Effects of Prescribed Fire on Wildlife and Wildlife Habitat in Selected Ecosystems of North America

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Edited by

William M. Block and L. Mike Conner

Cover Image

Controlled burn in Chihuahuan Desert grassland at the Sevilleta National Wildlife Refuge, New Mexico. Credit: U.S. Fish and Wildlife Service

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Foreword

Sawback prescribed fire in Banff National Park.
Credit: Chris Siddall

Presidents of The Wildlife Society occasionally appoint ad hoc committees to study and report on select conservation issues. The reports ordinarily appear as either a Technical Review or a Position Statement. Review papers present technical information and the views of the appointed committee members, but not necessarily the views of their employers. Position Statements are based on the review papers, and the preliminary versions are made available for comment by Society members. Following the comment period, revision, and Council's approval, the statements are published as official positions of The Wildlife Society.

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Prescribed fire in a longleaf pine forest in southwestern Georgia.
Credit: Gail Morris, Joseph W. Jones Ecological Research Center.

Executive Summary

Prescribed fires in semi-desert grasslands in Arizona.

Credit: Andrea Litt

Prescribed fire is applied widely as a management tool in North America to meet various objectives such as reducing fuel loads and fuel continuity, returning fire to an ecosystem, enhancing wildlife habitats, improving forage, preparing seedbeds, improving watershed conditions, enhancing nutrient cycling, controlling exotic weeds, and enhancing resilience from climate change. Regardless of the particular objective, fire affects ecosystem structure, composition, and function in many ways.

We used a regional approach, focusing on selected vegetation types for our review (Figure 1). Included were southeastern pine (*Pinus* spp.) and mixed pine-oak (*Quercus* spp.) forests, eastern coastal marshes, midwestern jack pine forests, sagebrush (*Artemisia* spp.) ecosystems of the interior West, mixed-severity forests of the northern Rocky Mountains, subalpine and montane forests of the Canadian Rockies, southwestern ponderosa pine forests, desert grasslands, and shortgrass steppe ecosystems. We structured each regional account by reviewing historical and current uses of fire, and then discussed fire effects on wildlife and the challenges of using prescribed fire in each system.

Prescribed fire affects wildlife in various ways. Population responses by species can be positive, negative, or neutral, short-term or long-term, and they often vary across spatial scales. Whereas prescribed fire can create or maintain habitats for some species, it can also remove or alter conditions in ways that render it unsuitable for other species. Furthermore, a species may benefit from fire in one situation but not another. Given the variations in fire and in species responses, the only real generalization one can make is that exceptions occur. Fire does not occur uniformly across a landscape, instead manifesting as a heterogeneous mosaic that provides habitats for different species, thereby influencing wildlife diversity. Practitioners

should try to emulate natural mosaic patterns by designing and implementing a set of prescriptions rather than applying one prescription across a landscape.

Social issues, particularly those surrounding smoke and emissions, constrain where, when, and how managers can burn vegetation. Certainly, emissions standards enforced by state and federal environmental agencies limit windows of opportunity for burning. Smoke billowing into human communities is a health concern, especially for people with existing respiratory ailments. Many publics associate smoke with fire and conclude that fire is bad. Progress has been made in educating the public concerning benefits of prescribed fire to both reduce threats of wildfire to people and property and to maintain or enhance ecological communities, but much work remains.

In conclusion, benefits of prescribed fire far outweigh negative effects. The science of prescribed fire continues to provide better information and options for resource managers to incorporate into management plans. Prescribed fire should be applied within a structured adaptive management framework, which requires developing and implementing monitoring systems to evaluate the efficacy of specific fire prescriptions. Depending on monitoring results, prescriptions could be applied elsewhere or adjusted to meet management objectives. Either way, prescribed fire is an important resource management tool that can be effective at maintaining or enhancing habitats for many species of wildlife.

Longleaf pines require periodic fires to persist on the landscape.
Courtesy of the Orienne Society

Introduction

Elk grazing in the Carrot Creek prescribed fire area in Banff National Park.

Credit: Ian Pengelly

Wildland fires occur throughout North America (Pyne 1997), and some suggest that as much as 60% of North American landscapes have been shaped by low-intensity fires (Melvin 2012). Prescribed fires, defined as human-ignited fires intended to accomplish a particular management objective, have been used for centuries as a vegetation and wildlife management tool (Poulos 2015). Prior to this time, fire-maintained ecosystems evolved as a result of lightning ignition (Rorig and Ferguson 1999). In many instances, Native Americans were instrumental in applying fire on landscapes (Delcourt and Delcourt 1997, Pyne 1997). Indeed, Native Americans should be considered the first practitioners of prescribed fire in North America, as ample evidence suggests that they used fire to modify their surroundings (Pyne 1997).

Fire frequency in North America declined following European settlement. Fire suppression due to changing land-use pat-

terns occurred after the Civil War, leading to a further decline in fire frequency (Cutter and Guyette 1994). During the late 1800s and well into the 20th century, numerous government programs were enacted to suppress fire; perhaps the most effective of these campaigns was "Smokey Bear" (Pyne 1997). As fire suppression became commonplace, tree densities increased and coarse woody debris and litter accumulated. Increased fuels and fuel continuity led to larger and hotter fires (Varner et al. 2005), which often had sufficient intensity to kill fire-adapted plant species. Today, the importance of fire within ecosystems is largely recognized, and use of prescribed fire as a restoration and management tool is considered valuable (Debano et al. 1998, Melvin 2012). Prescribed fires with specific wildlife habitat management objectives are now common (Krausman et al. 2011).

Within virtually all ecosystems, wildlife and other biota fall along a continuum from fire-intolerant species to those species that could not exist in the absence of periodic fire (i.e., fire-dependent or fire-obligate species). Wildlife responses to prescribed fire also can be broadly classified into direct responses to fire events, indirect responses that occur due to conditions created by fire, and evolutionary responses that influence where a species falls on the fire-intolerant to fire-dependent continuum (Whelan et al. 2002, Engstrom 2010). Although direct mortality occurs, it is generally confined to a few individuals within populations (Conner et al. 2011). Surviving a fire event often can be attributable to a behavioral response (e.g., fleeing to an unburned area, finding refugia in burrows, etc.) to avoid fire-induced injury or death.

Indirect effects associated with fire events also elicit a wildlife response. Most commonly, these responses are associated with changes in vegetation (Engstrom 2010) or snag production (Zamoch et al. 2014) as a result of fire, but may also include attraction of predators to feed on prey displaced by a fire (Komarek 1969) and mortality events associated with fire-facilitated predation (Conner et al. 2011, Morris et al. 2011). However, in the absence of fire, these same species may become locally extinct due to vegetation succession and subsequent decline in habitat quantity or quality (Morris et al. 2011).

Finally, evolutionary responses occur as the result of wildlife being exposed to fires for many generations. These responses result in adaptations that ultimately determine the position of species along a continuum from fire-intolerant to fire-obligate species and presumably contribute to observed diversity of animal communities in areas that are exposed to fire events. Fire history, especially fire-return interval, greatly affects composition of animal communities relative to the fire-intolerant to fire-obligate continuum (Handley 1969).
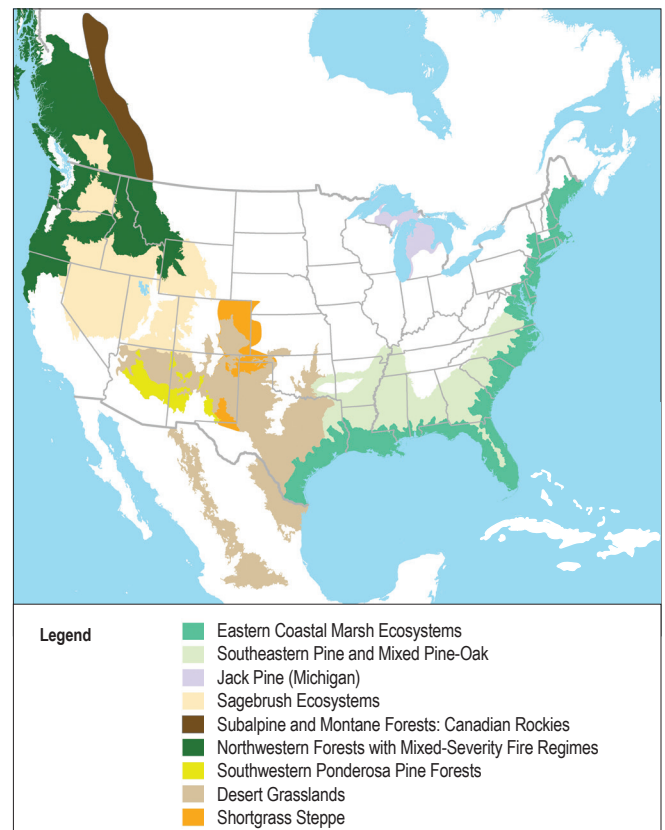
Fire-return intervals vary by ecosystem; for example, subalpine forests burn every 300-400 years (Romme 1982), boreal forests burn every 69-132 years (Bergeron et al. 2001), ponderosa pine (see Appendix A for scientific names) forests burn every 1-125 years (Veblen et al. 2000), and longleaf pine forests burn every 2-10 years (Ware et al. 1993). In systems where fire occurs infrequently, wildfire events often result in stand or system replacement and may profoundly impact wildlife populations. In frequently-burned systems, fire intensity is considerably lower and unlikely to result in pronounced mortality of native species or shift in community composition. Effectively, fire can be used to maintain or alter vegetation associations or seral stages, thereby influencing habitats and wildlife communities (Box 1. See page 63). Indeed, within ecosystems that historically experienced frequent fires, fire suppression should be considered a disturbance because it leads to altered vegetation composition (Fill et al. 2015).

Basic uses of fire as a forest management technique include: wildfire hazard reduction, controlling competing vegetation (usually hardwoods), thinning and release of crop trees, disease control, site preparation (for both artificial and natural regeneration), increasing quantity and quality of forage for livestock grazing, and managing and improving wildlife habitat (Lotan et al. 1978, Crow and Shilling 1980, Van Lear et al.1985). Recognizing the role of fire within North American landscapes does not eliminate problems associated with its use, and a myriad of issues threatens our ability to continue to apply prescribed fire as a management tool. Concerns about human health, a lack of trained prescribed fire practitioners, landowner or land manager liability, and decreased forest productivity are but a few reasons that prescribed fire can be difficult to implement (Melvin 2012, 2015). However, fire practitioners and state forestry agencies are making headway toward addressing bottlenecks associated with use of prescribed fire to meet management objectives.

To provide a science-based understanding of impacts of prescribed fire from a wildlife management perspective, The Wildlife Society was petitioned to provide a technical review of effects of prescribed fire on wildlife populations, communities, and wildlife habitat. The purpose of this review is to: 1) review the history of natural and prescribed fire in North America; 2) discuss effects of prescribed fire on vegetation and wildlife communities; 3) describe current and perceived future obstacles to continued application of prescribed fire; 4) examine the potential future use of prescribed fire and policy needed for continued use of this tool; and, 5) suggest information gaps and research needs to improve our ability to use prescribed fire to better meet desired management goals. To address these purposes in a relatively concise document, the authors of the review chose to approach the review from an ecosystem perspective (Figure 1). Each ecosystem is treated separately in an attempt to show the widespread use of prescribed fire in North America and to provide ecosystem-specific examples of prescribed fire use and effects.

Fig. 1. Map of North American types reviewed in this assessment.

Legend
- Eastern Coastal Marsh Ecosystems
- Southeastern Pine and Mixed Pine-Oak
- Jack Pine (Michigan)
- Sagebrush Ecosystems
- Subalpine and Montane Forests: Canadian Rockies
- Northwestern Forests with Mixed-Severity Fire Regimes
- Southwestern Ponderosa Pine Forests
- Desert Grasslands
- Shortgrass Steppe

Southeastern Pine and Mixed Pine-Oak

The oak-pine forest type is the largest cover type in the eastern United States (Lotan et al. 1978). Primary pine species within the southeastern United States include shortleaf, longleaf, loblolly, and slash pines. Fire has played a major role in development and maintenance of southern pine ecosystems (Garren 1943, Komarek 1974, Van Lear et al. 1985). Fire in the oak-pine forest type results in pine dominance over oak to form a disclimax association rather than an oak climax association (Garren 1943, Oosting 1956). In the absence of fire, succession progresses from oak-pine to oak-hickory climax (Braun 1950, Oosting 1956). Depending on the biophysical site conditions and fire frequency, oaks and other hardwoods may vary in abundance because of their individual fire tolerance and site adaptability.

In ecosystems where natural disturbance processes, particularly frequent fire, are allowed to operate freely, old-growth stands may be characterized by low basal area, open canopy, pure or nearly pure pine stands with limited midstory, and a grass-dominated understory (Komarek 1974, Fryar 1991, Masters et al. 1995, Sparks and Masters 1996, Batek et al. 1999). Oaks and other hardwoods may be present to varying degrees depending on site characteristics (Vogl 1972, Fryar 1991, Kreiter 1994, Masters et al. 1995). A distinct woody component will be present in the understory but suppressed by fire (Sparks et al. 1999, 2002). With increasing time since fire, woody stems in the understory gradually grow into the lower midstory (Masters et al. 2002).

Historical and Current Use of Fire

Historical fire-return intervals range from 1 to 3 years in the Lower Coastal Plain, 4 to 6 years in the Upper Coastal Plain, 7 to 12 years in the Piedmont and Tablelands, to 13 to 25+ years in mountainous regions (Frost 1998). Across much of the southern United States and in the southern Appalachians, timing of lightning-set fires occurs on a bimodal distribution, most frequently in late-spring and early summer with another, smaller peak in early fall (Komarek 1968, Barden and Woods 1973). Relative area burned by lightning fires is limited north and west of Florida; therefore, it is not axiomatic that lightning-set fires perpetuate dominance of pine across its range (Masters et al. 1995, Ison 2000). Prevalence of fire-derived cover types in areas of limited lightning supports the hypothesis that anthropogenic fire maintained vegetation conditions in the southern Appalachians and Cumberland Plateau regions, dating back 9,500 years before present (Ison 2000).

Frequent fire of anthropogenic origin prior to the mid-1850s is mentioned in numerous historical accounts in the Interior Highlands of Arkansas, Missouri, and Oklahoma where shortleaf pine occurs (Beilmann and Brenner 1951*a,b*; Masters et al. 1995). Similar historical accounts also note frequent fire in the Gulf Coastal Plain from east Texas across Louisiana to Georgia and north into the Carolinas and Virginia and in the Cumberland Plateau region (William Bartram in 1773 see Vogl 1972, Ison 2000, Jurney et al. 2004). Native Americans likely were the most important source of ignition, compared to lightning, as distance from the Lower Coastal Plain and Florida increases to the west (Frost 1998). Pine-grassland community development was attributed in part to frequent burning by Native Americans and persisted across the southern United States well into the 1900s as a result of the adoption of this practice by early settlers to manage free-ranging livestock (Vogl 1972, Waldrop et al. 1992). Annual burning throughout the southern pine region was commonly practiced in the early 1900s (Mattoon 1915). Fire has been used as a forest management tool in the southeastern United States since early settlement. Most research, however, has examined shortleaf, loblolly, longleaf, and slash pines in Coastal Plain areas (Lotan et al. 1978, Wright and Bailey 1982, Murphy and Farrar 1985).

Fire Effects on Wildlife

Fire improves forage for wildlife by increasing palatability, nutrient content, digestibility, productivity, and availability of grasses and forbs (Lay 1967, Komarek 1974, Reeves and Halls 1977). Lay (1956) and Oosting (1944) also documented plant species composition change and

increased forage production after burning. Fire exclusion has led to declines in herbaceous ground cover (Kucera and Koelling 1964, Lewis and Harshbarger 1976). Lewis and Harshbarger (1976) studied several seasonal and cyclic fire treatments and observed that in all instances, forage production increased after fire compared to unburned controls. Although fire increases forage quality, Lashley et al. (2015) suggested lack of cover following fire may result in wildlife avoidance of these areas.

Fire in woodlands can promote sprouting and increase cover of hardwoods at the expense of wildlife forage production (Shrauder and Miller 1969), with frequent fire leading to dominance by fire-tolerant grasses that may not be used as forage. Frequent fire may also negatively impact wildlife species that depend upon soft mast (e.g., blackberry, huckleberry; Lay 1956), which is generally absent on new growth.

Although hardwood midstories can be detrimental to forage production, fire may negatively impact hardwoods critical for some wildlife such as squirrels (*Sciurus* spp.), white-tailed deer, northern bobwhite, and wild turkeys (Heirs et al. 2014). Hardwoods may also provide cavities for squirrels, bats, and cavity-nesting birds, and hardwood bark often harbors insects consumed by birds. Although hardwoods are important to fox squirrels in a longleaf pine forest (Perkins et al. 2008), Conner et al. (1999) suggested that suppressing fire would increase hardwood dominance, ultimately resulting in gray squirrels replacing fox squirrels.

Snag retention can be problematic in frequently-burned woodlands. Snags are essential for primary and secondary cavity-nesting species (Masters et al. 2002, Taulman and Smith 2004). Periodic, low-intensity fire can be beneficial by creating future snags (Zamoch et al. 2014), but fires that occur under extended dry conditions will consume snags. Burning when snags have high moisture content (>25%) (Scott and Burgan 2005), or when the Keetch-Byram Drought Index (KBDI) is low, will reduce snag loss (Masters 2007).

Fire may be the most important factor affecting abundance of forest birds. Aside from changing habitat structure, fire directly affects food availability for both seed-eating and insectivorous birds (Komarek 1974, Landers 1987). At ground level, short-term abundance of litter-dwelling

invertebrates may be reduced by fire, but as succulent herbaceous regrowth occurs, herbivorous insects increase (Dickson 1981). These changes in composition of the invertebrate community may affect breeding success of some birds, because invertebrates are a critical source of nutrients for many breeding birds (Landers 1987).

Stands of mature, shortleaf pine-bluestems with abundant herbaceous ground cover and little-to-no hardwood midstory that are managed with late-dormant season fire at 3-year intervals have diverse and abundant small mammals and songbirds (Wilson et al. 1995; Masters et al. 1998, 2001, 2002). Similarly, frequent prescribed fires within the longleaf pine-wiregrass forest are associated with increased diversity of birds (Landers and Crawford 1995, Steen et al. 2013*a*) and small mammals (Landers 1987). Frequent fire essentially re-sets the succession clock in the understory by lowering density and cover of woody vegetation, creating habitat for some bird species, such as the red-cockaded woodpecker (Ligon et al. 1986). Michael and Thornburgh (1971) noted increased abundance of birds within pine-hardwood stands subjected to partial hardwood removal and fire, and Steen et al. (2013*a*) observed that prescribed fire applied over a 15-year period within hardwood-encroached longleaf pine stands was sufficient for re-occupancy by bird species regarded as specialists in longleaf pine systems.

At least 10 species of breeding birds are considered pine-grassland obligates and are benefited by prescribed fire (Wilson et al. 1995, Conner et al. 2002, Masters et al. 2002, Cox and Widener 2008). Another 11 species increase in abundance with pine-grassland management (Masters et al. 2002), which likely is related to retention of oaks and other hardwoods within pine-grasslands and associated hardwoods along ephemeral drainages within stands (Masters et al. 2002).

There is a rapid successional progression of bird species not considered to be pine-grassland obligates that are associated with increasing height of lower-midstory hardwoods and pine, depending on time since the last burn (Landers and Crawford 1995, Masters et al. 2002, Cox and Widener 2008). Importance of fire in maintaining suitable habitat structure was well illustrated in a study by Walsh (2004) in which northern bobwhite avoided early seral stands and mature stands that had not been burned

for 3 to 5 years. Understory structure of pine forests largely determines composition of bird (Johnston and Odum 1956) and small mammal communities. Desirable forest structure can be altered or maintained naturally by periodic fire (Masters et al. 2002, Steen et al. 2013*b*).

When fire reduced the midstory hardwood component in mixed pine-hardwood forests, structural complexity and cavity availability were also reduced, leading to declines in avian diversity (Dickson 1981, Landers 1987). However, this is more pronounced in mid-successional, second-growth stands and may not apply in old-growth stands because of a continual supply of trees with cavities and snags.

Small mammal communities often benefit from pine-grassland management. Both small mammal richness and total captures increase in response to thinning and fire (Masters et al. 1998, 2001). However, fire-facilitated predation results in dramatic, yet short-term, declines in cotton rat abundance and survival (Morris et al. 2011).

O'Donnell et al. (2015) studied response of terrestrial salamanders to prescribed fire. They suggested that managers focus prescribed fires during periods when salamanders were not surface-active to reduce detrimental effects of fire on salamander populations. In a recent meta-analysis of forest management practices within southeastern pine forests, Greene et al. (2016) observed that prescribed fire resulted in a decrease in amphibian diversity. However, they also suggested herpetofauna response to fire within managed pine forests was in need of further study.

Low-basal-area pine-bluestem stands managed with frequent fire also provide more than adequate high quality forage for white-tailed deer and elk (Masters 1991*a*; Masters et al. 1993, 1996, 1997). Black bears used unburned areas more than burned areas, but among burned areas preferred those that had been burned 3-5 years prior, presumably because of increased production of soft mast within the 3-5-year post-burn period (Stratman and Pelton 2007).

Challenges

Melvin (2012, 2015) ranked 9 impediments to prescribed fire in the southeastern United States relative to the remainder of the nation. Prescribed fire practitioners ranked liability, capacity (i.e., having appropriate personnel and equipment), and air quality or smoke management concerns as the greatest challenges to prescribed fire in this region.

A major concern revolves around application of prescribed fire during the growing season. Specifically, little is known about effects of this on nesting birds, particularly in association with ground-nesting birds. Some research on wild turkeys has been encouraging; Little et al. (2014) concluded that growing season prescribed fire had little impact on nest success of wild turkeys and Pittman and Krementz (2016) suggested that early growing season fires had no direct effect on turkey nests because the majority of early growing season fires occurred prior to peak nest initiation. However, Pittman and Krementz (2016) also concluded that reintroduction of prescribed fire did not seem to benefit wild turkeys.

Little is known of the effects of fire frequency on wildlife. The preferred return interval for prescribed fire differs among plant species. Some species prefer frequent burns (≤ 2 years), whereas less frequent fires are suggested for other species. Little et al. (2014) noted that growing season fires were used to promote flowering of native groundcover plants for wild turkeys. However, prescribed fires need not occur every growing season to maintain these plants (e.g., fires may occur every other growing season [Little et al. 2014]). Streich et al. (2015) studied effects of prescribed fire on wild turkey nesting habitat and concluded that a more frequent burn regime was consistent with wild turkey management within longleaf pine forests. Effects of fire-return interval, however, remain poorly known for the vast number of wildlife species. Clearly, this topic should be the focus of future research to help guide application of fire as a management tool.

Eastern Coastal Marsh Ecosystems

Approximately 2.5 million ha of coastal marshes occur in the United States (Alexander et al. 1986, Chabreck 1988). Coastal marshes form a comparatively narrow ecotone between upland and marine areas, protecting shorelines from erosion, providing nursery areas for estuarine and marine organisms (Greenberg et al. 2006), and providing critical primary productivity inputs to estuaries (Zedler and Kercher 2005, Bernhard et al. 2012). In North America, tidal marshes support a high proportion of endemic species in their vertebrate communities (Greenberg 2006).

Historical and Current Use of Fire

Many authors have conjectured that historical fire, whether resulting from lightning strikes, spontaneous combustion, or Native American activities, has always been an important driver in the ecology of coastal marshes (Lynch 1941, Givens 1962, Nyman and Chabreck 1995). However, the natural fire frequency of tidal marshes along eastern North America is difficult to ascertain in the absence of woody vegetation, tree scars, and reliable written records. Authors have estimated historical fire regimes in eastern tidal marshes based largely on fire spread models, amount of marsh landscape uninterrupted by fire breaks ("fuel compartments"), and estimated natural ignition (e.g., lightning) frequency (Frost 1995, 1998). Some authors suggest that during pre-European times, the natural frequency of fires in tidal marshes of the southeastern United States was high and varied by latitude, with mid-Atlantic marshes having a slightly longer fire-return interval (4 – 6 years) than more southerly and Gulf Coast marshes (1 – 3 years) (Frost 1998, Baily et al. 2007). European settlers reportedly practiced marsh-burning, perhaps emulating Native Americans (Nyman and Chabreck 1995).

Although the historical fire-return interval in coastal marshes is not well-described, this interval has likely increased significantly during the past century. Humans have caused this directly through fire suppression activities and indirectly through widespread coastal urban development. Development infrastructure, such as roads, parking areas, and mowed lawns, has greatly increased firebreaks (e.g., non-burnable cover types) in tidal marsh landscapes.

Since at least the 1930s, wildlife managers have used prescribed burning in eastern tidal marshes to improve habitats for waterfowl and furbearers, control invasive species, and reduce wildfire risk (Griffith 1940, Hoffpauir 1961, Givens 1962, Hackney and de la Cruz 1981, Nyman and Chabreck 1995). Prescribed fire is purported by wildlife managers to: 1) promote or maintain productivity of marsh plants, especially those important to waterfowl and furbearers, 2) recycle nutrients trapped in dead plant material, and 3) stimulate primary productivity by marsh graminoids while reducing cover of woody plants (Nyman and Chabreck 1995, Kern et al. 2012). Managers in the eastern United States also use prescribed fire to remove cover of invasive common reed, after herbicide control, to facilitate recovery by native marsh plants (Cross and Fleming 1989). Research on effects of these prescribed burns on nongame vertebrates, many of which are of conservation concern, has been limited (Mitchell et al. 2006).

Fire Effects on Wildlife

Nearly all research conducted on effects of prescribed fire in eastern coastal marshes has focused on birds. This is hardly surprising as coastal marshlands provide critical habitat for many species of migratory birds. Many state and federal wildlife management units along the Atlantic and Gulf coasts were established to conserve and protect migratory waterfowl in particular, and other waterbirds. Wildlife studies in these conservation areas often have focused on these species.

A traditional assumption by wildlife managers in the past century is that controlled winter burns in coastal marshes enhance wintering and foraging habitat for waterfowl. In coastal Louisiana, Lynch (1941) observed that prescribed

burns attracted geese and ducks, presumably by removing dense vegetation that interfered with growth of waterfowl foods, increasing access to seeds and rhizomes, and possibly increasing nutritional quality of forage. Givens (1962), Hoffpauir (1968), and Perkins (1968) reported that marsh burning increased biomasses of forage plants while maintaining a shrub-free, open marsh preferred by ducks and geese. In contrast, Flores and Bounds (2003) documented that controlled fire increased above-ground biomass of inland saltgrass and salt meadow cordgrass, 2 grasses that are considered unimportant in waterfowl diets. We are aware of only 1 study (Gabrey et al. 1999) in which investigators measured waterfowl response to controlled burns in coastal marshes. The authors reported that flocks of white geese (e.g., Ross's goose), used only recently-burned marshes as opposed to unburned areas, during a single December-February period on a 30,700-ha state wildlife refuge in coastal Louisiana.

Several species of endemic, tidal marsh sparrows, occurring from Maine to Texas, are among priority species in several coastal Bird Conservation Regions, and are on the National Audubon Society's Watch List (National Audubon Society 2007). These include several discrete, recognized populations of seaside sparrows, Nelson's sharp-tailed sparrow, and saltmarsh sharp-tailed sparrow. Primary threats to these tidal marsh specialists include marsh loss to development and sea level rise, marsh fragmentation, and wetland degradation, although some management techniques also may have negative impacts (Mitchell et al. 2006).

Authors have studied effects of prescribed fire on various subspecies of seaside sparrows. The Cape Sable seaside sparrow is an endangered, non-migratory, subspecies of seaside sparrow of sub-tropical marshes and seasonally flooded prairies of southern Florida, which are subjected to frequent wildfires and prescribed fires, with Werner (1975) suggesting a fairly frequent (4-5 year return interval) fire regime. However, others suggest longer intervals (8-10 years, Taylor 1983; >10 years, Curnutt et al. 1998) or that the sparrow tolerates, but does not benefit from prescribed fire (La Puma et al. 2007). Gabrey et al. (1999) concluded that winter burns reduced suitability of winter habitat for the Louisiana seaside sparrow for a few months immediately following the burn; leading researchers to

recommend a fire frequency of >2 years to maintain habitat for this subspecies (Gabrey and Afton 2000, Gabrey et al. 2001). Kern et al. (2012) studied effects of prescribed, winter burns on northern seaside sparrows and reported that nest and territory densities were greatest on marshes <1 year post-burn. Densities of nests and territories declined with time since fire, but fledgling density did not differ among fire-return intervals. Kern et al. (2012) recommend 1–4-year return intervals to maintain habitat quality for breeding seaside sparrows. Ultimately, prescribed fires increased probability of seaside sparrow persistence (Kern and Shriver 2014).

Impact of prescribed fire on sparrows is generally indirect through changes in habitat quality. Kern (2010) detected saltmarsh sparrows throughout a study area and among fire regimes, concluding that prescribed fire did not affect occupancy by this sparrow species. The author also found that Coastal Plain swamp sparrows occurred only in specific, shrubby vegetation in the high marsh, and also did not respond strongly to fire. Legare et al. (2000) captured and banded 5 swamp sparrows and 1 was recovered dead and burned following a prescribed fire. Gabrey et al. (1999) observed that winter burning reduced suitability of a marsh as winter habitat for Nelson's sharp-tailed sparrows. Gabrey et al. (2001) concluded that populations on the Chenier Coastal Plain benefited from periodic, infrequent fires that remove dense, dead vegetation.

Boat-tailed grackles and red-winged blackbirds preferred recently burned plots, possibly because burns reduce visual obstruction and ground cover, facilitating foraging for prey, contact with conspecifics, and detection of predators (Gabrey et al. 1999). Marsh wrens occurred more frequently in unburned than in burned plots, whereas common yellowthroats and sedge wrens avoided recently burned marshes entirely, but were present the following winter. The authors concluded that for certain wintering bird species of coastal marshes, such as tidal marsh sparrows and wrens, habitat suitability was reduced temporarily following winter burning, but these species recolonized burned areas by the second winter, after plant cover had returned to pre-burn levels.

Gabrey et al. (2001) reported that winter burning did not affect breeding bird species richness or species composition in Gulf Coast marshes. They concluded that managed burns to enhance habitat for wintering waterfowl appear compatible with maintaining populations of certain other marsh birds, provided that large contiguous marsh areas are not burned in any single winter, and >2 years are allowed between burns.

On the Chesapeake Bay, Kern (2010) evaluated single- and multi-season occupancy of 4 relatively abundant marsh bird species in response to prescribed burning, using spot-map and call-back survey methodology. Least bittern occupancy was positively influenced by fire, and burning had no discernible effect on Coastal Plain swamp sparrow and Virginia rail occupancy. Kern (2010) noted that the natural fire frequency of their study area had been estimated to be 4-6 years, indicating that marsh birds may have adapted to occasional fire events and recommended patchy burning approximately once every 4 years.

Legare et al. (1998) recorded direct mortality of black rails as a result of prescribed winter burns. In contrast, when patchy, incomplete prescribed burns were conducted during August, black rails and other bird species survived in unburned patches within burn units. Legare et al. (1998) recommend that controlled burns in coastal marshes be conducted to provide a well-interspersed patchwork of unburned areas.

Anecdotal evidence suggests that raptors use smoke and fire as a foraging cue, feeding opportunistically on prey affected or exposed by marsh burns (Stevenson and Meitzen 1946, Tewes 1984, Chavez-Ramirez and Prieto 1994). Raptors move out of burned areas rapidly post-fire, suggesting that enhanced foraging opportunities are likely short-lived (Tewes 1984). Chavez-Ramirez and Prieto (1994) concluded that winter burns did not affect numbers of wintering raptors using burned areas, but burns did affect species composition, with northern harriers decreasing and American kestrels increasing, post-burn. The authors speculated that northern harriers decreased post-burn because these raptors are surprise hunters and generally capture prey in dense grassland or shrubland vegetation. In contrast, American kestrels are more successful hunters in open vegetative conditions (Toland 1987).

Challenges

Knowledge of natural fire regimes in coastal mashes is unclear with respect to frequency, timing, and severity. As a result, managers have limited information for developing prescriptions that emulate historical regimes. As sea levels rise, marshes must rise through the accumulation of organic material to keep pace with rising water. Whether or not prescribed fire inadvertently limits the accumulation of organic material and the marsh build-up is unknown, but should be the subject of future research. Finally, many coastal marshes are imbedded in a landscape of mixed private and public ownership. Coordinating application of fire in these landscapes requires extensive communication and collaboration.

Much of our knowledge is observational, with only limited understanding of the underlying mechanisms. Wildlife managers have observed that waterfowl are attracted to winter-burned coastal marshes, but mechanisms for this attraction remain unclear. Prescribed fires often promote growth of some waterfowl plant foods (Chabreck 1981, Pendleton and Stevenson 1983, Turner 1987, DeSzalay and Resh 1997, Stevenson et al. 2001), but not others (Flores and Bounds 2001, Gabrey and Afton 2001), and effects of burning on nutritional quality of marsh vegetation are ambiguous (McAtee et al. 1979, Schmalzer and Hinkle 1993). Few studies have focused on how fire affects invertebrates, which provide food for waterfowl (Matta and Clouse 1972, Turner 1987). Most authors concur that controlled fires in coastal marshes should be used to create a mosaic during any given management year: maintaining recently burned areas, areas that have had a recovery period of several years, and unburned areas as refugia for marsh species (Legare et al. 2000, Gabrey et al. 2001, Almario et al. 2009, Kern et al. 2012).

Subalpine and Montane Forests: The Canadian Rockies

Forests that cover most of the Canadian Rockies can be categorized into elevation- dependent forest types: 1) montane, which ranges from approximately 1,000 to 1,600 m in elevation and consists primarily of Douglas-fir, trembling aspen, white spruce, and lodgepole pine, 2) lower subalpine, which occurs from 1,300 to 2,100 m in elevation and is dominated by dense stands of mature lodgepole pine transitioning to subalpine fir and Engelmann spruce, and 3) upper subalpine, which occurs just below the un-forested alpine between 1,600 and 2,300 m in elevation and is dominated by Englemann spruce and subalpine fir (Holland and Coen 1983). In addition to forested areas, shrub and grassland meadows also are common at all elevations. A large amount (21,900 km²) of these areas is managed as federal or provincial park lands.

Historical and Current Use of Fire

Fire regimes in montane and sub-alpine forests of the Canadian Rockies have been summarized by Van Wagner et al. (2006) but have also been the subject of numerous studies across the region (Hawkes 1979; Tande 1979; White 1985; Johnson 1987; Johnson and Fryer 1987; Masters 1990; Johnson and Larsen 1991; Rogeau and Gilbride 1994; Rogeau 1994*a,b*, 1996). Along the east slopes of the Canadian Rockies, lightning and lightning-caused fires do not occur frequently (Wierzchowski et al. 2002), yet evidence from studies of fire history show that fires occurred frequently in many montane and subalpine forests of the area prior to the 1880s, the start of the era of European settlement and railway construction (Tande 1979, Hawkes 1979). Furthermore, most of these fires burned during periods of infrequent lightning and before the typical season for major summer thunderstorms (White et al. 2001). This incongruence between fire frequency and season of burning is an indication of anthropogenic burning by local First Nations peoples in the area to provide food for game species in valley bottoms (White 1985, Kay et al. 1999).

Fire frequencies range between 20 and 50 years in the montane forests, whereas forests at slightly higher elevations (lower subalpine) have longer intervals between 50 and 100 years on south- and west-facing slopes and 100 and 150 years on north- and east-facing slopes (White and Hart 2007). The longest fire-return intervals (>150 years) occur in upper subalpine forests where climate and snowpack likely affect fuel moisture and ignition.

In addition to frequency, fire size, intensity, and severity also may be influenced by elevation. In valley bottoms, fires were often smaller and less intense and severe, compared to higher elevations; anthropogenic burning in the spring to create favorable habitats for game species may have contributed to these characteristics (Kay and White 1995). In the lower and upper subalpine, fires likely occurred only in those years when weather and fuel conditions would support large, stand-replacing fires (Hawkes 1979, Johnson and Larsen 1991).

Decades of fire suppression have led to large tracts of decadent forests composed of lodgepole pine at lower and mid-elevations and spruce and subalpine fir at upper elevations (Rhemtulla et al. 2002). As a consequence, recent wildfires have been very large, intense, and severe. In 2014 and 2015 alone, over 7,500 km² of Canadian park land burned as the result of wildfire (Parks Canada, unpublished data). After an era of fire suppression, a new understanding of the interaction between fire as a natural disturbance and ecosystem function (vegetation and wildlife) was beginning to develop. By 1983, Parks Canada began experimental prescribed fires within Banff National Park, and by 1990 several national parks had begun prescribed fire programs to restore fire to the landscape. The key goal in the Canadian National Parks has been to restore 50% of the long-term fire cycle, which is an expression of mean frequency and size of fires over a land base through time (Van Wagner 1978, Johnson et al. 1995).

Current Canadian National Park prescribed fire programs include complex, landscape-level burns and smaller burn

units to achieve a variety of ecological and management objectives. Although primary objectives of prescribed fires may be to improve habitats for specific species, the overall goal is always multi-faceted and ecosystem-based. Furthermore, fire managers seek to create a mosaic of burn severities within a unit, rather than creating landscapes that have been burned uniformly.

The most recent, large prescribed fires have had several common objectives:

- Restoring open forest types such as Douglas-fir grasslands by removing in-growth by lodgepole pine and immature Douglas-fir;

- Reducing shrub and tree encroachment in montane grassland meadows;

- Restoring rough fescue ecosystems through high-intensity, low-severity prescribed fire;

- Enhancing habitats for grizzly bears, ungulates, and wolves;

- Reducing stand size and extent of mature lodgepole pine forests susceptible to mountain pine beetle infestation.

Fire Effects on Wildlife

Mammals. Ecosystems within montane and sub-alpine forests of the Canadian Rockies have been strongly impacted by human disturbance via fire exclusion, development (transportation corridors and settlement), predator control, and resource use. Cumulatively, these factors have contributed to temporal fluctuations in multiple ecosystem components. For example, exclusion of fire and increase in elk resulting from predator control in the 1950s and 1960s have led to a significant decrease in aspens and willows (White et al. 1998, Kay et al. 1999, Nietvelt 2001). Furthermore, exclusion of fire from many of these forests has led to a paucity of early successional, open forest conditions (aspen, grasslands, Douglas-fir) preferred by grizzly bears, ungulates, and wolves. Instead, large, dense tracts of overmature lodgepole pine exist that, combined with changes in regional climate, have recently been under increased pressure from forest insects and disease such as the mountain pine beetle (Safranyik et al. 1974, Safranyik and Wilson 2007, Ritchie 2008) and do not provide high-

quality habitats for much of the wildlife in the area. Moose might exhibit a short-term positive response to beetle infestation, but may decline in the long-term from intensive forest management following the outbreak (Ritchie 2008). Furthermore, decadent stands also contribute to large amounts of downed-woody debris that present barriers to movement for a variety of wildlife species.

Reintroduction of fire onto this landscape affects wildlife such as birds, grizzly bears, ungulates, small mammals, and predators in a variety of ways. Stand-replacing fires that cause extensive mortality of lodgepole pine result in a temporary increase in sun penetration and an increase in understory shrubs and forbs that are important to grizzly bears, such as sweetvetch and Canada buffaloberry (Hamer 1996, Pengelly and Hamer 2006). Moreover, prescribed fire increases forage abundance and suitability for elk (Sachro et al. 2005). However, in areas with high densities of elk and low predation rates by wolves, fire can have a negative influence on amount of aspen available for forage (White et al. 1998, 2003). Fire is also important to maintain rough fescue grasslands that are highly valuable to ungulates such as elk, mule deer, and bighorn sheep (Robinson et al. 2010). Over time, shrub encroachment and plant maturity reduce quantity and quality (nutritional content) of available grass for ungulates (Van Soest 1982, Benn et al. 1988, Hebblewhite et al. 2008). Prescribed fire applied to these meadows in periods of high soil moisture or during dormancy can be beneficial to wildlife as it removes heavy litter buildups that might be avoided by elk. However, fire suppression can cause high litter loads, shrubs, and coarse woody debris to accumulate, resulting in increased potential for high severity wildfires that lead to a decrease in dominance of rough fescue and to an increasing proportion of unpalatable grass species (Fleenor 2011).

Prescribed fire has an indirect, positive effect on large carnivore populations due to the high quality ungulate habitat it creates. Both cougar and wolf abundance are strongly correlated with ungulate abundance (Paquet et al. 1996, Riley and Malecki 2001). Furthermore, prescribed fires result in increased amounts of coarse woody debris important to forest carnivores such as fishers, martens, wolverines, and Canada lynx. Martens and Canada lynx in particular are associated with early post-fire conditions (Koeler and Aubry 1994).

Mountain caribou have a complicated relationship with fire. Currently listed as endangered under the Canadian Species at Risk Act (2002), mountain caribou rely on a diet of arboreal hair lichens that are associated with old-growth forests (Seip and Cichowski 1996). Whereas this species is generally negatively affected by prescribed fire through decrease in suitable habitat (Shepherd et al. 2007) and increased predator abundance in response to increased prey abundance, caribou may still benefit from strategic use of prescribed fire. Fire-excluded landscapes are particularly prone to widespread, stand-replacing fires. In this context, prescribed fire could be used to protect important areas from large-scale wildfires, and provide for habitat security during a period when most research shows a trend towards larger, more severe wildfires (Flannigan and Van Wagner 1991). This strategy has been used to protect watersheds in fire-prone areas through promotion of a mosaic of vegetation age classes that reduces fire severity and extent during a wildfire (Riggan et al. 1994, Conard and Weise 1998). Furthermore, Klein (1982) highlighted the need for fire in the long term to maintain lichens in old-growth forests. However, conservation of mountain caribou requires significant consideration of additional important factors such as human disturbance, motorized access, and habitat loss and fragmentation as the result of both human and natural events (Apps and McLellan 2006).

Birds. Hutto (1995) reported that 15 species of birds in the Rocky Mountains were associated with post-burn plant communities and more than 87 species were found in previously burned areas. Research on fire effects in Banff National Park revealed higher species abundance, richness, and heterogeneity in burned versus control sites associated with forest structure and life history characteristics (Chruszcz and Breniser 2003). They reported that birds requiring open spaces and snags were more abundant in burns than those requiring foliage for nesting or foraging. The olive-sided flycatcher, a threatened species under the Canadian Species at Risk Act (2002), has a strong association to recently burned areas and open forest types and would benefit from prescribed fires.

Challenges

Challenges associated with reintroducing fire into these landscapes largely are a function of the cumulative effects of misguided management practices that have led to imbalances among predators, herbivores, and surrounding vegetation. Furthermore, rate and extent of human development throughout these areas have necessitated significant cooperation with neighboring jurisdictions, public education, and safety mitigations.

Multiple factors must be considered to develop an ignition prescription to meet a variety of ecological objectives. In addition to operational and technical constraints, human development can also complicate implementing prescribed fire. Large communities and major transportation corridors now exist in low-elevation valleys, requiring consideration of smoke, socio-economic (e.g., air quality/health, industry, tourism), and safety effects. Fire managers in these areas now spend years planning prescribed fires and building trust with stakeholders to ensure that adequate communication and education have been conducted prior to ignition. Tolerance for air quality impacts (i.e., smoke and ash) is finite, but public acceptance has increased with increased education on potential benefits of short-lived prescribed fires compared to large, severe wildfires. McFarlane et al. (2007) showed that the public's support of the prescribed fire program in Banff National Park increased significantly between 1994 and 2007.

Another significant challenge associated with human development is mitigation of safety of communities and facilities adjacent to burn units. When communities occur downwind of large complex burn units, proactive fuel management must be completed ahead of ignition to ensure safety. As such, many large prescribed fires have been conducted following implementation of large, landscape-level fuel breaks.

Despite the major challenges of implementing large, landscape-level prescribed fires, multiple agencies in the Canadian Rocky Mountains (Parks Canada, Government of Alberta, Alberta Parks, Government of British Columbia, BC Parks) have all made progress in developing prescribed fire programs, facilitating inter-agency collaboration on multiple occasions.

Jack Pine

Aband of jack pine forests and savannas occurs across the north-central states of the United States extending north into the boreal forests across Canada. Jack pines possess a number of fire-dependent characteristics to prevent succession to another vegetation type. Jack pines have serotinous cones, which require interaction of the heat of fire with the cones' thermal conductivity to open and disperse seeds (McRae 1979, Johnson and Gutsell 1993). Once seeds are dispersed, jack pines require bare mineral soil or an extremely thin duff layer to germinate successfully and become established (McRae 1979, Thomas and Wein 1985). Chrosciewicz (1974) demonstrated a negative exponential relationship between post-burn duff layer depth and jack pine seedling germination and growth, with thin residual duff (0.5 cm deep) providing the best combination for the 2 response variables.

Within jack pine forests and savannas, other structural and compositional components also rely on fire. Many shrubs and forbs are reduced after fire, whereas other species may increase dramatically (e.g., sedges, sweet ferns; Ahlgren 1970). Immediately following a post-harvest burn, transitory seed-producing species invade, including geranium, willow-herb, and knotweed, all of which decline in abundance 3-5 years later (Ahlgren 1970).

Historical and Current Use of Fire

Fire has always been a disturbance factor in jack pine barrens. Historically, these barrens were maintained by naturally-occurring wildfires. Jack pines held little value for the early lumbermen who came in search of white pines. Once logging activity ended in the 1880s, continuing forest fires helped increase the range of jack pines (Michigan Department of Natural Resources and Environment 2011).

Jack pine forests and savannas probably were maintained naturally by very different fire regimes. Some evidence suggests that if a stand-replacing fire occurs in the early stages of jack pine forest development (<20 years old), nutrient cycling may be impaired, which may lower stand productivity and lead to site degradation. Jack pine savannas, on the other hand, may have been maintained by light, frequent burns (i.e., every 10-20 years) that maintained openness. In a study of a New York jack pine savanna, fire did not appear to adversely affect macronutrient cycling, even within 20 years after a burn (Stergas and Adams 1989). Dense, even-aged jack pine forests were probably maintained by intense, infrequent fires (i.e., every 40-50 years).

After decades of fire suppression, land managers and ecologists of the 1960s realized that fires were a natural part of many ecosystems rather than a destructive force and that reintroducing fire into these systems could restore their structure, function, and processes, and improve wildlife habitats for some species (Johnson and Miyanishi 1995). Prescribed burning in jack pine ecosystems evolved from this shift in attitude. Although such a premise has merits, using prescribed burning as a restoration tool is only advisable to achieve specific goals (Johnson and Miyanishi 1995).

Prescribed burning goals and measures of success should vary in a jack pine savanna ecosystem depending on forest age and structure and desired conditions. A successful burn for ecosystem restoration in jack pine might include a stand-killing fire that initiates not only jack pine regeneration, but also important understory species. A savanna ecosystem from which fire has long been excluded might require an initial thinning of trees to savanna densities either with a hot burn or by harvesting. The fire prescription in this situation would include killing a certain percentage of trees and shrubs to shift composition of the understory toward a desired species mixture. A fire prescription for an intact savanna system might simply strive to maintain the understory species mixture and canopy openness.

Fire Effects on Wildlife

Kirtland's warbler, an iconic species with very restrictive habitat requirements, is most commonly associated

with fire management and jack pines. Kirtland's warbler prefers young jack pine stands >30 ha in size and depends on young jack pines after fire removes older trees and rejuvenates growth. Jack pine forests provide the primary nesting habitat for Kirtland's warbler. Stands that are most suitable for breeding are characterized by dense clumps of trees interspersed with numerous small, grassy openings, sedges, ferns, and low shrubs (Michigan Department of Natural Resources and Environment 2011). Nests generally are concealed in mixed vegetation of grasses and shrubs below the living branches of 5- to 20-year-old jack pines.

With modern fire protection and suppression limiting wildfire, regeneration of jack pines has suffered. Consequently, nesting habitat for Kirtland's warbler declined and populations plummeted (Probst 1986). To provide appropriate habitat for Kirtland's warbler, the U.S. Forest Service and Michigan Department of Natural Resources created 4 areas within state and national forests to be managed specifically for Kirtland's warbler nesting habitat between 1957 and 1962. By 1973, these areas contained 53% of the nesting population. However, additional areas of jack pines were necessary to increase the warbler population. During the mid-1970s, 54,000 ha of jack pines were designated for management as nesting habitat for Kirtland's warbler within 24 management areas of state and national forests. Additional lands were added through the 1990s to bring the total public land specifically managed for the Kirtland's warbler to more than 60,000 ha (Kepler et al. 1996). Results from annual singing bird surveys documented 2,365 males in 2015, well above the low of 167 males recorded in 1974 (www.fws.gov/MIDWEST/endangered/birds/Kirtland/Kwpop.html; accessed: 8 February 2016).

Challenges

The limited number of days when weather is appropriate to burn safely has hindered and continues to hinder rapid expansion of prescribed burning in jack pine (Buckman 1961). For example, weather appropriate for prescribed burning rarely lasts more than 1 day during spring in lower Michigan (Simard et al. 1983). In addition to this physical limitation are social concerns. The stigma of the Mack Lake fire in Michigan continues to cast prescribed fire as an ineffective and sometimes destructive tool (Simard et al. 1983). Fire, in general, is often perceived by many publics as something to be controlled rather than promoted. Furthermore, other methods (e.g., chemical, mechanical, and silvicultural) are garnering wide support as alternative ways to manage jack pine forests (Buckman 1964). Other challenges include urbanization, escaped fires, and smoke management.

Sagebrush Ecosystems

The sagebrush biome occurs across approximately 480,000 km^2 of western North America, including areas in 14 states and 3 Canadian provinces (U.S. Geological Survey 2005). This biome often is split between the sagebrush steppe in the northern part of the biome and the Great Basin sagebrush area in the southern part of the biome (Bureau of Land Management 2002). The sagebrush steppe is cooler and moister than the Great Basin, with sagebrush communities consisting of sagebrush mixed with grasses and forbs. In the Great Basin, amount of grasses and forbs is substantially reduced. The sagebrush biome contains a diverse array of ecosystems dominated by several sagebrush species in late-seral conditions. McArthur (1999) and McArthur and Sanderson (1999) identified 11 species and 14 subspecies of sagebrush.

Fire played a varying historical role as a disturbance agent in these ecosystems, from being largely absent in some of the drier locations to being an important disturbance component in moister locations. Most of the current focus on sagebrush management centers around various subspecies of big sagebrush, because this species is the most widespread and supports species of current management concern, including sage-grouse.

Historical and Current Use of Fire

Historical fire regimes in sagebrush ecosystems varied considerably (Keane et al. 2008). Generally, fire intervals were long in sites with low productivity, as characterizes most of the Great Basin sagebrush, and increased in frequency with increased precipitation levels and overall site productivity. Miller and Rose (1999) reported mean fire-return intervals of 12-15 years for mountain big sagebrush and 60-110 years for Wyoming big sagebrush. Perryman and Laycock (2000) reported a mean fire-return interval of 7-11 years in Wyoming big sagebrush in the eastern extent of its range in the Rochelle Hills of eastern Wyoming. Sand sagebrush burns as frequently as every

5-10 years (Vermiere 2002), and returns to pre-burning conditions within 4 years. Low sagebrush rarely burns because of low productivity of these sites (Bureau of Land Management 2002). In sagebrush ecosystems such as sand sagebrush, relatively frequent fire events maintained a mosaic of grass, forbs, and shrubs that provided for a diversity of species adapted to this dynamic landscape pattern (Winter et al. 2012). At higher elevations and moister sites, including many mountain big sagebrush and sand sagebrush areas, fire kept species such as junipers from invading a site and becoming the dominant species (Miller et al. 2005, Bates and Svejcar 2009). On drier sites, fire could be a significant disturbance to sagebrush communities, with successional trajectories following fire in some areas being up to 100 years or more (Baker 2006, 2011). Miller and Heyerdahl (2008) examined estimated historical fire regimes within a 4000-ha area of California dominated by sagebrush and juniper and observed a wide range of return intervals within this relatively small area influenced by soils, topography, and other features.

Sagebrush ecosystems have experienced dramatic changes in the role of fire from historical conditions. Mountain big sagebrush and sand sagebrush ecosystems have been invaded by various species of juniper, substantially altering these ecosystems. Another major change involves invasion by cheatgrass, an annual exotic grass that has expanded across much of the drier sagebrush ecosystems, dramatically increasing fine fuels. When these areas burn, they subsequently are dominated by cheatgrass and are susceptible to a new regime of frequent fire that precludes sagebrush (Chambers et al. 2007, Epanchin-Niell et al. 2009, Condon et al. 2011, Davies et al. 2011), causing a loss of functional sagebrush ecosystems. Sagebrush has expanded into some areas that were previously maintained as grasslands by frequent fire (Perryman and Laycock 2000). Sagebrush ecosystems have been influenced by other factors including grazing by livestock and human development that have interacted

with fire to cause dramatic changes throughout much of the sagebrush biome (Davies et al. 2011), with concomitant effects on wildlife habitats.

The range of historical fire regimes among various ecosystems within the sagebrush biome produces a corresponding range in recommendations for using prescribed fire. For sand sagebrush ecosystems, prescribed fire is highly recommended as a tool to restore and rejuvenate these fire-dependent plant communities (Elmore et al. 2009, Winter et al. 2012). Patch-burning (pyric herbivory) is a method of prescribed burning linked with grazing that produces desirable responses by plant communities and improves habitat for lesser prairie-chickens (Elmore et al. 2009, Winter et al. 2012). Pyric herbivory in sand sagebrush also can increase overall habitat heterogeneity and abundance and diversity of macroinvertebrates (Doxon et al. 2011).

Lack of fire may allow invasion of juniper into sagebrush communities, especially mountain big sagebrush (Burkhardt and Tinsdale 1976, Miller and Rose 1999). Miller and Rose (1999) reported that lack of fire associated with intense grazing allowed for expansion of juniper in their Oregon study area. Maintaining the role of fire in these sagebrush areas is important to reverse these trends (Davies et al. 2011). Concerns exist about extent and timing of fires in mountain big sagebrush because an estimated fire-return interval of 35 years for southwestern Montana would result in a predominance of early- to mid-seral sagebrush in this area (Lesica et al. 2007). Davies et al. (2011) concluded that prescribed fire was more cost-effective than mechanical treatments to control conifer encroachment, because it could be applied across large landscapes and could control tree seedlings that would be missed with mechanical treatments. They also noted that residual woody debris produced by mechanical treatments of conifers would provide fuels that could also result in an accumulation of dry fuels that would pose a significant wildfire risk (see also Miller et al. 2005, Bates and Svejcar 2009). Landscape-scale treatments could conflict with other ecosystem services (Davies et al. 2011). Treating parts of the landscape on a rotational basis over decades could limit conifer encroachment and provide habitat for sagebrush-obligate species. Prescribed fire alone may not be effective in some situations. Bates et al.

(2011) observed that late successional juniper, which had invaded sagebrush communities in Idaho, would not burn effectively because of the lack of understory. They applied a cut-and-burn prescription, where areas with dense junipers were partially cut and then burned, and found this to be an effective treatment to control junipers and reestablish native perennial grasses. They cautioned that non-native annual grasses could invade these sites under certain conditions.

Fire played a varying historical role in Wyoming big sagebrush, from being relatively rare with very long return intervals in some locations (Baker 2011), to being more frequent and maintaining a predominant grassland condition in other areas (Perryman and Laycock 2000). The role of fire in this subspecies of big sagebrush that grows under drier conditions has been greatly exacerbated by the invasion of cheatgrass. This has increased the current fire-return interval in invaded areas (Condon et al. 2011, Davies et al. 2011) and can convert a site from sagebrush to cheatgrass (Chambers et al. 2007). Lesica et al. (2007) evaluated sagebrush recovery following fires in southwestern Montana. They observed that mountain big sagebrush canopy cover and heights returned to conditions of unburned sites approximately 32 years after a burn. In Wyoming big sagebrush, they estimated this return would be greater than 30 years, but were not confident in projecting return times because several burned Wyoming big sagebrush sites had no sagebrush present even 17 years post-burn. Lesica et al. (2007) suggested that sagebrush will recover on most sagebrush sites in Montana, but will require many years to fully recover from a fire. Baker (2011) estimated that Wyoming big sagebrush may require 25-100 years to recover from a fire. Dangi et al. (2010) reported that sagebrush on a 39-year-old mountain big sagebrush site had returned to pre-burn densities of sagebrush. They also reported that soil microbial communities had returned to pre-burn conditions 7 years post-burn.

Fire Effects on Wildlife

Various wildlife species associated with sagebrush have been impacted by changes in sagebrush ecosystems resulting from altered fire regimes. Sagebrush-associated species including greater sage-grouse, pronghorns, pygmy

rabbits, and lesser prairie-chickens have been impacted negatively by juniper invasion of areas historically dominated by sagebrush (Elmore et al. 2009, Rowland et al. 2011).

Galliformes. Over much of their range, lesser prairie-chickens persisted within sand sagebrush communities with a frequent-fire regime. Fire acted to keep sand sagebrush at appropriate densities and stimulated growth of grasses and forbs. Lesser prairie-chickens have used recent burns as leks and for brood-rearing (Elmore et al. 2009), but require sites >3 years post-burn for optimum nesting habitat. A mosaic of recent to older burns within a home range provides optimal juxtaposition of habitat needed for leks, nesting, and brood-rearing.

Greater sage-grouse occur in several sagebrush ecosystems but are primarily tied to big sagebrush plant communities (Connelly et al. 2000*a*). Fire has influenced sage-grouse habitat historically by maintaining some big sagebrush communities (especially mountain big sagebrush) and reducing presence of other big sagebrush communities (especially Wyoming big sagebrush). Prescribed fire does not improve sage-grouse habitat, at least not within a 10-20-year timeframe, the longest timeframe in which most studies have investigated direct responses to fire. Beck et al. (2009) observed that sagebrush cover following prescribed burns in Wyoming big sagebrush had not returned to high enough levels to provide good sage-grouse habitat for 14 years after the burn, even though other desirable habitat features had responded to the fire. Rhodes et al. (2010) investigated sage-grouse habitat features 6 years following a burn in Wyoming big sagebrush and reported a 50% decrease in tall grasses and shrubs needed by sage-grouse, a decrease in ant populations, and no increase in forbs considered desirable to sage-grouse. Hess and Beck (2012) similarly reported that Wyoming big sagebrush did not return to desired conditions for sage-grouse even after 19 years in their study area, and Davis and Crawford (2014) reported that mountain big sagebrush did not meet conditions for sage-grouse 10-11 years post burn.. They did find a positive response by grasses, but suggested that other management tools, such as adjustments to grazing regimes, were preferable to prescribed fire for improving sage-grouse habitat in Wyoming big sagebrush.

Pyle and Crawford (1996) reported that prescribed fire in Oregon increased total forb cover and diversity, suggesting an improvement in brood-rearing habitat. Fischer et al. (1996) found that forb cover was comparable in burned and unburned areas of Wyoming big sagebrush in Idaho and concluded that fire did not enhance brood-rearing and nesting habitat in mountain big sagebrush stands. Effects on brood-rearing habitat may be negative and prolonged (Nelle et al. 2000) to the point that sage-grouse avoid using an area post-fire (Byrne 2002). Drought might exacerbate negative effects of fire, because Connelly et al. (2000*b*) documented a large decline of the sage-grouse breeding population following prescribed fire. In contrast, Slater (2003) observed sage-grouse using areas with both prescribed and wildfires, but use was related to age of the burn and presence of alternative shrub species. Lockyer et al. (2015) modeled habitat use following fire and found that sagebrush cover was consistently the best predictor of nest survival in northwestern Nevada. Pedersen et al. (2003) modelled effects of fire and concluded that small fires may benefit sage-grouse, but large fires (>10% of the spring-use area) occurring at high frequencies (17 years between fires) could result in their extirpation.

Ungulates. Fire is important to pronghorn because it creates the desired density of grasses and forbs and improves quality of forbs for foraging (Yoakum 2004). Fire can also maintain shrub cover at desirable densities and heights for pronghorn. Van Dyke and Darragh (2007) reported that elk increased use of a sagebrush burn for 2 years post-burn, but then returned to similar levels of use as unburned areas. Heterogeneity of grasses and forbs persisted for 10 years post-burn, but sagebrush did not substantially return within the 10 years of the study (Van Dyke and Darragh 2007).

Other vertebrates. Pygmy rabbits are an obligate species in sagebrush ecosystems. Changes to historical fire regimes allow expansion of pygmy rabbits into new areas where livestock grazing and fire suppression have resulted in expansion of sagebrush communities and cause a loss of habitat in other areas where juniper invade due to lack of fire (Larrucea and Brussard 2008). McGee (1982) reported fewer species of small mammals following a sagebrush burn, but that richness returned to those of unburned control plots 3 years after fire. Humple and

Prescribed burn in a sagebrush/grassland vegetation mix in Thunder Basin, Wyoming.

Credit: Ecosystem Management Research Institute.

Holmes (2006) reported that densities of loggerhead shrikes dropped by one-half following a fire that reduced sagebrush cover by more than 50%. Nest success also was lower after fire, which they attributed to reduction in cover and patchy distribution of sagebrush.

Challenges

The studies reported here display the range of responses exhibited by different sagebrush ecosystems to prescribed fire. Prescribed fire is an important tool in sand sagebrush communities, and appears to offer significant benefits in some mountain big sagebrush communities. Managers applying prescribed fire in these sagebrush communities should consider its spatial arrangement and extent, because mosaic patterns can create a juxtaposition of conditions to benefit various wildlife species that depend on sagebrush. In Wyoming big sagebrush communities, reduced habitat quality for sage-grouse and other sagebrush-associated wildlife species for long periods after fire, coupled with increased opportunities for invasion by cheatgrass, have led to numerous recommendations against use of prescribed fire in these ecosystems. Fire never was a major disturbance in more arid sagebrush ecosystems, so prescribed fire is not a recommended management tool in these areas.

Northwestern Forests with Mixed-severity Fire Regimes

Historical fire regimes exhibited tremendous variation in forest types found in the northwest regions of North America. Good descriptions of these fire regimes can be found in Agee (1993) and Hessburg et al. (2016), and coarse-scale mapping of historical fire regimes is presented in Landfire (www.landfire.gov, accessed 31 August 2015). Coastal rainforests from Alaska to Oregon did not experience fire because of rain, fog, and lush vegetation of these areas. Further inland, fires transitioned to infrequent, high-severity fire events in cool moist and wet forest types and to frequent, understory fires that occurred in warmer and dryer forest types. Other areas experienced intermediate, mixed-severity fire regimes that produced complex spatial and structural vegetation characteristics (Arno et al. 1991, Agee 2004, Taylor 2004, Hessburg et al. 2004, 2016). Grass and shrub communities had varying fire regimes, ranging from frequent fire events in some areas to protected sites that allowed junipers and other shrubs to predominate. Prescribed fire is being used in drier forests of the Northwest to return low-severity fire conditions to appropriate forest types. Use of prescribed fire in these forest types has many similarities to that described for ponderosa pine ecosystems (see below and later in this Technical Review). Here, we provide a description of fire histories and prescribed fire for mixed-severity fire regimes in forest ecosystems of the northwestern United States. We also describe the role of fire in sagebrush ecosystems, while pointing out that much of the sagebrush biome occurs in other parts of the United States (also see sagebrush section in this Technical Review).

Historical and Current Use of Fire

Many northwestern coniferous forests are found along 2 gradients: dry to wet and cold to warm. These often vary by elevation and aspect, and influence fire extent and behavior depending on where a forest type is found along the gradients. Forests that historically were influenced by mixed-severity fire regimes in the Pacific Northwest occurred in the transition zones between drier and warmer forest types. Warmer forest types typically experienced a frequent (<25-year) fire-return interval and fires were predominantly of low severity. In contrast, cool and moist forests rarely burned (>100-year fire-return interval) but when they did, fires were primarily high severity and stand replacing events. Thus, mixed-severity fires typically occurred in areas where fire-return intervals varied between 25 and 100 years, although Barrett (2004) noted that some mixed-severity fires occurred at longer fire-return intervals in more patchy, high-elevation, cold forest types. Mixed-severity fire regimes were discussed as one type of fire regime with considerable variation in its expression by Hardy et al. (1998) and Agee (2004). Mehl et al. (2010) discussed 2 classes of mixed-severity fire regime (25-50-year and 50-100-year fire-return intervals). Gray (2004) also identified 2 types of mixed-severity fire regimes (0to 35-year and 35to 100-year fire-return intervals). The primary difference between these types of mixed-severity fire regimes was the spatial heterogeneity produced by the burns. Mehl et al. (2010) discussed how restoration for mixed-severity fire conditions needed to consider the various types of forest compositions and structures and their spatial arrangement. They used a scale of 20 ha and described mixed-severity fire regime A as having a fire-return interval of 25-50 years, resulting in predominantly low severity fire effects with between 10 and 50% of a 20-ha stand displaying higher severity fire effects (>50% of overstory mortality). Mixed-severity fire regime B (fire-return interval of 50-100 years) would have >50% of a 20-ha stand subjected to the higher severity fire effects with a proportionally smaller percentage of low-severity fire effects. Similarly, Hessburg et al. (2004) reported on the need to examine areas as patches rather than points. They reported that using a patch analysis resulted in classifying 3 landscapes in eastern Washington and Oregon as being dominated (approximately 60%) by the mixed-severity fire regime with much lower levels of low- or high-severity fire

regimes. Larson et al. (2009) examined fire histories in 3 whitebark pine communities in western Montana and reported that the mixed-severity fire regime predominated, although substantial differences in fire-return intervals and conditions were present among the 3 sites.

The complexity and variability of mixed-severity fire regimes have made their description and restoration difficult. Specific efforts to understand and address this need have developed only in the last 10-20 years. This is an important need, however, given concerns about maintaining conditions that represent this fire regime in appropriate landscapes.

A primary focus on using prescribed fire in the northern Rocky Mountains is to assist with thinning of forests to reduce fuel loadings and restore low-severity fire regimes in ponderosa pine and other low elevation forests. The description of southwestern ponderosa pine forests later in this Technical Review and the role of prescribed fire in these forests is a good example of this type of restoration. For warm and dry forest types at lower elevations of the northwestern United States, this is an appropriate approach and is an important application of prescribed fire. In these forests, prescribed fire can be used to maintain desired forest conditions, particularly once the buildup of fuels that has occurred over the past 50-100 years has been reduced to levels that will allow large trees to survive a fire. In other forest types, such as cooler and moister forest types of the northern Rocky Mountains, historical fire patterns were more complex, combining elements of low-severity fire regimes with high-severity fire regimes in a spatially heterogeneous arrangement (Arno et al. 1991, 2000; Agee 2004). As Agee (2004) described, these forests contained areas where fire could act as an understory disturbance, thinning out smaller and more fire sensitive trees, areas where fire would be high intensity and would kill all trees, and areas in between these 2 conditions, with varying levels of mortality to overstory trees. These varying conditions could occur in an array of patch sizes, producing a spatial heterogeneity that is a characteristic of the mixed-severity fire regime forests.

Because mixed-severity fire regimes are a relatively new focus for researchers and managers, coupled with the difficulty of quantifying changes from historical conditions in this complex fire regime, few studies have quantified current conditions or evaluated cumulative effects to mixed-severity fire regimes. More typically, mixed-severity fire regimes are included with low-severity fire regimes, and a relatively uniform prescription for thinning of understory trees and reducing overstory canopy has been suggested. However, as indicated above, mixed-severity fire regimes are important for landscape heterogeneity and habitats they provide for many wildlife species.

Fire Effects on Wildlife

Effects of mixed-severity fire regimes on wildlife have been little studied. Lehmkuhl (2004) examined wildlife species expected to occur in the mixed-conifer forests of Oregon and Washington, a forest type associated with mixed-severity fire regimes. When he compared these species to those associated with forest types at low elevations (low-severity fire regimes) and higher elevations (high-severity fire regime), he found the mixed-conifer forests supported wildlife species associated with both forest types (and fire regimes). He also noted that downed woody debris and snags in mixed-severity fire conditions would be beneficial to many wildlife species.

Vegetation heterogeneity produced by mixed-severity fire regimes is favored by some wildlife species. One example is the Canada lynx that uses stands of dense large trees with blowdowns and other sources of large woody debris as denning sites, with surrounding forests of heterogeneous conditions supporting snowshoe hares and other prey species. Northern flying squirrels also may use varying stand conditions produced in mixed-severity fire regime forests (Lehmkuhl 2004). Finally, northern goshawks prefer nesting in stands of dense large trees with fairly open understories, but with a variety of other forest conditions of varying density where they can forage on various prey species (Reynolds et al. 2008). However, no studies have specifically examined the relationship between requirements of these species and habitats occurring within mixed-severity fire regime forests.

Challenges

Restoration of mixed-severity fire regime forests has only recently been a management focus. Graham and

Jain (2004) discussed silvicultural tools that might be useful in such restoration. Prescribed fire was included as an important tool for restoration of mixed-severity fire regimes, but this presents several challenges. First, prescribed burning is seldom conducted during dry conditions that can produce high-severity fires. Difficulties in controlling fire under these conditions and possible consequences of losing control of a prescribed burn make managers apprehensive, even within a mixed-severity application. Current efforts such as those emphasized by the Collaborative Forest Landscape Restoration Program of the U.S. Forest Service emphasize addressing landscape-level fire management. As more landscapes are managed at these larger scales and better fire management capabilities are designed into landscape prescriptions, use of prescribed fire to more closely resemble historical mixed-severity patterns may be feasible.

A second challenge, related to the first, is seasonal application of prescribed fire. Feller (2004) reported on influence of season of fire on plant species; spring burns resulted in different responses than summer burns. In the Kamloops Forest Region of Canada, 48% of the lightning caused fires from 1919 to 1960 occurred in July and 51% occurred in August (Feller 2004). Historically, some burning by Native Americans may have occurred in the fall or spring, but summer was the primary burning season. White et al. (2004) reported that historical fires occurred primarily in the summer in Banff National Park in Alberta. The Park has used prescribed burning, but not during the prime fire season, resulting in a much lower kill of trees than predicted from models of historical fire intensity or severity. Today, using prescribed fire during this period is limited by difficulty of its control. Taylor (2004) discussed the need to factor in topography and other landscape features to design restoration efforts that produce the mosaic of conditions desired for mixed-severity fire regime forests. Similarly, Wimberly and Kennedy (2007) modeled mixed-severity fire regimes for the interior Pacific Northwest and reported that closed canopy patches were rare in landscapes with a fire-return interval of 50 years or less, but emphasized importance of interactions among fire spread, landscape vegetation patterns, and the underlying physical landscape features.

Most current uses of prescribed burning in mixed-severity forest areas occur in the early spring, before substantial green-up of vegetation, or after fall rains have reduced fire danger. These relatively low-severity fires can provide helpful reductions in understory fuels and some thinning and mortality of smaller trees, but do not produce the heterogeneity of conditions produced by true mixed-severity fires. Developing forest conditions that will allow mixed-severity fires to again be used in landscapes will be a challenge.

A third challenge is the need for large trees to be present to produce the desired mix of forest compositions and structures. Because of past logging activities and recent high-severity fires, large trees are under-represented in many if not most historical mixed-severity fire locations (Perry et al. 2011). Planning for long-term restoration could provide for growth of large trees in appropriate locations, but that could require 100+ years to reach acceptable conditions. A current focus is to concentrate on maintaining large trees and their functions in locations where they still occur. Management actions include protecting these trees from logging and from high-severity fire events. In mixed-severity fire areas where large larches, ponderosa pines, and Douglas-firs are present, typical management includes mechanical or hand thinning of smaller trees and understory vegetation so that prescribed burning can be used to maintain desired stand conditions.

Because of the small number of stands containing large trees in mixed-severity fire areas, remaining stands with large trees often dictate priority areas for restoration and mixed-severity fire conditions that can be restored. Where substantial areas of large trees remain, mixed-severity fire conditions that represent the drier end of this fire regime with more low-severity fire conditions may be restored. Where only small patches of large trees remain, conditions favorable for moderate- and high-severity fire might be restored; however, managers would need to assess whether the lack of large trees was the result of having higher-severity fires in that location historically or the result of logging or other anthropogenic changes. Optimally, prescribed burning can be used in conjunction with other stand treatments that can reduce fuel loadings in areas supporting large trees to maintain these trees, and then producing varying conditions around the large tree areas.

Prescribed burn of predominantly poderosa pine along with some Gambel oak on Flagstaff Ranger District, Coconino National Forest in Arizona.

Credit: Shaula Hedwall, U.S. Fish and Wildlife Service

Taylor (2004) and Hessburg et al. (2004) recommended using topographic-edaphic variables in determining desired fire severity conditions for an area. Potential vegetation type classifications can indicate probability of low-, high-, or mixed-severity fires occurring, but considerable overlap and variation can occur in response to the topographic-edaphic site conditions. Gray (2004) identified landscape features that could help design where to place different types of mixed-severity fire conditions within a landscape.

A final challenge in using prescribed burning for restoration of mixed-severity fire regimes is integration with other resource management objectives. Haufler and Rieman (2011) identified challenges of restoring terrestrial forest ecosystems while also addressing fuel management concerns in the wildland-urban interface. They also addressed aquatic restoration concerns that may emphasize minimizing any additional disturbances within key watersheds. New levels of landscape planning will be required to sort through these potential conflicts and identify appropriate areas for reinstating the role of fire, particularly for mixed-severity fire regimes.

Southwestern Ponderosa Pine Forests

Ponderosa pine is a primary forest type in western North America (Daubenmire 1978). It can occur in monotypic stands or mixed with xerophytic vegetation at lower elevations and mesophytic species at higher elevations. Lower montane-zone pine forests (2,150-2,600 m) are often mixed with Gambel or Arizona white oaks and grade into pinyon-juniper woodland and grassland, whereas forests at higher elevations (2,400-3,000 m) grade into mixed-conifer forest comprised of ponderosa pines, Douglas-fir, white fir, southwestern white pine, and other conifer and hardwood species (Moir et al. 1997). The largest contiguous belt of ponderosa pine in North America occurs along the Mogollon Rim extending from central Arizona to western New Mexico.

Historical and Current Use of Fire

Fire is perhaps the most important natural disturbance in southwestern ponderosa pine forests, and frequent, low-intensity fires were part of their evolutionary history (Pyne 1996, Moir et al. 1997). These fires burned every 2-12 years, maintaining an open park-like structure with a variable and patchy tree distribution (Cooper 1961, White 1985). Fires were lightning-ignited and occurred in late spring to early summer prior to onset of monsoon season (Moir et al. 1997). Trees often occurred in even- and uneven-aged groups or clumps, separated by open, grassy interspaces (Cooper 1961, Covington and Moore 1994). Large, mature pines tended to dominate tree distributions (Biswell et al. 1973). Fires largely remained on the surface, carried by the grassy understory, and served to maintain forest structure and open interspaces. Mesophytic pine forests had a more mixed-severity fire regime, but were still dominated by low-intensity surface fires. Crown fires occurred, but were rare (Iniguez et al. 2009).

Management of pine forests in the Southwest following European settlement changed the structure of these forests dramatically. Large trees were harvested selectively, fires were suppressed, and livestock (cattle and sheep) grazing removed much of the fine fuel that carried surface fires. A combination of these factors and widespread tree reproduction in 1919 drastically changed the structure of pine forests (Covington and Moore 1994, Allen et al. 2002). What once had been a heterogeneous landscape consisting of groups of trees separated by grassy openings became a homogenous forest of dense, small-diameter trees that filled interspaces (Biswell et al. 1973).

These changes in forest structure led to a concomitant change in fire regime. Fire suppression agencies continued to extinguish most, but not all fires. Fires that were not controlled during initial suppression attempts often became large, stand-replacement wildfires. Resource managers have recognized the need to address this situation by reducing fuel loads and disrupting fuel continuity across the landscape via mechanical tree removal (i.e., thinning and logging), prescribed fire, or a combination thereof (Strahan et al. 2015). Mechanical removal is required because tree densities in many areas are too great to use prescribed fire safely. Prescribed fire is applied using both planned and unplanned ignitions. Planned ignitions occur often in early spring or fall, outside the natural burn season, when moister conditions allow for greater control. Unplanned ignitions can occur during any part of the year and are allowed to burn only if the fire burns within prescription.

Fire Effects on Wildlife

Wildfire. Several studies have evaluated wildfire effects on wildlife in southwestern ponderosa pine forests (Lowe et al. 1978, Overturf 1979, Blake 1982, Dwyer and Block 2000, Kyle and Block 2000, Bock and Block 2005, Converse et al. 2006b). Some general trends emerging from these studies were increases in populations of ground-foraging and wood-boring bird species following fire (Lowe et al. 1978, Overturf 1979), and decreases in populations of foliage-gleaning species. Blake (1982) studied response of non-breeding birds to fire and noted positive responses by ground-foraging and aerial

insectivores, but negative responses by foliage-gleaning species. Population responses by species corresponded to changes in vegetation and remaining vegetation structure. Wildfire often kills trees, replacing them with snags that provide both foraging and nesting substrates for species that use dead wood. Wood-boring avian species often have short-term responses, corresponding to an increase in insect prey 2-3 years following fire (Covert-Bratland et al. 2006). With fewer trees, green foliage used as a foraging and nesting substrate by certain birds is also reduced, thereby leading to a reduction in population sizes. Conversely, opening the canopy leads to growth of a woody and herbaceous understory, providing habitats for ground-dwelling birds. Latif et al. (2016) found that more avian species responded negatively to wildfire than positively, possibly because recent fires deviate so drastically from the historical low-severity fire regime characterizing the Southwest.

This change in vegetation structure also affects small mammal species. Converse et al. (2006*b*) observed an increase in biomass of small mammals following wildfire, including a positive numerical response by deer mice. Kyle and Block (2000) reported significantly larger deer mouse populations within severely burned forest than in unburned controls, but no significant difference between numbers in moderately burned forest and controls. Dwyer and Block (2000) studied secondary cavity-nesting birds on the same fires and reported that, as a group, these birds were more abundant on moderately-burned and unburned sites than on severely-burned sites. At the species level, however, western bluebirds benefitted from severe- and moderate-fire, white-breasted and pygmy nuthatches benefitted by moderate-fire, but mountain chickadees were negatively affected by any fire. In a broader community analysis of the same sites, bird numbers and species richness seemed to increase shortly after fire (Bock and Block 2005). Three years post-fire, more species of breeding birds were detected in areas where fires were severe and moderate than in adjacent unburned forests, with a similar trend during the nonbreeding season. Woodpeckers, flycatchers, and thrushes were among the species groups that were more abundant in response to fire. In contrast, many foliage-gleaning birds were detected less frequently within severe fire areas.

Prescribed Fire and Thinning. The Fire/Fire Surrogates study (Schwilk et al. 2009) was a national study focusing on effects of thinning and prescribed fire, used singly and in combination, on a variety of response variables in pine systems across the United States. Two replicates occurred in the Southwest, 1 in New Mexico and the other in Arizona. Hurteau et al. (2008) reported that the populations of some species, such as western bluebirds, increased following prescribed fire, whereas others, such as mountain chickadees, decreased in response to thinning treatments. Home-range sizes for western bluebirds were 1.5 times larger in the thin-only treatments than in the control units, but approximately 30% smaller in thin-and-burn treatments than control units (Hurteau et al. 2010). The largest home ranges occurred in the burn-only treatments. Nesting attributes, such as number of eggs or nestlings, did not differ statistically among treatments. Hurteau et al. (2010) concluded that forest treatments such as thinning and prescribed fire are generally beneficial to western bluebirds, but that low snag retention may be an issue in areas subjected to prescribed fire.

Converse et al. (2006*a,b*) evaluated effects of thinning and prescribed fire on habitats and densities of 4 species of small mammals. Treatments increased herbaceous vegetation, decreased shrub density, and decreased woody debris. As a result of these treatments, densities of deer mice increased and densities of gray-collared chipmunks decreased. Golden-mantled ground squirrels were positively related to shrub cover, and Mexican woodrats were positively related to shrub cover and woody debris. Converse et al. (2006*a*) concluded that reduction of shrubs and woody debris with prescribed fire may reduce densities of small mammals. Strahan et al. (2015) concluded that thinning and prescribed fire increased understory diversity and were valuable restoration tools within ponderosa pine forests.

Kailes et al. (2010) conducted a meta-analysis of 25 studies in northern Arizona to compare the effects of small-diameter removal, prescribed fire, thin/burn, selective harvest, overstory removal, and wildfire on birds and small mammals. Generally, prescribed fire and thin/burn treatments benefitted passerine bird and small mammal populations, whereas overstory removal and wildfire were mostly detrimental. Ground-foraging birds and rodents showed neutral population responses to thinning and burning, whereas aerial-, tree-, and bole-foraging birds exhibited neutral to positive responses.

Prescribed Fire. A large study was initiated in 2002 to evaluate effects of prescribed fire on habitats of birds throughout the Interior West (Saab et al. 2007). This study was replicated at 14 locations, including 4 in the Southwest. It differed from previous efforts because the burn units exceeded 200 ha, which enabled more complete sampling of the avian community. We consider results from the Southwest here.

For breeding birds, response to treatments appeared to be scale-dependent (Dickson et al. 2009). At the unit level, few treatment effects were observed, and none of those were strong relationships. Stronger relationships emerged at the scale of the sampling point, where only the American robin and hairy woodpecker appeared to respond positively to fire. Dickson et al. (2009) concluded that breeding birds were fairly tolerant to conditions 2-3 years post-fire.

Pope and Block (2010) reported similar results for birds during winter. Bird communities were similar between treatments and years, and the rank abundances of species between burn and control units were correlated. However, species-specific differences were noted among 3 bark-foraging birds: hairy woodpecker, pygmy nuthatches, and white-breasted nuthatches (Pope et al. 2009). Density of hairy woodpeckers increased 5-fold in burned units, whereas white-breasted nuthatches and pygmy nuthatches showed no significant differences. This difference was attributed to foraging mode because hairy woodpeckers selected trees with bark beetles, which were more abundant in the burned plots. Pope and Block (2010) concluded that forest managers could use prescribed fire treatments without detrimental effects to winter avian communities.

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 for 1 and 2 years after. They observed few changes in bird abundance; northern flickers and violet-green swallows decreased, and mountain chickadees increased. However, care should be taken when applying prescribed fire to ensure retention and development of key habitat elements. Jentsch et al. (2008), for example, reported that bird species richness was positively associated with abundance of large Gambel oaks. Safeguards (e.g., lining of oaks) might be warranted to minimize loss of these components. Furthermore, prescribed burning could stimulate growth of Gambel oak thickets, which appear important to some bird species in pine-oak forests. Prescribed fire might also lead to loss of snags and logs. Randall-Parker and Miller (2002) noted that 50% of downed logs and 20% of snags were lost to prescribed fire. In contrast, Saab et al. (2006) noted significant reductions in logs and live trees, but no significant reduction in snags. Neither study provided information on numbers of snags nor number of logs needed for specific species of wildlife, so interpretation of effects on wildlife is difficult.

Response of small mammal communities to prescribed fire was studied by Roberts et al. (2015). Here researchers studied small mammal communities in 20 forests (10 burned within the past 15 years and 10 unburned). Small mammal abundance was greater in the unburned forests, but burned forests had greater species evenness. They suggested that application of prescribed fire to enhance landscape heterogeneity, including the presence of unburned patches, would help maintain diverse small mammal communities.

Challenges

Ponderosa pine is a fire-adapted ecosystem that requires periodic fire to maintain forest structure. More than a century of human intervention has altered these forests and fire regimes from one of frequent, low-severity fires to infrequent, high-severity fires. As a result, resource managers are exploring options for reducing fuels and disrupting fuel continuity to restore forest structure and returning to natural fire regimes. Two primary options are available: mechanical treatments (i.e., tree removal) and prescribed fire, used singly or in combination.

Information on effects of prescribed fire is largely limited to birds and small mammals; data on other taxa are clearly needed to better understand effects. Responses by species to fuels reduction vary, but by-and-large, effects of prescribed fire on species appear beneficial or benign. This is not surprising, given that native species evolved with fire and its effects. Constraints to applying these treatments over greater landscapes appear more social than biological.

Desert Grasslands

Semi-desert grasslands are dominated by perennial grasses, interspersed with shrubs and small trees, and have the lowest biomass of grasslands in North America (Sims and Singh 1978). Semi-desert grasslands are distributed throughout 13 states in Mexico and reach their northern extent in Arizona, New Mexico, and Texas (Schmutz et al. 1991). These arid grasslands occur between 1,100 and 1,800 m in elevation (up to 2,500 m in Mexico) and are naturally fragmented on the landscape, creating a mosaic with oak woodlands, chaparral, desert scrub, and other vegetation communities (Burgess 1995, McAuliffe 1995). Precipitation averages 250-450 mm annually (Schnapp and Kinucan 2010), although semi-desert grasslands in Mexico may receive as much as 600 mm of rainfall per year (Schmutz et al. 1991). Much of the rainfall occurs between May and October and coincides with growth of predominate warm-season grasses (McClaran 1995).

Historical and Current Use of Fire

Historically, fires ignited naturally with dry lightning that preceded onset of summer monsoon rains (Humphrey 1949, Bahre 1991); lightning strikes are common in the southwestern United States (Pyne 1982). Native Americans also applied fire to the landscape for many purposes, including hunting and improving pasture conditions (Pyne 1982), which provided additional anthropogenic sources of ignition (Bahre 1991). Fires were low-intensity, patchy, and wide-ranging, sometimes extending hundreds of square kilometers, and were limited only by the continuity of fine fuels (Bahre 1991, Dick-Peddie 1993, McPherson 1995). The typical fire-return interval was 7-10 years, which was less frequent than that of other grassland types (Wright and Bailey 1982, Schmutz et al. 1985) and rainfall served as the main driver of fuel production (Burgess 1995).

Overgrazing was prevalent in the southwestern United States in the late 1800s and early 1900s, which altered fire frequency and extent due to reduced fuel availability (Bahre and Shelton 1993, McPherson 1995). Fire suppression and other changes to the fire regime and land use contributed to increased soil erosion and woody dominance on the once grassy landscape (Wright and Bailey 1982, Bahre and Shelton 1993, McAuliffe 1995, van Devender 1995, Dickerson 2010).

Nonnative grasses were introduced to semi-desert grasslands in the late 19th and early 20th centuries, in an attempt to reduce soil erosion and improve range conditions in this altered landscape (Crider 1945, Cox et al. 1988, Bahre 1991, Burgess et al. 1991, Roundy and Biedenbender 1995). These species have increased in dominance and distribution throughout the southwestern United States and northern Mexico (e.g., Cox and Ruyle 1986, Anable et al. 1992, Schussman et al. 2006) and have contributed to further changes in fire regime because of an increase in abundance and continuity of fine fuels. Lehmann lovegrass, for example, produces more litter and up to 4 times more biomass than native grass species (Cable 1971, Cox et al. 1990, Anable et al. 1992, Geiger 2006). These nonnative plants are well-adapted to fire, with germination rates and dominance sometimes increasing after fire (Cable 1965, Ruyle et al. 1988, Sumrall et al. 1991, Bock, J. H. and Bock 1992), although evidence for a positive feedback grass-fire cycle (sensu D'Antonio and Vitousek 1992, Mack and D'Antonio 1998) in these semi-desert grasslands has been mixed (Anable et al. 1992, Bock, J. H. and Bock 1992, Geiger and McPherson 2005, Geiger 2006, Litt and Steidl 2011, McGlone 2013).

Prescribed fire typically has been applied during winter and spring months because of the cooler ambient temperatures, increased humidity, and higher fuel and soil moisture. Although these cooler fires reduce biomass, mortality generally occurs only for cool-season plants, which are less common in semi-desert grasslands (McPherson 1995). Summer fires, consistent with historical fire regimes, result in effects that are of

greater magnitude and longer duration (Glendening and Paulsen 1955).

Fire Effects on Wildlife

Vertebrates in semi-desert grasslands have evolved under the influence of patchy, low-intensity fire, and direct mortality resulting from fire is relatively uncommon (McPherson 1995). Most species avoid fire by making use of speed or underground burrows, but species with above-ground nests (e.g., woodrats) may experience some direct mortality (Simons 1991). Vertebrate responses to fire are species-specific and based on habitat requirements, which may change through an animal's life history. In general, species that prefer high cover and vertical structure decrease in presence and abundance following fire and species that prefer more open environments and foods that are stimulated by burning (e.g., seeds, Bock et al. 1976) increase in presence and abundance (Bock and Bock 1978, Bock et al. 1986, Bock and Bock 1988, Bock, C. E. and Bock 1992, McPherson 1995, Fitzgerald et al. 2001, Litt and Steidl 2011). Raptor populations may increase after fire because prey populations are more exposed (Bock and Bock 1978, Lyon et al. 2000), and a high diversity of granivorous species (e.g., small mammals and birds) benefits from new growth of grasses and forbs (Bock and Bock 1978, Bock et al. 1986, Litt and Steidl 2011).

Changes in presence and abundance of vertebrate species after fire typically are relatively ephemeral, and populations recover within 1-4 years (Bock and Bock 1978, Bock and Bock 1988, Albrecht et al. 2008, Litt and Steidl 2011), depending on post-fire precipitation and vegetation growth (Cable 1967, Wright and Bailey 1982, Bock, J. H. and Bock 1992). Changes in season of burn may have implications for species that are reproducing or have young at the time of the fire (Erwin and Stasiak 1979); many species of grassland birds are ground-nesters (van Devender 1995) and would be negatively impacted by fires during nesting season.

Challenges

Grasslands are among the most endangered plant communities in North America (Noss et al. 1995), due in part to invasion by nonnative plants and changes in land use. Fire regimes in remaining grasslands have been altered greatly, through changes in return interval, intensity, and fire season. Anthropogenic fragmentation of remaining grasslands further alters fire regimes (McPherson 1995) and reduces feasibility of applying prescribed fire.

One of the largest challenges in managing semi-desert grasslands currently is that the interactive effects of fire, nonnative plants, and other landscape changes on grassland plants and animals are largely unknown (Steidl and Litt 2009, Fleishman et al. 2011). Under these novel conditions, fire may operate outside the natural range (D'Antonio et al. 1999, Brooks et al. 2004) and no longer may behave in a predictable way or serve as an effective restoration tool (Raffa et al. 2008, Steidl and Litt 2009, Litt and Steidl 2011). Increases in greenhouse gases could result in further changes in fuel loads because of increases in woody cover and decreases in grass cover (McPherson 1995), and changes in temperature and precipitation patterns may also affect primary productivity and species persistence. Such compounded stresses may act synergistically and drive local extirpation of species that are unable to tolerate altered conditions (Hobbs and Huenneke 1992, Paine et al. 1998).

Diverse species composition of flora and fauna in semi-desert grasslands likely was maintained historically by variability in fire frequency and intensity (Rice et al. 2008). Management strategies that maximize heterogeneity of vegetation structure and composition, distribution of fuels, and resulting fires in grasslands could ensure that a diversity of taxa can meet habitat requirements at all life stages (Bock and Bock 1978, Fuhlendorf et al. 2006, Litt and Steidl 2011).

Shortgrass Steppe

Steppe is a mid-latitude, semi-arid, generally treeless grassland, dominated by short grasses and bunchgrasses, and characterized by large grazing mammals and burrowing animals (Lincoln et al. 1998). It has a wide distribution ranging from Eurasia to the Great Plains of central North America, including the American Southwest. Vegetation characteristic of the North American steppe includes perennial grasses: buffalograss, a sod-forming shortgrass, and blue grama, a bunchgrass (Bailey 1995, Ford and Johnson 2006). The Great Plains climate has severe, windy, dry winters, with little snow accumulation, relatively moist springs, and summers are often droughty and punctuated by thunderstorms (Borchert 1950, Sims and Risser 2000). Natural fires and those ignited by Native Americans moved uninterrupted across the relatively level plains at sufficient frequency to restrict occurrence of trees and shrubs (Sims and Risser 2000).

The southern Great Plains includes the eastern third of New Mexico, the northern two-thirds of Texas, and most of Oklahoma (Wright and Bailey 1982). Almost all of the grassland in this region is composed of mixed or shortgrass communities (Brown 1994). Although these communities have been altered by grazing and indirect effects of fire suppression followed by shrub invasion, much of the landscape remains dominated by perennial grasses (Brown 1994). The Rio Grande plains of south Texas represent the southern-most extension of the Great Plains grasslands. Fire, along with other climatic variables such as drought, presumably maintained the honey mesquite savannas and interspersed grasslands of pre-European settlement in South Texas (Scifres and Hamilton 1993). Frequency of fire appeared to have been highly variable and ranged from 5 to 30 years (Wright and Bailey, 1982, Ruthven III et al. 2008).

Historical and Current Use of Fire

In general, response of shortgrass steppe to fire seems to depend primarily on pre- and post-fire levels of precipitation. Therefore, using fire as a management tool in a drought year should be carefully considered and aligned with management goals (Ford et al. 2004). Perceptions about value of fire in shortgrass steppe may have been influenced by a desire for rapid increases in grassland productivity to benefit domestic livestock (Ford 1999). This resulted in effect of fire on shortgrass steppe viewed as negative, largely based on conclusions from studies primarily focused on using fire as a tool to increase forage value of grassland vegetation. However, an analysis of early fire-effects literature spanning 42 years (Ford 1999) revealed that responses to fire appear to be predominantly neutral or positive and depend mainly on levels of precipitation.

Fire Effects on Wildlife

Numerous studies (e.g., Komarek 1969, Kaufman et al. 1990, Whelan et al. 2002, Engstrom 2010) have shown that animals respond differentially to disturbance by fire, due in part because fire can have both direct and indirect effects. Direct effects are acute but ephemeral (i.e., fire-induced mortality). Indirect effects (i.e., alterations in conditions) are long-lasting and usually more important (Ford and McPherson 1996). Prescribed fire currently is used in shortgrass steppe as a management tool to improve wildlife habitat, reduce fuel loading, restrict spread of shrubs, and better align timing and intensity of fire to increase ecosystem benefits.

Shortgrass steppe is used by hundreds of bird species. Many of these birds are migrants, whereas others breed in the Great Plains, or can be classified as summer, winter, or yearlong residents. Svingen and Giesen (1999) observed higher densities of mountain plovers during migration on prescribed burns than on unburned shortgrass steppe, and Augustine and Skagen (2014) suggested prescribed fire was important for creating suitable nesting habitat when other forms of disturbance were absent. In addition, prescribed burns in combination with active black-tailed prairie dog colonies may enhance

breeding habitat for mountain plovers in shortgrass steppe (Augustine 2011).

In general, birds are most vulnerable to fire during nesting and fledging periods. Fires can be devastating to ground-nesting birds owing to destruction of existing nests, removal of protective cover, and elimination of insect food resources (Daubenmire 1968) that may be associated with ground litter and vegetation. Therefore, timing of prescribed burns should be a primary consideration to resource managers concerned with declining avian populations that breed in shortgrass steppe.

Because birds are highly mobile, fires rarely kill birds directly, but rather affect population levels indirectly by altering habitat structure, abundance of competing species, and food levels (Dickson 1981, Bock and Bock 1990, Rotenberry et al. 1995). For example, populations of burrowing owls reportedly have declined on grasslands with increases in litter cover, suggesting that using fire to reduce litter cover may be beneficial to this species (Komarek 1969, Kramp et al. 1983). Birds of prey are particularly attracted to fire and smoke, which appears to be related to vulnerability and ease of capture of prey species forced to flee from the flames. Several other species of birds are attracted to recently-burned grasslands (Clark 1935, Handley 1969, Komarek 1969, Kramp et al. 1983, Lyon and Marzluff 1984, Tomback 1986, Ford and McPherson 1996).

Data on effects of fire on herpetofauna are lacking. With increased use of prescribed fire to manage rangelands in South Texas for wildlife and livestock, a better understanding of effects of fire on herpetofauna is needed (Ruthven et al. 2008). Prescribed-burning regimes that incorporate both dormant- and growing-season fire have little short-term effect on diversity of herpetofauna (Keyser et al. 2004, Wilgers and Horne 2006, Ruthven III et al. 2008). Overall, abundance of lizards, snakes, and amphibians is unaffected by dormant-season fires. Texas spotted whiptails decreased slightly in abundance in response to winter burns, whereas six-lined racerunners increased in abundance during the first year after fire. Inclusion of summer fires had little effect on the whiptail; yet encounters of the racerunner were 10 times greater on burned sites compared to unburned areas. Six-lined racerunners typically inhabit open, xeric vegetation types

(Carpenter 1959, Greenberg et al. 1994), and increases in abundance following fire are likely the result of increases in bare ground and reductions of woody plant cover (Ruthven et al. 2002, 2003). A heterogeneous fire regime can maximize diversity of this species group (Mushinsky 1985, Greenberg et al. 1994, Ruthven et al. 2008, Knapp et al. 2009).

Effects of fire on mammals are a function of animal size and vagility. Deer and elk easily avoid injury during fire (McCulloch 1969, Dills 1970, Boeker et al. 1972, Hallisey and Wood 1976), although young ungulates frequently are killed by large fires (Daubenmire 1968, Kramp et al. 1983). Most small mammals can escape fires by hiding in burrows or rock crevices (Howard et al. 1959, Heinselman 1973), where soil provides insulation (Bendell 1974, Kramp et al. 1983). Small mammals die most commonly from a combination of heat effects and asphyxiation. Other causes of death include physiological stress from overexertion while trying to escape, trampling as large mammals stampede, and predation as small mammals flee from fire (Kaufman et al. 1990).

Fires that remove food and cover (litter and standing dead vegetation) temporarily may be detrimental to small rodents immediately after fire (Daubenmire 1968, Kaufman et al. 1990). However, repopulation of such areas is reported to be nearly complete within 6 months (Cook 1959). Mice and rodent populations often increase in response to increased availability of forb seeds and insects. In addition, burned areas often support more diverse animal populations than comparable unburned sites because of increased habitat diversity (Beck and Vogl 1972, Wirtz 1977).

Mammals that respond negatively to fire include species that forage on invertebrates in the litter layer, species that live in relatively dense vegetation and eat plant foliage, and species that use, at least partially, aboveground nests of plant debris. Examples in the southern Great Plains include cotton rats, Bailey's pocket mice, pinyon mice, white-tailed antelope, ground squirrels, southern red-backed voles, white-throated woodrats, western harvest mice, and meadow voles (Komarek 1969, Beck and Vogl 1972, Bradley and Mauer 1973, Bock et al. 1976, Bock and Bock 1978, Geier and Best 1980, Mazurek 1981, Kramp et al. 1983, Kaufman et al. 1990, Ford 2002).

Mammals that respond positively to fire include species that use ambulatory locomotion in microhabitats with a relatively open herbaceous layer and feed on seeds and insects and that use saltatorial locomotion (Kaufman et al. 1990). Population size and habitat use increase after fire because of a concomitant increase in availability of forb seeds, insects, and newly greening vegetation, creation of open areas in otherwise dense vegetation, and eventually an increase in forb cover. Increases may occur immediately or gradually as areas begin to revegetate and habitat diversity increases. Small mammals that show a positive response include deer mice, white-footed mice, eastern cotton-tailed rabbits, kangaroo rats, grasshopper mice, Nuttall's cotton-tailed rabbits, thirteen-lined ground squirrels, and hispid pocket mice (Cook 1959, Cable 1967, Daubenmire 1968, Komarek 1969, Beck and Vogl 1972, Bradley and Mauer 1973, Kramp et al. 1983, Kaufman et al. 1990, Ford 2002).

Factors influencing distribution and abundance of black-tailed prairie dog colonies are of interest to rangeland managers because of the significant influence prairie dogs can exert on both livestock and biodiversity (Augustine et al. 2007). Research on influence of 4 prescribed burns and 1 wildfire on rate and direction of colony expansion in shortgrass steppe of southeastern Colorado indicated that burning can increase rate of colony expansion even with low vegetative structure. This effect was minor at the scale of the overall colony complex, because some unburned colonies were also able to expand at high rates. This result highlights the need to evaluate effects of fire on colony expansion during above-average rainfall years, when expansion into unburned grassland may be considerably lower (Augustine et al. 2007).

Carnivores that occur in the southern Great Plains include badgers, bobcats, swift foxes, and coyotes. These species may increase select vegetation types in response to fire-enhanced rodent prey populations (Wirtz 1977, Gruell 1980, Kramp et al. 1983). Swift foxes are shortgrass specialists and, as a result, are heavily dependent upon disturbance to maintain high-quality habitat (Thompson et al. 2008). Habitat quality for swift foxes represents a balance between prey availability and exposure to predation (Thompson and Gese 2007), which can be created with low intensity fire. Prescribed burning is

therefore an appropriate method to maintain high-quality habitat for swift fox (Thompson et al. 2008).

Population size and habitat use of most native ungulates, including bison, white-tailed deer, elk, and pronghorn increase after fire (Ford and McPherson 1996). These increases are reportedly due to an increase in forage quality and quantity in newly burned areas (Ford and McPherson 1996).

Challenges

Timing for conducting prescribed burns to meet wildlife objectives can be challenging. Brockway et al. (2002) suggested that burning during the dormant season favored native plant restoration and enhanced nutrient cycling. However, burn windows that consider wind speed and direction greatly limit number of days suitable for dormant-season burning (Roberts et al. 1999). Furthermore, dormant-season burns occur outside of the natural summer fire season and may not be as effective at controlling encroachment of woody species (Ansley and Castellano 2007). More information is needed to better understand response of wildlife to different timing alternatives.

Much of the land base within the range of shortgrass steppe is privately owned. As a result, there is public concern over unintended consequences of prescribed fire. Some landowners fear that a prescribed fire may escape containment and move onto their lands burning crops and property. Others express health concerns over effects of smoke on those with heart or respiratory ailments.

Conclusion

Fire as a management tool long predates European settlement of North America. Indeed, Native American and First Nations peoples were well-versed in application and benefits of prescribed fire. Prescribed fire is a tool used by contemporary resource managers to meet numerous objectives, including reducing fuel loads and continuity, returning fire to an ecosystem, enhancing wildlife habitat, improving forage, preparing seedbeds, improving watershed conditions, enhancing nutrient cycling, controlling exotic weeds, and enhancing resilience from climate change. Regardless of the particular objective, fire affects ecosystem structure, composition, and function in many ways.

As many of the regional accounts describe, prescribed fire varies widely in application and effects. Factors that influence fire effects are vegetation type and seral stage, fuel conditions, topography, weather, climate, fire size, burning prescription, fire intensity, fire frequency, and fire seasonality. In many, if not most, situations, prescribed fire is used in vegetation types where fire is a natural disturbance and a critical process influencing ecosystem structure and function. Fire suppression over the past century has disrupted natural fire regimes, and resulting ecosystems deviate considerably from what existed historically. Prescribed fire is gaining support as a restoration management tool and the practice of applying it is improving with new information.

With the realities of global climate change becoming more apparent, we have only a limited understanding of its effects on ecosystems attributes, including wildlife (Sommers et al. 2011). This is partly because resulting changes will alter ecological systems and the underlying biotic relationships. Vegetation changes may render areas suitable for some plant and animal species, but unsuitable for others. Vegetation composition and structure may form communities never observed before, hence wildlife responses to these new communities may be unpredictable. New mixes of plant species may lead to the emergence of novel wildlife communities with unforeseen

biotic interactions (e.g., competition, predation). Changes may occur at varying spatial scales, from micro- to macrohabitats and to landscapes and regions. Given these uncertainties, trying to mitigate these changes will be difficult. One approach is to increase ecosystem resiliency (Reynolds et al. 2013). Both mechanical tree removal and prescribed fire are critical tools to enhance resiliency by reducing stem densities towards historical levels. The premise is that many of these ecosystems persisted for thousands of years and experienced a wide range of environmental conditions in temperature and moisture. Presumably, restoring these systems to the range of historical conditions provides the best chance for systems to persist in the face of climate change.

Generalized effects on wildlife

Prescribed fire affects wildlife in various ways. Population responses by species can be positive, negative, or neutral; short- or long-term (or both); and they often change with time. Whereas prescribed fire can create or maintain habitats for some species, fire can remove or alter conditions in ways that render it unsuitable for other species. Furthermore, a species may benefit from fire in 1 situation but not another. Given variations in fire and in species responses, the only real generalization one can make is that exceptions occur. Fire does not occur uniformly across a landscape, instead manifesting as a heterogeneous mosaic that provides habitats for different species, thereby influencing wildlife diversity. Practitioners should try to emulate natural mosaic patterns by designing and implementing a set of prescriptions rather than applying one prescription across a landscape.

Scale and timing are critical considerations when prescribed fire is used. Scale relates to both time and space. Natural fire ignitions often correspond to the season(s) when lightning occurs. Plants and animals co-evolved with fire occurring during this time of year and exhibit adaptations to breed, survive, and even flourish with fire. When possible, prescribed fire should

occur during the natural fire season, and spatial scale of a prescription should emulate natural fire. Often, low-intensity surface fires burned extensive areas, whereas high-intensity crown fires tended to be more limited in extent (e.g., stand scale).

The science of prescribed fire and our understanding of effects on wildlife are improving. Many studies are observational or quasi-experimental, but opportunities exist to conduct well-replicated experiments. Experiments require coordination with fire managers to design and implement treatments. Experimental units must be sufficiently large to assess population response, which will vary according to the species under study. Saab et al. (2007), for example, required units ≥200 ha for sampling passerine birds. Larger units may be required for ungulates and rare species with large home ranges (e.g., carnivores), whereas smaller units might suffice for common species with small home ranges (e.g., small mammals).

Much of our knowledge on effects of prescribed fire is derived from studies on birds, small mammals, and ungulates. We found few studies that addressed effects on furbearers, reptiles, and amphibians. Clearly, research on these taxa is needed to more fully understand relationships between wildlife and prescribed fire.

Knowledge gaps remain in our understanding of effects of timing of prescribed fire. Presumably, prescribed fire applied within the time of year when fires occur naturally would be most beneficial to wildlife. However, fire managers may be forced to ignite fires during other times of the year when likelihood of fires burning outside prescription are reduced. For example, fires in the southwestern United States occurred naturally from late spring to early summer. These were lightning-ignited fires prior to onset of heavy monsoon rains. Typically, this time of year is also characterized by high winds, which can cause fires to spread quickly and become out of control. As a result, managers conduct burns in late summer, fall, or late winter when conditions are moister and the winds reduced.

Social issues, particularly those surrounding smoke and emissions, constrain where, when, and how managers can burn. Certainly, emissions standards enforced by state and federal environmental agencies limit windows of opportunity for burning. Smoke billowing into human communities is a health concern, especially for people with existing respiratory ailments. Many publics associate smoke with fire and conclude that fire is bad. Progress has been made at educating the public concerning benefits of prescribed fire to reduce threats of wildfire to people and property and also benefits to ecological communities, but much work remains.

In conclusion, benefits of prescribed fire far outweigh negative effects. The science of prescribed fire continues to provide better information and options for resources managers to incorporate into management plans. Prescribed fire should be applied within a structured adaptive management framework (Walters 1986), which requires developing and implementing monitoring systems to evaluate efficacy of specific fire prescriptions. Depending on monitoring results, prescriptions could be applied elsewhere or adjusted to meet management objectives. Either way, prescribed fire is an important resource management tool that can be effective at maintaining or enhancing habitats for many species of wildlife.

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Box 1. Forest Succession and Wildlife-Habitat Relations

Prescribed fire can influence forest succession by reverting it to an earlier stage, maintaining it at its current stage, or assisting progress towards an older stage. As succession progresses from early to late stages, vegetation composition and structure change, which changes the array of habitats and wildlife species present. To illustrate these relationships, we present species-habitat relations for birds and mammals in the southeastern United States shortleaf pine-bluestem forests and how changing habitat structure and conditions results in different mixes of species in the wildlife community.

Early Succession. Following disturbance that moves a stand to an early seral stage, a fairly predictable chronosequence of vegetation replacement occurs (Johnston and Odum 1956; Meyers and Johnson 1978; Masters 1991*a,b;* Masters et al. 2006). The first stage is represented by herbaceous vegetation with an array of grasses and forbs. If the stand was clearcut and the site prepared for planting, the first stage may have considerable bare ground. Within 2 years of the clearcut, herbaceous vegetation will dominate the site and some woody component will develop (Masters 1991*a,b*; Masters et al. 2006). Soft mast production, important for many mammals and birds, typically recovers by the 3rd growing season and is more abundant than in mature mixed pine-hardwood stands (Perry et al. 2004). Herbaceous and woody current annual growth will increase until canopy closure, generally within 6-8 years (Fenwood et al. 1984; Masters et al. 1993, 2006). Forage and browse production will be from 10 to 25 times greater than that in mature oak-pine stands over this short period of time (Masters et al. 2006). Within 4 to 6 years, woody vegetation begins to assert dominance as a distinct grass-shrub stage (Johnston and Odum 1956, Masters et al. 2006). Then by 8 to 10 years a distinct sapling stage occurs. The replacement sequence and relative dominance of woody species can be redirected by subsequent disturbances such as fire (Masters 1991*a*; Masters et al. 2005, 2006).

The chronosequence of mammals and birds that follow stages of vegetation replacement are also somewhat predictable and fairly well documented. From the first herbaceous dominated stages, as cover develops, small mammals colonize quickly (Atkeson and Johnson 1979, Thill et al. 2004), and eastern cotton-tailed rabbits, white-tailed deer and elk begin using the site (Masters 1991*a,b;* Masters et al. 1997; Fig. 2). However flying squirrels (Taulman and Smith 2004), gray squirrels, and fox squirrels show dramatic declines compared to those in mature stands in these earliest seral stages (Flyger and Gates 1982). These groups of species continue using these sites through the shrub stage and into the sapling stage. However, by the 5th growing season small mammal density (Thill et al. 2004) and squirrel use decline dramatically (Flyger and Gates 1982). Any benefit to small- and medium-size mammals also benefited mammalian predators (Landers 1987).

Small mammal survival in burned areas depends on uniformity, duration, and intensity of fire, in addition to an animal's mobility and position in relation to soil surfaces (Wright and Bailey 1982) and litter structure (Landers 1987). During the first and second years post-burn, herbivorous and gramnivorous species become dominant and insectivorous species decline. Many small mammals require early- to mid-successional conditions, created or maintained by fire (Landers 1987).

Sapling stands provide beneficial escape and bedding cover and browse for white-tailed deer and elk in naturally or artificially-regenerated stands. However, cotton-tailed rabbit use declines (Masters 1991*a,b;* Masters et al. 1993, 1997). As crowns closure begins, herbaceous vegetation begins declining (Masters et al. 1993) as does small mammal richness and density (Atkeson and Johnson 1979). By age 10 and at crown closure, rabbit,

elk, and deer dramatically curtail use of either naturally-regenerated or clearcut stands (Masters et al. 1997). Use of these stands is extended when prescribed fire is introduced early and at least on a 3-year late-dormant season cycle (Masters et al. 1997; Fig. 3). Prescribed fire reduces density of small (<2 m) woody stems (Sparks et al. 1999) and maintains herbaceous understory production at high levels (Masters et al. 1993, 1996).

From the earliest stages of secondary succession (bare ground), mourning doves begin using such sites. When the herbaceous stage is extended, such as in old-field situations or in some clearcuts, eastern meadowlarks, field sparrows, and grasshopper sparrows also use this stage (Johnston and Odum 1956, Meyers and Johnson 1978, Dickson et al. 1993). Other early-succession bird species such as northern bobwhites, northern cardinals, indigo buntings, blue grosbeaks, and less frequently Bachman's sparrows make some use of the grass-shrub stage found in regenerated stands as long as adequate ground cover and fairly dense brushy woody plants are present (Fig. 4). Eastern bluebirds will use these sites where suitable snags are found. Where ground cover is predominantly needle litter in dense sapling to post-sized stands, species like prairie warblers and hooded warblers may occur (Jennelle 2000). Periodic burning on at least a 3-year rotation in young sapling stands extends the period of use by early sere wildlife species such as numerous small mammals, northern bobwhite, wild turkeys, and numerous songbirds that will continue to use stands as they develop (Masters 1991*a*, Stewart 1999, Jennelle 2000, Walsh 2004; Fig. 5).

Mid-Succession. The mid-succession stage occurs from about 12 to 60 years of age. A common characteristic in stands where fires have been excluded are closed canopies with sparse patches of relatively few herbaceous plants in the understory (Oosting 1942, Meyers and Johnson 1978, Masters et al. 2006). Stand density varies throughout this age span, but dense stands generally decline in density over time as competition-induced mortality takes place. Lower density stands will become denser during the early part of this stage for a short period. But in either instance, by the later part of this successional stage, density will be similar (Oosting 1942). Once a mixed oak-pine stand enters the post size-class (10-

15 cm, diameter at breast height), use by many wildlife species will decline dramatically as will density, especially in dense stands where fire is excluded. By age 15, stands support low numbers of small mammals (Atkeson and Johnson 1979). By age 18-20, flying squirrels begin using these developing mixed stands (Landers and Crawford 1995). Only during the latter part of this stage will significant numbers of fox or gray squirrels begin using the stand. In the later part of this stage, fox and gray squirrels may be more abundant than in late seral stages (Flyger and Gates 1982).

At age 12-15 depending on the site index, some songbird species more characteristic of later stages of succession will once again begin using canopies of southern pine species (Engstrom et al. 1984, Jennelle 2000). Species such as red-eyed vireos, hooded warblers, and wood thrushes become increasingly common, but ground dwelling and nesting species and some shrub associated species decline (Engstrom et al. 1984, Landers and Crawford 1995). Importance of fire in retaining early seral wildlife species was recently shown in a study on the Ouachita National Forest, Arkansas, that examined northern bobwhite use of even-aged stands 12-15 years of age. Following only 3-4 seasons of fire exclusion, northern bobwhite began avoiding stands that ranged from 240 to 280 stems/ha and that previously had showed extensive use (Walsh 2004).

In stands from about age 25 to 60, low densities of breeding birds characterize most dense southern pine forests (Johnston and Odum 1956). However, a host of songbirds use canopies of pole-sized stands and to a much greater extent the understory where frequent fire is used and lower stand density (<16 m²/ha) is maintained (Fig. 5). The complement of songbird species in pole stands is similar to that in mature stands (Wilson et al. 1995, Jennelle 2000, Masters et al. 2002). In mid-succession stands excluded from fire, both species richness and density of small mammals and songbirds decline markedly as midstory hardwoods develop and the herbaceous layer declines from litter buildup and shading by hardwoods (Engstrom et al. 1984, Landers and Crawford 1995, Masters et al. 2002).

Late Succession. Late seral-stage mixed oak-pine stands may be characterized by a distribution of uneven-

aged diameters, sparse herbaceous understory, and considerable horizontal and vertical structure (Meyers and Johnson 1978, Kreiter 1994, Smith et al. 1997). Often the canopy may have periodic gaps of different sizes. A snag component is evident.

The small mammal community density, species richness, and diversity are typically lower and composition somewhat different than in early seral stages (Tappe et al. 1994, Masters et al. 1998, 2002). Southern flying squirrels are considered to be a representative small mammal of mature mixed oak-pine forests (Taulman and Thill 1994) as are fox and gray squirrels, depending on the mix of oaks and other hard-mast producing hardwoods (Flyger and Gates 1982).

Ovenbird, scarlet tanagers, summer tanagers, great-crested flycatchers, Acadian flycatchers, tufted titmice, Carolina chickadees, Kentucky warblers, pine warblers, worm-eating warblers, yellow-billed cuckoos, northern cardinals, pileated woodpeckers, hairy woodpeckers, downy woodpeckers, chuck-will's widows, whip-poor-wills, wood thrushes, tufted titmice, Carolina wrens, broad-winged hawks, red-eyed vireos, and possibly yellow-throated vireos are characteristic species of late succession mixed hardwood-pine hardwood stands (Johnston and Odum 1956, Meyers and Johnson 1978, Wilson et al. 1995, Masters et al. 2002). However, many of these are also characteristic of mature hardwood stands (Meyers and Johnson 1978). There is a paucity of conifer-specialized bird species in the southern forests compared with northern forests (Johnston and Odum 1956).
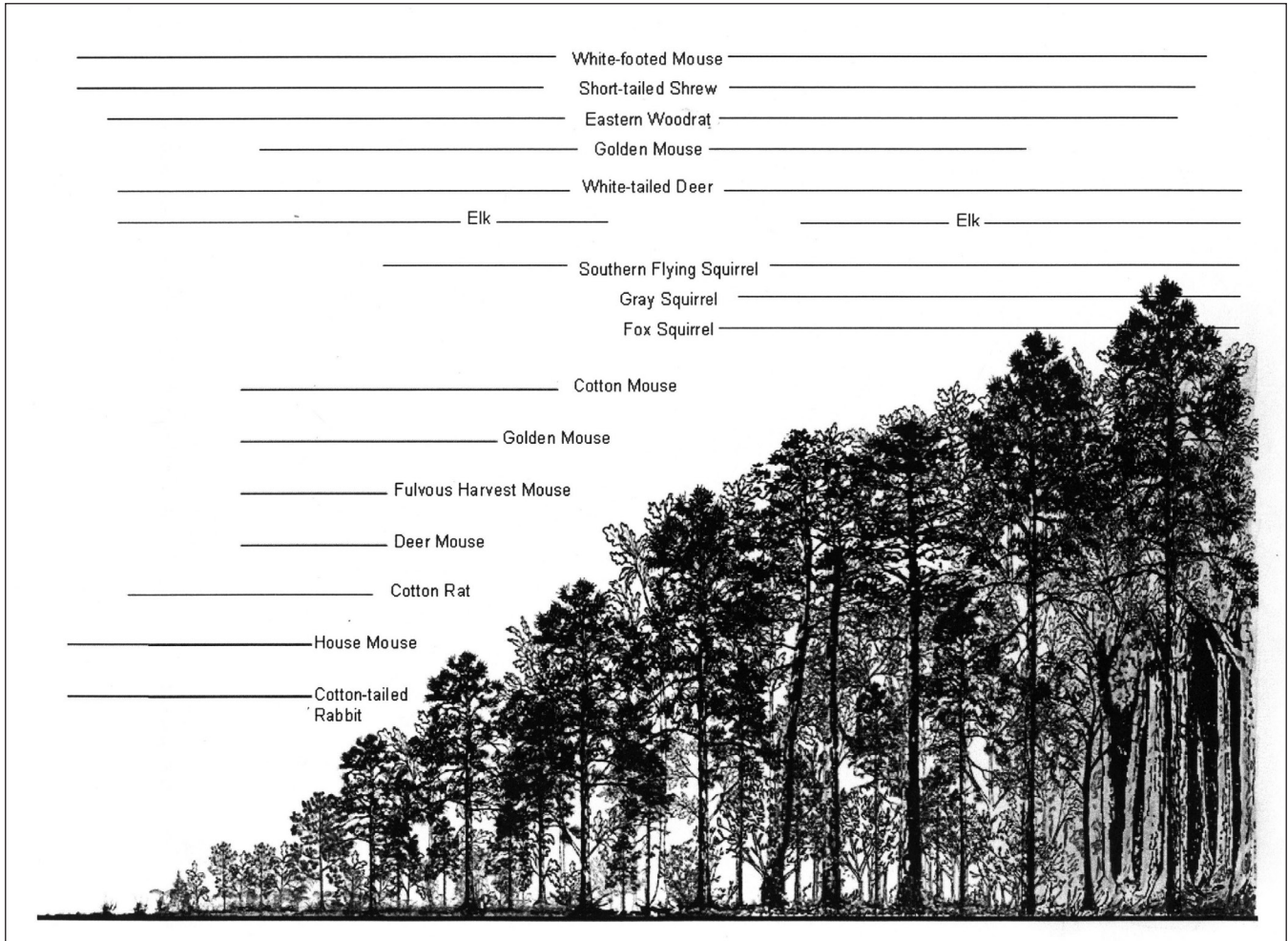
Fig. 2. Plant succession and mammal community succession model of occurrence of selected common species associated with different stages of succession within shortleaf pine-bluestem forests in the absence of fire. Horizontal lines indicate only the presence of the named species at a particular successional stage. Based on Atkeson and Johnson (1979), Tappe et al. (1994, 2004), and Masters et al. (1998, 2002).
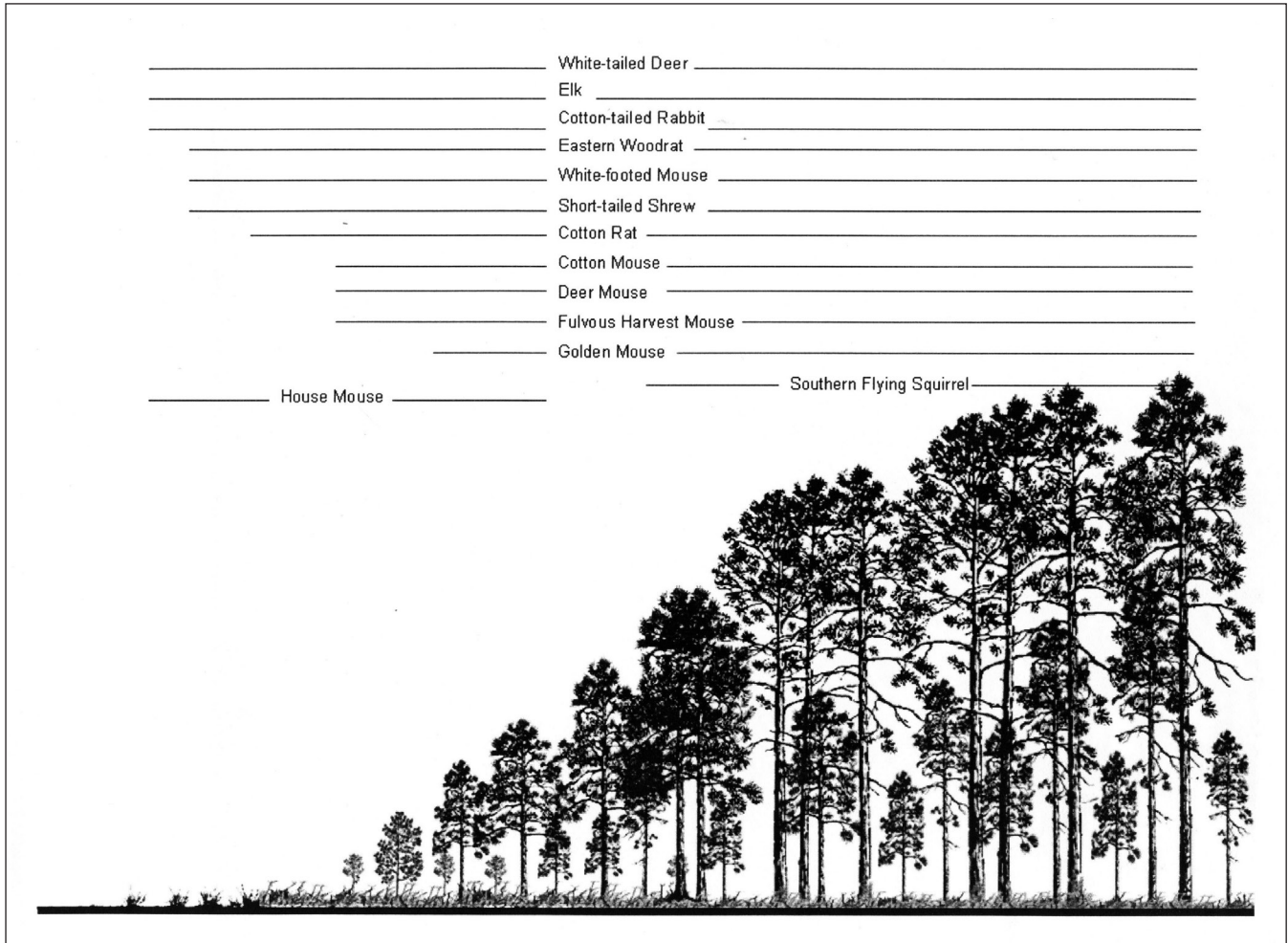
Fig. 3. Plant succession and mammal community succession model of selected common species occurrence associated with different stages of succession within shortleaf pine-bluestem forests with frequent fire of at least 1- 5-year intervals. Horizontal lines indicate only the presence of the named species at a particular successional stage. Based on Masters et al. (1998, 2002).
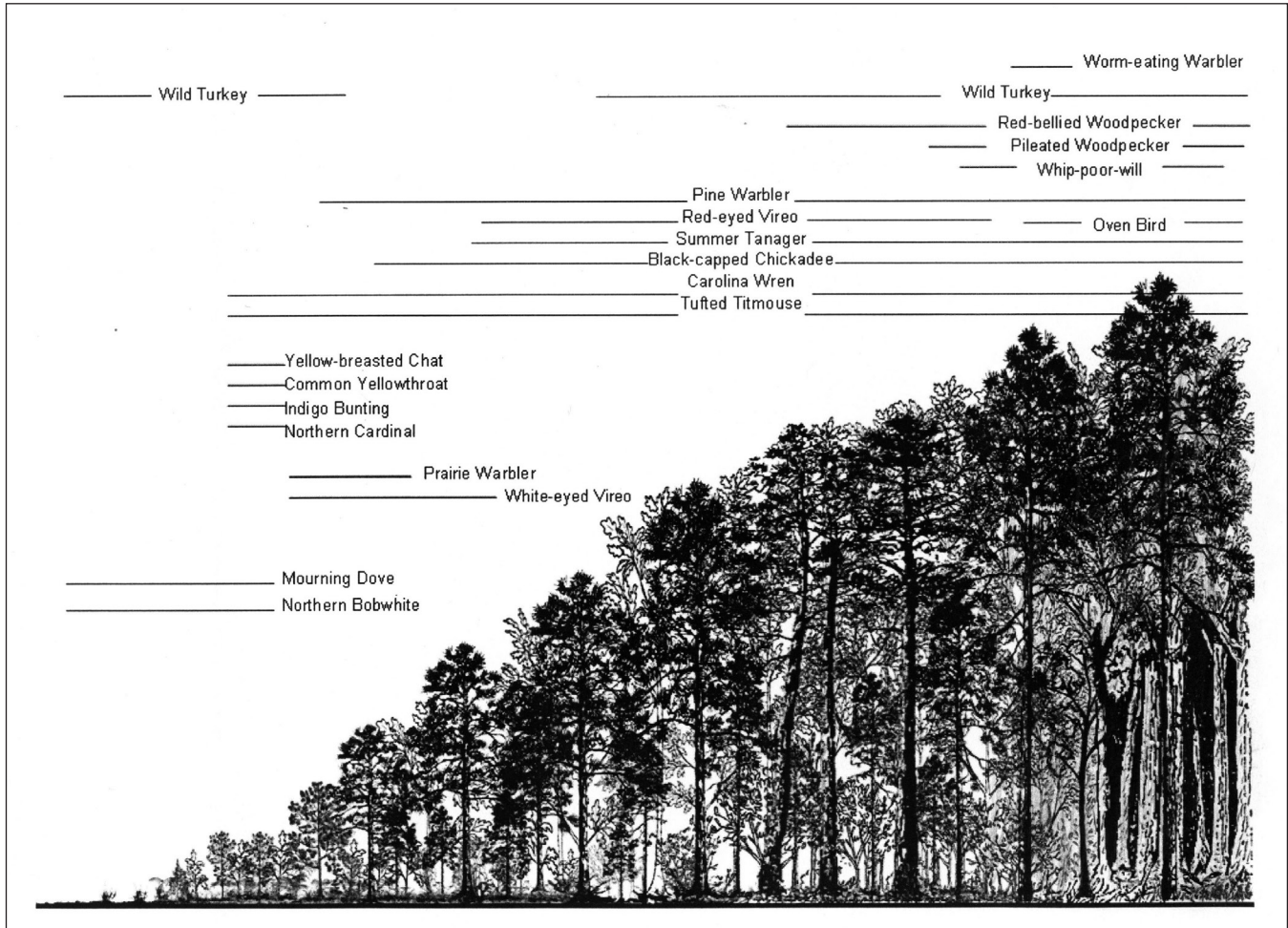
Fig. 4. Plant succession and breeding bird community succession model of selected common species occurrence associated with different stages of succession within shortleaf pine-bluestem forests in the absence of fire. Horizontal lines indicate only the presence of the named species at a particular successional stage. Based on Johnston and Odum (1956), Meyers and Johnson (1978), Engstrom et al. 1984, Wilson et al. (1995), Jennelle (2000), and Masters et al. (2002).
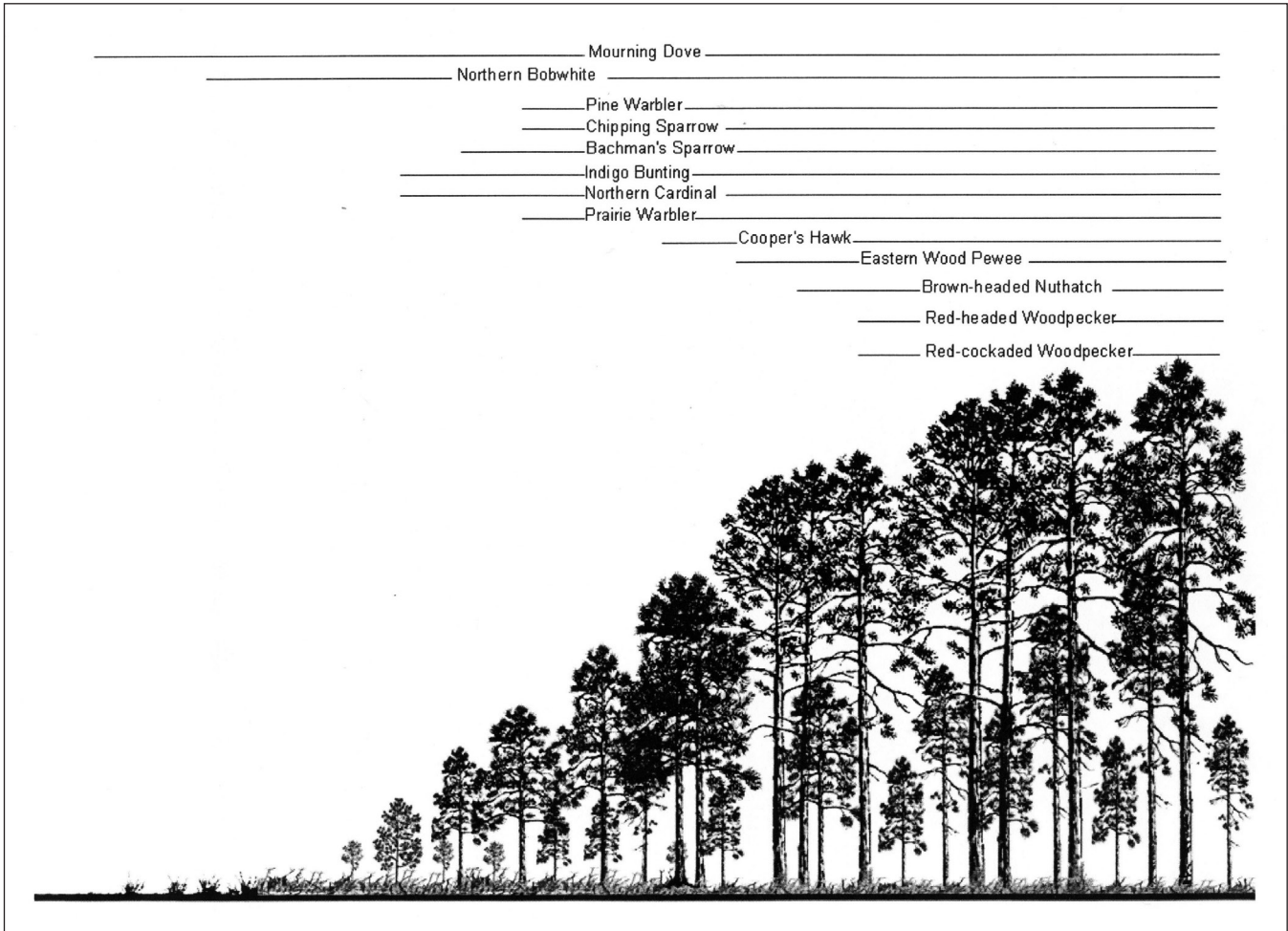
Fig. 5. Plant succession and breeding bird community succession model of selected common species occurrence associated with different stages of succession within shortleaf pine-bluestem forests with frequent fire of at least 1- to 5-year intervals. Most of the bird species from Fig. 4 will be found here as well if even 3.4 m2 of hardwood basal area per hectare is present in the stand. Horizontal lines indicate only the presence of the named species at a particular successional stage. Based on Wilson et al. (1995), Jennelle (2000), and Masters et al. (2002).

Appendix A.
List of Species Included in the Document

Common name	Scientific name
Plants	
Subalpine/Corkbark fir	*Abies lasioscarpa*
White fir	*A. concolor*
Big bluestem	*Andropogon gerardi*
Wiregrass	*Aristida spp.*
Low sagebrush	*Artemesia arbuscula*
Sand sagebrush	*A. filifolia*
Big sagebrush	*A. tridentata*
Mountain big sagebrush	*A. t. vaseyana*
Wyoming big sagebrush	*A. t. wyomingensis*
Buffalograss	*Bouteloua dactyloides*
Blue grama	*B. gracilis*
Cheatgrass	*Bromus tectorum*
Sedge	*Carex spp.*
Hickory	*Carya spp.*
Sweet fern	*Comptonia peregrina*
Inland saltgrass	*Distichlis spicata*
Willow-herb	*Epilobium angustifolium*
Lehmann lovegrass	*Eragrostis lehmanniana*
Rough fescue	*Festuca campestus*
Geranium	*Geranium bicknellii*
Sweetvetch	*Hedysarum* spp.
Juniper	*Juniperus* spp.
Larch	*Larix occidentalis*
Common reed	*Phragmites australis*
White spruce	*Picea glauca*
Engelmann spruce	*P. engelmanii*
Whitebark pine	*Pinus albicaulis*
Jack pine	*P. banksiana*
Lodgepole pine	*P. contorta*
Shortleaf pine	*P. echinata*
Slash pine	*P. elliottii*
Pinyon	*P. edulis*
Longleaf pine	*P. palustris*
Loblolly pine	*P. taeda*
Ponderosa pine	*P. ponderosa*
Southwestern white pine	*P. strobiformis*
Monterey pine	*P. radiata*
Knotweed	*Polygonum cilinode*
Trembling aspen	*Populus tremuloides*
Honey mesquite	*Prosopis glandulosa*
Douglas-fir	*Pseudotsuga menziesii*
Arizona white oak	*Quercus arizonica*
Gambel oak	*Q. gambelii*
Huckleberry	*Vaccinium* spp
Blackberry	*Rubus* spp.
Canada buffaloberry	*Sheperdia canadensis*
Smooth cordgrass	*Spartina alterniflora*
Salt meadow cordgrass	*S. patens*
Invertebrates	
Katydid	*Conocephalus* sp.
Periwinkle snail	*Littorarea irrorata*
Mountain pine beetle	*Dendroctonus ponderosae*
Reptiles	
Texas spotted whiptail	*Cnemidophorus gularis*
Six-lined racerunner	*C. sexlineatus*
Birds	
Least bittern	*Ixobrychus exilis*
Ross's goose	*Chen rossii*
American black duck	*Anas rubripes*
Northern goshawk	*Accipiter gentilis*
Cooper's hawk	*A. cooperii*
Broad-winged hawk	*Buteo platypterus*
Northern harrier	*Circus cyaneus*
American kestrel	*Falco sparverius*
Lesser prairie chickens	*Tympanuchus cupido*
Greater sage-grouse	*Centrocercus urophasianus*
Northern bobwhite	*Colinus virginianus*
Wild turkey	*Meleagris gallopavo*
Virginia rail	*Rallus limicola*
Black rail	*Laterallus jamaicensus*
Mountain plover	*Charadrius montanus*
Mourning dove	*Zenaida macroura*
Chuck-will's widow	*Antrostomus carolinensis*
Yellow-billed cuckoo	*Coccyzus americanus*
Burrowing owl	*Athene cumicularia*
Northern flicker	*Colaptes auratus*
Pileated woodpecker	*Hylatomus pileatus*

Red-bellied woodpecker	*Melanerpes carolinus*
Red-headed woodpecker	*M. erythrocephalus*
Hairy woodpecker	*Picoides villosus*
Downy woodpecker	*P. pubescens*
Red-cockaded woodpecker	*P. borealis*
Violet-green swallow	*Tachycineta thalassima*
Great-crested flycatcher	*Myiarchus crinitus*
Eastern wood-pewee	*Contopus virens*
Acadian flycatcher	*Empidonax virescens*
Olive-sided flycatcher	*Contopus cooperi*
Black-capped chickadee	*Poecile atricapillus*
Carolina chickadee	*P. carolinensis*
Mountain chickadee	*P. gambeli*
Tufted titmouse	*Baeolophus bicolor*
White-breasted nuthatch	*Sitta carolinensis*
Brown-headed nuthatch	*S. pusilla*
Pygmy nuthatch	*S. pygmaea*
Carolina wren	*Thryothorus ludovicianus*
Marsh wren	*Cistothorus palustris*
Sedge wren	*C. platensis*
American robin	*Turdus migratorius*
Wood thrush	*Hylocichla mustelina*
Eastern bluebird	*Sialia sialis*
Western bluebird	*S. mexicana*
Loggerhead shrike	*Lanius ludovicianus*
White-eyed vireo	*Vireo griseus*
Yellow-throated vireo	*V. flavifrons*
Red-eyed vireo	*V. olivaceus*
Worm-eating warbler	*Helmitheros vermivorum*
Pine warbler	*Setophaga pinus*
Kirtland's warbler	*S. kirtlandii*
Prairie warbler	*S. discolor*
Hooded warbler	*S. citrina*
Ovenbird	*Seiurus aurocapilla*
Kentucky warbler	*Geothlypis formosa*
Common yellowthroat	*G. trichas*
Yellow-breasted chat	*Icteria virens*
Eastern meadowlark	*Sturnella magna*
Scarlet tanager	*Piranga olivacea*
Summer tanager	*P. rubra*
Northern cardinal	*Cardinalis cardinalis*
Blue grosbeak	*Passerina caerulea*
Indigo bunting	*P. cyanea*
Grasshopper sparrow	*Ammodramus savannarum*
Seaside sparrow	*A. maritimus*
Cape Sable seaside sparrow	*A. m. mirabilis*
Louisiana seaside sparrow	*A. m. fisheri*
Northern seaside sparrow	*A. m. maritimus*
Nelson's sharp-tailed sparrow	*A. nelson*
Saltmarsh sharp-tailed sparrow	*A. cautacutus*
Bachman's sparrow	*Aimophila aestivalis*
Chipping sparrow	*Spizella passerina*
Field sparrow	*S. pusilla*
Swamp sparrow	*Melospiza georgiana*
Coastal Plain swamp sparrow	*M. g. nigrescens*
Eastern meadowlark	*Sturnella magna*
Red-winged blackbird	*Agelaius phoenecius*
Boat-tailed grackle	*Quiscalus major*

Mammals

Short-tailed shrew	*Blarina brevicauda*
Black bear	*Ursus americanus*
Grizzly bear	*U. horribilis*
Badger	*Taxidea taxus*
Coyote	*Canis latrans*
Gray wolf	*C. lupus*
Swift fox	*Vulpes velox*
Bobcat	*Felis rufus*
Canada lynx	*Lynx canadensis*
Cougar	*Puma concolor*
Black-tailed prairie dog	*Cynomys ludovicianus*
Thirteen-lined ground squirrel	*Spermophilus tridecemlineatus*
Golden-mantled ground squirrel	*S. lateralis*
White-tailed antelope ground squirrel	*Ammospermophilus leucurus*
Gray-collared chipmunk	*Tamias cinereicollis*
Eastern gray squirrel	*Sciurus carolinensis*
Fox squirrel	*S. niger*
Northern flying squirrel	*Glaucomys sabrinus*
Southern flying squirrel	*Glaucomys volans*
Bailey's pocket mouse	*Perognathus baileyi*
Hispid pocket mouse	*Chaetodipus hispidus*
Ord kangaroo rat	*Dipodomys ordi*
Merriam kangaroo rat	*D. merriami*
Western harvest mouse	*Reithrodontomys megalotis*
Fulvous harvest mouse	*R. fulvescens*
Deer mouse	*Peromyscus maniculatus*
White-footed mouse	*P. leucopus*
Cotton mouse	*P. gossypinus*
Pinyon mouse	*P. truei*
Golden mouse	*Ochrotomys nuttalli*
Northern grasshopper mouse	*O. leucogaster*
Southern grasshopper mouse	*O. torridus*
Eastern woodrat	*Neotoma floridana*
White-throated woodrat	*N. albigula*
Mexican woodrat	*N. mexicana*
Hispid cotton rat	*Sigmodon hispidus*

Southern red-backed vole	*Clethrionomys gapperi*
House mouse	*Mus musculus*
Meadow vole	*Microtus pennsylvanicus*
Snowshoe hare	*Lepus americanus*
Eastern cottontail	*Sylvilagus floridanus*
Nuttall's cottontail	*S. nuttallii*
Pygmy rabbit	*Brachylagus idahoensis*
Elk	*Cervus elaphus*
White-tailed deer	*Odocoileus virginianus*
Mule deer	*O. hemionus*
Moose	*Alces alces*
Pronghorn	*Antilocapra americanus*
Bison	*Bison bison*
Bighorn sheep	*Ovis canadensis*
Mountain caribou	*Rangifer tarandus caribou*