	8 b, 4 u	0	2
(*Empidonax virescens*)						
American Goldfinch	MN	1	8–18	5 b, 2 u	+	3
(*Carduelis tristis*)						
American Redstart	OH	1–2	20–30	8 b, 4 u	0	2
(*Setophaga ruticilla*)						
American Robin	OH	1–2	20–30	8 b, 4 u	+	2
(*Turdus migratorius*)	MN	1	8–18	5 b, 2 u	+	3
Baltimore Oriole	MN	1	8–18	5 b, 2 u	+	3
(*Icterus galbula*)						
Cedar Waxwing	MN	1	8–18	5 b, 2 u	+	3
(*Bombycilla cedrorum*)						
Northern Cardinal	OH	1–2	20–30	8 b, 4 u	–	2
(*Cardinalis cardinalis*)						
Red-eyed Vireo	OH	1–2	20–30	8 b, 4 u	0	2
(*Vireo olivaceus*)	MN	1	8–18	5 b, 2 u	–	3
Wood Thrush	OH	1–2	20–30	8 b, 4 u	0	2
(*Hylocichla mustelina*)						

TABLE 2. CONTINUED.

Species by nest site position	State	Years after fire	Size of fire (ha)	No. replicate sites [a]	Response [b]	Reference[c]
Yellow-billed Cuckoo (*Coccyzus americanus*)	OH	1–2	20–30	8 b, 4 u	0	2
Canopy						
Blue-gray Gnatcatcher (*Polioptila caerulea*)	OH	1–2	20–30	8 b, 4 u	0	2
Blue Jay (*Cyanocitta cristata*)	OH	1–2	20–30	8 b, 4 u	0	2
Cerulean Warbler (*Dendroica cerulea*)	OH	1–2	20–30	8 b, 4 u	0	2
Eastern Kingbird (*Tyrannus tyrannus*)	MN	1	8–18	5 b, 2 u	+	3
Eastern Wood-Pewee (*Contopus virens*)	OH	1–2	20–30	8 b, 4 u	+	2
Least Flycatcher (*Empidonax minimus*)	MN	1	8–18	5 b, 2 u	–	3
Scarlet Tanager (*Piranga olivacea*)	OH	1–2	20–30	8 b, 4 u	0	2
Summer Tanager (*Piranga rubra*)	OH	1–2	20–30	8 b, 4 u	0	2
Yellow-throated Vireo (*Vireo flavifrons*)	OH	1–2	20–30	8 b, 4 u	0	2
Cavity						
Carolina Chickadee (*Poecile carolinensis*)	OH	1–2	20–30	8 b, 4 u	0	2
Downy Woodpecker (*Picoides pubescens*)	OH	1–2	20–30	8 b, 4 u	0	2
Eastern Bluebird (*Sialia sialis*)	MN	1	8–18	5 b, 2 u	+	3
Great Crested Flycatcher	OH	1–2	20–30	8 b, 4 u	0	2
(*Myiarchus crinitus*)	MN	1	8–18	5 b, 2 u	–	3
Hairy Woodpecker (*Picoides villosus*)	OH	1–2	20–30	8 b, 4 u	0	2
Northern Flicker (*Colaptes auratus*)	OH	1–2	20–30	8 b, 4 u	0	2
Pileated Woodpecker (*Dryocopus pileatus*)	OH	1–2	20–30	8 b, 4 u	0	2
Red-bellied Woodpecker (*Melanerpes carolinus*)	OH	1–2	20–30	8 b, 4 u	0	2
Red-headed Woodpecker (*Melanerpes erythrocephalus*)	MN	1	8–18	5 b, 2 u	+	3
Tufted Titmouse (*Baeolophus bicolor*)	OH	1–2	20–30	8 b, 4 u	0	2
White-breasted Nuthatch (*Sitta carolinensis*)	OH	1–2	20–30	8 b, 4 u	0	2
Other						
Brown-headed Cowbird	IN	2–3	140	1 b, 1 u	0	1
(*Molothrus ater*)	MN	1	8–18	5 b, 2 u	+	3
Eastern Phoebe (*Sayornis phoebe*)	OH	1–2	20–30	8 b, 4 u	0	2

[a] All studies prescribed fire; b = number of burned sites; u = number of unburned sites.

[b] + = increase; – = decrease; 0 = no effect or study inconclusive.

[c] References: 1 = Aquilani et al. 2000; 2 = Artman et al. 2001; 3 = Davis et al. 2000; 4 = Rogers and Samuel 1984; 5 = Palmer et al. 1996.

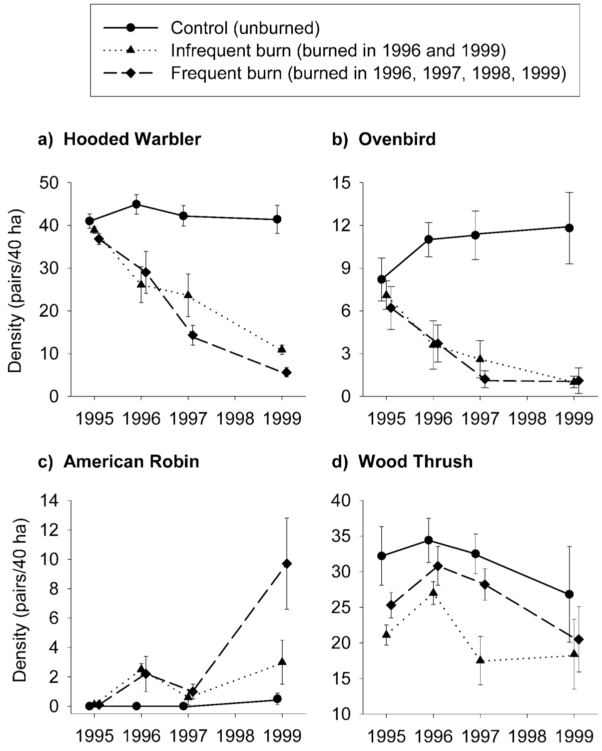

FIGURE 3. Mean (standard error) densities of bird species in relation to prescribed burning treatments in mixed-oak forests, southern Ohio; 1995 represents pre-burn conditions (Artman et al. 2001).

shifts in the composition of the breeding bird community may result from declines of ground- and low-shrub-nesting bird species (Artman et al. 2001).

Population levels of two bird species, the Eastern Wood-Pewee (*Contopus virens*) and American Robin (*Turdus migratorius*), increased in response to the fires in southern Ohio (Artman et al. 2001). Eastern Wood-Pewees were common in both burned and unburned areas, but burning may have improved their foraging habitat by creating more open and park-like conditions in the understory. American Robins did not occur in unburned areas but population levels gradually increased in response to repeated burning (Fig. 3c). Burning may increase food accessibility for ground-foraging birds such as robins by removing leaf litter, brush, and dense vegetation, exposing both seeds and insects. Ground-foraging bird species, including robins, Ovenbirds, Brown-headed Cowbirds (*Molothrus ater*), and Wood Thrushes (*Hylocichla mustelina*) were frequently observed feeding in recently burned areas in southern Ohio (Artman et al. 2001). Indeed, prescribed fire is recognized as an appropriate management strategy to improve habitat for ground-foraging gamebirds such as the Wild Turkey (*Meleagris gallopavo*) and Ruffed Grouse (*Bonasa umbellus*) (Rogers and Samuel 1984, Palmer et al. 1996).

Other bird species may be unaffected by prescribed fire, as long as low-intensity, surface fires maintain the closed-canopy forest structure. The objective of prescribed burning in southern Ohio was to maintain the existing oak-dominated forest, not to restore a different habitat type. Population levels of canopy-nesting bird species, including the Cerulean Warbler (*Dendroica cerulea*), were unaffected by the low-intensity fires in southern Ohio because the fires did not affect the density of over-story trees (Artman et al. 2001). Flexibility in habitat selection minimized effects of prescribed fire on other forest bird species. Population levels of the mid-story-nesting Wood Thrush did not differ between burned and unburned areas in southern Ohio (Fig. 3d), despite mortality of shrubs and saplings. Instead Wood Thrushes continued to inhabit recently burned areas, selecting nest patches where fire intensity was lower and placing their nests higher above the ground and in larger trees in burned than unburned areas (Artman and Downhower 2003). Nesting success of Wood

Thrushes did not differ between burned and unburned areas, suggesting that their shifts in nest site selection had no adverse consequences in terms of breeding productivity (Artman and Downhower 2003).

Prescribed Burning and Shelterwood/Thinning

Prescribed fire alone may be insufficient to maintain oak-dominated forests. Instead, a combination of prescribed fire with thinning of the canopy may be necessary to provide more light to the understory, thus promoting growth of oak recruitment. Research is currently being conducted to assess the combined effects of prescribed fire and thinning on forest bird populations in southern Ohio (D. Miles, Ohio University, pers. commun.). A combination of burning and thinning may provide habitat for a diverse community of birds, including a mix of both forest-interior species and disturbance-dependent species (Lanham et al. 2002). Shelter-wood harvesting in Missouri, for example, supported a greater diversity of birds than uncut forests, although abundance of some forest-interior species, such as the Acadian Flycatcher (*Empidonax virens*), Wood Thrush, Red-eyed Vireo (*Vireo olivaceus*), and Ovenbird, was lower in shelter-wood stands than uncut stands (Annand and Thompson 1997).

Savanna Restoration

In the transitional zone between eastern deciduous forests and midwestern prairies, prescribed fire is being used in combination with mechanical removal of vegetation to convert closed-canopy forests into a mix of forest and open grasslands to restore savannas. These treatments result in more substantial changes in bird communities, with forest-interior bird species being replaced by disturbance-dependent bird species. Research has been conducted to assess effects of savanna restoration on bird populations in Minnesota (Davis et al. 2000). Prescribed fires were applied over a 32-yr period, from 1964–1995. Fires were applied over a range of frequencies, from nearly every year to complete fire exclusion. The size of the burned areas ranged from 8–18 ha. Bird populations were monitored during 2 yr after burning (in 1995 and 1996). Restored savannas supported increased numbers of open-country and disturbance-dependent bird species, including the Red-headed Woodpecker (*Melanerpes erythrocephalus*), Eastern Bluebird (*Sialia sialis*), Baltimore Oriole (*Icterus galbula*), Indigo Bunting (*Passerina cyanea*), and Brown Thrasher (*Toxostoma rufum*). Abundance of some forest-interior bird species, including the Ovenbird, Red-eyed Vireo, and Scarlet Tanager (*Piranga olivacea*), were lower in savannas than unburned forests (Davis et al. 2000).

Studies of the local abundances of passage migrants in the Chicago area, an important migratory stopover site in the Midwest, have suggested that restoration sites offer better foraging opportunities than closed-canopy forests (Brawn and Stotz 2000). Open woodlands and early-successional habitats tend to exhibit earlier budbreak and flowering, and, presumably, arthropod abundances in these habitats are higher during the migration period (late April-May) than in closed-canopy forests that are weeks later phenologically (Brawn and Stotz 2000).

CONSERVATION IMPLICATIONS

The use of fire in eastern deciduous forests requires tradeoffs in terms of management and conservation because some bird species benefit from fire while others are negatively affected, depending on the degree to which fire changes habitat features. Frequent burning creates less favorable conditions for forest birds that nest on the ground and in low shrubs, but provides more favorable conditions for disturbance-dependent birds associated with savannas and woodlands.

Is reintroduction of fire to eastern deciduous forests restoring bird communities to what they were when fire was more prevalent in the region? It is impossible to speculate because effects of pre-European fire regimes on regional bird populations are unknown. Bird populations undoubtedly have undergone massive retractions and expansions in response to land use changes within the region. Widespread clearing of forest during the 19th century may have contributed to the extinction of the Passenger Pigeon (*Ectopistes migratorius*) and Carolina Parakeet (*Conuropsis carolinensis*) (Whitney 1994, Askins 2000). Open-country and disturbance-dependent bird species (e.g., American Crow [*Corvus brachyrhynchos*] and Red-tailed Hawk [*Buteo jamaicensis*]) replaced closely related forest species (e.g., Common Raven [*Corvus corax*] and Red-shouldered Hawk [*Buteo lineatus*]) (Whitney 1994). Restoration of forest habitat began during the early 20th century, with forest regeneration occurring on abandoned farmlands and initiation of fire suppression activities. Given extensive forest regeneration and fire suppression, population levels of some forest bird species may be at their highest level since European settlement. Widespread declines of disturbance-dependent bird species have been occurring in the region, but declines have also been observed for some forest-interior bird species (Askins 2000, Brawn et al. 2001, Sauer et al. 2001). One of the key strategies for conservation and management within the region is to maintain a balance between restoring disturbance regimes and minimizing forest fragmentation.

In general, prescribed burning is unlikely to be applied on a widespread or frequent basis in the region, given specific management objectives, economic costs, and other constraints such as land ownership. Restoration of disturbance regimes such as fire may be appropriate in more fragmented landscapes, thus minimizing effects on forest-interior bird species. The consideration of tradeoffs is necessary, however, as forest managers and conservation ecologists balance the need to maintain viable populations of bird species dependent on the entire range of successional habitats. The effectiveness of conservation strategies for birds in eastern deciduous forests requires maintaining a mosaic of habitats covering the entire successional range within and across landscapes.

FUTURE RESEARCH NEEDS

Appropriate questions for future research are:

1. What are the long-term effects of prescribed burning of varying frequencies on bird population levels, nesting success, and population sustainability?
2. What are the effects of prescribed burning on life-history characteristics such as territory size, mating success, survival, and food availability of different bird species, including forest-interior and disturbance-dependent bird species?
3. Does prescribed fire or do shifts in forest composition affect habitat suitability for forest bird species of concern, such as the Cerulean Warbler?
4. How do microsite conditions, patchiness within burns, and seasonality of fires affect bird populations?
5. What are the long-term effects of excluding and suppressing fire on bird populations and other community and ecosystem components in the region?
6. What are the appropriate criteria for deciding where and when to use prescribed fire in the context of ecosystem management?
7. Should prescribed fire be used on a more widespread or frequent basis in the region, given the historical context, specific management objectives, economic costs, and ownership constraints?
8. What is the appropriate balance of multiple resources and habitats (early-successional, savanna, late-successional, burned, unburned) given conservation concerns?

One of the most critical needs for research is to address the effects of fire frequency on forest bird populations. Previous research has focused on the immediate and short-term response of forest bird communities to prescribed fires but long-term effects and the amount of time necessary for potential recovery of reduced populations are unknown. It is essential to monitor the response of forest bird populations to a burning regime that replicates the fire-return interval of 5–7 yr that occurred before and after European settlement. Other changes may also occur on a long-term basis that are not detectable during short-term monitoring.

The importance of forest composition to bird communities in the region also remains to be determined. If current successional trends continue, oaks and hickories may be replaced by other tree species such as maple. The consequences of this shift in forest composition depend on the specific habitat requirements of particular wildlife species. Oak-dominated forests are often identified as important habitat because acorns provide a valuable and energy-rich food resource for many wildlife species (Martin et al. 1961, Kirkpatrick and Pekins 2002). Many resident bird species consume acorns but other forest species, including most Neotropical migrants, are not directly dependent on acorns or other resources provided specifically by oaks.

Studies in Avian Biology No. 30:139–146

INFLUENCE OF FIRE AND OTHER ANTHROPOGENIC PRACTICES ON GRASSLAND AND SHRUBLAND BIRDS IN NEW ENGLAND

Peter D. Vickery, Benjamin Zuckerberg, Andrea L. Jones, W. Gregory Shriver, and Andrew P. Weik

Abstract. The extent of grassland and shrubland habitat in New England has changed dramatically over the past 400 yr as a result of changing land uses. Presently, grasslands and shrublands in New England have been created and maintained primarily as a result of four types of habitat management: mowing, livestock grazing, clearcutting, and prescribed burning. Hayfields and pastures comprise the largest proportion of open land, approximately 718,500 ha. Clearcutting has created extensive shrubland patches in northern Maine, where 3.5% (243,000 ha) of the commercial forestland has been harvested in the past 20 yr, creating ephemeral, early successional shrublands used by a wide variety of warblers, sparrows, and other birds. The most widespread use of prescribed fire is agricultural and takes place on commercial lowbush blueberry (*Vaccinium angustifolium*) barrens in Maine, where approximately 3,000 ha are burned annually. These barrens are especially important habitats for Upland Sandpipers (*Bartramia longicauda*) and Vesper Sparrows (*Pooecetes gramineus*). The scale of ecological prescribed burns in New England for habitat management of endangered ecosystems has been small; in recent years fewer than 300 ha have been burned annually. The effects of burning differ in grasslands versus shrublands. In native grasslands, burning has a strong effect on vegetation structure, which, in turn, has clear effects on most grassland specialist birds. Shrubland fires have less impact on shrubland birds because most of the woody structure remains intact.

Key Words: blueberry barrens, farmland, grassland birds, New England, prescribed fire, shrubland birds.

INFLUENCIA DEL FUEGO Y OTRAS PRÁCTICAS ANTROPOGÉNICAS EN AVES DE PASTIZALES Y ARBUSTOS EN NUEVA INGLATERRA

Resumen. La extensión de hábitats de pastizales y matorrales ha cambiado drásticamente en los últimos 400 años en Nueva Inglaterra, debido a los cambios en el uso del suelo. Actualmente, los pastizales y matorrales en Nueva Inglaterra han sido creados y mantenidos principalmente por el resultado de cuatro tipos de manejo del habitat: segar, pastoreo, tala-rasa, y quemas prescritas. Campos de heno y pastizales comprenden la proporción más grande de tierras abiertas, aproximadamente 718,500 ha. Los aprovechamientos forestales han creado extensos parches de matorral en la parte norte de Maine, donde 3.5% ((243,000 ha) del bosque comercial ha sido aprovechado en los últimos 20 años, creando matorrales efímeros de sucesión temprana, utilizados por gran cantidad de aves (*Dendroica* spp.) y (*Ammodramus* spp.), entre otras. El uso más recurrido en quemas prescritas, es el de la agricultura, y tiene lugar en arbustos bajos de (*Vaccinium angustifolium*) in Maine, donde aproximadamente 3,000 ha son quemadas anualmente. Estas campo de arbustos bajos, son especialmente habitats importantes para aves tales como (*Bartramia longicauda*) y (*Pooecetes gramineus*). La escala de las quemas ecológicas prescritas para manejo del habiatat de ecosistemas en peligro en Nueva Inglaterra ha sido baja; en años recientes menos de 300 ha han sido quemadas anualmente. Los efectos del fuego difieren en los pastizales contra los matorrales. En pastizales nativos, los incendios tienen un fuerte efecto en la estructura de la vegetación, lo cual, por el otro lado, tiene efectos claros en la mayoría de las aves especializadas de pastizales. Los incendios en matorrales tienen menor impacto en las aves de matorral, debido a que la mayor parte de la estructura de madera permanece intacta.

Native grasslands and shrublands in New England were historically the result of natural disturbances (e.g., wind, fire, disease, beaver [*Castor canadensis*] meadows, insect damage, or a combination of these forces). Although fires were not usually a frequent form of disturbance in New England forests, they had profound effects on vegetation, and therefore birds, and sometimes burned thousands of hectares (Whitney 1994). Fire and other disturbances created habitat for a distinctive suite of grassland and shrubland birds, including the now extinct Heath Hen (*Tympanuchus cupido cupido*), the eastern form of the Greater Prairie-Chicken, which once ranged from southern Maine to Virginia and Maryland but disappeared in the 1930s (Gross 1932). The steep population declines of many species of grassland and shrubland birds in the past 35 yr (Peterjohn et al. 1999), and the extinction of grassland taxa such as the Heath Hen, has created an awareness that these species and their habitats should be a high conservation priority (Vickery 1992, Askins 2000).

Early successional habitats have declined sharply and become more fragmented and isolated as a result of the decline in agriculture since the late nineteenth century, increased development, and active fire suppression (Litvaitis et al. 1999). Indeed, wildfires are now vigorously suppressed, which means other forms of disturbance, or habitat maintenance, have become more important for providing habitat for grassland and shrubland birds. These habitats are now more commonly a product of human disturbances, including farming, silviculture, and active grassland and shrubland habitat management (Askins 1999, 2000).

NEW ENGLAND FIRE HISTORY

Fire before European Settlement

Fire has been an important, if infrequent, part of the New England landscape since at least the last ice age, some 12,000 yr before present (Patterson and Sassaman 1988). Fire has had important ecological and evolutionary effects for the biota in the Northeast. For example, all native plants found in eastern sandplain grasslands are adapted to fire (Vickery and Dunwiddie 1997), and flowering and reproductive phenology for some northeastern grassland plant species have clearly evolved with fire (Vickery 2002).

Some New England forest types burn more regularly than others (Parshall and Foster 2002), and fire has been more frequent on dry sandy outwash plain and glaciomarine delta soils than richer, more mesic soils (Winne 1997, Fig. 1). For example, the sandy pine barrens (10,600 ha) in Plymouth, Massachusetts, have burned three times in the past 40 yr, with major fires in 1964, 1974, and 1991 (T. Maloney, pers. comm.).

It is generally thought that American Indians (numerous tribes collectively known as Eastern Algonquians; Patterson and Sassaman 1988) probably ignited most fires and that only a small proportion of wildfires were the result of lightning strikes (Pyne 1984). However, an alternate view holds that fires in pitch pine (*Pinus rigida*) and oak (*Quercus* spp.) forests in south coastal New England were more likely natural in origin (Parshall and Foster 2002). It seems clear that fires were more common in southern New England, from the Saco River region in southern Maine to coastal Massachusetts and the Middle Atlantic states (Patterson and Sassaman 1988). But fire was also an important part of the landscape in parts of eastern Maine; Winne (1997) analyzed pollen from pond sediments in Washington County, Maine, and determined that the xeric blueberry barrens (glaciomarine deltas) in this area had been in some form of open grassland–pine/shrub barrens for at least the past 1,700 yr.

The spatial scale of fires started by American Indians was shaped by their needs (Cronon 1983). Prescribed fires near permanent settlements along the coast were likely for agriculture and game management; such fires would have been smaller and less intense than fires in more remote areas, which were probably less frequent but more intense and probably larger (Patterson and Sassaman 1988). At this point it remains unclear whether New England grasslands were shaped primarily by pre-European human influences or by climate, soil, and vegetation (Parshall and Foster 2002).

Fire after European Settlement

European settlement brought profound changes to the New England landscape that potentially benefited grassland birds by reducing forest cover and increasing coastal heathlands (Askins 2000). By the 18th and 19th centuries, more than 60% of the forests in Massachusetts, Rhode Island, and Connecticut were cleared and converted to pasture and agriculture (Cronon 1983, Whitney 1994). The reduction in forest cover over this period is thought to have provided novel habitats for grassland birds, which responded by extending ranges and increasing populations into the once-forested New England landscape (Askins 1999). In addition to vastly increasing the amount of open grassland, Europeans introduced many species of exotic grasses, forbs, and shrubs. Cool-season grasses such as timothy (*Phleum pratense*) were usually rhizomatous, creating a substantially thicker vegetation structure and density, which benefited grassland habitat generalists such as Savannah Sparrow (*Passerculus sandwichensis*) and Bobolink (*Dolichonyx oryzivorus*).

Along south coastal New England, especially in Massachusetts, maritime heathlands increased to become a major component of the landscape as settlers cleared oak and pine forests from the sandy, easily eroded outwash soils (Dunwiddie 1989). European grasses generally did not thrive in these acidic, low-nutrient soils, and native plants expanded. Livestock grazing and prescribed fire maintained these heathland plants (Dunwiddie 1989), providing important nesting habitat for grassland birds.

Since the beginning of the twentieth century, wildfires have been suppressed in New England to reduce property damage and to minimize loss

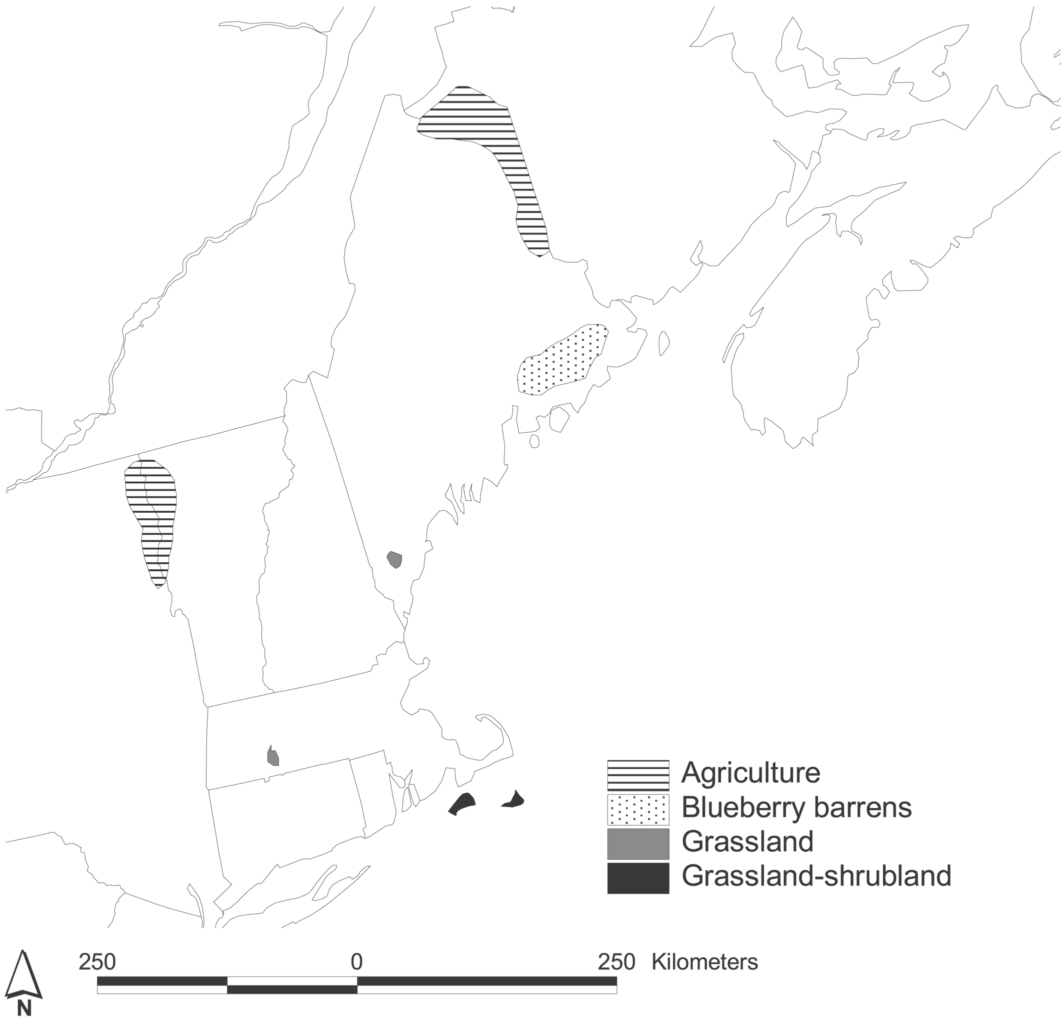

FIGURE 1. Ecological regions of New England and New York, as defined by The Nature Conservancy. Large contiguous patches of agricultural habitat occur in northern Maine and northeastern Vermont. Major grassland habitats, including blueberry barrens, occur in eastern and southern Maine and in western Massachusetts. Substantial grassland and shrubland habitats also occur on the islands south of Cape Cod. There are also many smaller farms, grasslands, and shrub patches interspersed throughout this region. Historically, fires were more frequent along the coastal plain, defined here as the North Atlantic coast. Fires also occurred regularly on the sandy glacio-marine deltas inland from the coast of eastern Maine.

of merchantable timber (Whitney 1994). For example, in Maine, 0.4% of forest area burned annually between 1903 and 1910, but this number was reduced to 0.02% by 1961–1970 (Fahey and Reiners 1981). Active fire suppression continues to the present and even has a strong effect on prescribed burns on conservation land. On Nantucket Island, Massachusetts, prescribed fires can only be conducted during the dormant season between October and April (E. Steinauer, pers. comm.) despite the fact that growing-season burns appear to be more effective in controlling shrubs and maintaining grasslands (Rudnicky et al. 1999).

CONTEMPORARY USE OF FIRE

Contemporary prescribed fires are primarily used for two reasons in New England: habitat management of rare plant and animal assemblages, and pruning of commercial lowbush blueberry fields. In the first case, prescribed fires are used to conserve rare, pyrogenically mediated habitats such as sandplain grasslands, coastal heathlands, and pitch pine-scrub oak (*Quercus ilicifolia*) barrens. Prescribed fires are used to maintain vegetation structure and composition, reduce fuel loads, and provide an important mechanism to protect and enhance globally rare plants and animals (Dunwiddie and Caljouw 1990).

Importantly, the scale of prescribed burns in New England for management of threatened ecosystems tends to be small. In the past 10 yr, fewer than 400 ha of grassland and shrubland have been burned annually and burns were rarely larger than 15 ha. For example, in 2002, 301 ha of native grassland and heathland were burned in New England; average burn size was 10 ha (T. Maloney, pers. comm.), although somewhat larger burns (60–65 ha) have taken place on Nantucket Island (E. Steinauer, pers. comm.). Since 1996, an average of 12.0 ± 2.3 ha (SE) have been burned annually on the Kennebunk Plains, Maine; the largest burn unit was 31.8 ha (P. Schuerman, pers. comm.). The size of fires on blueberry lands is not accurately recorded but these ignitions are undoubtedly much larger than the prescribed burns on conservation lands, probably on the order of 20–100+ ha (P. Vickery, pers. obs.).

FIRE EFFECTS ON GRASSLANDS

On a landscape level, fire is relatively unimportant for maintaining large tracts of grassland habitat in New England. Agricultural land clearly represents the largest proportion of graminoid-dominated open land. In 1997, 1,760,000 ha of open farmland existed in New England. Approximately 718,500 ha were hayfields, pastures, and idle cropland (National Agricultural Statistics Service 2002), habitats that are most likely to provide suitable nesting sites for grassland birds. The 354,500 ha of hayfields in New England are rarely burned but are mowed or cut one or more times annually.

In eastern Maine, commercial lowbush blueberry production covers approximately 26,000 ha (D. Yarborough, pers. comm.), creating a low-stature vegetation type (<15 cm), commonly called blueberry barrens, that are better described as grassland barrens (Vickery et al. 1994). Grassland birds use this mosaic of short shrubs and grasslands. Prescribed fire on these barrens represents the greatest extent of fire management in New England. These grassland barrens are managed for commercial production on a 2-yr rotation: berries are harvested one year and the plants are then mowed or burned (sometimes both) in the second year. In the past 10 yr, approximately 20–30% of the non-harvest-year fields, or ca. 3,000 ha, have been burned annually. The remaining non-harvest fields are generally flail mowed (D. Yarborough, pers. comm.).

Blueberry barrens provide especially important nesting habitat for Upland Sandpipers (*Bartramia longicauda*) and Vesper Sparrows (*Pooecetes gramineus*; Weik 1998, Shriver et al. In press). A regional survey of New England and New York from 1997–2000 revealed that both species had similar ranges and that they often occurred together; 85% of these sites were located on the commercial blueberry barrens of eastern Maine (Fig. 2; Shriver et al. In press). At least 140 territorial male Upland Sandpipers and 350 Vesper Sparrows were found on these barrens, representing a substantial proportion of the entire population for these two species throughout New England and New York, 45% and >70%, respectively (Weik 1998, Shriver et al. In press).

Livestock grazing is an important form of habitat management that affects grassland birds. In New York, Smith (1997) found that moderate grazing with stocking rates of 0.12–0.24 head of cattle per hectare provided adequate habitat for Henslow's Sparrows (*Ammodramus henslowii*) and Grasshopper Sparrows (*Ammodramus savannarum*) in the Fingers Lake National Forest. The same stocking rates are likely to be applicable for New England as well.

FIRE EFFECTS ON GRASSLAND BIRDS

Despite their small size, conservation burns can have important benefits for grassland birds, at least locally (Table 1). In Maine, the 210-ha Kennebunk Plains supports a rich assemblage of grassland birds that clearly benefit from fire management (Vickery et al. 1999a). In an 8-yr study at this site, prescribed fire affected all eight species that breed there (Vickery et al. 1999a). Savannah Sparrow, Grasshopper Sparrow, Bobolink, and Eastern Meadowlark (*Sturnella magna*) densities declined for 1 yr following fire but remained high for 5–7 yr following prescribed burns (Fig. 2). Horned Larks (*Eremophila alpestris*) and Vesper Sparrows preferred recently burned sites; abundances of both these species and Upland Sandpipers declined with time since fire. Field Sparrows (*Spizella pusiila*) preferred sites that had not been burned or mowed in 5 yr (Fig. 3; Vickery et al. 1999a). A study of the effects of fire on Grasshopper Sparrows at Katama Plains, Martha's Vineyard, Massachusetts, was consistent with the Maine findings; sparrows generally preferred recently burned sites and avoided sites that had not been burned for ≥ 5 yr (Harris 1998).

Prescribed fires in coastal grasslands in Massachusetts primarily benefit Savannah Sparrows,

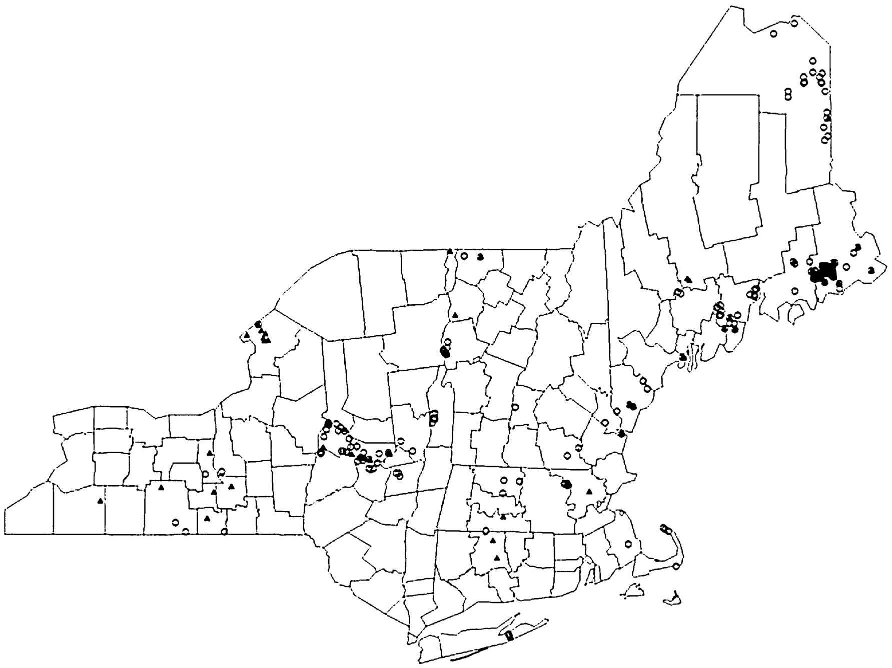

FIGURE 2. A grassland bird inventory of New England and New York, 1997–2000, revealed that Upland Sandpipers (filled triangle) and Vespers Sparrows (open circle) were most common on the large commercial blueberry barrens in eastern Maine. These two species frequently occurred together on these sites (adapted from Shriver et al. 2003).

Eastern Meadowlarks, Bobolinks, and foraging Northern Harriers (*Circus cyaneus*) (Zuckerberg 2002). On Nantucket Island, Massachusetts, Savannah Sparrow territory densities did not differ in grasslands that had been burned, mowed, or left unmanaged (Zuckerberg 2002).

EFFECTS OF FIRE AND OTHER DISTURBANCES IN SHRUBLANDS

Because wild fires are assiduously suppressed in New England, fire has not been a major factor affecting shrubland birds. Clearcutting, a silvicultural practice that removes all standing wood, was a common practice in the 1980s and early 1990s, especially in northern Maine. This practice has created a continuum of early successional shrubland habitats used by a wide variety of shrubland warblers and sparrows, especially Chestnut-sided Warbler (*Dendroica pensylvanica*), Palm Warbler (*Dendroica palmarum*), Mourning Warbler (*Oporornis philadelphia*), Common Yellowthroat (*Geothlypis trichas*), Wilson's Warbler (*Wilsonia pusilla*), Lincoln's Sparrow (*Melospiza lincolnii*), and White-throated Sparrow (*Zonotrichia albicollis;* King et al. 2001). Although the extent of this silvicultural practice has declined in the past 10 yr, approximately 3.5% (243,000 ha) of the commercial forest land has been clearcut within the past 20 yr (Maine Forest Service 2001). Maine GAP analysis, using 1993 satellite imagery, revealed that an estimated 2% (127,000 ha) of Maine's forests consisted of clearcuts with an additional 4% (267,000 ha) in selective cuts (Krohn et al. 1998). In general, clearcuts are ephemeral, providing suitable shrubland habitat for an average of 10 years in northern hardwood forests (Thompson and DeGraaf 2001).

Fire has played a more important role in pitch pine–scrub oak habitats. These areas are priorities for conservation in New England because they support several rare plant and animal species (Schweitzer and Rawinski 1988; Barbour et al. 1999). On the Montague Plain in central Massachusetts, fire has been an important historical factor for promoting the stability of scrub-oak stands by removing hardwood canopy trees and initiating vigorous sprouting of shrubs (Motzkin et al. 1996), benefiting Whip-poor-wills (*Caprimulgus vociferus*), Prairie Warblers (*Dendroica discolor*), and Field Sparrows. Within the past 10 yr prescribed fire has also been used to

TABLE 1. SUMMARY OF AVAILABLE LITERATURE ON THE RESPONSE (CHANGE IN ABUNDANCE) OF BREEDING GRASSLAND BIRDS TO PRESCRIBED FIRE IN GRASSLAND HABITATS IN NEW ENGLAND (FIG. 3).

Species	State	Years after fire	Size of fire (ha)	No. of sites	Response	Reference[a]
Upland Sandpiper (*Bartramia longicauda*)	ME	4–8	6–24	1–4	–	1
Horned Lark (*Eremophila alpestris*)	ME	1–8	6–24	1–12	–	1
Field Sparrow (*Spizella pusilla*)	ME	3–8	6–24	1–4	+	1
Vesper Sparrow (*Pooecetes gramineus*)	ME	2–8	6–24	1–4	–	1
Savannah Sparrow	ME	1–6	6–24	1–12	+	1
(*Passerculus sandwichensis*)	MA	1–2	4-31	1-7	0	2
Grasshopper Sparrow	ME	1–4	6–24	1–12	very +	1
(*Ammodramus savannarum*)	ME	5–7	6–24	1–4	slightly +	1
	MA	1–4	4–18	1–4	+	3
Bobolink	ME	1–2	6–24	4–12	very +	1
(*Dolichonyx oryzivorus*)	ME	3–6	6–24	1–4	moderately +	1
Eastern Meadowlark (*Sturnella magna*)	ME	1–7	6–24	1–12	very +	1

[a] References: 1 = Vickery et al. 1999a; 2 = Zuckerberg 2002; 3 = Harris 1998.

manage pine barrens in Plymouth, Massachusetts; the reasons for these burns have been primarily to reduce fuel loads and avoid uncontrolled fires that could damage houses and other structures (T. Maloney, pers. comm.).

Large power lines also provide persistent shrubland habitat used by many species, including Gray Catbird (*Dumetella carolinensis*), Blue-winged Warbler (*Vermivora pinus*), Prairie Warbler, Common Yellowthroat, and Indigo Bunting (*Passerina cyanea;* King and Byers 2002).

FIRE EFFECTS ON SHRUBLAND BIRDS

The effects of fire on shrubland birds have received little attention in New England (Table 1). Most shrubland studies have examined the effects of various silvicultural practices on shrubland birds (e.g., King et al. 2001). For example, a study of clearcuts in southeastern Connecticut found that vegetation structure (e.g., canopy height), as well as surrounding landscape features, influenced shrubland bird occupancy (R. A. Askins, B. Zuckerberg, pers. comm.). These clearcuts provided important breeding habitat for Blue-winged Warbler, Chestnut-sided Warbler, Prairie Warbler, Common Yellowthroat, and Eastern Towhee.

A recent study on Nantucket Island shrublands in Massachusetts found that Eastern Towhees (*Pipilo erythrophthalmus*) were more abundant in areas that had been burned or were left unmanaged compared to areas that had been mowed (Zuckerberg 2002). Conversely, Song Sparrow (*Melospiza melodia*) territory densities in shrublands were similar in burned, mowed, and unmanaged units (Zuckerberg 2002).

In general, these results indicate that burning has a stronger effect on grassland birds than on shrubland birds, although the response of shrubland birds to fire has not been adequately studied in New England. Not surprisingly, mowing has a more substantial effect on bird occupancy in shrubland habitats because this form of habitat manipulation has a much more pronounced effect on vegetation structure (Zuckerberg 2002).

CRITICAL MANAGEMENT AND RESEARCH ISSUES

Large-scale prescribed burning in most of New England will continue to be a difficult management issue because of the density and spatial distribution of houses and other structures. Consequently, prescribed fires will generally continue to be small and isolated, usually occurring in the dormant season (October–April). It is unlikely that dormant-season fires mimic the effects of natural wildfires and summer fires are most effective in killing woody shrubs (Rudnicky et al. 1999), a high priority in most grassland burn programs. Additionally, small-scale prescribed fires alone are unlikely to increase habitat

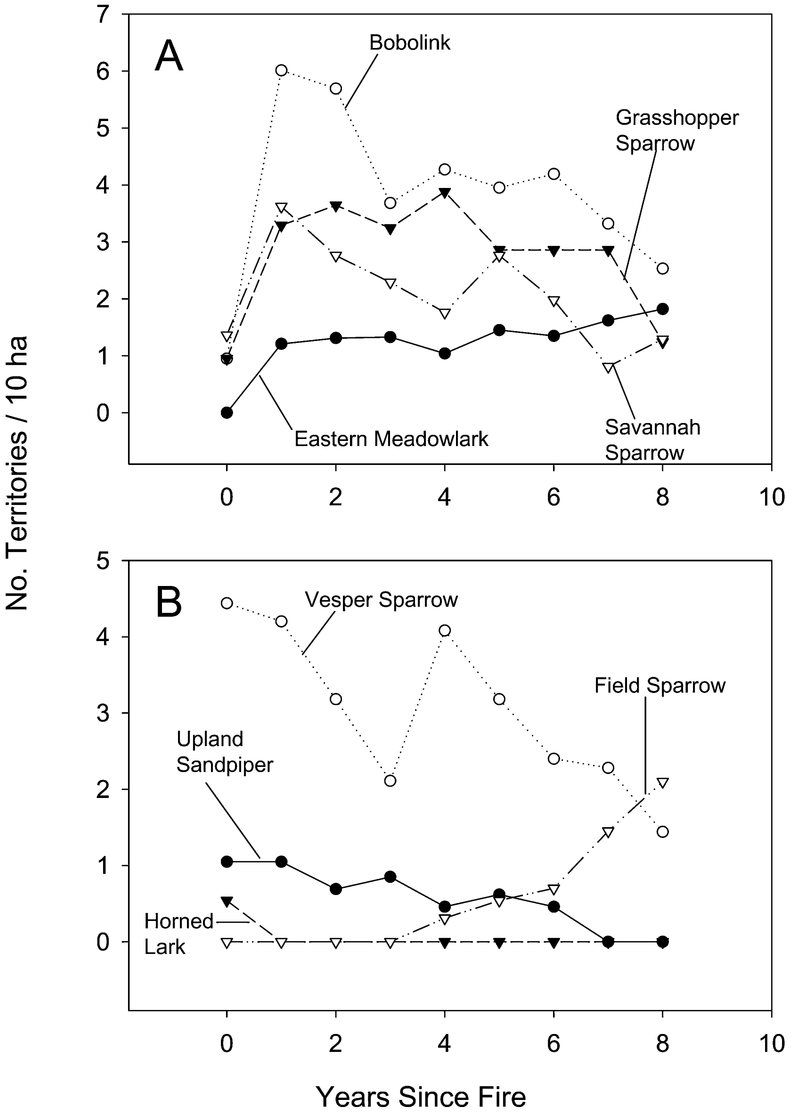

FIGURE 3. Eight species of grassland birds responded differently to prescribed fire at Kennebunk, Maine, 1984–1991. Four species (A) followed the same general pattern; breeding densities were very low during the burn-year but increased markedly in the year following the burn. Eastern Meadowlark densities remained high for 8 yr following fire. Bobolink and Savannah Sparrow densities were high in the year following but generally decreased thereafter. Grasshopper Sparrow densities remained high for 4 yr following fire but then decreased. Four other species responded differently to prescribed fires (B). Breeding densities of Upland Sandpipers and Vesper Sparrows were greatest in the burn-year but then generally declined with time since fire. Horned Larks only used burn-year sites whereas Field Sparrows only used sites that had not been burned for 4 yr. Standard errors, not shown, were <0.2 territories per 10 ha (adapted from Vickery et al. 1999a).

for declining grassland birds in New England. These fires improve the habitat quality of existing grasslands; they do not create additional habitat.

Grassland restoration may be a viable alternative for creating and, ultimately, managing large areas for grassland birds. Several sites in Rhode Island (Ninigret National Wildlife Refuge) and Massachusetts (Allen's Pond, Dartmouth) have been restored since 1990. However, because these sites are relatively small (<50 ha), they are unlikely to support grassland birds that are strongly area-sensitive (e.g., Upland Sandpiper). It seems likely that these sites will eventually be managed by a combination of burning, mowing, and grazing. It will be important to determine which types of grassland restoration and which combinations of management practices (burning, mowing, grazing) will be most beneficial to grassland birds.

There has been no research into the effects of commercial blueberry barrens management, including fire, on Upland Sandpipers and Vesper Sparrows in eastern Maine. Given the importance of these barrens for these two species (Weik 1998, Shriver et al. In press), this should be a high research priority.

Landscape-scale patterns in land use have been shown to affect the regional patterns of grassland bird distributions and reproductive success in the Midwest (e.g., Johnson and Igl 2001). It would be valuable to determine the extent to which similar landscape metrics influence grassland bird distributions and reproductive success in New England. Species distributions and relative abundances have been estimated recently (Shriver et al. In press) and could be coupled with land-use data to determine landscape-scale effects on species distribution patterns.

Since many of the natural disturbances that once created and sustained shrubland habitats throughout the northeastern United States are now gone or diminishing, it is increasingly important that shrubland management be considered at a regional scale (Askins 1998). Conservation planning should focus on the proportion and configuration of early seral habitats within a landscape (Litvaitis et al. 1999). Large-scale shrubland management has been a key issue for several agencies. In 1997, the Massachusetts Division of Fisheries and Wildlife initiated a program to increase the proportion of state-owned properties that are maintained as shrubland; currently the program has provided and maintained over 200 ha (Litvaitis et al. 1999). In the White Mountain National Forest in New Hampshire and Maine, the goal of the U.S. Forest Service is to manage 10% (30,000 ha) of the forest in a regeneration stage (USDA Forest Service 1986). Although both these programs are unique initiatives, public opposition to clearcutting remains a major obstacle in achieving these and other management goals (Litvaitis et al. 1999). To the greatest degree possible, management of early successional habitats within a landscape context should attempt to mimic the natural and historical processes that initially created them (Askins 1998). Conservation efforts should emphasize existing shrubland habitats (e.g., abandoned farmlands, silviculture, powerline corridors) in an attempt to consolidate and create larger shrubland patches.

ACKNOWLEDGMENTS

Robert Askins, Tom Hodgman, Tom Maloney, Ernie Steinauer, and David Yarborough are warmly acknowledged for providing thoughtful suggestions and unpublished information. The comments of two anonymous reviewers substantially improved the manuscript.

Studies in Avian Biology No. 30:147–160

EFFECTS OF FIRE REGIME ON BIRDS IN SOUTHEASTERN PINE SAVANNAS AND NATIVE PRAIRIES

R. Todd Engstrom, Peter D. Vickery, Dustin W. Perkins, and W. Gregory Shriver

Abstract. Fire, both natural and anthropogenic, has played a critical role in shaping vegetation structure and composition of many of the plant communities of the southeastern United States. Pine savannas, especially longleaf pine (*Pinus palustris*), that were dominant over much of the upland coastal plain, have declined by approximately 97% over the past 100 yr. The inferred natural fire regime of this vegetation type was a fire frequency of 2–8 yr with typically low-severity fires that occurred during the lightning season (June–August). Currently, dormant-season (January through April) fires are used most frequently. Approximately 110–120 species, excluding migrants, comprise the avian community of southeastern pine savannas; and some of these are among the most rapidly declining bird species in the eastern United States. Disruption of the natural fire regime by fire exclusion or lengthened fire interval was detrimental to bird species associated with tree (e.g., Red-cockaded Woodpecker [*Picoides borealis*] and ground cover components (e.g., Bachman's Sparrow [*Aimophila aestivalis*] of the ecosystem. Lightning-season fire has mixed effects on birds (e.g., loss of some nests, but improved brood habitat); therefore, creation of patches of different burn treatments should be carefully considered. The foremost management and conservation challenge is to increase the number of acres of southeastern pine savannas burned frequently through thoughtful application of prescribed burning. Important research challenges include measuring tradeoffs among bird species and other wildlife for different fire regimes, evaluating metapopulation effects of different landscape applications of fire, and considering the nutrient dynamics of different fire regimes on bird populations.

Key Words: birds, fire, longleaf pine, prairie, southeastern United States.

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EFECTOS DE RÉGIMEN DEL FUEGO EN AVES DE SABANAS DE PINO Y PRADERAS NATIVAS DEL SURESTE

Resumen. El fuego ha jugado un importante papel para darle forma a la estructura de la vegetación, así como a la composición de varias comunidades de plantas del sureste de los Estados Unidos. Las sabanas de pino, especialmente de pino (*Pinus palustris*) (las cuales dominaban las tierras altas de la planicie costera), han disminuido aproximadamente en un 97% durante los últimos 100 años. La consecuencia de este régimen natural de este tipo de vegetación era de un frecuencia de incendios de 2–8 años, con incendios típicos de baja severidad, los cuales ocurrieron durante la temporada de relámpagos (junio–agosto). Actualmente, en temporada de inactividad (enero a abril), se utilizan las quemas. Aproximadamente de 110–120 especies (excluyendo a las migratorias), comprenden la comunidad de aves del sureste de sabanas de pino, y algunas de estas se encuentran dentro de las especies de aves con declive mas rápido en el este de los Estados Unidos. La interrupción en el proceso del régimen natural del fuego por la exclusión del fuego o el alargamiento en el intervalo de incendios, fue determinante para las especies de aves asociadas a los árboles (e.g., Pájaro carpintero [*Picoides borealis*], en la composición de la cobertura del suelo del ecosistema (e.g., *Aimophila aestivalis*). Incendios en temporada de relámpagos tienen efectos mezclados en aves (ej. pérdida de algunos de los nidos, pero el mejoramiento del habitat de empollamiento); es por esto, que la creación de parches de distintos tratamientos de los incendios debe ser cuidadosamente considerada. El reto mayor en el manejo y la conservación, es incrementar el número de acres de sabanas de pino del sureste frecuentemente incendiadas, a través de la aplicación de quemas prescritas. Importantes retos para la investigación, incluyen la medición de los intercambios entre las especies de aves y otra fauna para los diferentes regimenes, la evaluación de los efectos de la metapoblación de distintas aplicaciones del fuego en el paisaje, y la consideración de las dinámicas de los nutrientes de los distintos regimenes de incendios en poblaciones de aves.

Many plant communities of the southeastern US have been shaped by fire for thousands of years (Komarek 1974, Myers and Ewel 1990, Boyce and Martin 1993, Frost 1998). Schmidt et al. (2002) identified 23 potential natural vegetation groups that were derived from 43 groups described by Küchler (1964) for the southeastern US (USDA Ecoregion 8: Virginia, North and South Carolina, Kentucky, Tennessee, Alabama, Mississippi, Arkansas, Louisiana, Oklahoma, and Texas). Southeastern vegetation types range along a fire-return-interval continuum from fire-free (e.g., southern floodplain forest and mangrove) to fire every 1–3 yr on average (e.g., longleaf pine [*Pinus* *palustris*] savanna, pocosin, southern cordgrass [*Spartina*] prairie, Florida dry prairie; Abrahamson and Hartnett 1990, Frost 1998). Of course, fire does not behave uniformly within any vegetation type, and each of the broad vegetation classes has other plant communities embedded within it. These communities are variably affected by fire depending on elevation, moisture gradients, and edaphic conditions. We focus this review on the southern mixed forest and wet grassland (groups 56 and 36, respectively; Schmidt et al. 2002) that form the mosaic of pine-dominated woodlands and savannas (Platt 1999) and grass-dominated prairies (Abrahamson and Hartnett 1990) in the southeastern US.

Like all disturbances, fire can be characterized by spatial distribution, frequency, return interval, rotation period, predictability, area or size, magnitude (intensity and severity), synergism, and timing or season (White and Pickett 1985). Fire in contemporary landscapes is further influenced by anthropogenic vegetation communities (e.g., post-agricultural old fields) and prescribed-fire lighting patterns. Many of these aspects of fire are interdependent. In this review we summarize studies of individual bird species and communities within the context of modern day occurrences of fire in pine savannas and native prairies in the southeastern United States.

FIRE IN SOUTHEASTERN PINE SAVANNAS AND NATIVE PRAIRIES

SPATIAL EXTENT AND CHARACTERISTIC PLANT SPECIES

Pre-Columbian pine savannas maintained by fire extended from southeastern Virginia to the Florida Keys and westward to Louisiana and Texas (Fig. 1). These savannas can be divided into five general classes: longleaf pine transition savannas (along the northern and western boundaries); longleaf pine-bluestem (*Andropogon* sp.) savannas (in regions of the eastern Coastal Plain and throughout the western Coastal Plain); longleaf pine-wiregrass (*Aristida* spp.) savannas (Atlantic coast and in the eastern Gulf Coastal plain south to central Florida); longleaf-slash (*Pinus elliotii*) pine wiregrass savannas (central Florida); and south Florida slash pine savannas (subtropical Florida south to the keys) (Fig. 2.1 in Platt 1999). Longleaf pine dominated or shared dominance over an estimated 37,000,000 ha of the southeastern Coastal Plain, but this amount has declined by approximately 97%, and much of what remains is in a highly altered condition (Frost 1998). Less than 1% of longleaf pine savannas remain in old-growth condition (Means 1996, Landers and Boyer 1999).

Longleaf pine savannas can be classified into four series (xeric, subxeric, mesic, and seasonally wet) and at least 23 different types based on geographic and edaphic conditions (Peet and Allard 1995). Canopy composition varies from a virtual longleaf monoculture (Schwarz 1907, Wahlenberg 1946) to a mixture of hardwoods (*Quercus, Carya*, etc.) and longleaf pine (Harcombe et al. 1995). Frequently, canopy trees are widely spaced giving an open appearance (30–40% canopy cover) that fosters development of a rich ground flora dominated by perennial plants (Drew et al. 1998). Naturally treeless prairies and pitcher plant (*Sarracenia* spp.) bogs are closely tied to and embedded in southeastern pine savannas creating a mosaic of woodland and prairie with distinct ecotones. The woodland-prairie mosaic is maintained by drainage patterns, soil types, fire, and precipitation (Frost et al. 1986, Abrahamson and Hartnett 1990). Grasslands within the longleaf pine ecosystem are among the most species-rich per unit area (30–50 species per square meter) in the Western Hemisphere (Peet and Allard 1995). In general, however, grasslands in the southeastern United States have received relatively little attention (Vogl 1972, DeSelm and Murdock 1993).

Other southeastern pines occur in stands shaped by fire, but none were as extensive as longleaf. Two pine species are less tolerant of fire than longleaf pine: slash pine is typically found in wetter sites, and loblolly pine (*Pinus taeda*) occurs in hardwood-pine mixtures, ecotones, and is extensively planted for silviculture. On the Ozark Plateau, shortleaf pine (*Pinus echinata*) is a dominant species in fire-maintained savannas, has similar structural characteristics to longleaf savannas, and supports populations of Red-cockaded Woodpecker (*Picoides borealis*) (Sparks et al. 1999). In old fields loblolly and shortleaf pines can replace longleaf pine and form a structural analog to longleaf pine savanna, although the plant community composition can be quite different (Engstrom and Palmer, in press).

Dry prairies occur in flat areas in south-central Florida. Although much of this ecosystem (830,000 ha; Kautz et al. 1993) has been converted to improved pasture, significant preserves of native prairie exist on some public and private lands (e.g., Three Lakes Wildlife Management Area, Kissimmee Prairie State Preserve, National Audubon Society Ordway-Whittell Kissimmee Prairie Sancturary, and Avon Park Bombing Range). These native prairies are treeless, fire-dependent grasslands with scattered shrubs such as saw palmetto (*Serenoa repens*), dwarf oak (*Quercus minima*), fetterbush (*Lyonia lucida*), and gallberry

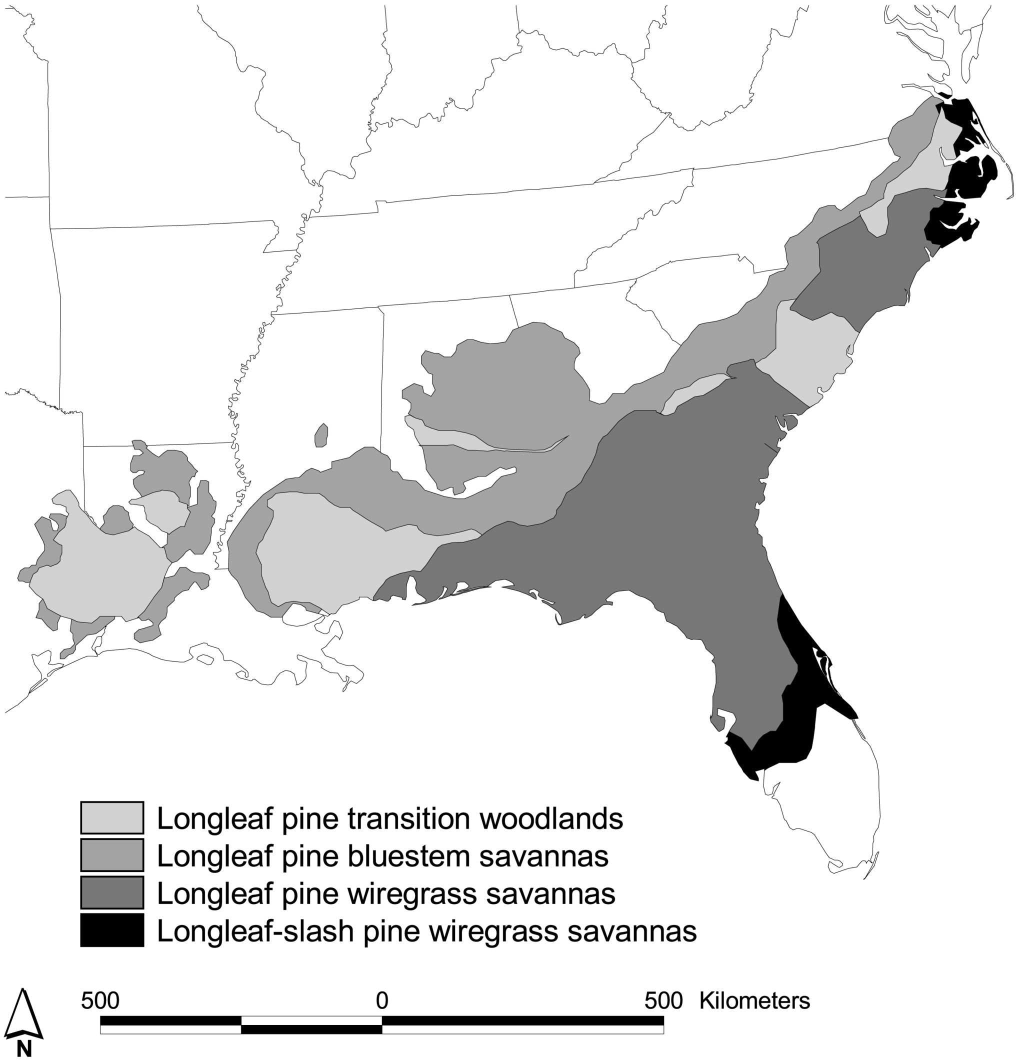

FIGURE 1. Extent of southeastern pine savannas and grasslands (after Platt 1999).

(*Ilex glabra*). Dominant grasses include wiregrass, toothache grass (*Ctenium aromaticum*), bluestem (*Andropogon* spp.), and beakrush (*Rhynchospora* spp.; Perkins et al. 1998).

Fire Regime

Fire is essential to maintenance of the structure and composition of southeastern pine savannas (Christensen 1981). Fire frequency varies according to ground cover characteristics and landscape context, but typically low fires burn only the understory vegetation and rarely burn into the canopy or kill canopy trees (Greene 1931, Harper 1962, Christensen 1981). Lightning-started fires during the peak of the thunderstorm season (May–July) probably were the most common type of fires in Florida longleaf savannas (Komarek 1968, Robbins and Myers 1992) before human settlement. American Indians in the Southeast likely used fire on the landscape for purposes such as hunting, game management, and warfare (Swanton 1946, Robbins and Myers 1992, Williams 2002), but his is not extensively documented. Fires that start in upland longleaf pine woodland can burn into adjacent habitat types depending on moisture and weather conditions, which creates a gradient of plant occurrence based on tolerance to fire and water.

The natural fire frequency in the region prior to settlement by European colonists is poorly documented, but has been estimated at every 3–4 yr (Chapman 1932) and 2–8 yr (Christensen 1981). These estimates are based on the observations that (1) lightning frequency in the Southeast is among the highest in the world with annual rates of 1–10 cloud-to-ground lightning flashes per square kilometer; (2) fuel from pyrogenic grasses and shrubs accumulates rapidly in the absence of fire; and (3) the dominant plants of southeastern pine savannas thrive in the presence of frequent fire and are commonly replaced by less fire tolerant plants over longer fire-return intervals (Chapman1932, Wahlenberg 1946, Christensen 1981, Waldrop et al. 1992, Platt 1999). The fact that open pine savannas were commonly reported by some of the earliest written accounts of vegetation conditions in southeastern coastal plain uplands strongly suggests that lightning-started fire and fires used by American Indians occurred typically more than once every 10 yr (Robbins and Myers 1992, Platt 1999). Fire intervals within pine savannas undoubtedly varied according to vegetation associated within a range of edaphic and hydrological conditions and drought cycles (Brenner 1991, Robbins and Myers 1992, Peet and Allard 1995).

Little is known about the natural fire regime of dry prairies, but the vegetation association clearly has a great tolerance of fire and many species persist because of its occurrence (Abrahamson and Hartnett 1990). Frequent (1–3 yr) fires prevent succession from graminoid to woody vegetation domination.

MODIFICATIONS TO THE FIRE REGIME

Compared to the presettlement fire regime, fire interval in contemporary southeastern pine savannas commonly has been greatly lengthened or fire has been altogether excluded. (For photographic documentation of the effects of long-term fire exclusion on vegetation structure, see Myers [1990], Engstrom et al. [1984], and Woolfenden and Fitzpatrick [1984]). Fire in southeastern pine savannas has the general effect of favoring pines and grasses and suppressing hardwoods (Waldrop et al. 1992, Glitzenstein et al. 1995). Kush et al. (1999) described the effects of 45 yr of fire removal on an old-growth longleaf pine stand in the Flomaton Natural Area in Alabama. In the absence of fire, a substantial midstory dominated by water oak (*Quercus nigra*), laurel oak (*Quercus laurifolia*), southern red oak (*Quercus falcata*), and black cherry (*Prunus serotina*) developed. This hardwood midstory shaded the understory to the point that only 5% of all regenerating saplings were longleaf. This description closely follows the effects of fire exclusion on an old field pineland in north Florida (Engstrom et al. 1984) that will be described in further detail.

The modern landscape fragmented by roads, urban areas, and agricultural fields has broken up what were extensive pine savannas. Some of the earliest (16th and 17th century) explorers in the region described vast pinelands dissected by creeks and rivers (see Robbins and Myers 1992). Major roads and urban areas typically require fire-free buffers and careful smoke management that are challenges within a fire-dependent ecosystem.

PRESCRIBED FIRE

The southeastern US has a long tradition of application of fire by humans for land management purposes from prehistoric use by American Indians to the present (Komarek 1981, Johnson and Hale 2002). Few details are known about fire techniques used by American Indians in the Southeast compared to other native cultures, such as Australian aborigines (Lewis 1989), but documents indicate it was used extensively (Robbins and Myers 1992). Early Europeans, particularly English and Scottish settlers, readily adopted the use of fire for range management (Pyne 1982). Traditional uses of fire in the Southeast persisted despite a strong campaign against its use in the early twentieth century, and fire practitioners in the Southeast can be considered some of the leaders in recognizing the ecological role of fire (Johnson and Hale 2002).

Fire in the Southeast is used by a wide variety of practitioners, and the region is unique because fire is used on many private and public (especially federal) lands. Historically, fire has been used for a variety of agricultural and wildlife management purposes, and two bird species, Northern Bobwhite (*Colinus virginianus*) and Red-cockaded Woodpecker, have played especially important roles. (See discussion of these species below.) Where fire has been applied frequently in pine savannas over a long period of time (e.g., private hunting estates in Georgia, Florida, and South Carolina), prescribed fire is often applied by workers on foot using drip torches typically shortly after the end of the bobwhite hunting season. Applications on public land are more variable. Use of helicopters to apply fire is common and the season of fire is broader. Currently, prescribed burning is widely acknowledged as being essential for the long-term ecological health of the longleaf pine ecosystem (Platt 1999), but the long-term use of burning is dependent on societal acknowledgment and permission (Wade 1993).

CHARACTERISTIC BIRD SPECIES OF SAVANNAS AND PRAIRIES

The avian community of this once-extensive ecosystem is composed of approximately 110–120 species, excluding species that occur only as migrants (Jackson 1988, Engstrom 1993, Hunter et al. 2001). Depending on location in woodland subtypes, approximately 40% of this avifauna is resident, 34% is found during the breeding season only, and 26% is found during the winter only (Engstrom 1993). Indicative of the importance of ground cover in this ecosystem, about one third of the species that characterize the ecosystem forage on or close to the ground or in shrubs in mature, fire-maintained woodlands. Of all southeastern pinewoods bird species, the Red-cockaded Woodpecker, Brown-headed Nuthatch (*Sitta pusilla*), and Bachman's Sparrow (*Aimophila aestivalis*) use longleaf habitats extensively and are largely sympatric with southeastern pine savannas. An endangered subspecies, Florida Grasshopper Sparrow (*Ammodramus savannarum floridanus*) that is restricted to dry prairies, Northern Bobwhite (*Colinus virginianus*), because of its economic importance and historic role in use of fire, and a wintering species, Henslow's Sparrow (*Ammodramus henslowii*), are also characteristic of the region and are covered in more detail below.

EFFECTS OF CHANGES TO FIRE REGIME

Fire Frequency Including Fire Exclusion

More than any other component of fire regime, fire frequency has profound effects on vegetation and associated bird life in southeastern pine savannas and prairies. After long-term fire removal, shifts from herbaceous-dominated, open pine savannas (25–60% crown closure) to hardwood pine woodland (>60% canopy cover) have contributed to dramatic declines in pine savanna bird species. Askins (1993) drew attention to widespread declines in grassland and shrubland birds and attributed the declines to loss of early successional habitat. Fire is the primary ecological factor that shaped southeastern pine savannas and native prairies, and prescribed fire is the management tool that will enable pine savanna ecosystems to persist.

Most studies of the effects of alteration of fire frequency on birds in southeastern pine savannas can be separated into two types: fire exclusion and fire reintroduction. We compared the results of two studies of the effects of fire exclusion on bird species (Engstrom et al. 1984, White et al. 1999).

Engstrom et al. (1984) reported the results of annual spot-mapping of the breeding-season avian community of an 8.9-ha study plot (named NB66). The site was an old-field pine woodland that had been burned annually until 1967, at which point fire was excluded. The woodland had developed on abandoned agricultural fields, and although it was dominated by loblolly and shortleaf pines, it was a structural analog to longleaf pine woodland. Frequent (annual or biannual) application of prescribed fire can maintain the structure of longleaf pine woodlands for decades, although recent evidence suggests that the community in old-field pine woodlands, composed of less pyrogenic plants, is not so stable (Engstrom et al. 1999). The size-class distribution of pines in the 1966 data indicated a shortage of pine recruits. Without intensive management, including soil disturbance, loblolly and shortleaf pines were not regenerating in the frequent fire regime.

During the 15 yr from 1967 through 1981, the breeding bird community lost species richness at an average rate of 0.5 species per year. Of 44 species encountered, 17 showed no clear changes following fire exclusion, 19 declined, and eight responded positively to fire exclusion (Table 1). Many of the bird species that rapidly declined on NB66 were pine woods specialists that occurred in all years on a nearby old-growth longleaf pine site and were never recorded at a nearby American beech (*Fagus grandifolia*)-southern magnolia (*Magnolia grandiflora*) forest (Engstrom et al. 1984). These same species are also declining throughout the southeastern United States (Hunter et al. 2001). Although NB66 was not replicated, had no control, and no pretreatment data were collected, the patterns of bird species loss are consistent with large-scale bird population trends. This is a strong indication of fire's role in determining vegetation composition and structure that is critical for selected bird species. The plant succession and changes in the avian community observed by Engstrom et al. (1984) may be typical of widespread habitat alteration throughout the Southeast as application of prescribed fire has declined. For example, the avian community of an old-growth longleaf pine woodland in central Florida that had obvious signs of decades of fire suppression (i.e., large diameter water oaks) lacked several of the longleaf pine specialists, such as Brown-headed Nuthatch, Red-cockaded Woodpecker, and Bachman's Sparrow (Hirth et al. 1991).

White et al. (1999) compared point-count results on 18 postfire sites (eight 1-yr postfire, six 2-yr postfire, and four 3-yr postfire) and six sites that were not burned for >20 yr during 1993–1995. Results of the 18 postfire sites were pooled because no differences

TABLE 1. RESPONSE OF INDIVIDUAL BIRD SPECIES TO FIRE EXCLUSION, FIRE REINTRODUCTION, AND FIRE SEASON. STUDY SEASON: B = BREEDING, W = WINTER. RESPONSE TO FIRE EXCLUSION WOULD BE EXPECTED TO BE THE OPPOSITE OF RESPONSE TO FIRE REINTRODUCTION. THE TWO SYMBOLS IN THE FIRE REINTRODUCTION COLUMN REFER TO RESPONSES OBSERVED IN CONTROL AND BURNED PLOTS, RESPECTIVELY.

Species	Study season	Response to fire exclusion	Response to fire reintroduction	Response to fire season (growing vs. dormant)	Reference[a]
Black Vulture	breeding			0	1
(*Coragyps atratus*)					
Turkey Vulture	dormant			0	1
(*Cathartes aura*)					
Wood Duck	breeding	–			2
(*Aix sponsa*)					
Red-shouldered Hawk	dormant			0	1
(*Buteo lineatus*)					
American Kestrel	breeding		0/0		3
(*Falco sparverius*)	dormant			0	1
Wild Turkey	breeding	0			4
(*Meleagris gallopavo*)	dormant			0	1
Northern Bobwhite	breeding	–			2
(*Colinus virginianus*)	breeding	0			4
	breeding		+/+		3
	breeding			–	6
Common Snipe	dormant			0	1
(*Gallinago gallinago*)					
Mourning Dove	breeding	0			2
(*Zenaida macroura*)	breeding	+			4
	dormant			0	1
	breeding			0	5
Yellow-billed Cuckoo	breeding	+			2
(*Coccyzus americanus*)	breeding	+			4
Common Nighthawk	breeding		0/0		3
(*Chordeiles minor*)	breeding			0	5
Red-headed Woodpecker	breeding	–			2
(*Melanerpes erythrocephalus*)	breeding	0			4
	dormant			0	1
	breeding			0	5
Red-bellied Woodpecker	breeding	0			2
(*Melanerpes carolinus*)	breeding	+			4
	dormant		0/0		6
	breeding		+/0		3
	dormant			0	1
	breeding			0	5
Yellow-bellied Sapsucker	dormant		0/0		6
(*Sphyrapicus varius*)	dormant			0	1
Downy Woodpecker	breeding	0			2
(*Picoides pubescens*)	dormant		0/0		6
	breeding	0			4
	dormant			0	1
Hairy Woodpecker	breeding	0			2
(*Picoides villosus*)	breeding	0			4
	dormant		0/0		6
	dormant			0	1
Red-cockaded Woodpecker	breeding	–			2
(*Picoides borealis*)	breeding	–			4
	dormant		+/0		6
	breeding		+/+		3
	dormant			0	1
	breeding			0	5

TABLE 1. CONTINUED.

Species	Study season	Response to fire exclusion	Response to fire reintroduction	Response to fire season (growing vs. dormant)	Reference[a]
Northern Flicker	dormant	0			2
(*Colaptes auratus*)	breeding	–			4
	breeding		+/+		3
	dormant			0	1
	breeding			0	5
Pileated Woodpecker	breeding	0			2
(*Dryocopus pileatus*)	breeding	0			4
	breeding			0	5
Eastern Wood-Pewee	breeding	–			2
(*Contopus virens*)	breeding	–			4
	dormant			0	1
Eastern Phoebe	dormant		0/0		6
(*Sayornis phoebe*)	dormant			0	1
Acadian Flycatcher (*Empidonax virescens*)	breeding	–			4
Great Crested Flycatcher	breeding	0			2
(*Myiarchus crinitus*)	breeding	+			4
	breeding			0	5
Eastern Kingbird	breeding	–			2
(*Tyrannus tyrannus*)	breeding			0	5
Loggerhead Shrike (*Lanius ludovicianus*)	breeding	–			2
White-eyed Vireo	breeding	+			2
(*Vireo griseus*)	breeding	0			4
Yellow-throated Vireo	breeding	0			2
(*Vireo flavifrons*)	breeding	–			4
Blue-headed Vireo	dormant		0/0		6
(*Vireo solitarius*)	breeding	–			4
	dormant			0	1
Red-eyed Vireo	breeding	+			2
(*Vireo olivaceus*)	breeding	–			4
Blue Jay	breeding	0			2
(*Cyanocitta cristata*)	breeding	+			4
	dormant			0	1
American Crow	breeding	0			4
(*Corvus brachyrhynchos*)	dormant			0	1
Carolina Chickadee	breeding	0			2
(*Poecile carolinensis*)	breeding	0			4
	dormant		0/0		6
	dormant			0	1
	breeding			0	5
Tufted Titmouse	breeding	0			2
(*Baeolophus bicolor*)	breeding	0			4
	dormant		0/0		6
	breeding		–/–		3
	dormant			0	1
Red-breasted Nuthatch (*Sitta canadensis*)	dormant			0	1
White-breasted Nuthatch	breeding	–			2
(*Sitta carolinensis*)	dormant			0	1
Brown-headed Nutchatch	breeding	0			2
(*Sitta pusilla*)	breeding	–			4
	dormant		0/0		6
	dormant			0	1
	breeding			0	5

TABLE 1. CONTINUED.

Species	Study season	Response to fire exclusion	Response to fire reintroduction	Response to fire season (growing vs. dormant)	Reference[a]
Carolina Wren	breeding	0			2
(*Thryothorus ludovicianus*)	breeding	–			4
	dormant			0	1
House Wren (*Troglodytes aedon*)	dormant		0/0		6
Golden-crowned Kinglet	dormant		x/0		6
(*Regulus satrapa*)	dormant			0	1
Ruby-crowned Kinglet	dormant		0/0		6
(*Regulus regulus*)	dormant			0	1
Blue-gray Gnatcatcher	breeding	0			2
(*Polioptila caerulea*)	breeding	–			4
	dormant		0/0		6
	breeding			0	5
Eastern Bluebird	breeding	–			2
(*Sialia sialis*)	dormant		0/+		6
	dormant			0	1
	breeding			0	5
Hermit Thrush	dormant		0/0		6
(*Catharus guttatus*)	dormant			0	1
Wood Thrush	breeding	+			2
(*Hylocichla mustelina*)	breeding	0			4
American Robin	breeding	0			4
(*Turdus migratorius*)	dormant			0	1
Gray Catbird (*Dumetella carolinensis*)	dormant			0	1
Brown Thrasher	breeding	0			2
(*Toxostoma rufum*)	breeding	0			4
	breeding		–/0		3
Cedar Waxwing (*Bombycilla cedrorum*)	dormant			0	1
Northern Parula	breeding	+			2
(*Parula americana*)	breeding	–			4
Yellow-rumped Warbler	dormant		0/0		6
(*Dendroica coronata*)	dormant			0	1
Yellow-throated Warbler	breeding	+			2
(*Dendroica dominica*)	breeding	–			4
Pine Warbler	breeding	+			2
(*Dendroica pinus*)	breeding	–			4
	dormant		0/0		6
	dormant			0	1
	breeding			0	5
Prairie Warbler	breeding	–			2
(*Dendroica discolor*)	breeding	–			4
	dormant			0	1
Palm Warbler	dormant		0/0		6
(*Dendroica palmarum*)	dormant			0	1
Black-and-White Warbler (*Mniotilta varis*)	breeding	+			4
Kentucky Warbler (*Oporornis formosus*)	breeding	0			4
Common Yellowthroat	breeding	–			2
(*Geothlypis trichas*)	breeding	–			4
	dormant			0	1
	breeding			0	5

TABLE 1. CONTINUED.

Species	Study season	Response to fire exclusion	Response to fire reintroduction	Response to fire season (growing vs. dormant)	Reference[a]
Hooded Warbler	breeding	+			2
(*Wilsonia citrina*)	breeding	0			4
Yellow-breasted Chat	breeding	–			2
(*Icteria virens*)	breeding	–			4
Summer Tanager	breeding	–			2
(*Piranga rubra*)	breeding	0			4
	breeding			0	5
Eastern Towhee	breeding	–			2
(*Pipilo erythrophthalmus*)	breeding		0/+		3
	breeding	–			4
	dormant			0	1
	breeding			0	5
Bachman's Sparrow	breeding	–			2
(*Aimophila aestivalis*)	breeding				7
	breeding	–			4
	dormant			0	1
Chipping Sparrow	dormant		0/0		6
(*Spizella passerina*)	breeding	–			4
	dormant			0	1
Field Sparrow					
(*Spizella pusilla*)	breeding	–			2
	breeding	–			4
Fox Sparrow	dormant			0	1
(*Passerella iliaca*)					
Song Sparrow	dormant			0	1
(*Melospiza melodia*)					
White-throated Sparrow	dormant			0	1
(*Zonotrichia albicollis*)					
Dark-eyed Junco	dormant		0/0		6
(*Junco hyemalis*)	dormant			0	1
Northern Cardinal	breeding	0			2
(*Cardinalis cardinalis*)	breeding	–			4
	dormant			0	1
Blue Grosbeak	breeding	–			2
(*Guiraca caerulea*)	breeding		+/+		3
Indigo Bunting	breeding	–			2
(*Passerina cyanea*)	breeding	–			4
Eastern Meadowlark	breeding			0	5
(*Sturnella magna*)					
Common Grackle	dormant			0	1
(*Quiscalus quiscula*)					
Brown-headed Cowbird	breeding	0			2
(*Molothrus ater*)	breeding	–			4
Orchard Oriole	breeding	–			2
(*Icterus spurius*)					
American Goldfinch	breeding	–			4
(*Carduelis tristis*)	dormant			0	1

[a] References: 1 = King et al. (1998); 2 = Engstrom et al. (1984); 3 = Provencher et al. (2002b); 4 = White et al. (1999); 5 = Engstrom et al. (1996); 6 = Provencher et al. (2002a); 7 = Shriver and Vickery (2001).

were detected. A comparison of the burned sites versus the fire-excluded sites indicated that of a total of 46 species, 16 showed no differences between burned and fire-excluded sites, 24 species declined, and six increased after fire was excluded (Table 1).

Thirty-seven of 53 total species were encountered in both studies (Engstrom et al. 1984, White et al. 1999). Of these 37 species six had no response to fire exclusion, the Yellow-billed Cuckoo (*Coccyzus americanus*) had a consistently positive response in both studies, nine species consistently declined, 18 species had no response in one of the studies despite showing a response in the other, and three species had contrary responses (Table 1).

Hardwood removal using herbicides or mechanical means and reintroduction of fire is being employed widely to improve Red-cockaded Woodpecker habitat on many federal lands. Breeding birds such as Northern Bobwhite and Bachman's Sparrow, that are associated with open grass- and pine-dominated savannas (Hunter et al. 2001), responded positively to hardwood removal (Burger et al. 1998, Brennan et al. 1995, Masters et al. 2002).

Experimental habitat restoration of fire-excluded longleaf pine savannas was recently conducted in northern Florida, and the effects of restoration were measured for winter (Provencher et al. 2002a) and breeding birds (Provencher et al. 2002b). Six plots (81 ha each) were randomly chosen for each of three experimental treatments and a control (no treatment) for a total of 24 plots. Habitat restoration treatments (primarily oak reduction) were: herbicides, chainsaw felling and girdling, and growing-season burns. Plots were burned in 1995 and birds were sampled in 1998 and 1999. The symbols in Table 1 (e.g., 0/0) reported for these two studies reflect the contrast of the control vs. burned plots for each of the 2 yr (1998 and 1999). For example, the '+/+' for Northern Bobwhite (Table 1) means that statistically significant increases in detections of bobwhite were made in both 1998 and 1999. A total of 29 species were counted during the 2 studies combined, but, somewhat surprisingly, only three, Red-bellied Woodpecker (*Melanerpes carolinus*), Red-cockaded Woodpecker, and Tufted Titmouse (*Baeolophus bicolor*), were found in both the winter (Provencher et al. 2002a) and breeding season (Provencher et al. 2002b). Of these three species, the Red-cockaded Woodpecker came close to increases in both years in both seasons; the Red-bellied Woodpecker showed no change in response to reintroduction of fire in all contrasts except for an increase in breeding-season detections in 1999; and the Tufted Titmouse declined in response to fire when measured in the breeding season, but showed no effect in the winter (Table 1). During the breeding-season study only, three additional species responded positively to fire (Northern Bobwhite, Northern Flicker (*Colaptes auratus*), and Blue Grosbeak (*Passerina caerulea*); Provencher et al. 2002b). During the winter study, species richness was not significantly different among the control and three treatments over the 2-yr study period, but flock size on the treated plots was larger than control plots. This increase was primarily influenced by the abundance of Chipping Sparrows (*Spizella passerina*; Provencher et al. 2002a).

Season

Debate in the Southeast about the proper season of fire developed from the observation that lightning-started fires predominantly occur between June and August, whereas most land managers century have applied fire during the dormant season (December–March) (Robbins and Myers 1992, Brennan et al. 2000; Fig. 1). The strongly seasonal natural fire regime over thousands of years must have exerted selection pressure on organisms that inhabited pine savannas (Komarek 1965). Concern about wiregrass, a pyrogenic species that has a physiological trigger to flower in the fall following fire (or other disturbance) during the late spring—early summer (Clewell 1989), further pushed the debate, because it is functionally important within portions of the southeastern pine-woodland complex (Noss 1989). Use of prescribed fire during the lightning season to better mimic the season of natural fire has increased on some land ownerships such as national forests (Ferguson 1998).

Application of prescribed fire during the lightning season is more effective at killing hardwoods and shrubs than winter or dormant-season prescribed burning (Waldrop et al. 1992). This results in maintenance of herbaceous vegetation typical of grassland communities. The possibility of more effective control of hardwoods makes lightning-season fire an attractive management technique. Counterbalancing interest in use of lightning-season, prescribed fires for vegetation management is concern that such fires will have strongly negative effects on nesting birds, particularly ground-nesting game birds (Stoddard 1931) and insects such as rare butterflies (Swengel 2001).

In field experiments over 2 yr on four replicate pairs of 12-ha plots (one dormant-season and one growing-season plot per pair), the effects of biennial dormant- and growing-season prescribed fire on bird populations in longleaf pine savannas in northern Florida were measured (Engstrom et al. 1996). Spot-mapping and nest data were collected before and after dormant- (January-February), and growing-season (May–July) prescribed fires during the treatment year (1995) and during the breeding season in the non-treatment year (1994). Breeding bird densities ranged from 11–15 pairs per plot, and 250 nests of mostly cavity-nesting and canopy species were located. No statistically significant differences in species richness or the number of territories were found between growing-season and dormant-season paired plots, nor were statistically significant differences found between pre-fire and postfire bird species richness or number of individuals in the dormant-season plots during years in which fire was applied. Growing-season prescribed fires have limited short-term effects on bird communities in longleaf pine woodland (Table 1; Engstrom et al. 1996). King et al. (1998) in a study of the effects of growing-season versus dormant-season fire in Georgia pinelands detected no significant differences in abundance in 47 species counted (Table 1).

Severity

As in many ecosystems, fire severity in southeastern pine savannas can be inversely related to fire frequency. In general, the frequent fires in well-managed longleaf pine savannas are low severity and cause little mortality in the dominant plant species. When the fire regime is disrupted and fire is excluded for extended periods, reintroduction of fire can kill even the most fire-tolerant species, such as mature longleaf pines. In a study of restoration of an old-growth longleaf pine woodland in Flomaton, Alabama, in which many large hardwoods had grown over years of fire exclusion, a low intensity-fire killed some of the oldest longleaf pine trees by severely pruning overstory feeder roots that had grown into the duff layer (Wade et al. 1998). The challenge of reintroducing fire into longleaf pine savannas after long periods of fire exclusion is being faced at several locations throughout the Southeast (e.g., Eglin Air Force Base, Florida; Moody Tract, Georgia; Chinsegut Preserve, Florida). Little documentation has been made of the avian response to severe fires that cause extensive areas of overstory mortality in southeastern pine savannas.

FIRE EFFECTS ON CHARACTERISTIC BIRD SPECIES OF SAVANNAS AND PRAIRIES

NORTHERN BOBWHITE

Research on population ecology of the Northern Bobwhite played a pivotal role in development of fire ecology in the southeastern US (Johnson and Hale 2002). Herbert Stoddard's work on the Northern Bobwhite stands as a classic monograph on wildlife management of a bird species and is additionally influential because it recognized the utility of fire as a management technique and provided an ecological basis for the role of fire in southeastern upland ecosystems (Stoddard 1931). Stoddard established the critical role of fire in maintaining ecosystem health, but he was highly concerned about negative effects (primarily loss of nests and young) of lightning-season fire on bobwhites and ground-nesting birds in general (Stoddard 1931, 1963). Seasonal application of prescribed fire in the area of north Florida to south Georgia where Stoddard lived and worked tended to occur during a narrow window immediately after the bobwhite hunting season and before bobwhites initiated nesting. As previously noted, this is not when natural, lightning-caused fires happen. Stoddard's opposition cast a long shadow on use of prescribed fire during the lightning-season when maintaining populations of bobwhites was the primary management objective. In a recent study, application of prescribed fire during May and June resulted in slight increases in arthropod biomass and slightly increased hunting success on sites burned in the lightning season versus those burned during the dormant season (Brennan et al. 2000). The authors recommended that small-scale application of lightning-season fire could be used to control hardwoods without short-term negative effects on bobwhites.

RED-COCKADED WOODPECKER

Since the 1970s, concern for populations of the endangered Red-cockaded Woodpecker has played a significant role in re-evaluation of the role of fire in management of southeastern pine savannas, particularly on federal lands (Ferguson 1998, Provencher et al. 2002a, 2002b). The woodpecker typically forages on living pine trees and excavates its roosting and nesting cavities in old living pine trees (Conner et al. 2001). Lengthened fire interval is one of the key agents in declines in habitat quality and population size of the Red-cockaded Woodpecker (Conner et al. 2001, Saenz et al. 2001), because this facilitates an increase in hardwoods and eventual elimination of pine regeneration that results in a slow transition from a pine-dominated to a hardwood-dominated forest. The exact mechanism that causes the Red-cockaded Woodpecker to abandon hardwood-encroached pine habitats is not fully understood, but the species avoids hardwood dominated forests and pinelands in which a hardwood midstory is thickly developed (Conner et al. 2001).

Fire also has more subtle effects on the life history of the Red-cockaded Woodpecker than setting the successional stage. The species' distinctive habit of creating wounds on the tree bole that exude resin around the cavity creates a highly flammable zone. Cavities that have copious and extensive resin flow or are low on the tree may be particularly vulnerable. Effects of burning this resin may be as minor as a temporary loss of predator or competitor inhibition, but it can cause tree death and abandonment by the woodpecker of the cavity tree. This may be most devastating if burning the resin barrier results in loss of a nesting effort, but any loss of cavity trees is important, because of the high investment by the woodpeckers to excavate the cavities. Minimizing loss of cavity trees to fire may be particularly critical in the younger pinelands following extensive harvest in the early twentieth century to the point that fuels are often reduced manually on public lands on which woodpecker population recovery is a high priority.

Use of growing season prescribed fire has been identified as a critical component of habitat management to enhance Red-cockaded Woodpecker population recovery (USDI Fish and Wildlife 2000, Conner et al. 2001). In a woodland in which fire increased nesting productivity in the first year after a fire, James et al. (1997) also found that some of the variation in group size (an important indicator of population health) could be explained by variation in composition of the ground cover. They hypothesized that nutrient cycling and variation in the arboreal arthropod community, particularly ants, are influenced by the fire regime and could play important roles in regulation of woodpecker populations.

BROWN-HEADED NUTHATCH

This species occurs almost exclusively in southeastern pine forests (Withgott and Smith 1998) where it forages on living pines and often nests in well-decayed snags and stumps. Brown-headed Nuthatch median nest height of 1.5 m throughout its range (McNair 1984) is among the lowest of North American cavity nesters (Withgott and Smith 1998). The mean egg date is 9 April ± 19 days, and 90% of the clutches are complete by 5 May (McNair 1984). The combination of low nest height and early nesting could make some nests of this species vulnerable to late dormant-season fires, although the effects of fire on nuthatch nests has not been studied to date. Fire exclusion resulted in slow decline in numbers of this species in north Florida (Table 1; Engstrom et al. 1984), and no change in abundance resulted from application of different seasons of prescribed fire (Table1).

FLORIDA GRASSHOPPER SPARROW

Prescribed burning is the primary management option to maintain habitat in Florida dry prairies, a formerly extensive vegetation association embedded within longleaf/south Florida slash pine savannas (Kautz et al. 1993). Fire affects vegetation by reducing litter, exposing bare ground, and reducing shrub encroachment. In a 3-yr spot-mapping study, densities and indices of reproductive success of the Florida Grasshopper Sparrow, an endangered grassland specialist, were greater in units that had been dormant-season burned within the past 6 mo compared to units that were 1.5 or 2.5 yr postfire (Shriver and Vickery 2001). To optimize dry prairie habitat for Florida Grasshopper Sparrows, burns should be conducted every 2–3 yr. This burn regime will optimize habitat for Grasshopper Sparrows without adversely affecting Bachman's Sparrows (Shriver and Vickery 2001). In a point-count study of Florida Grasshopper Sparrow response to growing-season fire (June), Shriver et al. (1999) noted that male sparrows established territories on sites within a week of the fires and initiated a second bout of breeding activity that extended into mid-August and early September. This contrasted with a steady decline in sparrow breeding activity on control plots that had been burned 3 yr earlier.

BACHMAN'S SPARROW

Fire creates and maintains the open structure within southeastern pine savannas that are the primary habitat of this species, although it also occurs in utility right-of-ways, clearcuts, and abandoned agricultural fields. In the southern part of its range, egg dates are from late April to late August (85% in May–July) in cupped or domed ground nests (Dunning 1993). Bachman's Sparrows abandoned a site after 3 yr of fire exclusion in north Florida (Engstrom et al. 1984), but no difference in Bachman's Sparrow density was noted in a 3-yr spot-mapping study of three burn classes (0.5-yr, 1.5-yr, and 2.5-yr postfire) in dry prairie (Shriver and Vickery 2001). Counts of singing males did not differ between growing season and dormant season burned plots in north Florida (Engstrom et al. 1996); however, Seaman and Krementz (2000) found that 18 marked Bachman's Sparrows abandoned two stands burned in the growing season and did not return. They suggested that displacement of all of the marked sparrows from the growing-season burned areas could have had a negative effect on reproduction and cautioned managers against burning too much suitable breeding habitat within the same year. Seaman and Krementz (2000) did not discuss use of sites burned in the growing-season as post-breeding habitat.

HENSLOW'S SPARROW

Henslow's Sparrow has shown one of the most extreme population declines of any landbird in eastern North America (Wells and Rosenberg 1999). This decline is caused in part by loss or degradation of grassland habitats on both the winter and breeding ranges (Peterjohn et al. 1994, Pruitt 1996, Wells and Rosenberg 1999). The winter range of Henslow's Sparrow is largely congruent with the lower coastal plain of the southeastern United States, where longleaf pine woodland was once the dominant ecosystem. Winter populations of Henslow's Sparrows have become fragmented even in the center of the winter range on the north Gulf Coastal Plain (Pruitt 1996). Some of the largest known remaining populations are located in Mississippi (Chandler and Woodrey 1995), Louisiana (Carrie et al., unpubl. data), Alabama (Plentovich et al. 1999), and northwest Florida (McNair, unpubl. data). Henslow's Sparrows in winter are often found in wet prairies and bogs that have been recently burned (<6 yr postfire); maximum abundance of sparrows occurred on sites that were burned or disturbed one growing season previously in Alabama (Plentovich et al. 1999) and on sites that had been burned within 1 yr in Louisiana (Bechtoldt and Schaefer, unpubl. report). The role of fire in management of its breeding habitat in the midwestern United States indicates that sparrow populations decline the first growing season after fire (Herkert 1994, Swengel 1996), but increase in subsequent years. Reduced populations of Henslow's Sparrows in the first year postfire appear to be related to the species' preference for dense vegetation with a well-developed litter layer and a high density of standing dead vegetation (Zimmerman 1988).

CONCLUSIONS

Some general conclusions about use of fire for conservation and management of birds in southeastern pine savannas seem clear:

1. More burning is needed in pine woodlands, savannas, and associated grasslands to retard hardwood intrusion. The continuing reduction in the number of acres burned annually in southeastern pine savannas has the effect of lengthening the fire interval. This will increase the fuel load and could increase fire severity. Planning for prescribed fire to minimize severity (i.e., overstory mortality) when a heavy fuel load is present will inevitably narrow the weather and fuel moisture conditions that are acceptable to meet management objectives. This means that fewer days may be available for burning and the risk of wildfire will increase. Use of herbicides to maintain a desired vegetation structure as an alternative to burning has been proposed (Wigley et al. 2002), but this is more expensive and its long-term effects on vegetation are unknown. At least for some rare plants (e.g., *Schwabea*), herbicides are unlikely to be an effective substitute for fire (Kirkman et al. 1998). In no way do we endorse a call for more burning at any cost. Prescribed fire must be applied thoughtfully to reduce fire severity, especially in chronically fire suppressed situations.
2. Efforts to determine natural fire regime may be overdrawn. Mimicking nature may be impossible when the relative influences of anthropogenic and natural fires are impossible to separate (e.g., natural and Native American fire regimes). We agree with Whelan (1995) and Agee (1993) that a more practical approach would be to measure the response of organisms, populations, and communities to experimentally imposed fire regimes and to set goals based on those results. Efforts to understand natural fire regimes are useful within the context of establishing a starting point for adaptive management (Engstrom et al. 1999), not as an end in itself.
3. One of our most important research challenges is to assess the tradeoffs among different species of different seasonal and landscape patterns of prescribed fire. Any management action, including use or exclusion of fire, affects bird populations. For example, use of prescribed fire improved gross habitat structure for the Red-cockaded Woodpecker, Northern Bobwhite, and other grassland birds (Brennan et al.1995, Masters et al. 2002), but negatively affected bird species associated with hardwoods. Dormant-season fire, particularly midwinter, removes cover and foraging substrate of species that are active close to the ground. Growing-season fire can eliminate the reproductive effort of some individuals (loss of eggs and young), although it may enhance the reproductive effort of others through improved

brood habitat, which sets up a compensatory dynamic within a population of a single species. Better understanding of these relations can only be derived from further scientific study, but until then, it seems practical to adopt a strategy of application of fire that is diverse in time (season and frequency) and space.

ACKNOWLEDGMENTS

We thank Frances James, an anonymous reviewer, and Hugh Powell and Vicki Saab, for their comments on this paper.

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