

THE ROLE OF FIRE IN STRUCTURING SAGEBRUSH HABITATS AND BIRD COMMUNITIES

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

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

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

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

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

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

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

In this review, we discuss the role of fire in influencing the composition and configuration of sagebrush systems and subsequent effects on birds living in these communities. We summarize information on the historical role of fire and the mechanisms by which land use and management practices have altered the fire regime. We then describe the effects of fire on bird communities caused by changes in the local vegetation and surrounding landscape. Because

more fire-related research has been conducted on Greater Sage-Grouse (*Centrocercus urophasianus*) than nongame species, we present findings separately. Finally, we identify the critical management needs and research issues.

HISTORICAL PATTERNS OF VEGETATION DYNAMICS AND BIRD COMMUNITIES

VEGETATION DYNAMICS

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

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

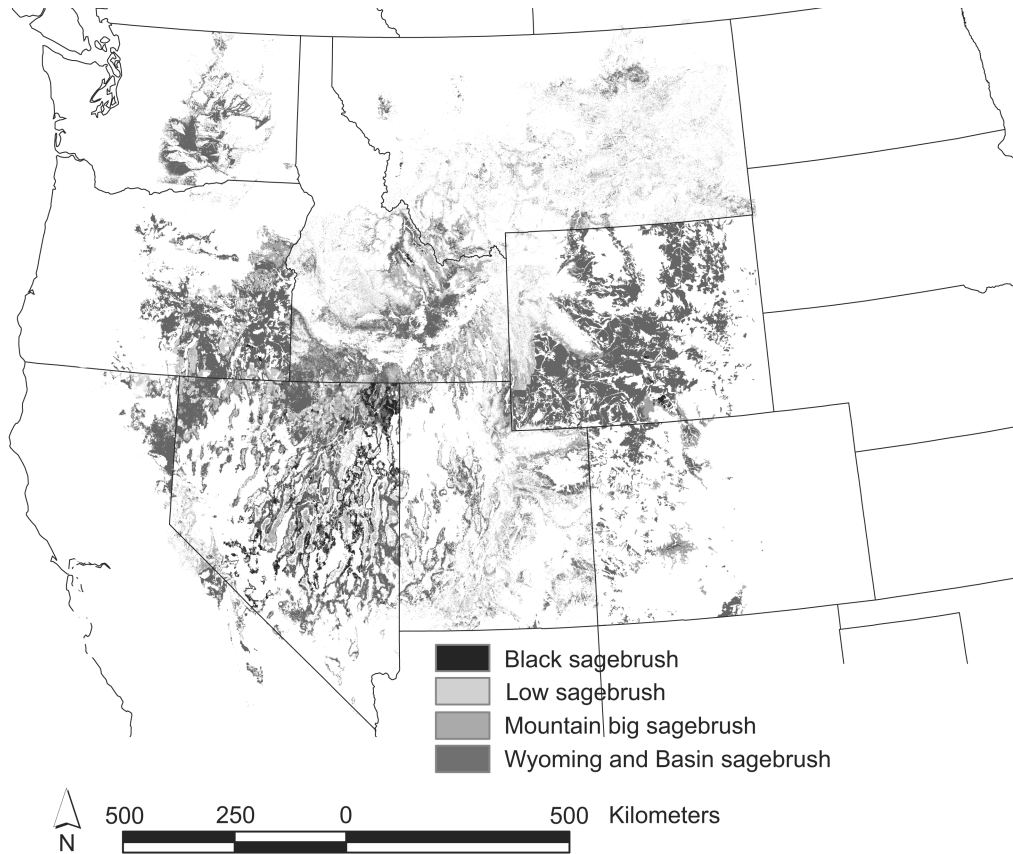


FIGURE 1. Sagebrush habitats cover approximately 43,000,000 ha in western North America. The map depicts the current distribution of the primary species of dwarf and tall sagebrush species (Comer *et al.* 2002). Sagebrush areas are not shown for states and provinces having limited geographic distribution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

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

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

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

BASIN BIG SAGEBRUSH

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

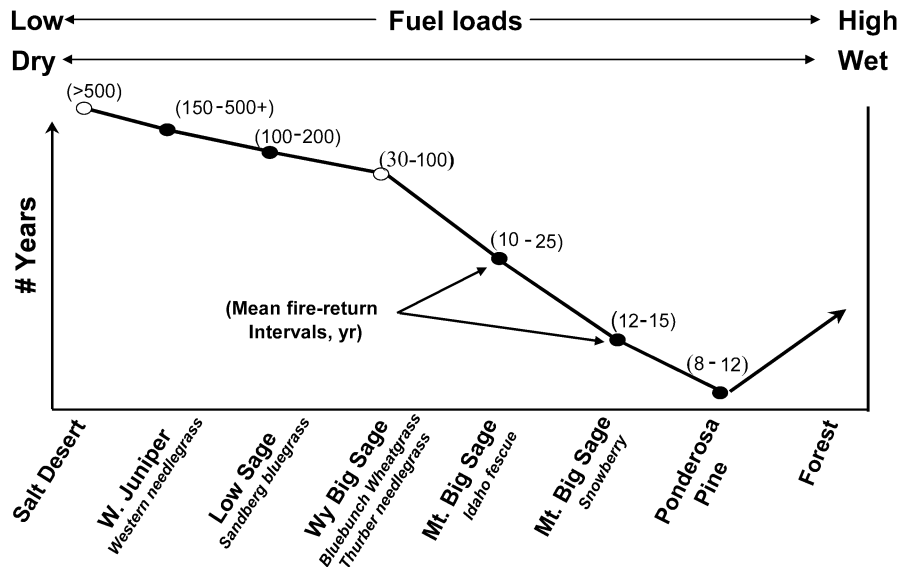


FIGURE 2. Presettlement mean fire-return intervals (MFRI) for salt desert, old growth western juniper-western needlegrass (*Stipa occidentalis*), low sagebrush (*Artemisia arbuscula* Nutt.)-Sandberg bluegrass (*Poa sandbergii* Vasey), Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Welsh.)-bluebunch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

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

WYOMING BIG SAGEBRUSH

Wyoming big sagebrush is widely distributed through the Intermountain (McArthur 1994). Wyoming big sagebrush grows in shallower soils and more xeric conditions (20–30 cm/yr annual precipitation) compared to basin big sagebrush. The average size of Wyoming big sagebrush is 45–100 cm (Winward and Tisdale 1977). Very little direct information exists to document pre-settlement fire regimes in regions dominated by Wyoming big sagebrush; estimated fire-return intervals range from 50 to >100 yr (Wright and Bailey 1982). Fire occurrence,

severity, size, and complexity were probably highly variable in space and time. Due to limited fuels, most fires in the pre-settlement landscape probably were patchy, uneven burns that left islands of sagebrush within the burn that provided seed sources to initiate recovery to a shrubland landscape. However, occasional fires with limited spatial complexity probably occurred under severe weather conditions and in years following above average moisture resulting in the build up of fine fuels.

MOUNTAIN BIG SAGEBRUSH

Mountain big sagebrush grows at higher elevations (usually >1600 m) than basin or Wyoming big sagebrush. Mountain big sagebrush communities generally are more resilient to disturbance and recovers more rapidly than either basin or Wyoming big sagebrush because of greater precipitation (>30 cm/yr) and possibly longer seed viability. Mountain big sagebrush sites also are less susceptible to invasion by alien weeds than the other subspecies of big sagebrush. Historical fire-return intervals are thought to be relatively frequent (10–25 yr) in the more productive communities (Miller and Rose 1999, Miller

et al. 2000). However, drier sites with reduced fuel loadings may have had less frequent returns with moderate severity fires occurring between 30–70 yr. The fire regime for mountain big sagebrush associations in arid locations on pumice influenced soils was characterized by infrequent but high severity, stand replacement fires that occurred only under severe weather conditions and may have been >150 yr (Miller and Tausch 2001).

DWARF SAGEBRUSH

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

Salt Desert Shrub

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

BIRD COMMUNITIES IN SAGEBRUSH ECOSYSTEMS

Bird species whose distribution is closely tied to sagebrush habitats during at least part of the year are considered sagebrush obligates (Braun *et al.* 1976, Paige and Ritter 1999). These include Greater Sagegrouse, Gunnison Sage-Grouse (*Centrocercus minimus*), Sage Thrasher (*Oreoscoptes montanus*), Sage Sparrow (*Amphispiza belli*), and Brewer's Sparrow (*Spizella breweri*) although these species also may use other shrubland habitats. Gray Flycatcher

(*Empidonax wrightii*) relies heavily, although not exclusively, on sagebrush habitats (Sterling 1999). The above species place their nests in or beneath big sagebrush shrubs and occur in a wide spectrum of structural conditions. Other widespread species that use sagebrush habitats include Lark Sparrow (*Chondestes grammacus*) and Black-throated Sparrow (*Amphispiza bilineata*). Green-tailed Towhee (*Pipilo chlorurus*) is common in mesic sagebrush communities and the Loggerhead Shrike (*Lanius ludovicianus*) occurs throughout most of the sagebrush biome, with the highest densities associated with the taller shrub communities (Yosef 1996). Species primarily associated with grasslands adjacent to sagebrush habitats include Burrowing Owl (*Athene cunicularia*), Western Meadowlark (*Sturnella neglecta*), Horned Lark (*Eremophila alpestris*), Vesper Sparrow (*Pooecetes gramineus*), Grasshopper Sparrow (*Ammodramus savannarum*), and Long-billed Curlew (*Numenius americanus*) (Knick and Rotenberry 2002). Grasshopper and Vesper sparrows are associated with perennial bunchgrass cover (Janes 1983, Vander Haegen *et al.* 2000). Long-billed Curlews (*Numenius americanus*) and Burrowing Owls (*Athene cunicularia*) are generally associated with shorter stature grasslands in open habitats (Green and Anthony 1989, Pampush and Anthony 1993).

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

Bird assemblages in presettlement sagebrush-dominated sites near the end of a fire cycle likely were dominated by the sagebrush obligate species. Grassland species, such as Vesper and Grasshopper sparrows (*Ammodramus savannarum*), Western Meadowlarks (*Sturnella neglecta*), and Horned Larks (*Eremophila alpestris*) would increase following a fire as a function of shrub removal. Songbird species obligate to sagebrush habitats may not respond immediately to landscapes in which <50% of original shrub canopy cover is reduced (Petersen and Best 1987). However, larger, high severity burns

like those in Wyoming big sagebrush-bunchgrass communities in which shrub removal is more complete likely resulted in reductions in these birds that use sagebrush, and even rendered blocks of habitat unsuitable for years until shrubs reestablished. In relatively mesic plant communities in the mountain big sagebrush cover type where mean fire-return intervals were <20 yr, burns also probably were spatially complex due to their low severity. Increased fire occurrence in this cover type usually resulted in more but smaller fires (Miller and Rose 1999).

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

DISRUPTIONS TO NATURAL FIRE REGIMES IN SAGEBRUSH COMMUNITIES

LIVESTOCK GRAZING

Livestock grazing over the past 140 yr is the single most important influence that has changed sagebrush habitats and influenced fire regimes throughout the Intermountain West (Robertson 1954, Bock et al. 1993, West and Young 2000). Livestock grazing can increase the frequency of fires by disturbing soils and reducing competition from native grasses to facilitate spread of the highly flammable cheatgrass (Shaw et al. 1999). In mesic sagebrush communities not favorable to cheatgrass, grazing by livestock on perennial grasses and forbs reduced the fine fuels available to spread fires across a landscape and increased the interval between fires (Miller and Rose 1999, Miller and Tausch 2001). Excessive grazing of herbaceous components in these systems increases shrub density and cover. In south central Oregon, the role of fire was greatly reduced after 1870, just after the introduction of large numbers of livestock, but 46 yr before organized fire suppression (Miller and Rose 1999). Active fire suppression (especially after the 1940s) and a reduction in human ignition furthered the reduction in fires (Miller and Rose 1999). Finally, management of sagebrush landscapes has been directed primarily toward increasing forage biomass and conditions for

livestock grazing. Prescribed fires have been used to eradicate sagebrush (Vale 1974, Braun et al. 1976) and large areas replanted to nonnative perennial grasses, such as crested wheatgrass (*Agropyron cristatum*) (Hull 1974, Evans and Young 1978, Young 1994). However, shrub eradication also may increase the susceptibility of the area to weed invasions and increased risk to subsequent fires.

ENCROACHMENT BY JUNIPER AND PINYON PINE WOODLANDS

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

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

NON-NATIVE PLANT INVASIONS

CHEATGRASS

The introduction of cheatgrass to the arid portions of the sagebrush biome has fundamentally and perhaps irreversibly altered the natural fire regime by increasing the frequency and severity of fires (West

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

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

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

OTHER NON-NATIVE PLANT INVADERS

We have focused on cheatgrass in this review because of its ability to change the form and function

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

USE OF PRESCRIBED FIRE IN SAGEBRUSH ECOSYSTEMS

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

Prescribed burning may reduce cheatgrass on a short-term basis but original densities can return within 2 yr from seeds remaining in the seed bank

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

THE EFFECT OF FIRE ON BIRDS IN SAGEBRUSH HABITATS

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

EFFECTS OF FIRE

Birds that use sagebrush as their primary habitat declined dramatically in landscapes where shrub removal was complete and at large scales (Bock and Bock 1987, Knick and Rotenberry 1995, Knick and Rotenberry 1999). Loggerhead Shrikes, which also rely on shrublands for nesting habitat, were reduced by approximately 50% following a large mosaic burn in a basin and Wyoming sagebrush community (Humble and Holmes, unpubl. data). Because extensive, high-severity fires are increasing in frequency in lower elevation xeric communities, substantial expanses of habitat unsuitable for shrub dependent

species are created until shrubs reinvade and establish appropriate cover. In unaltered systems this process can take decades (Hemstrom et al. 2002). When sagebrush re-establishment is precluded either by recurring wildfire or by lack of seed sources within the burned area, habitat loss for birds depending on sagebrush habitats may be permanent.

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

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

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

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

Only one study (Petersen and Best 1987) examined how fire influenced reproductive success of songbirds. Nestling growth or reproductive output for either Sage Sparrow or Brewer's Sparrow was unchanged in 3 yr following a fire that removed approximately 45% of the shrubs (Petersen and Best

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

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

TABLE 1. CONTINUED.

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

^a number of fires reported for each study = 1.

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

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

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

1987). The lack of measurable short-term responses in this and other studies of the effects of disturbance on shrubland birds may be in part attributable to time lags on individual and population responses stemming at least in part from site tenacity by breeding adults (Wiens *et al.* 1986, Knick and Rotenberry 2000).

EFFECTS OF FIRE SUPPRESSION

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

SAGE-GROUSE AND FIRE

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

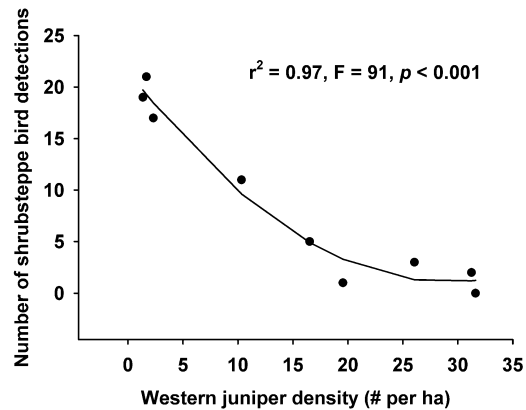


FIGURE 3. Abundance of ground and shrub nesting bird species in relation to density of western juniper trees >8 cm diameter at breast height in Lassen County, California 2002 (Point Reyes Bird Observatory, unpubl. data). Data points represent average values of four point count sampling stations within each study site. The abundance index is the mean number of detections per survey point within 100 m.

plant groups, and pattern and size of burn (Miller and Eddleman 2001).

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

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

Negative impacts from fire exist even in the more resilient mountain big sagebrush communities. For both nesting and brood rearing, Greater Sage-Grouse

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

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

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

avoided burns that were <20 yr old and lacked sagebrush cover (Byrne 2002). In landscapes with a short fire-return interval, unburned areas played an important role in population maintenance.

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

CRITICAL MANAGEMENT QUESTIONS AND RESEARCH ISSUES

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

Sagebrush is one of the few habitats in which

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

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

SUMMARY

Fire was a spatially and temporally complex disturbance in the sagebrush biome ranging from 10 to >200-yr return intervals with varying severities in communities dominated by sagebrush (*Artemisia* spp.) and may have been >500 yr in some salt-desert shrub communities. The frequency of fires that completely burn large areas has increased dramatically in some regions, particularly in Wyoming big sagebrush communities at low elevations containing a cheatgrass understory. In other regions, widespread reductions in fire frequency and extent followed the introduction of livestock to western rangelands and resulted in increased shrub cover, loss of herbaceous understory, and increasing rates of woodland encroachment. Populations of bird

species that use sagebrush as their primary habitat declined either from conversion of sagebrush landscapes to cheatgrass dominated grasslands or to increases in woodland cover. We expect that populations of grassland birds, including Long-billed Curlews, Horned Larks, and Burrowing Owls, will increase with greater proportions of grasslands in the landscape. Similarly, increases in pinyon and juniper should benefit populations of bird species associated woodlands.

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