

CHANGING FIRE REGIMES AND THE AVIFAUNA OF CALIFORNIA OAK WOODLANDS

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

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

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

Resumen. Alguna vez los incendios tanto naturales, como antropogénicos jugaron un importante papel en los bosques de encino de California. A pesar de que los incendios causados por relámpagos eran infrecuentes, los Indios de California utilizaban el fuego para modificar los bosques de encino por al menos 3,000 años. La elevada frecuencia y baja intensidad de incendios causó poca mortandad en encinos maduros, un renuevo bajo, pero continuo, vegetación secundaria abierta y un fino mosaico de parches de vegetación. Después del asentamiento de los Europeos a mediados de 1800s, quienes manejaban las tierras, quemaban para reducir la cobertura de arbustos y para incrementar el área de pastizales, así como la producción de forraje; eran comunes las superficies de incendios con un promedio de repetición de intervalos de 8–15 años. La supresión del fuego comenzó en 1940–1950, lo cual causó el incremento de combustible (tanto en superficie, como en copas), la invasión de vegetación forestal en la vegetación secundaria y un aumento en la densidad de árboles. En ausencia de demostraciones de los efectos del fuego en aves de bosques de encino, usamos cambios en la estructura de la vegetación, esperando lo que resulte del incendio, así como la supresión del mismo, para predecir la respuesta de las aves en bosques de encino a los incendios y a la supresión de estos, basados en habitats de anidamiento de 17 especies comunes reproductivas de aves de bosques de encino en el Rancho Experimental de San Joaquín, Condado de Madera, California. Nuestros resultados sugieren que las poblaciones de Tirano Pálido (*Tyrannus verticalis*), Azulejo Gorjiazul (*Sialia mexicana*), y Golondrina Cariblanca (*Tachycineta thalassina*), incrementarían en abundancia después de un incendio, dado que ellas constantemente anidan en habitats similares a aquellos esperados después de incendios frecuentes de baja intensidad. Las especies que se espera que respondan negativamente a los cambios resultantes de los incendios, difieren según las variables examinadas. Si el fuego produce un mosaico de parches de habitat, en lugar de un paisaje homogéneo,

esperamos que las necesidades de la mayoría de las especies del habitat que difiere serán proveídas. Así como con en el fuego, el cambio más obvio que resulta de la exclusión del ganado, es un incremento en la cobertura de arbustos. La pregunta surge naturalmente; hasta qué punto el pastoreo crea un habitat similar a aquel creado por el fuego históricamente? Pero esta pregunta permanece aún sin estudiar. Se requiere mayor investigación en la historia de los incendios, para entender regimenes pasados de incendios en bosques de encino y los efectos de estos (incluyendo quemas prescritas) en la vegetación y en las comunidades de aves. Nosotros animamos a otros a comprobar nuestra hipótesis, tomando en cuenta las respuestas de las aves a las variables que se espera sean alteradas por el fuego: cobertura arbustiva, densidad de árboles y número de tocones, muestreos y trozas. Finalmente, necesitamos comprobar la hipótesis con la cual trabajamos: un mosaico de parches de un habitat proveerá las condiciones que requiere el habitat para sustentar una alta diversidad de aves, característico de bosques de encino.

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

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

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

Here we review existing information on how fire as a disturbance regime has changed in California's oak woodlands, and how the various fire regimes and changes to them have affected the vegetation. We discuss existing information on historic burning by California Indians and the resulting effects on oak woodlands. Although prehistoric fire regimes are difficult to reconstruct and disagreement on the

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

CALIFORNIA OAK WOODLANDS

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

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

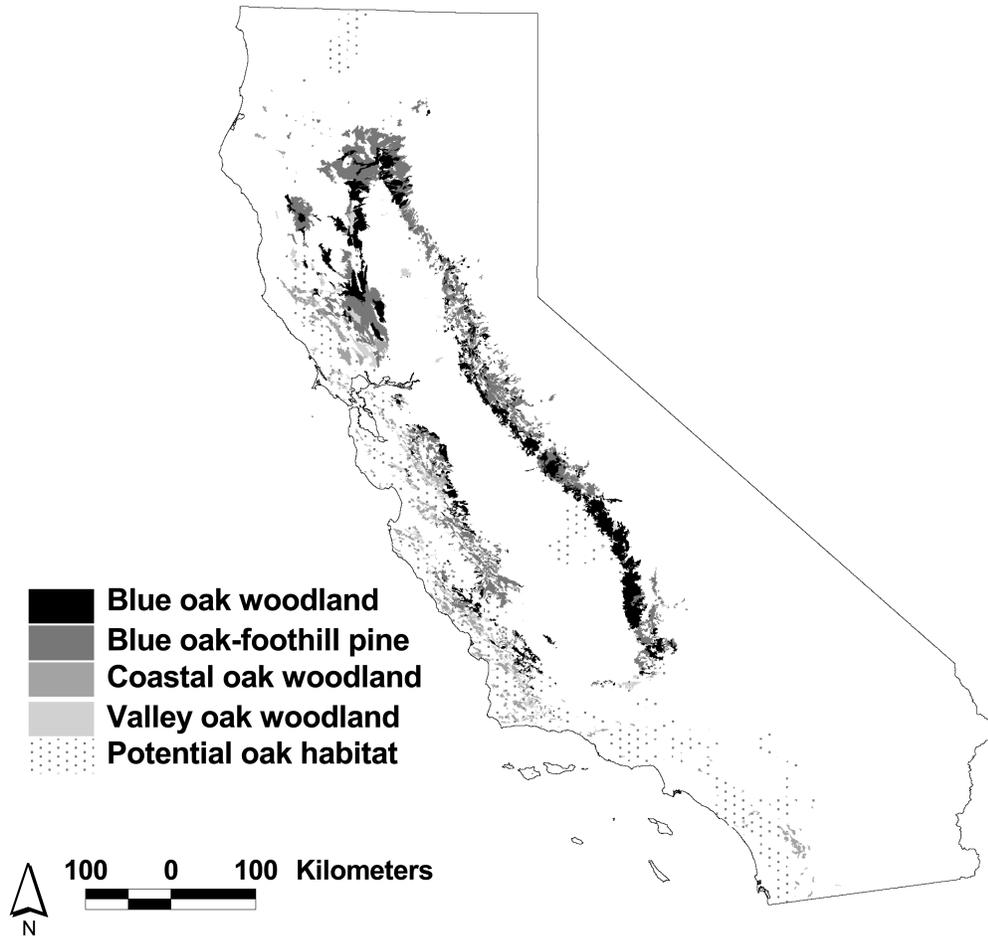


FIGURE 1. Approximate current coverage of valley and foothill oak woodland habitats throughout California based on the California GAP Analysis Project (Davis et al. 1998) and potential coverage based on Kuchler (1976) (adapted from California Partners in Flight 2002).

eastern foothills of the Coast Ranges. They range from open woodlands of scattered trees to stands with nearly closed canopies (Ritter 1988a). Blue oak is the dominant tree species, and the understory consists of annual grasses and forbs. Blue oak-foothill pine woodlands are more diverse both structurally and floristically (Verner 1988). Blue oaks and foothill pines dominate the canopy, with interior live oak (*Quercus wislizenii*), coast live oak, and valley oak often appearing as associated species. The understory may include patches of scattered shrubs in addition to annual grasses and forbs. This habitat is nearly continuous in the western foothills of the Sierra Nevada and discontinuous in the Coast Range west of the Central Valley and the Transverse Range of southern California. Coastal oak wood-

lands occur in coastal foothills and valleys and are variable in terms of species composition in both overstory and understory (Holland 1988). Oregon white oak (*Quercus garryana*) is common in the North Coast Range to Sonoma County, while coast live oak dominates to the south. Additional tree species occur in both more mesic and drier sites, and the understory may consist of annual grasses with scattered shrubs in open stands, dense shrubs, or a lush cover of shade-tolerant plants in closed stands. Valley oak woodlands occur in remnant patches in the Central Valley, the Sierra Nevada foothills, the Tehachapi Mountains, and valleys of the Coast Ranges (Ritter 1988b). They are dominated by valley oaks, with denser stands occurring in deep soils along river margins.

FIRE HISTORY OF CALIFORNIA OAK WOODLANDS

BURNING BY CALIFORNIA INDIANS

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

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

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

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

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

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

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

EFFECTS OF BURNING BY CALIFORNIA INDIANS

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

Due to the high frequency of burning, fires were of low intensity with little mortality of mature trees. Grass fires reduced encroachment by shrubs and conifers, which can act as fuel ladders to oak trees, and protected the oaks. Jepson (1910:11) suggested the open stands of valley oak and interior live oak he saw were the results of annual burning by California Indians. Those low-intensity frequent fires are often invoked as maintaining the open structure of pre-settlement valley oak woodlands (Jepson 1923:167). At Big Oak Flat in the Sierra Nevada foothills, Paden and Schlichtmann (1959:121) described the results of frequent burning by the Miwoks on the vegetation structure. The California Indians took an active role

in manipulating the vegetation, and following the reduction in burning by California Indians, vegetation structure changed and the understory became more dense (Steward 1935:40–41 in Anderson 1993). The extent of burning in the foothills of the southern Sierra Nevada is discussed by a Chukchansi informant in Gayton (1948:176).

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

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

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

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

EURO-AMERICAN BURNING

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

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

EFFECTS OF EURO-AMERICAN BURNING

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

While recruitment of oaks appears to have been slow and steady during the California Indian occupation of the oak woodlands, high rates of regeneration and recruitment occurred in some areas in the mid-1800s, coincident with European settlement in the region (Mensing 1992). Pulses of blue oak regeneration may have resulted from sprouting of top-killed saplings and trees. Swiecki and Bernhardt (1998),

however, believe they resulted from the release of understory seedlings, caused by cutting and burning of the overstory between the 1850s and the first decades of the twentieth century. Because Euro-American settlers burned concurrently with clearing for agriculture, fuel wood, mining, and range improvement, it is difficult to decouple the effects of fire and clearing on overall tree density. Where blue oak woodlands were entirely cleared followed by repeated disturbance, conversion to annual grassland was essentially permanent and the extent of oak woodlands was reduced (Swiecki and Bernhardt 1998). Where blue oaks persisted due to sprouting and release of understory seedlings, they clearly rebounded and the overall change was an initial decrease in oak density and canopy cover followed by even-aged stands of oaks (Holzman and Allen-Diaz 1991, Swiecki and Bernhardt 1998).

FIRE SUPPRESSION

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

PRESCRIBED BURNING

Although interest in prescribed burning has increased recently due to concerns about fuel accumulation, many oak woodlands in California were burned by ranchers beginning in the late 1800s up to the 1950s (Biswell 1989, Stephens 1997). Depending on the prescription, the effects of prescribed fire may be similar in many ways to those of California Indian fires. Prescribed fire can kill or thin woody vegetation (Vreeland and Tietje 1998). Lawrence (1966) found that prescribed fire significantly reduced shrub cover with a corresponding increase in grasses and forbs, and did little damage to trees, although foothill pines were largely eliminated. Fry (2002) found low tree mortality following low-intensity, prescribed fires, and little change in overall stand structure in an area

with a relatively dense pre-fire canopy cover of 50% and negligible shrub cover. The species assemblage at this site varied from nearly pure stands of California black oak (*Quercus kelloggii*), blue oak, and valley oak to stands of mixed codominance. At the same site, M. Homrighausen (unpubl. data) found a substantial increase in bare ground and cover of native forbs immediately following the fire.

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

GENERAL EFFECTS OF FREQUENT, LOW-INTENSITY FIRE

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

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

Foothill pines are susceptible to damage by fire due to their thin bark, high resin content, and the

presence of congealed resins from wounds (Lawrence 1966, Powers 1990). Foothill pines increased in an area ungrazed since 1934 and unburned since 1929 at the San Joaquin Experimental Range (Woolfolk and Reppert 1963).

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

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

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

EFFECTS OF FIRE ON THE LANDSCAPE

At the landscape scale, we expect frequent, low-intensity fire to create a complex mosaic of habitats, resulting in an overall structure of irregular patches and abundant edges. The fine-grained mosaics we expect resulted from high-frequency, low-intensity

fires such as those ignited by California Indians differ from fragmentation of oak woodland habitat resulting from other types of disturbance.

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

RESPONSE OF THE BIRD COMMUNITY

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

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

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

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

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

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

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

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

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

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

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

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

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

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

PREDICTING BIRD RESPONSES FROM HABITAT DATA

Knowledge of habitat relations of oak woodland birds should enable the prediction of responses of birds to fire by examining the expected changes in vegetation structure (Rotenberry et al. 1995). At the San Joaquin Experimental Range (37°06'N, 119°44'W) in the western foothills of the Sierra

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

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

Starling (*Sturnus vulgaris*), followed closely by the House Finch (Table 2).

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

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

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

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

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

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

^c Percent cover of all shrubs combined.

^d Basal area of live trees (m²/ha) around the nest.

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

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

^g Percent cover of logs (\geq 5 cm dia).

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

GRAZING AND FIRE

Grazing has often been considered helpful, and even necessary, to reducing the risk of wildfire. Because an increase in shrub understory has been the primary response to reduced fire frequency in California oak woodlands and our own work has

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

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

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

CONCLUSION

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

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

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

To conserve avian diversity, we need to monitor bird population trends in oak woodlands and to understand the conditions needed to maintain healthy populations. With so little work done on fire's effects on birds in oak woodlands, we need tests of our hypotheses on species' response to decreased shrub cover, lowered tree density, and decreased numbers of snags, saplings, and logs following fire. Other

unstudied questions relate to response to increased surface water following fire, and responses of seed-eating, ground-foraging birds to fire, including the duration of the response. Finally, we need to test our working hypothesis that a mosaic of habitat patches will provide the habitat conditions needed to sustain high avian diversity in oak woodlands. This information is crucial to our understanding of avian diversity and habitat relations in oak woodlands, and answers to these questions will be useful to landowners and land managers and planners.

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