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FIRE AND AVIAN ECOLOGY IN NORTH AMERICA: PROCESS INFLUENCING PATTERN

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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 shrubsteppe, 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,

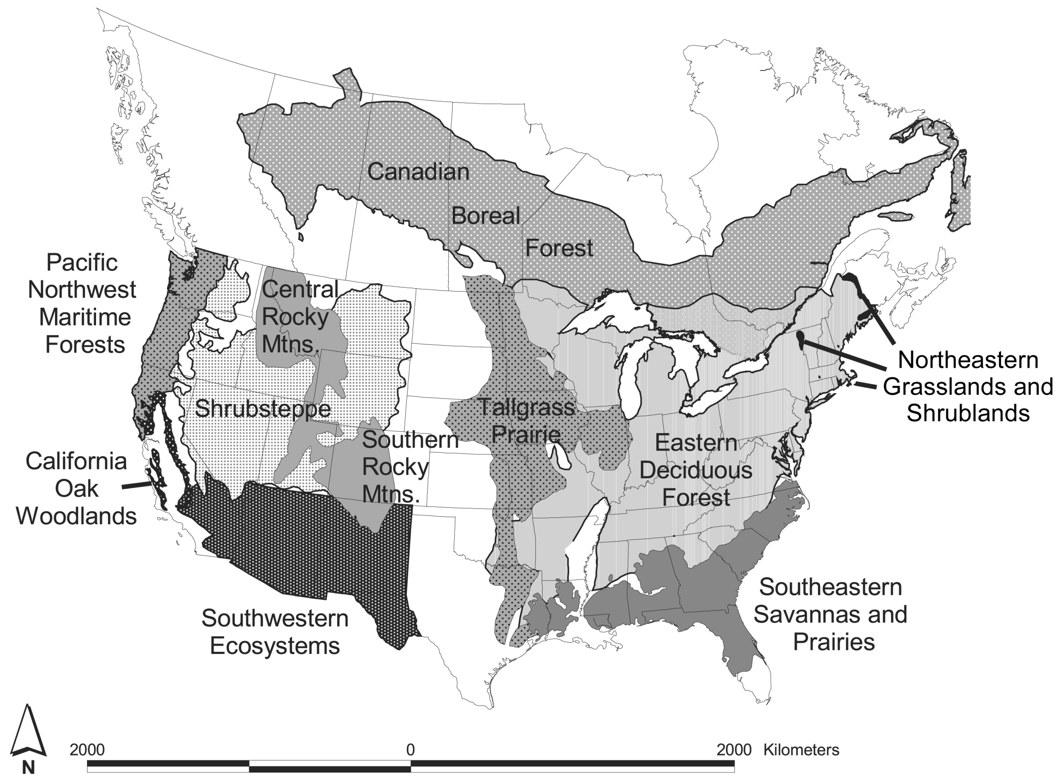

FIGURE 1. Spacial extent of the 10 geographic regions covered in this volume.

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.

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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.