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Effects of Fire and Restoration on Habitats and Populations of Western Hummingbirds: A Literature Review

John D. Alexander, Elizabeth J. Williams, Caitlyn R. Gillespie, Sarahy Contreras-Martínez, and Deborah M. Finch

Abstract

To inform future restoration efforts, we reviewed the known effects of fire and habitat management and restoration on hummingbirds in four key habitat types in North America. We examined seven species that most commonly occur west of the Rocky Mountains: Rufous (*Selasphorus rufus*), Calliope (*Selasphorus calliope*), Broad-tailed (*Selasphorus platycercus*), Costa's (*Calypte costae*), Black-chinned (*Archilochus alexandri*), Anna's (*Calypte anna*), and Allen's (*Selasphorus sasin*). Our review found that most western hummingbird species respond positively to wild or prescribed fire in forested and chaparral habitats of the western United States, although some hummingbird occurrence declines following fire, possibly due to the loss of preferred nesting habitat in mature forests. Restoration practices that eradicate exotic plants, encourage the regeneration of native shrubs and flowering plants (especially understory vegetation), and promote early and mid-successional habitats connected with native stand trees will benefit hummingbirds by providing foraging habitat in migration and on breeding grounds. Restoration practices that encourage the regeneration of native shrubs, understory vegetation, and native epiphytes, while maintaining forest canopy, can also benefit hummingbirds. We also identify many critical research questions and needs which, if addressed, would improve the quantification of pre- and postfire and habitat management impacts on hummingbirds, especially Allen's and Rufous populations, which are experiencing steep population declines.

Cover:
Photo 1. Broad-tailed hummingbird (*Selasphorus platycercus*) pollinates a variety of flowering plants in different seasons (Calder et al. 2013). Photo by Mark Chappell.
Photo 2 inset. Wholeleaf Indian Paintbrush (*Castilleja integra*) in Arizona is frequently pollinated by the Black-chinned Hummingbird (*Archilochus alexandri*) (Brown and Kodric-Brown 1979). Photo by Robert Sivinski.

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Introduction and Scope

Hummingbirds are one of the most diverse families of birds in the world, with 338 recorded species (McGuire et al. 2014). They are exclusive to the western hemisphere, with the highest diversity of species occurring in the tropics (Greenewalt 1960). Although hummingbirds breed as far north as Canada and Alaska, their highest diversity in the United States occurs in the pine-oak woodlands of southeastern Arizona (Wethington and Finley 2009). Hummingbirds use a variety of habitats throughout their range, including second-growth forests, alpine meadows, desert habitats, and riparian woodlands. They have been found at elevations from 0 to 4,800 m (15,748 ft) (Stolz et al. 1996). Hummingbirds are specialized nectar feeders and play an important ecological role in plant pollination (Brown and Bowers 1985; Gegear and Burns 2007; Stiles 1981; Temeles and Kress 2003).

Due to a number of factors, including their small size, limited energy reserves, rapid movements, high-pitched vocalizations, timing of migration, and polygynous mating systems, it is thought that hummingbirds cannot be monitored as easily as many other landbirds (Wethington and Finley 2009). Because of this, population data are limited to results from North American Breeding Bird Surveys, and relatively little is known about the basic biology and life history of many hummingbirds. Nests have not been described for over 60 percent of the 48 known vulnerable, threatened, or endangered hummingbird species on the International Union for the Conservation of Nature's Red List (Wethington and Finley 2009).

Available data suggest declines in many species of hummingbirds, although the causes of these declines are unknown. In 2009, 48 of the 338 known species of hummingbirds, or over 14 percent of the hummingbird family, were listed as vulnerable, threatened, or endangered. Twenty-three species were listed as critically endangered or endangered on the International Union for the Conservation of Nature's Red List, and an additional 25 species are listed as near threatened or vulnerable (Wethington and Finley 2009). As of 2019, 60 of 367 Trochilidae species are listed as either vulnerable, near threatened, or endangered (Schumann et al. 1999). Partners in Flight (PIF) has identified Rufous Hummingbird (*Selasphorus rufus*) and Allen's Hummingbird (*Selasphorus sasin*) as Watch List species of continental concern (Rosenberg et al. 2016). Watchlist species are of concern due to small populations, declining population trends, narrow distribution, high threats, restricted distributions, or some combination of these (Rich et al. 2004).

In order to advance hummingbird conservation, it is important to identify key information gaps related to hummingbird biology, movements, and habitat relationships. All species in the western United States (genera *Archilochus, Calypte,* and *Selasphorus*) migrate long distances annually between temperate and tropical regions, facing thermogenic demand. Five are endemic to the western North America area (*Archilochus alexandri, Calypte costae, Selasphorus rufus, Selasphorus sasin,* and *Selasphorus calliope*). In 2002, the Hummingbird Monitoring Network was developed to inform hummingbird management and conservation. In 2009, a group of scientists, land managers, and conservation professionals convened for the first major meeting of the Western Hummingbird Partnership (WHP), a multi-party network with the goal to advance hummingbird conservation through "science-based monitoring, research, habitat restoration/enhancement, and education/outreach efforts," with an initial focus on western North America (Wethington et al. 2010).

The WHP identified the study of fire and restoration effects on populations of humming-birds as a key priority (Wethington et al. 2010). While a number of studies have addressed avian responses to fire, fuel reduction, thinning, and other restoration practices (e.g., Bock and Block 2005; Huff et al. 2005; Kotliar et al. 2002; Saab and Powell 2005; Saab et al. 2005; Saab et al. 2007), virtually none have focused on hummingbirds. There is concern that changes in forest or plant community structure as a result of wildfire, prescribed fire, or other restoration practices will alter habitats and change the availability of nectar resources, thus impacting hummingbird populations (Contreras-Martínez 2015). In turn, as hummingbirds are important pollinators in western ecosystems, impacts that result in changes in their abundance and distribution are likely to affect hummingbird-pollinated plants, many of which are endemic or endangered.

The WHP also identified global climate change, invasive species, and habitat loss as significant threats to hummingbird populations (Wethington et al. 2010). Because humming-birds are specialized nectar feeders, they are likely to be particularly vulnerable to effects of climate change that cause shifts in plant communities or floral phenology (Croonquist and Brooks 1991). Some species, like Anna's Hummingbird (*Calypte anna*), have demonstrated an ability to quickly adapt to human development and food sources, while other species, like Allen's and Costa's Hummingbird, are more restricted in their movements and habitats. Some hummingbird species may persist in the face of climate change while others with more sensitive habitat or food requirements will decline in population size or occurrence and possibly face extirpation. In order to slow or prevent these declines, it is critical to understand the limiting factors on hummingbird populations and the potential impacts, both positive and negative, of climate change.

In order to reduce fuel loads and fire risk, and to increase the resiliency of forest and aridland habitats to potential climate change impacts, land managers across the western United States are initiating a variety of restoration projects. For example, the USDA Forest Service is currently initiating a series of adaptive restoration projects on National Forest lands through the Collaborative Landscape Restoration Program (USDA Forest Service 2012). In an effort to inform these restoration efforts, and to address information gaps in our understanding of hummingbirds, this review presents the results of studies examining the known or potential impacts of fire and restoration on hummingbirds that breed primarily in the western United States.

This review first provides an overview of the region of interest, and of general hummingbird biology and habitat relationships, before describing the range, habitat relationships, key plant species, and conservation status of the seven hummingbird focus species. It then provides a summary, organized by geographical region, of literature related to fire, restoration, and hummingbirds, along with preliminary management implications. Where appropriate, relevant inferences are drawn from studies of fire and avian ecology, fire effects on vegetation, or climate change effects on vegetation. These sections are followed by a discussion and a summary of research, inventory, and monitoring priorities for western hummingbirds.

It is important to note that the results presented in this review of fire, restoration effects, and avian ecology studies are not comprehensive. Instead, this review is focused on results that include detections of western hummingbirds or results that can potentially inform an understanding of hummingbirds' responses to fire, restoration, and climate change. For a more complete treatment of the fire and avian ecology literature, consult reviews such as Bock

and Block (2005); Huff et al. (2005); Kotliar et al. (2002); Saab and Powell (2005); Saab et al. (2005); and Saab et al. (2007). Or, refer to the sources cited within this review.

Region of Interest

The region of interest is the western United States, with the following States considered: Washington, Oregon, California, Idaho, Montana, Wyoming, Arizona, Colorado, New México, Utah, and Nevada. In order to organize relevant findings and facilitate their integration into North American Bird Conservation Initiative (NABCI) and other bird conservation planning contexts, we utilized Bird Conservation Regions (BCRs). BCRs were developed by NABCI to facilitate bird conservation planning throughout North America (Rich et al. 2004). They are large, ecologically distinct units that share relatively homogenous bird communities, habitats, and resource management issues (fig. 1). Within the region and States of interest, the following nine BCRs were identified:

BCR 5: Northern Pacific Rainforest
BCR 9: Great Basin
BCR 10: Northern Rockies
BCR 15: Sierra Nevada
BCR 16: Southern Rockies/Colorado Plateau
BCR 32: Coastal California
BCR 33: Sonoran and Mojave Deserts
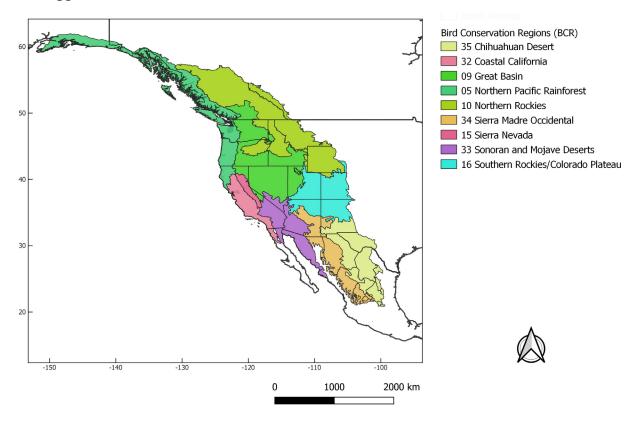BCR 34: Sierra Madre Occidental
BCR 35: Chihuahuan Desert

Figure 1. Bird Conservation Regions of North America included in this review.

The "Fire, Restoration, and Hummingbirds" section below provides an overview of the habitats, historic fire regimes, and priority management issues for each of the nine BCRs.

In compiling results from the literature, it became clear that some BCRs are well represented in the fire and restoration literature, while others have received little to no study. In order to aggregate information in a regional context as well as provide a broad organizational framework for the review, we grouped the BCRs of interest into four geographical regions as follows:

Southwestern Desert and Riparian (BCRs 33, 34, and 35)
Coastal California/Sierra Nevada/Great Basin (BCRs 9, 15, 32)
Pacific Northwest/Northern Rockies (BCRs 5, 10)
Southern Rockies (BCR 16)

These regions broadly correspond to the core breeding ranges of each of the seven focus species for this review.

Hummingbird Biology and Habitat Relationships

All North American hummingbirds belong to the subfamily *Trochilinae* and the order *Apodiformes*. The hummingbird order has many genera, most of which contain only a few species. Hummingbird hybridization is relatively common (Banks and Johnson 1961). Hummingbirds have a number of unique adaptations that set them apart from other birds. They are the smallest birds, with weights of North American species ranging from 2.5 to about 5.0 g (Calder and Calder 1994; Russell 1996). They have long, slender bills and are adapted primarily to feeding on nectar from flowers, but they will also feed on a variety of small insects. The figure-eight motion of their wings allows them to hover while feeding as well as to fly up, down, sideways, and even upside down for brief periods (Elphick et al. 2001). Hummingbirds have the ability to lower their body temperature to 13 °C (55 °F) to conserve energy (Hiebert 1990).

Hummingbirds play an important role in plant pollination and are thought to have played a role in the speciation of several plants (Grant and Grant 1966). Hummingbird and plant co-evolution is especially notable in the tropics (Wolf et al. 1976). Although they are often associated with red, tubular flowers, hummingbirds will feed on a variety of flower shapes and colors (Grant 1966). Being highly mobile, hummingbirds can quickly exploit new food sources, and most species feed from a variety of flower species (Feinsinger 1978; Snow and Snow 1972; Wolf 1970; Wolf et al. 1976). Hummingbirds are known to visit flowers in a predictable sequence called "traplining" and some defend territories of food resources. In a study in Arizona, Brown and Kodric-Brown (1979) found that hummingbirds were not selective in the flowers they visited, and that some individuals carried four or more types of pollen. The flowers in this study were all convergent in flower size, shape, and color.

Hummingbird movements and the timing of hummingbird migration are not well under-stood but are thought to relate to flowering plant phenology (Baltosser 1989). As described in the species descriptions, the Rufous, Allen's, and Calliope Hummingbird, all of which breed in latitudes north of Arizona, are thought to migrate following an elliptical route, flying south along the Rocky Mountain flyway postbreeding and north in the spring farther west and at lower elevations (Calder 1993; Calder and Calder 1994; Phillips 1975). Other species, such as

the Black-chinned (*Archilochus alexandri*) and Broad-tailed Hummingbird, migrate through Arizona in the fall but their timing and routes are poorly understood (Baltosser and Russell 2000; Calder and Calder 1992).

Migration is also thought to vary with the age and sex of individuals. Adult male Rufous Hummingbirds typically migrate before adult females, and in the fall, females precede the juveniles (Calder 1993; Phillips 1975). Male Black-chinned and Costa's Hummingbirds precede females but the young migrate at approximately the same time as females (Baltosser and Russell 2000; Baltosser and Scott 1996). Citizen-science data from eBird has revealed evidence of seasonal geographic variation in migratory routes for Rufous, Black-chinned, Calliope, and Broad-tailed Hummingbirds, although more research is needed to understand how hummingbird species respond to environmental change and conditions en route (Supp et al. 2015).

Hummingbirds are territorial and will actively defend their feeding and nest sites against conspecifics and potential predators. They usually do so through performing an elaborate dive display which is repeated several times. Males warn off intruders with a variety of tactics including vocalizations, flashing of the gorget and/or the crown feathers, or even a physical assault punctuated with diving displays (Elphick et al. 2001). Both male and female hummingbirds establish territories, usually in different locations. Hummingbirds do not maintain pair bonds, and males will try to mate with as many females as possible. It is thought that males set up territories in relation to food supplies, although other factors may influence territory selection, such as proximity to females' nest sites or open views of the surrounding area (Armstrong 1987; Pitelka 1942; Powers 1987).

Female hummingbirds build an open cup-shaped nest on a branch or other supporting structure. They typically nest in the canopy or sub-canopy, less than 15 m above the ground (Saab and Powell 2005). They construct their nest out of soft, silky materials like spider webs, caterpillar silk, feathers, down, bark, or lichen. Predation is a major cause of nest failure for many hummingbirds (Baltosser 1986). Greeney and Wethington (2009), however, found that nests within 300 m of active accipiter nests had significantly higher probabilities of successfully fledging young. It is thought that the presence of accipiters kept away potential hummingbird nest predators like jays.

Species of Interest

It is outside of the scope of this review to consider all of the hummingbird species that occur within the region of interest. Instead, we chose to focus on those species that have much of their global distribution in the western United States. In managing habitats for these species, other hummingbird species that occur in the same habitats should benefit. In order to determine the focus species, the Partners in Flight (PIF) Landbird Population Estimates Database was queried to determine the percent of global distribution and estimated population of western hummingbirds within the States and BCRs of interest (Blancher et al. 2007). The following seven species were identified as having 40 percent or more of their global distribution in the region of interest:

Allen's Hummingbird
Anna's Hummingbird
Black-chinned Hummingbird
Broad-tailed Hummingbird

Calliope Hummingbird
Costa's Hummingbird
Rufous Hummingbird

In this section, we briefly describe the range, movements, habitat relationships, key plant species, and conservation status of the seven focus species.

Anna's Hummingbird (*Calypte anna*)

The Anna's Hummingbird (fig. 2) breeds from southern British Columbia to the Baja Peninsula of California (Russell 1996), although it is likely the range has expanded northward (Battey 2019; Davidson et al. 2015). During the postbreeding period, it is found along the Pacific Coast from southeastern Alaska to northern México. Its postbreeding movements are not well understood but are thought to take advantage of localized, seasonal blooms. In California, individuals are thought to move to higher elevations postbreeding, coinciding with the flowering of high-elevation plants, as well as to the south and east, where movements coincide with the onset of summer rains and the availability of flowering plants and insects (Russell 1996).

Figure 2. Anna's Hummingbird (photo: Jim Livaudais, used with permission).

The Anna's Hummingbird feeds on a variety of flowering plants, including chaparral currant (*Ribes malvaceum*), fuchsia-flowered gooseberry (*Ribes speciosum*), monkeyflower (*Mimulus* spp.), penstemon (*Keckiella cordifolia*) (fig. 3), fuchsia (*Epilobium cana*), woolly blue curls (*Trichostema lanatum*), manzanita (*Arctostaphylos* spp.), pitcher-sage (*Salvia spathacea*), western columbine (*Aquilegia formosa*), and Indian warrior (*Pedicularis densiflora*) (Grant and Grant 1966; Russell 1996; Stiles 1973). It is considered an important pollinator throughout its range. Breeding coincides with the onset of winter rains as chaparral currant begins to bloom. In California, nesting begins as early as mid-November and usually ends in May, although both earlier and later nesting have been recorded. Broods fledge from March through June, coinciding with the blooming of fuchsia-flowered gooseberry and other flowers (Russell 1996).

Figure 3. *Keckiella cordifolia* (photo: Tim Miller, used with permission).

The Anna's Hummingbird breeds primarily in chaparral habitats interspersed with open woodlands (Pitelka 1951; Stiles 1973). Males set up territories on slopes in chaparral, while females typically nest in live oak (*Quercus agrifolia*) woodlands in canyon bottoms, with nests located 2 to 20 m above the ground (Grinnell and Wythe 1927). Anna's Hummingbirds also use riparian woodlands, coastal scrub, and urban and suburban areas with exotic flowering plants for breeding (Shuford 1993; Small 1994). Its range is thought to have expanded significantly since the 1930s as urban and suburban development have introduced new year-round food sources. Because of its expanded range, the Anna's Hummingbird is not currently of conservation concern (Russell 1996).

Allen's Hummingbird (*Selasphorus sasin*)

The Allen's Hummingbird (fig. 4) is a short to medium distance migrant that breeds in a narrow strip along the Pacific Coast of California and southwestern Oregon and winters in a small area of central México (Mitchell 2000). It is rarely found in Mojave Desert scrub habitats (Cody 1968; Rosenberg et al. 1991). There are two known subspecies: the migratory *Selasphorus sasin sasin* and the resident *S. s. sedentarius*, found on the Channel Islands of California and on adjacent small sections of the mainland, although the mainland range has expanded in southern California since 1970 (Clark 2017). The Allen's Hummingbird breeds in coastal scrub or riparian shrub/woodland habitat, generally within 30 km of the coast, and occasionally uses coastal pine forests or live oak woodlands (Grinnell and Miller 1944). In western México, it is a rare species in cloud forests and coniferous-oak forests, and its abundance is influenced by floral abundance after a fire. It prefers sites with a scrub layer and a thin canopy adjacent to territories with native trees. It starts to arrive during the second week of November and departs in March (Contreras-Martínez 2015). There is a large population at the Sierra de Manantlán in December (Santana 2000).

Figure 4. Allen's Hummingbird (photo: Mark Chappell, used with permission).

Most migratory hummingbird species reduce their ranges in winter compared to their breeding ranges; however, Allen's Hummingbird increases its range in winter (Contreras-Martínez and Schondube 2009) using the Neovolcanic Transverse Belt, an important overwintering region with flowering plants at high elevations as the season progresses. Allen's Hummingbirds use this region to move from eastern to western México (Contreras-Martínez 2015), but more study is needed to understand the habitat use and distribution of Allen's Hummingbird in winter.

The Allen's Hummingbird is known for the extremely early timing of its migration. Northbound migration begins as early as December, and southward migration can begin as early as mid-May. Northbound migration follows the Pacific Coast, corresponding to the flowering of winter-blooming plants, while southward movements are thought to follow an inland route through the coast range or the Sierra Nevada mountains, corresponding to higher elevation blooms (Phillips 1975). Nesting usually takes place from early to mid-February through June (Pitelka 1951). Male Allen's Hummingbirds establish territories in open coastal scrub or riparian shrub habitat. Females select their nest sites in areas of dense vegetation, and nests are usually 5 to 15 m above the ground (Legg and Pitelka 1956).

The migratory *sasin* subspecies feeds on a variety of flowers, including bush monkeyflower (*Mimulus aurantiacus*), Indian paintbrush (*Castilleja* spp.), columbine (*Aquilegia formosa*), currants and gooseberries (*Ribes* spp.), Indian pink (*Silene laciniata, S. californica*), Indian warrior (*Pedicularis densiflora*), twinflower (*Lonicera involucrata*), penstemon (*Penstemon* and *Keckia* spp.), ceanothus (*Ceanothus* spp.), pitcher-sage (*Salvia spathacea*), madrone (*Arbutus menziesii*), and manzanita (*Arctostaphylos* spp.) (Bent 1940; Grant and Grant 1966). It is also known to pollinate several lily species along the coast of California, including the federally endangered western lily (*Lilium occidentale*) (fig. 5). The *sedentarius* subspecies feeds on a number of endemic plant species on the Channel Islands, including island snapdragon (*Galvezia speciosa*), island monkeyflower (*Mimulus flemingii*), and Indian paintbrush (*Castilleja lanata hololeuca*) (Mitchell 2000).

Figure 5. *Lilium occidentale* (photo: 2000 John Game, used with permission).

The Allen's Hummingbird is a PIF Watchlist species due to its small geographic range, particularly the range of *S. s. sedentarius* (Rosenberg et al. 2016). It is also listed as a U.S. Fish and Wildlife Service (USFWS) 2008 Bird of Conservation Concern. Breeding Bird Survey data suggest potential declines in the Allen's Hummingbird, although the reasons for these declines are unknown (Sauer et al. 2008). The mainland range of *S. s. sedentarius* has expanded more than 23 percent in mainland California since 1970, primarily in urban areas (Clark 2017). The Allen's Hummingbird is difficult to distinguish from the Rufous Hummingbird, which presents a challenge for field identification based on physical appearance, but other indicators such as dive type and sonation are distinctive between species (Calder 1993; Mitchell 2000). The expansion of the Anna's Hummingbirds' range in recent decades is also of some concern, as the Allen's Hummingbird is thought to be at a competitive disadvantage to the Anna's Hummingbird (Mitchell 2000).

Black-chinned Hummingbird (*Archilochus alexandri*)

The Black-chinned Hummingbird (fig. 6) breeds in a variety of habitats throughout the western United States, Texas, and northeastern México, and winters in west-central México (Baltosser and Russell 2000; Karr and Freemark 1983). During breeding it is most abundant in the southern portion of its range, particularly in riparian habitats of southern Arizona and southern New México, but it also breeds throughout the southern, central, and northern Rocky Mountains. Males arrive on breeding grounds from mid-March to May, depending on latitude, and typically depart in July and August, before the females and young migrate (Russell 1996).

Figure 6. Black-chinned Hummingbird (photo: Jim Livaudais, used with permission).

The Black-chinned Hummingbird nests in riparian or woodland habitats that include oaks (*Quercus* spp.), sycamores (*Platanus* spp.), cottonwoods (*Populus* spp.), and willow (*Salix* spp.). Strong and Bock (1990) found that in southeastern Arizona, Black-chinned Hummingbirds used lowland areas with relatively large riparian trees, especially Arizona sycamore (*Platanus wrightii*), and that they selected drier areas than other species. It also uses a variety of altered habitats, including urban environments, and in the lower Colorado River Valley it nests almost exclusively in introduced tamarisk (*Tamarix ramosissima*), or salt-cedar, habitats (Rosenberg et al. 1987). Females often nest in canyon bottoms, floodplains, or dry washes, while males are often found on adjacent drier slopes. Nests are typically less than 4 m above the ground (Baltosser 1989). In the Sonoran Desert, nesting is usually limited to a single brood (Strong and Bock 1990). Postbreeding habitat is thought to be similar to breeding habitat, and postbreeding movements appear to follow food availability (Baltosser and Russell 2000).

The Black-chinned Hummingbird is an important pollinator throughout its range. In the mountains of Arizona, it pollinates beard-lip penstemon (*Penstemon barbatus*) and squaw-feather (*Castilleja integra*) (fig. 7) (Brown and Kodric-Brown 1979). The Black-chinned Hummingbird's range has expanded as artificial food sources and nesting habitats, especially tamarisk habitats, have grown. There is little conservation concern for the species rangewide, although it is thought that the loss or severe alteration of riparian habitats could affect local populations (Baltosser and Russell 2000). Population growth is thought to be limited due to high levels of nest predation (Baltosser 1986).

Figure 7. *Castilleja integra* (photo: 2004 Robert Sivinski, used with permission).

Broad-tailed Hummingbird (*Selasphorus platycercus*)

The Broad-tailed Hummingbird (fig. 8) breeds throughout the southern and central Rocky Mountains and uses a variety of habitats in upper Sonoran and montane habitats of east-central California, Arizona, New México, Colorado, western Texas, Nevada, Utah, and Wyoming (Calder and Calder 1992). It is also found year-round in oak and oak-pine forests throughout central México. In California, it breeds in upper Sonoran habitats containing pinyon (*Pinus monophylla*), juniper (*Juniperus californica*), and mountain mahogany (*Cercocarpus* spp.), in willow thickets, and in riparian areas (Grinnell and Miller 1944). In Arizona, it breeds in ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), Engelmann spruce (*Picea engelmannii*), and fir (*Abies concolor, A. lasiocarpa*) forests, as well as in oak woodlands and riparian habitats (Phillips et al. 1964). In Colorado, Utah, and Wyoming, it breeds in foothill and montane environments containing aspen (*Populus tremuloides*), ponderosa pine, Engelmann spruce, subalpine fir, and Douglas-fir, as well as in shrub patches within woodlands (Finch 1989). In western México, it is restricted to higher elevations in the mountains, and some individuals breed in winter sites (Contreras-Martínez 2015). Its presence coincides with the flowering peak of plants in the genera Salvia, Lobelia, Calliandra, Ipomea, and Senecio (Schondube et al. 2004).

Figure 8. Broad-tailed Hummingbird (photo: Mark Chappell, used with permission).

The Broad-tailed Hummingbird is thought to prefer moderately to heavily disturbed habitats for breeding and is often found in or near meadows or in shrubby habitats along forest edges (Szaro and Balda 1982). It is known to nest to 3,230 m (10,597 ft) (Bagne and Finch 2005; Bock and Block 2005). Nests are usually located 0.3 to 1.5 m above the ground, and nest sites often have an overhanging branch or other object to shield the nest and conserve heat (Calder 1973). Successful nesting corresponds to peaks in flower blossoms, and late nests have lower success rates (Calder 1973; Waser 1976). The Broad-tailed Hummingbird arrives on its breeding grounds between early March and late May, depending on latitude, and departs on its postbreeding migration in August or September. Although its migration is not well understood, it is thought to follow an elliptical migration similar to other *Selasphorus* hummingbirds, traveling north in the spring, then east to its breeding grounds, then south along the Rocky Mountain flyway postbreeding (Calder and Calder 1994; Phillips 1975).

The Broad-tailed Hummingbird feeds on a variety of red tubular flowers including penstemon (*Penstemon* spp.), delphinium (*Delphinium* spp.), columbine (*Aquilegia elegantula, A. triternata*), scarlet gilia (*Ipomopsis aggregata*), Mexican fire pink (*Silene laciniata*) (fig. 9), Indian paintbrush (*Castilleja* spp.), sage (*Salvia* spp.), bouvardia (*Bouvardia ternifolia*), scarlet mint (*Stachys coccinea*), and manzanita (*Arctostaphylos* spp.) (Waser 1978). At lower elevations in southeastern Arizona it uses ocotillo (*Fouquieria splendens*). The Broad-tailed Hummingbird also feeds on a variety of flowers that are not typical for hummingbirds, including pussy willow (*Salix* spp.), glacier lily (*Erythronium grandiflorum*), ball-head waterleaf (*Hydrophyllum capitatum*), and mountain cowslip (*Mertensia oblongifolia*) (Brown and Kodric-Brown 1979; Waser 1978).

Figure 9. *Silene laciniata* (photo: Tim Miller, used with permission).

There are concerns over declines in Broad-tailed Hummingbirds. Norvell et al. (2005) noted significant declines in riparian areas of Utah from 1992 to 2001, and Hejl (1994) reported declines in western coniferous forests. Bagne and Finch (2005) reported a 15 to 49 percent decline in the southern Rockies of New México. The reasons for these declines are not well understood. It has been suggested that the large-scale provision of feeders may artificially elevate populations and contribute to large-scale mortality in the winter months. It is also thought that land-use practices like fire suppression, timber harvest, and grazing may be contributing to declines (Brawn and Balda 1988; Hejl 1994). Contreras-Martínez (2015) suggested that the species can be associated with a mix of factors such as temperature, basal area of trees, and the availability of flowers. Phenological mismatch between early spring food resources from flowering plants and spring arrival of Broad-tailed Hummingbirds has also shifted and may contribute to reduced nest success in the future (McKinney et al. 2012). Broad-tailed Hummingbirds are not on the 2016 Partners in Flight Watch List but are noted as one of many species that have experienced population declines (Rosenberg et al. 2016).

Calliope Hummingbird (*Stellula calliope*)

The Calliope Hummingbird (fig. 10) breeds in montane habitats of western North America from British Columbia and Alberta through California and winters in southern México. It is the smallest breeding bird in North America, known for breeding in high-elevation habitats and undertaking a long-distance migration despite its small size. It is thought that the Calliope Hummingbird migrates in an elliptical pattern similar to the Rufous and Broad-tailed Hummingbird, flying north along the Pacific Coast in spring, then east to its breeding grounds, and then south along the Rocky Mountain flyway postbreeding (Calder and Calder 1994). Recent analysis of eBird data demonstrates annual east-west variation in western humming-bird migration paths, including Calliope Hummingbirds, that suggests that they may be able to adjust their routes due to weather and resource distribution while still moving north-south at similar rates across years (Supp et al. 2015).

The Calliope Hummingbird breeds in forested montane environments of British Columbia, the Pacific Northwest, the central and northern Rocky Mountains, Nevada, and California's Sierra Nevada mountains. It selects open montane forests and early successional forests for breeding (Marcot 1984). During fall migration, it uses primarily subalpine and alpine montane meadows but is also seen at low-elevation feeders. In both California and Oregon, it is known to nest in forests in the shrub-sapling stage of succession, 8 to 15 years after clearcutting or burning (Marcot 1984; Meslow and Wight 1975). In winter, it is restricted to the higher parts of the mountains in coniferous-oak forest, edges forest, and shrub, but it is an uncommon species in the wintering habitat in México. During its northward spring migration, the Calliope Hummingbird uses desert washes and low coastal mountains, as well as coastal riparian habitats. It feeds on red tubular flowers as well as a variety of other flowers, including larkspur (*Delphinium* spp.) (fig. 11), columbine (*Aquilegia* spp.), squaw currant (*Ribes cereum*), paint-brush, and bearded tongues (*Penstemon* spp.) (Armstrong 1987; Bent 1940; Martin 1988). Male Calliope Hummingbirds set up breeding territories in open areas such as forest open-ings, meadows, or clearings, while females nest in forests or in aspen or willow thickets along streams (Ryser 1985). Nests are usually positioned under an overhanging branch to shield from precipitation and heat loss (Bent 1940; Calder 1973).

Figure 10. Calliope Hummingbird (photo: Jim Livaudais, used with permission).

Figure 11. *Delphinium nudicaule* (photo: Tim Miller, used with permission).

The Calliope Hummingbird was a 2004 PIF Watch List Species and a USFWS 2008 Bird of Conservation Concern (Rich et al. 2004) but was not a 2016 PIF Watch List Species (Rosenberg et al. 2016). Current species assessment scores rank Calliope Hummingbird as a "Yellow" Watch list species due to range restriction (PIF [Partners in Flight] 2017). It is thought that the provision of feeders may artificially elevate populations and contributing to high mortality during winter. The distribution of Calliope Hummingbird is more limited in México and it displays strong site fidelity (Contreras-Martínez and Schondube 2009), but habitat loss may be related to threats from agricultural development (Contreras-Martínez, personal observation, 2019).

Costa's Hummingbird (*Calypte costae*)

The Costa's Hummingbird (fig. 12) breeds in Sonoran Desert scrub habitats of Arizona, southern and Baja California, Nevada, Utah, and Sonora, México (Baltosser and Scott 1996). It is less common, but widespread during breeding in Mojave Desert habitats of Nevada, southwestern Utah, northeastern Arizona, and parts of eastern California, as well as in California coastal shrub and chaparral habitats (Johnsgard 1983). In the Sonoran Desert, breeding takes place from February to May, after which most individuals are thought to migrate to the Pacific Coast of southern and Baja California (Phillips et al. 1964). These individuals are thought to return to Arizona and California deserts beginning in October, coinciding with the blooming of chuparosa (*Justicia californica*) or desert lavender (*Hyptis emoryi*) (fig. 13), where they remain through the breeding season (Weathers 1983). Individuals that breed in the Mojave Desert arrive there between February and April and remain into May or June, after which most are thought to winter in México, although some individuals overwinter (Baltosser and Scott 1996). In southern California, breeding occurs in coastal sage and chaparral habitats from March through September, and most individuals are thought to winter in México.

In the Sonoran Desert, the Costa's Hummingbird breeds in dry, low-elevation scrubby habitats. In the Mojave Desert, it breeds near springs and in riparian woodlands, washes, and canyons. In California, it breeds in chaparral and sage scrub habitats (Stiles 1973). During migration, it uses xeric habitats, although it may follow riparian corridors or canyons (Baltosser and Scott 1996). Nests are usually built in a tree or shrub 1 to 2 m above the ground, and vegetative cover around the nest is often sparse. Along the Colorado River, Costa's Hummingbird nests were located in catclaw acacia (*Acacia greggii*), graythorn (*Condalia globosa*), and in flowering stalks of Utah agave (*Agave globosa*) (Brown 1992).

The Costa's Hummingbird feeds on nectar from a variety of flowering shrubs, trees, cacti, and agaves. Chuparosa is a reliable source of midwinter nectar, while ocotillo is used in March and April during breeding (Scott 1994; Waser 1976). Other nectar sources include desert lavender (*Hyptis emoryi*), creosote bush (*Larrea tridentata)*, fairy duster (*Calliandra eriophylla*), paloverde (*Parkinsonia* spp.), saguaro (*Carnegiea gigantea*), bladderpod (*Peritoma arborea*), desert willow (*Chilopsis linearis*), ironwood (*Olneya tesota*), barestem larkspur (*Delphinium scaposum*), bush penstemon (*Keckiella antirrhinoides*), desert honeysuckle (*Anisacanthus thurberi*), squaw cabbage (*Stanleya* spp.), black sage (*Salvia mellifera*), white sage (*Salvia apiana*), tree tobacco (*Nicotiana glauca*), woolly bluecurl (*Trichostema lanatum*), bush monkeyflower (*Diplacus longiflorus*), Mojave beardtongue (*Penstemon pseudospectabilis*), and heart-leaved penstemon (*Penstemon cordifolius*) (Baltosser and Scott 1996; Grinnell and Miller 1944).

Figure 12. Costa's Hummingbird (photo: Alan Schmierer, U.S. Fish and Wildlife Service).

Figure 13. *Hyptis emoryi* (photo: 2013 Robert F. Norris, used with permission).

The Costa's Hummingbird was listed as a PIF Watch List Species in 2004 and a USFWS 2008 Bird of Conservation Concern (Rich et al. 2004), but is not a PIF Watch List Species in 2016 (Rosenberg et al. 2016). It is listed as threatened in New México. Its greatest threat is habitat alteration and loss, especially in California desert scrub, coastal scrub, and chaparral habitats, but also in Sonoran Desert scrub habitats. In many areas of the southwestern United States, it is thought that human development has favored the Anna's Hummingbird, which readily uses urban and suburban habitats, at the expense of the Costa's Hummingbird (Bolger et al. 1997). Intensive cattle grazing and the invasion of buffelgrass (*Pennisetum ciliare)* and other exotic grasses into Sonoran Desert scrub habitats are also thought to be negatively affecting the Costa's Hummingbird (Baltosser and Scott 1996; Yetman and Búrquez 1994).

Rufous Hummingbird (*Selasphorus rufus*)

The Rufous Hummingbird (fig. 14) has the northernmost range and the longest migration of any western hummingbird. It utilized the greatest number of BCRs during the spring and fall migrations. It breeds from southeastern Alaska through British Columbia, Washington, Oregon, northern California, western Alberta, and the northern Rockies of Idaho and western Montana. It winters throughout Baja California and northern and central México (Calder 1993). The Rufous Hummingbird is known for its use of high-elevation habitats and has been observed in alpine meadows at 3,840 m (12,600 ft) in the Sierra Nevada of California (Small 1994). Like other *Selasphorus* hummingbirds, the Rufous Hummingbird is thought to have an elliptical migration, following a lowland coastal route north in the spring and a high-elevation route south in the summer and fall along the Rocky Mountain flyway, or through the Coast Range and Sierra Nevada mountains (Phillips 1975). The Rufous Hummingbirds' movements are thought to correspond to floral phenology (Calder 1993). Migrants arrive on their breeding grounds from February to May, depending on latitude, and depart in July or

Figure 14. Rufous Hummingbird (photo: Jim Livaudais, used with permission).

August.

The Rufous Hummingbird breeds in second-growth forests and forest openings, as well as in mature forests, riparian areas, parks, fields, meadows, and other open areas. In western Oregon, nests were found in second-growth forests from 16 to 120 years old (Meslow and Wight 1975). Nests are usually well-concealed in trees and shrubs, and colonies of up to 20 nests within a small area have been found (Bent 1940). During summer and fall migration, the Rufous Hummingbird uses primarily high-elevation meadows and other openings, and during late winter and spring it uses low coastal mountains and coastal riparian habitats (Calder 1993).

The Rufous Hummingbird feeds on a variety of red tubular flowers including red columbine (*Aquilegia formosa*), scarlet gilia (*Ipomopsis aggregata*) (fig. 15), bearded tongues (*Penstemon* spp.), and paintbrushes (*Castilleja* spp.). It also feeds on a variety of other flowers including sage (*Salvia* spp.), bouvardia (*Bouvardia ternifolia*), mint (*Stachys coccinea*), lilies (*Erythronium grandiflorum, Lilium columbianum*), purple larkspur (*Delphinium barbeyi* and *D. geranioides*), heath (*Vaccinium ovatum, Menziesia ferruginea*), currant (*Ribes sanguineum*), salmonberry (*Rubus spectabilis*), honeysuckle (*Lonicera* spp.), fireweed (*Epilobium angustifolium*), horsemint (*Monarda menthifolia*), toad-flax (*Linaria vulgaris*), snapdragon (*Scrophularia montana*), and bee-flower (*Cleome serrulata*) (Calder 1993).

The Rufous Hummingbird is a PIF and Audubon Watch List Species and is listed as a US-FWS 2008 Bird of Conservation Concern (Rich et al. 2004). It is a Partners in Flight Focal Species for nectar-producing plants in early seral forests (Altman 2005). Breeding bird survey data show an estimated 63 percent decline in Rufous Hummingbird since the 1960s, although reasons for these declines are unknown (Berlanga et al. 2010). The Rufus Hummingbird is a 2016 PIF Watch List species of continental concern (Rosenberg et al. 2016).

Figure 9. *Ipomopsis aggregata bridgesii* (photo: Tim Miller, used with permission).

Fire, Restoration, and Hummingbirds: Key Findings By Region

Southwestern Desert and Riparian

Habitats and Fire Regimes

The Sonoran and Mojave Deserts (BCR 33) cover much of the southwestern United States. The Mojave Desert region extends from southeastern California through southern Nevada and portions of Arizona and Utah. Dominant Mojave Desert scrub vegetation includes creosote bush, Joshua tree (*Yucca brevifolia*), and mesquite (*Prosopis* spp.), while juniper (*Juniperus* spp.) and white fir (*Abies concolor*) forests are found at higher elevations. The Sonoran Desert extends through much of southern Arizona and southwestern New México, as well as into Baja California and Sonora, México. The Sonoran Desert region is dominated by cacti including saguaro (*Carnegiea gigantea*) and cholla (*Cylindropuntia* spp.), as well as shrubs like creosote bush and bursage (*Ambrosia dumosa*), and small trees like mesquite (*Prosopis* spp.), paloverde (*Parkinsonia florida*), desert ironwood (*Olneya tesota*), desert willow (*Chilopsis linearis* ssp. *arcuata*), and ocotillo (*Fouquieria splendens*) (Shreve and Wiggins 1964). At higher elevations, Sonoran Desert scrub transitions into chaparral or desert grasslands in the north and desert thornscrub to the south (Búrquez et al. 1992).

Fires were historically rare in Sonoran and Mojave Desert habitats, and many native desert plants are not fire-adapted (Humphrey 1974). In recent decades, exotic grasses and shrubs like buffelgrass, which is planted for cattle forage, and red brome (*Bromus rubens*), have invaded southwestern desert habitats (Yetman and Búrquez 1994). These fire-prone exotic plants have increased fuel loads, leading to more frequent, high-severity fires that cause mortality of non-fire-adapted desert plants (Bock and Block 2005; D'Antonio and Vitousek 1992; Schmid and Rogers 1988). Population estimates for BCR 33 are presented in table 1.

Table 1—Western hummingbird percent global population and population estimates for BCR 33: Sonoran and Mojave Deserts.

Species	% Global population	Population estimate
Costa's Hummingbird	31.3	900,000
Total		900,000

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

The Sierra Madre Occidental (BCR 34) is a mountain range that extends from southeastern Arizona through central México. It is characterized by pine, pine-oak, and fir forests at higher elevations and by semiarid scrub habitats on the eastern slopes (NABCI 2012). Little is known about historic fire regimes in these habitats, but it is thought that the pine and pine-oak forests of the Sierra Madre Occidental historically experienced frequent, low- to mid-severity fires similar to ponderosa pine forests of the southwestern United States (Fule and Covington 1997).

Wildfires are the most important environmental disturbances in this region and are known to trigger the succession process in forested areas (Jardel-Peláez et al. 2006). However, fire exclusion, largely as a result of grazing, is thought to have increased the volume of woody vegetation, leading to more intense fires and mortality of mature oaks (Johnson et al. 1962). Population estimates for hummingbirds in BCR 34 are presented in table 2.

Table 2—Western hummingbird percent global population and population estimates for BCR 34: Sierra Madre Occidental.

Species	% Global population	Population estimate
Anna's Hummingbird	2.2	100,000
Black-chinned Humming-bird	8.9	400,000
Broad-tailed Hummingbird	4.1	400,000
Costa's Hummingbird	4.1	120,000
Total		1,020,000

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

The Chihuahuan Desert (BCR 35) borders the Sierra Madre Occidental to the east, extending from southern New México and extreme southeastern Arizona through central México. Lower elevations are dominated by desert scrub vegetation including creosote bush, mesquite, and tarbush (*Flourensia cernua*), as well as desert grasslands dominated by native black grama (*Bouteloua eriopoda*), with evergreen, pinyon-juniper, and pine-oak woodlands at higher elevations (Bock and Block 2005).

Like the Sonoran and Mojave Deserts, fire was likely rare historically in Chihuahuan desert and grassland habitats. Due to the combined effects of grazing and fire exclusion, native Chihuahuan desert grasslands have experienced extensive conversion to exotic shrublands (Bock and Block 2005). Climate change is expected to increase aridity and the frequency of fire in Chihuahuan desert habitats, which will accelerate the decline in range and occurrence of native desert grasses like black grama (Kilgore et al. 2009). Population estimates for hummingbirds in BCR 35 are presented in table 3.

Southwestern riparian habitat is not identified as a BCR, but we include it as a habitat type within the Southwestern Desert and Riparian region due to its high importance for breeding birds, including hummingbirds, in the southwestern United States. Riparian habitats are found throughout the southwestern United States and comprise a major source of vegetative and biological diversity in these habitats (Stamp 1978; Strong and Bock 1990). Native southwestern riparian vegetation includes cottonwood, Arizona sycamore (Platanus wrightii), willow, and netleaf hackberry (*Celtis reticulata*). These trees provide important breeding habitat for many resident and migratory birds, including several endangered or threatened species (Powell and Steidl 2000; Skagen et al. 1998; Szaro and Jakle 1985;). Riparian habitats in the southwestern United States provide breeding habitat for many bird species in this region, including rare or declining species that are not found elsewhere (Carothers et al. 1974; Cartron et al. 1999; Johnson et al. 1977; Naiman et al. 1993; Rosenberg et al. 1991; Strong and Bock 1990).

Table 3—Western hummingbird percent global population and population estimates for BCR 35: Chihuahuan Desert.

Species	% Global population	Population estimate
Black-chinned Hummingbird	15.8	700,000
Broad-tailed Hummingbird	5.4	500,000
Total		1,200,000

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

Over the past century, southwestern riparian habitats have been altered extensively through changes to hydrological regimes, fire suppression, grazing, and invasion by exotic plants, especially tamarisk (*Tamarix* spp.). Fleischner (1994) estimates that 90 to 95 percent of the original riparian habitat in the southwestern United States has been lost or degraded. These alterations have changed natural disturbance regimes, increasing fuel loads and the incidence of wildfires in riparian habitats (Bock and Block 2005; Schmid and Rogers 1988). The invasion of drought-resistant tamarisk into riparian habitats of the southwestern United States is thought to be contributing to more frequent, intense wildfires that are destructive to native vegetation (Busch 1995; Finch et al. 2006).

Wildfire and Hummingbirds

Fire was historically rare in southwestern desert habitats, and many desert plants are not well adapted to frequent fire (Humphrey 1974; McLaughlin and Bowers 1982). Because many desert bird species, including hummingbirds, rely on native vegetation for nesting and foraging, the loss or alteration of native vegetation due to fire and the spread of exotics is likely to have a profound effect on these species (Bock and Block 2005). A study of plant communities and birds following fire in the Sonoran Desert in Arizona found reduced bird species richness compared with unburned areas, both immediately and 4 years postfire (Esque et al. 2013) Because so few studies exist, the potential effects of fire on birds in desert habitats must be surmised from studies of the effects of fire on vegetation (Esque and Schwalbe 2002). There is a strong correlation between native vegetation volume, complexity, and bird diversity and abundance in Sonoran and Mojave Desert scrub habitats. The destruction of native vegetation through fire will likely have a negative effect on hummingbirds that breed in these habitats, for example the Costa's and Black-chinned Hummingbird (Mills et al. 1991; Tomoff 1974). While chuparosa responds well to fire in southern Arizona, many other desert plants that are used for both foraging and nesting by the Costa's Hummingbird, such as paloverde, agave, and many cacti species, are destroyed by fire (Baltosser and Scott 1996; Yetman and Búrquez 1994). Therefore, increases in the frequency and intensity of wildfire in desert scrub habitats are likely to negatively affect the Costa's Hummingbird and other hummingbirds that use these habitats.

Climate change, particularly decline in rainfall, is correlated to overall declines and collapse of bird communities in the Mojave Desert since the early 20th century (Iknayan and Beissinger 2018). Climate change may also negatively impact hummingbirds through its impacts on native

vegetation in southwestern desert habitats, although this needs more study. Smith et al. (2000) predicted that exotic grass seed production will be enhanced under projected climate change scenarios. White et al. (2011) modeled bird occurrence in northern Chihuahuan desert habitats using simulated vegetation changes associated with climate change. The model projected increases in the relative abundance of shrubland birds and decreases in the abundance of bird species associated with grassland, yucca (*Yucca* spp.), and ocotillo (*Fouquieria splendens*) habitats. The model predicted increases in shrubland because leaf-area index values were lower in shrubland. These results have potentially negative implications for the Costa's Hummingbird, which feeds on ocotillo flowers.

Because hummingbirds are not generally found in desert grasslands, this review does not address the results of studies examining avian responses to fire in grassland habitats in detail. In general, studies of postfire desert grassland bird habitat associations indicate declines in bird species that require dense cover, and increases in ground-foraging birds (Bock and Bock 1978; Bock and Bock 1988; Bock and Bock 1992).

In the Sierra Madre Occidental mountains of western México, fires are important for maintaining plant species diversity in the pine and pine-oak forest (Jardel-Peláez et al. 2009). Fires are part of the historical regime, and many plant species survive the effects of surface fires and regenerate quickly following severe fires (Jardel-Peláez et al. 2006; Llamas-Casillas 2009). However, when several fires occur in a short timeframe, regeneration in forests is inhibited and is replaced by secondary scrub. Jardel-Peláez et al. (2006) found that pines dominate early successional stages of tree regeneration, whereas broadleaf species dominate in later stages. In the understory, flowering herbaceous plants dominate in early postfire successional stages and are gradually replaced by woody plants with fewer flowers in later successional stages. Long-distance migratory hummingbirds respond to the successional stages of forest regeneration, as they depend on the abundance of plants that regenerate after the fires, for example abundant *Salvia iodantha* and *S. mexicana* (Arizmendi 2001). In Jalisco, Contreras-Martínez (2015) and Contreras-Martínez and Santana (1995) reported that hummingbird responses to postfire conditions varied. Out of the 10 common hummingbird species in pine-oak forest, 60 percent are migratory and occur within the regions included in this review. Hummingbirds are most abundant in the earlier successional stage after a fire, but changes in diversity of hummingbird species are not always correlated with the diversity of food plants at any given point in time, but are correlated with overall flower abundance (Contreras-Martínez 2015; Contreras-Martínez and Santana 1995).

In southwestern riparian habitats, native vegetation structure and diversity correlate with breeding bird diversity and abundance, as well as to nest success (Carothers et al. 1974; Powell and Steidl 2000; Strong and Bock 1990; Szaro and Jakle 1985). Avian diversity is also correlated to the presence of native cottonwoods in riparian habitats, and native Arizona sycamore is an important nest substrate (Carothers et al. 1974; Powell and Steidl 2000; Stamp 1978). In recent decades, there have been significant declines in bird abundance and diversity in many southwestern riparian habitats (Rosenburg et al. 1991; Skagen et al. 1998; Strong and Bock 1990). Southwestern riparian habitats are not adapted to frequent or intense fire, and recent wildfires in these habitats have caused the mortality of native trees including cottonwood (*Populus fremontii*) and sycamore (*Platanus wrightii*) (Bock and Bock 1988; Stuever 1997). In one of the few studies of the impacts of fire on birds in southwestern riparian habitats, Smith et al. (2006) studied breeding bird and native vegetation responses to wildfire

along the Middle Rio Grande River in New México. Black-chinned Hummingbirds were more abundant at control sites than at burned sites, suggesting a decrease in abundance after wildfire.

Restoration and Hummingbirds

Few studies have examined avian responses to restoration treatments in southwestern desert scrub habitats. More study is needed on the impacts of restoration treatments, including fencing to exclude grazing, replanting of native species, and exotic plant removal, on breeding bird species in these habitats. Prescribed fire is not indicated as a management tool, due to the destructive effects of fire on native vegetation. Herbicide application has shown some promise in killing buffelgrass, but its long-term effectiveness as well as its effects on native plants and birds are not well studied (Bovey et al. 1984; Tjelmeland et al. 2008).

Few studies have examined hummingbird responses following fire in western México. In Sierra Madre Occidental, fire is one of the most common natural and anthropogenic disturbances to wildlife habitats. Fire management in Mexican forested areas is a controversial issue, as many do not view fires as part of the normal dynamic nature of these ecosystems (Jardel-Peláez 2000). In addition, fire regimes have changed over time, and fires are becoming more frequent, more severe, and larger. Despite the importance and growing incidences of fire, no studies on vegetation restoration (food resources such as flowering shrubs) and hummingbirds have been conducted in western México. In general, the abiotic factors that affect the abundance of hummingbird species are the presence, frequency, and severity of the fire, altitude, and temperature (Contreras-Martínez 2015). The biotic factors that affect the abundance of hummingbirds are mainly the abundance of hummingbird-pollinated flowers and canopy cover. The challenges of habitat management and restoration following fire are different at the sites that hummingbirds use throughout their life cycles. Regardless of the location, fire can affect the diversity and density of floral nectar resources, in turn impacting hummingbird foraging (both positively and negatively), and thus limit hummingbird populations (Contreras-Martínez 2015; Contreras-Martínez and Santana 1995). More study is needed to address the timing of prescribed fires and the restoration of postfire habitat.

Few studies have examined avian responses to restoration treatments in southwestern riparian habitats. Still, many species of birds use invasive tamarisk as breeding habitat without any loss to productivity or nest success, suggesting that restoration projects focused on the removal of tamarisk should ensure it is replaced with high-quality native vegetation to mitigate the potential effects of restoration treatments on breeding birds (Sogge et al. 2008). From 2000 to 2005, vertebrate responses to a variety of restoration treatments designed to reduce fuel and remove invasive plants in riparian forests were studied along the Middle Rio Grande River in New México. Treatments included mechanical removal along with herbicide treatment, partial mechanical removal and herbicide treatment followed by prescribed fire, and mechanical removal followed by herbicide treatment and revegetation (Bateman et al. 2008; Finch 2008; Finch et al. 2006; Smith et al. 2009).

Finch et al. (2006) found that Black-chinned Hummingbirds were the most abundant species on all sites across all years of the study, but they declined in response to the treatment, likely due to reductions in nesting and foraging habitat (Finch 2008; Finch et al. 2006). Black-chinned Hummingbird nest success was slightly lower in native substrates than in exotic

substrates, but the analysis revealed nest success was not significantly related to exotic versus native plant use and Black-chinned Hummingbirds appeared to readily switch to native nesting substrates after exotics were removed during the first year following treatment (Finch et al. 2006).

Smith et al. (2009) further examined the effects of the treatments described above on nest-site selection and nest survival of Black-chinned Hummingbirds. Similar to the results of Finch et al. (2006), nest survival was higher in pretreatment plots and in exotic substrates than in posttreatment plots and native cottonwoods; however, treatments were not found to have a statistically significant effect on nest survival. Nest survival was found to be negatively associated with nest height, indicating that higher nests were more susceptible to predation. These results are similar to those of Baltosser (1983), who found an inverse relationship between nest height and nest survival for Black-chinned Hummingbirds. Both Smith et al. (2009) and Finch et al. (2006) found that nest survival rates varied significantly from year to year and across locations, indicating high variability in hummingbird abundance, movements, and habitat selection from year to year (Finch et al. 2006). Additional work examining nest success of Black-chinned Hummingbirds in riparian areas dominated by either nonnative or native plant species found similar or better nest success in nonnative Russian olive (*Elaeagnus angustifolia*) and salt-cedar (*Tamarix* spp.), suggesting that some nonnative shrub and tree species can still provide important habitat structure for nesting hummingbirds (Smith et al. 2014).

These results suggest that, while the removal of exotic vegetation may have a short-term negative impact on Black-chinned Hummingbird abundance and nest success, the species will readily adapt to nesting in native vegetation. The relative importance of nest height to Black-chinned Hummingbird nest success indicates that structural diversity in riparian vegetation is an important component of nesting habitat quality.

Management Implications

In Sonoran and Mojave Desert scrub habitats, the invasion of exotic grasses, particularly buffelgrass, and the subsequent risk for more frequent, intense fires destructive of native desert vegetation are serious management issues (Marshall et al. 2012). Increases in fire frequencies and the loss of native vegetation have potentially serious consequences for hummingbirds that nest and forage in desert scrub habitats, like the Costa's and Black-chinned Hummingbird. They also have potentially negative implications for species that use these habitats during migration, including Anna's, Calliope, and possibly Allen's Hummingbird.

Prescribed fire is not considered an appropriate management strategy in southwestern desert scrub habitats due to the destructive effects of fire on native desert vegetation. Manual or mechanical removal of exotic grasses may be effective, but the long-term effectiveness of these methods has not been assessed. Manual removal efforts should be monitored diligently to ensure success. Herbicide application has shown some promise in killing buffelgrass, but its long-term effectiveness as well as its effects on native plants and wildlife are not well studied (Bovey et al. 1984; Tjelmeland et al. 2008). More study is also needed on the viability of propagating and replanting native species in these habitats (CalPIF 2009).

According to Contreras-Martínez (2015), most specialist hummingbirds in pine-oak forests of the Sierra Madre Occidental are adapted to the conditions created after a fire. It is important to maintain the historical disturbance regime caused by forest fires. The landscape

matrix caused by diverse perturbation (natural and human activities) and the resulting mosaic of habitats can maintain hummingbird diversity. However, it is necessary to maintain burned areas with mostly low-severity fire and some small areas of high-severity fire (< 3 hectares), surrounded with forest cover of advanced successional stages (> 80 percent, Contreras-Martínez, personal observation, 2019) and a fire return interval between 11 and 30 years, (Jardel-Peláez et al. 2009). Bird species such as Rufous Hummingbird, Calliope Hummingbird, and Allen's Hummingbird, benefit from high-severity fire, with a positive response detected during the first 10 years after the fire (Contreras-Martínez 2015).

In southwestern riparian habitats, dense vegetation structure is correlated with nest success, and nest height is inversely related to nest success, for many avian species including the Black-chinned Hummingbird (Baltosser 1986; Finch et al. 2006; Mills et al. 1991; Powell and Steidl 2000). There are indications that native riparian species including cottonwood and willow are able to resprout after fire, although native plants may take longer to reestablish than exotics (Bateman et al. 2008; Finch et al. 2006). For example, cottonwoods may take up to 10 years to resprout after fire (Ellis 2001). Therefore, the challenge in riparian restoration is to reduce the risk of wildfire and the extent of exotic vegetation while retaining sufficient understory vegetation to ensure adequate nest success. A study of the effects of alternative understory management practices on bird abundance in the Middle Rio Grande found hand-thinning approaches to remove exotics resulted in no impact or greater abundance of understory nesting bird species, including Black-chinned Hummingbirds, while mechanical clearing treatments had negative effects on bird abundance (Brand et al. 2013). Prescribed fire, in combination with mechanical and herbicide treatments and the planting of native species, may help to reduce fuels and retard the spread of exotics (Finch et al. 2006). Fuel removal efforts should include planting of native species and the continued monitoring of restoration sites to ensure adequate native plant regeneration (Finch 2008).

Coastal California, Sierra Nevada, and Great Basin

Habitats and Fire Regimes

The Coastal California region (BCR 32) is characterized by mixed chaparral and coastal scrub habitats, oak/pine woodlands, and California Central Valley wetland and associated upland habitats. This review focuses on California coastal scrub and chaparral habitats as they provide important breeding habitat for Allen's, Anna's, and Costa's Hummingbird. Coastal California has a Mediterranean climate of hot, dry summers and wet, mild winters. California chaparral habitats support a variety of plant species including chamise (*Adenostoma fasciculatum*), California lilac (*Ceanothus* spp.), manzanita (*Arctostaphylos* spp.), and mountain mahogany (*Cercocarpus betuloides*) (CalPIF 2004). California coastal scrub habitats are comprised of plants such as coyote brush (*Baccharis pilularis*), yellow bush lupine (*Lupinus arboreus*), salal (*Gaultheria shallon*), and evergreen huckleberry (*Vaccinium ovatum*) (CalPIF 2004; Munz 1959).

Both California chaparral and coastal sage scrub habitats are fire-adapted, and many plants found in these habitats, including gooseberries and currants (*Ribes* spp.), trefoils (*Lotus* spp.), and blackberries (*Rubus* spp.), depend on fire to resprout (Brown and DeByle 1989; Keeley 1991; Lyon and Stickney 1976; Morgan and Neuenschwander 1988). In California, 57 of 58 herbaceous perennial species resprouted after a wildfire in chaparral (Keeley 1998). California

chaparral habitats historically experienced high-severity fire every 20 to 40 years, although some more southern areas historically experienced longer fire return intervals of 100 years or more (Hanes 1988; Keeley and Safford 2005; Kilgore 1981). California coastal scrub habitats are fire-adapted but are thought to have had a longer historic fire return interval (O'Leary 1990). Many coastal scrub plants are capable of resprouting or germinating after fire, but the persistence of some coastal scrub plant species is thought to be threatened by fires that occur every 40 years or less (Malanson 1985). Too-frequent fire intervals of less than 10 years can cause the conversion of California coastal shrub habitats to exotic grasslands (Keeley and Safford 2005; Malanson 1985). Fire suppression in California coastal scrub habitats can result in conversion to live oak woodland, although this is considered a lesser threat than grassland conversion (Callaway and Davis 1993).

Table 4—Western hummingbird percent global population and population estimates for BCR 32: Coastal California.

Species	% Global population	Population estimate
Allen's Hummingbird	57.5	400,000
Anna's Hummingbird	76.2	4,000,000
Costa's Hummingbird	12.2	400,000
Black-chinned Hummingbird	4.4	200,000
Calliope Hummingbird	0.2	5,000
Total		4,605,000

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

The greatest threats to California coastal scrub and chaparral habitats are loss, conversion, and fragmentation due to human development. California coastal scrub habitats have been virtually eliminated California, and chaparral habitats have declined significantly as well (CalPIF 2004). Increases in fire frequency due to climate change and human activities also represent a significant threat (Keeley et al. 1999). Population estimates for hummingbirds in BCR 32 are presented in table 4.

The mountain range of the Sierra Nevada (BCR 15) rises sharply from the Great Basin on the east and slopes toward the Central Valley of California on the west. Mixed-conifer forests of sugar pine (*Pinus lambertiana*), white fir, Douglas-fir, giant sequoia (*Sequoiadendron giganteum*), ponderosa pine, and incense cedar (*Calocedrus decurrens*) dominate the lower and mid-elevations on the west side, while red fir (*Abies magnifica*), Jeffrey pine (*Pinus jeffreyi*), whitebark pine (*Pinus albicaulis*), western white pine (*Pinus monticola*), and mountain hemlock (*Tsuga mertensiana*) dominate the montane and subalpine zones. The eastern Sierra is dominated by lodgepole pine (*Pinus contorta*), western white pine, and white-bark pine at high elevations, with pinyon-juniper forests at lower elevations.

Because of its Mediterranean climate of hot, dry summers and mild, wet winters, the Sierra Nevada region evolved with frequent fire. It is thought that Sierra Nevada forests historically experienced a patchy, mixed-severity fire regime with a typical fire return interval of less than 50 years (Agee 1993; Kilgore 1973; Skinner and Chang 1996). Fire suppression in Sierra Nevada forests is thought to have created a disproportionate amount of decadent, late-successional forest stands and an increase in fuels, contributing to more frequent, high-severity fires (Brown and Kapler Smith 2000; Husari and Hawk 1994). Population estimates for hummingbirds in BCR 15 are presented in table 5.

Table 5—Western hummingbird percent global population and population estimates for BCR 15: Sierra Nevada.

Species	% Global population	Population estimate
Anna's Hummingbird	7.3	300,000
Black-chinned Hummingbird	0.2	8,000
Calliope Hummingbird	5.0	120,000
Rufous Hummingbird	0.1	6,000
Total		434,000

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

The Great Basin region (BCR 9) includes the northern Basin and Range, the Columbia plateau, and the eastern slopes of the Cascade and Sierra Nevada mountain ranges in Oregon, California, Nevada, and Utah. The Great Basin receives little precipitation, mostly in the form of snow. Grasslands, sagebrush (*Artemisia* spp.), and other xeric shrubs dominate the lower elevations, while pinyon-juniper woodlands and open ponderosa pine forests are found at higher elevations. Lodgepole pine (*Pinus contorta*) and subalpine fir forests are found at higher elevations on north-facing slopes. Cottonwoods and quaking aspen are found in riparian habitats.

Great Basin habitats are thought to have been characterized by a low to moderate-severity fire regime, with seasonal burning by Native Americans (Kitchen 2010). Grazing, fire suppression, and the invasion of exotic grasses in these habitats have resulted in increased fire frequencies, more incidences of crown fires, and the expansion of woodland habitats into adjacent shrub-grasslands (Bock and Block 2005; Brooks and Pyke 2001; Keane et al. 2002). Population estimates for hummingbirds in BCR 9 are presented in table 6.

Table 6—Western hummingbird percent global population and population estimates for BCR 9: Great Basin.

Species	% Global population	Population estimate
Calliope Hummingbird	31.6	800,000
Rufous Hummingbird	6.6	700,000
Black-chinned Hummingbird	3.4	160,000
Anna's Hummingbird	0.8	40,000
Costa's Hummingbird	0.2	5,000
Broad-tailed Hummingbird	2.9	300,000
Total		2,005,000

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

Wildfire and Hummingbirds

While California coastal scrub habitats are sensitive to fire, California chaparral habitats evolved with frequent fire, and it is thought that the bird species associated with these habitats are adapted to fire as well (CalPIF 2004). There are indications that bird responses to fire in California chaparral habitats are relatively short-lived and that recolonization occurs during the first few years postfire (Moriarty et al. 1985). Other studies suggest that recently burned chaparral habitats support higher avian species richness and diversity than unburned habitats (Longhurst 1978; Wirtz 1982). Overall, fire appears to have a neutral to positive effect on bird species richness and abundance in California chaparral.

Several studies suggest that Anna's Hummingbird populations decline postfire in coastal sage scrub and chaparral habitats. In a study of avian responses to a wildfire in a variety of habitats in southern California, Mendelsohn et al. (2008) found that Anna's Hummingbirds declined significantly in low-elevation chaparral habitats 2 years postfire. The study found that overall species diversity increased postfire in low-elevation coastal sage scrub habitats. Shrub and tree covers were reduced significantly postfire in the coastal sage scrub and chaparral habitats. Anna's Hummingbird may have declined due to a loss of tree and shrub cover for nesting or perching.

Moriarty et al. (1985) compared bird populations in burned and unburned coastal sage scrub habitats following a wildfire in southern California. After an initial drop, the number of species at the burned site increased during the first year postfire, recovering 70 to 90 percent of the original species richness and abundance. Species associated with open habitats preferred the burned area, while birds associated with thick, shrubby areas favored the unburned area. Anna's Hummingbird declined postfire. Stanton (1986) studied avian community dynamics 2 and 3 years after the same fire. While bird abundance remained relatively constant throughout the year in the control habitat, it fluctuated in the burned habitat, with higher abundances during the breeding season.

Black-chinned Hummingbirds were more abundant in the burned habitat than in the control habitat by a ratio of 13:1. Anna's Hummingbirds were more abundant in the control habitat by a ratio of 95:60 and showed a statistically significant preference for the unburned habitat. These results align with those of Mendelsohn et al. (2008) and Moriarty et al. (1985). The reasons for declines in Anna's Hummingbirds after fire are unknown, but they possibly relate to the loss of tree and shrub cover in burned habitats, because the Anna's Hummingbird nests up to 20 m, and males often perch on tree branches overlooking their foraging territories. Anna's Hummingbirds also rapidly exploit new habitats and food sources, so it is possible that individuals disperse to new habitats after fire.

Limited information suggests that Costa's Hummingbirds may prefer burned habitats in both chaparral and coastal sage scrub habitats. Baltosser and Scott (1996) cited a study (Cogswell 1962) in which Costa's Hummingbirds reached their maximum density on plots that had burned 3 to 5 years earlier in coastal scrub and chaparral habitats in southern California. During this period, they were much more abundant than Anna's Hummingbirds. The reasons for this are unknown. It is possible that postfire habitats offer more food resources to Costa's Hummingbirds, or that the species, which nests low to the ground, prefers habitats in the stage of early shrub regeneration for nesting. Burned habitats may also present less territorial competition from Anna's Hummingbirds. Unfortunately, no information exists on the effects of wildfire on Allen's Hummingbird.

Studies of avian responses to wildfire in Sierra Nevada forests have found results similar to other studies of fire and avian ecology in western forests. Overall, studies have found that after fire, the abundance of ground and canopy foraging birds, as well as timber-drilling birds, increases, while the abundance of foliage-gleaning birds decreases (Bock and Lynch 1970; Burnett et al. 2011; Raphael et al. 1987). Responses to high and low/mixed-severity fire tend to be positive for Broad-tailed and Calliope Hummingbirds (Fontaine and Kennedy 2012). A number of studies indicate that Calliope Hummingbirds select early to mid-successional post-fire habitats in the Sierra Nevada. In a 2011 study of bird communities after wildfires in the northern Sierra Nevada that took place in 2000, 2007, and 2008, Burnett et al. (2011) found that Calliope Hummingbirds were most abundant on plots within the 2000 and 2007 fire areas, although they were not detected on plots that burned in the 2008 fire. The authors noted that Calliope Hummingbirds were rarely detected on private lands after fire, possibly because of the practice of removing shrubs to encourage conifer regeneration on these lands.

Raphael et al. (1987) summarized breeding bird censuses that were completed between 1966 and 1985, after a 1960 Sierra Nevada wildfire. In this study, Calliope Hummingbirds reached their highest mean densities on burned plots between 1975 and 1979, 15 to 19 years postfire, although their densities were also relatively high on unburned plots during the same period. Their abundance remained relatively high 21 to 25 years after fire on the burned plots (Raphael et al. 1987). Marcot (1984) found that Calliope Hummingbirds were associated with Douglas fir forests in the shrub-sapling stage of succession 14 years after fire in northwestern California.

It is likely that postfire habitats provide important stopover habitat for Rufous Hummingbirds in the Sierra Nevada during their postbreeding migration. In late summer of 2009 and 2011, Ryan Burnett (Director, Sierra Nevada Group, PRBO Conservation Science, personal communication, 2012) observed high numbers (thousands) of Rufous Hummingbirds foraging in open areas that had burned in a large 2007 wildfire. These areas contained many blooming wildflowers.

Little is known about the effects of wildfire on hummingbirds in Great Basin habitats. It is thought that fire exclusion and grazing have contributed to the expansion of pinyon-juniper woodlands into adjacent shrub-grasslands, which may affect Black-chinned, Broad-tailed, or Calliope Hummingbird, all of which breed in the Great Basin. The expansion of woodlands in Great Basin habitats may benefit the Black-chinned Hummingbird, which is known to nest in juniper trees (Balda 1969), although this has not been studied.

Restoration and Hummingbirds

Studies that have examined the effects of prescribed fire or other restoration practices on birds in California coastal scrub and chaparral habitats have not addressed hummingbird responses specifically. Lawrence (1966) found that bird densities increased during the first spring following a prescribed fire in a southern California foothill chaparral habitat but leveled off to prefire levels by the fourth year of the study. These results are similar to those of studies of avian responses to wildfire in chaparral.

There are indications that mechanical fuel reduction treatments, like mastication, result in lower diversities and abundances of birds than prescribed fire. A preliminary report of results from a study comparing prescribed fire and mastication treatments in California chaparral found that 40 bird species used postfire habitats, while only 14 species and many fewer individuals used postmastication habitat (Potts and Stephens 2007). The mastication plots also contained higher abundances of nonnative grasses. A study of chaparral bird community responses in coastal California to either prescribed fire treatments or mechanical mastication found that while bird communities recovered 3 years posttreatment following prescribed fire, mechanical treatments resulted in reduced species richness even 5 years following treatment (Newman et al. 2018).

The effects of prescribed fire on songbirds in Sierra Nevada forests are not well studied, but results are similar to those of wildfire and avian ecology studies in other habitats (Finch et al. 1997; Kotliar et al. 2002; Saab and Powell 2005). Bagne and Purcell (2011) studied the effects of prescribed fire applied to managed, fire-suppressed mixed conifer forests in the Sierra Nevada. Aerial foraging and riparian-associated birds increased 1-year postfire, while conifer-associated birds declined during the same period. Bark foraging and cavity nesting birds increased 3 to 6 years postfire. Anna's Hummingbirds decreased by 65 percent immediately postfire in this study, a result that aligns with Anna's Hummingbirds' responses to wildfire in chaparral. An examination of avian responses in the Sierra Nevada found that an interaction of time since fire and burn severity often interacted to predict response in a bird community (Taillie et al. 2018). While the analysis did not address hummingbird responses specifically, it highlighted the need to consider interacting effects when predicting avian response to mixed-severity fire.

Little to no information exists on the effects of restoration practices specifically for hummingbirds in the Great Basin, but studies examining restoration and management in pinyon-juniper woodlands on bird communities provide useful insights. In some pinyon-juniper woodland habitats, mechanical removal or "chaining" techniques have been applied to reduce the encroachment of woodland trees. The effects of these practices on birds have not been well studied. One study suggested that birds that depend on woodland trees for nesting and foraging responded negatively to the removal of trees through chaining (Balda and Masters 1980). The effects of these techniques on hummingbirds are not known. Black-chinned,

Broad-tailed, and Calliope Hummingbirds are known to nest in pinyon-juniper woodlands in the Great Basin, so these practices have the potential to affect breeding habitat quality for these species. In two studies of bird community response to management in pinyon-juniper woodlands, bird communities remained relatively stable following disturbance, though the response varied (Knick et al. 2014, 2017). A study of woodland reduction using mechanical treatments, including chaining, resulted in either no change or reduction in abundance of several species of birds for up to 2 years following treatment, although Black-chinned and Broad-tailed Hummingbirds did not show a significant decrease in habitat use following treatments relative to controls (Bombaci et al. 2017).

Management Implications

Studies indicate that many bird species are able to rapidly recolonize chaparral habitats postfire, and that these habitats return to preburn levels of avian abundance and richness within a few years (Moriarty et al. 1985). Furthermore, there is some indication that Costa's Hummingbird, a species of conservation concern that breeds in California chaparral and coastal sage scrub habitats, responds positively to fire. Therefore, management practices that encourage the restoration of fire to California chaparral habitats are likely to help maintain avian species richness and diversity in these habitats and will likely benefit the Costa's Hummingbird. Anna's Hummingbirds appear to decline in burned habitats postfire; however, there is little overall conservation concern for this species, which is thought to be able to rapidly exploit new habitats and food sources provided through human development.

The ability of birds, including the Costa's Hummingbird, to recolonize burned coastal scrub and chaparral habitats likely depends on the availability of suitable refugia within burned habitats, or of unburned habitat nearby, to escape to during and immediately after fire (Mayer and Wirtz 1995). Therefore, fire may be detrimental to birds in small or highly fragmented patches of chaparral or coastal scrub that are not adjacent to unburned habitat. Many species, including the Costa's Hummingbird, are thought to be highly sensitive to habitat fragmentation. Crooks et al. (2004) found a higher diversity of birds sensitive to urbanization in unfragmented sage scrub and chaparral habitats of coastal southern California. Bolger et al. (1997) found that Costa's Hummingbirds declined in response to fragmentation in coastal scrub and chaparral habitats in southern California and had significantly lower densities in habitats within 500 m of an edge. In contrast, Anna's Hummingbird was among the four species that increased in response to fragmentation. The study concluded that fragmentation was beneficial for species associated with human development and edge habitats, like the Anna's Hummingbird, and detrimental for species dependent on larger patches of unfragmented habitat, like the Costa's Hummingbird.

Management efforts that focus on preserving existing large, intact stands of coastal shrub and chaparral, and on restoring natural fire regimes within these habitats, are likely to be beneficial to the Costa's Hummingbird as well as other birds. Management practices should promote the development of a patchwork of habitats in various successional stages, from early to late seral, across the landscape to maximize the diversity and abundance of birds (CalPIF 2004; Chase et al. 2000). In areas with greater habitat fragmentation, efforts should focus on creating or maintaining intact corridors between habitat patches, as well as buffers between habitat patches and developed areas to reduce the risks of fire, predation, and the invasion of exotic plants. When possible, restoration sites should be located adjacent to intact, floristically

diverse habitats in order to promote the germination of native herbs (Allen et al. 2000). When fuel buffers to protect human development are necessary, small but effective fuel buffers are recommended over graded buffers that cover a large area (CalPIF 2004).

In chaparral, prescribed fire is recommended over mechanical removal or mastication because fire promotes the regeneration of flowering plants, and because mechanical mastication promotes the reseeding of exotic grasses at much higher rates than prescribed fire (Potts and Stephens 2007). Conversion to exotic grasslands is one of the greatest threats to California coastal scrub and chaparral habitats (Allen et al. 2000; CalPIF 2004). While some extent of mixed grassland/chaparral habitat may provide habitat heterogeneity and be beneficial for birds, homogenous exotic grasslands support a much lower diversity and abundance of birds than chaparral habitats. For example, in a study comparing south-western chaparral habitats with adjacent grassland and riparian habitats that had been repeatedly burned and seeded with exotic grasses, Szaro (1981) found that bird densities were significantly lower in the burned grassland habitats.

When necessary, mastication should be followed with mulching to discourage the reseeding of exotic grasses (Allen et al. 2000). Prescribed fire should be applied outside of the breeding seasons of hummingbirds and songbirds, which begins as early as February and ends around mid-August (CalPIF 2004). However, some evidence suggests that spring burns in coastal sage scrub may be more likely to promote native plant diversity than fall burns (Allen et al. 2000). More research is needed on the timing of prescribed fire in these habitats.

Several studies indicate that the Calliope Hummingbird, which breeds in the Sierra Nevada, selects early to mid-successional postfire habitats for nesting. Rufous Hummingbirds have been observed in large numbers in early postfire habitats in the Sierra Nevada during fall migration. Managing Sierra Nevada mixed-conifer forests for a mixed-severity fire regime, as was characteristic historically, should benefit these species. Management should allow for fires to burn at a variety of severities, including high severities, to promote flowering plant regeneration and provide habitat for a diversity of bird species. Many flowering plants in the Sierra Nevada are adapted to resprout after fire. For example, lupine can regenerate even when the entire crown of the plant is consumed (McLean 1969). Golden brodiaea, a perennial forb found in the Sierra Nevada, flowers when stimulated by increased light (Stone 1951).

In Sierra Nevada forests, prescribed fire is recommended as a management strategy alone or in combination with, thinning, logging, or mastication. Prescribed fire will encourage flowering plant regeneration as well as create spatial heterogeneity that will benefit a variety of bird species. Postfire habitat should be managed for the growth of a variety of native shrubs and forbs (rather than encouraging only conifer regeneration) to provide adequate nesting and forging habitat for Calliope and Rufous Hummingbird (Burnett et al. 2010). In foothill and montane chaparral habitats in the Sierra Nevada, restoring a fire return interval of 20–30 years, as was characteristic historically, will likely be beneficial to species that use these habitats (Barbour and Major 1988). Large, decadent patches of chaparral shrub can be treated with prescribed fire or mastication applied in small areas over several years to reduce the risk of catastrophic fire.

Birds in the Great Basin are thought to select habitats along elevational as well as successional gradients (Pavlacky 2004; Rosenstock and Van Riper 2001). The effects of fire or fire exclusion on hummingbirds in Great Basin habitats are unknown, but fire exclusion is thought to have altered successional processes and led to the encroachment of woodlands into adjacent grassland habitats (Bock and Block 2005; Brooks and Pyke 2001; Keane et al. 2002). Mechanical fuel reduction techniques like chaining may reduce woodland encroachment into grasslands, but some birds, including possibly hummingbirds, respond negatively to chaining (Balda and Masters 1980). The restoration of fire to Great Basin habitats will promote a variety of successional stages across the landscape that will benefit a variety of bird species (Pavlacky 2004). More study is needed on the effects of prescribed fire and on the potential effects of the reintroduction of fire into Great Basin habitats.

There is evidence that grazing, particularly in riparian habitats of the Great Basin, may negatively affect breeding birds that are associated with these habitats, including the Black-chinned and Broad-tailed Hummingbird (Dickson et al. 2009; Dobkin et al. 1998). A study of avian abundance in riparian and aspen woodlands in the Great Basin following livestock removal found an overall increase in bird abundance 10–12 years following removal, although there was a nonsignificant decrease in hummingbird species abundance (Earnst et al. 2012). More study is also needed in this area.

Pacific Northwest/Northern Rockies

Habitats and Fire Regimes

The Northern Pacific Rainforest region (BCR 5) in the northwestern United States encompasses the western portions of Washington, Oregon, and northern California and is characterized by high precipitation and mild temperatures. Along the Pacific Coast, western hemlock, Sitka spruce, and balsam fir forests dominate the northern regions, while Douglas fir and coast redwood dominate the southern regions (NABCI 2012). Montane forests of western hemlock (*Tsuga heterophylla*), Douglas fir, evergreen hardwood, white fir, grand fir (*Abies grandis*), and Pacific silver fir (*Abies amabilis*) dominate inland regions, along with oak woodland (*Quercus* spp.), oak savannah, and shrublands (Huff et al. 2005).

Historically, wet coastal forests in the Pacific Northwest experienced infrequent high-severity fire, with a fire return interval of over 100 years, while drier inland and montane forests were characterized by a mixed-severity fire regime with a fire return interval of 5 to 75 years (Agee 1991, 1993, 1998; Huff et al. 2005). In southwestern Oregon and northwestern California, it is thought that the mixed-conifer/hardwood forests that characterize this region historically burned frequently, supporting a variety of seral shrubs and fire-adapted hardwoods (Agee 1993). Due to the long historic fire return interval in wet coastal forests, fire suppression is not currently of management concern. In drier montane forests and lowland habitats, however, fire suppression is believed to have led to an accumulation of fuels, increased incidences of high-severity fires, and conifer encroachment in oak woodland and savannah habitats (Huff et al. 2005). In southwestern Oregon and northwestern California, fire suppression has altered forest structure in favor of conifers and at the expense of hardwood and mixed-conifer/hardwood forests (Betts et al. 2010). Population estimates for hummingbirds in BCR 5 are presented in table 7.

Table 7—Western hummingbird percent global population and population estimates for BCR 5: Northern Pacific Rainforest.

Species	% Global population	Population estimate
Allen's Hummingbird	42.1	300,000
Anna's Hummingbird	6.6	300,000
Rufous Hummingbird	75.3	8,000,000
Calliope Hummingbird	1.2	30,000
Black-chinned Hummingbird	0.0	1,500
Total		8,631,500

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

The Northern Rockies region (BCR 10) includes the Rocky Mountains and outlying ranges of Montana, Idaho, and northwestern Wyoming. This region is dominated by ponderosa pine, Douglas fir, and lodgepole pine forests at lower elevations, with Engelmann spruce (*Picea engelmannii*) and subalpine fir forests at higher elevations. The mesic north and west edges of the Rockies are dominated by western larch (*Larix occidentalis*), grand fir, western red cedar (*Thuja plicata*), and western hemlock forests. Northern Rockies forests historically experienced a range of fire frequencies and severities (Schoennagel et al. 2004). It is thought that lower elevation ponderosa pine forests historically experienced a frequent, low- to mid-severity fire regime, while mid- to high-elevation forests experienced less frequent, higher severity fires (Brown and Kapler Smith 2000; Veblen et al. 2000). It is thought that fire suppression in northern Rockies forests has led to heavy accumulations of dead and living fuels, uniform stands of late-successional forests, and an increased likelihood of uncharacteristically severe wildfires (Barrett et al. 1991). Population estimates for hummingbirds in BCR 10 are presented in table 8.

Table 8—Western hummingbird percent global population and population estimates for BCR 10: Northern Rockies.

Species	% Global population	Population estimate
Calliope Hummingbird	61.8	1,500,000
Black-chinned Hummingbird	2.8	130,000
Broad-tailed Hummingbird	1.2	110,000
Rufous Hummingbird	17.8	2,000,000
Total		3,740,000

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

Few studies have examined the effects of wildfire on birds in Pacific Northwest forests. Huff et al. (1985) studied postfire bird communities in montane forests of Olympic National Park, Washington. In this study, bird species richness and diversity were highest 19 years after fire. A higher percentage of species bred only in forests in the stand initiation stage from 1 to 19 years after fire, and during this period there were higher abundances of ground and shrub associated species and lower abundances of canopy-feeding species. Fontaine et al. (2009) found that in northwestern California and southwestern Oregon, repeatedly burned habitats were characterized by shrub-nesting and ground-foraging species, while unburned mature forests were characterized by conifer-nesting and foliage-gleaning species. These results are similar to those from other forest types in the western United States (Bock and Lynch 1970; Raphael et al. 1987; Saab et al. 2007). More recent studies have noted that fire severity plays an important role in individual species and community-level responses following wildfire (Stephens et al. 2015). Betts et al. (2010) noted that Rufous Hummingbirds were positively associated with early seral broadleaf forests in the Pacific Northwest. These habitats, which historically experienced frequent fire, are in decline across the region, likely due to combined effects of fire suppression and conifer-intensive management practices (Kennedy and Spies 2005).

In Huff's (1985) study, Rufous Hummingbird was one of the most abundant species 19 years after fire. In the same paper, however, Huff (1985) described the results of a chronosequence study of seven forested plots in Olympic National Park ranging from 1 to 515 years postfire. In this analysis, Rufous Hummingbird was found to have a "mixed" response to fire. Calder (1993) cites a study from Meslow and Wight (1975) which found that Rufous Hummingbirds nested in second-growth forests from 16 to 120 years old, as well as in mature forests greater than 120 years old. These results suggest that Rufous Hummingbirds use primarily mid-successional to mature forest habitats for nesting.

Little information is available on the response of the Calliope Hummingbird to fire in Pacific Northwest forests. Marcot (1984) found that Calliope Hummingbirds were associated with Douglas fir forests in the shrub-sapling stage of succession 14 years after fire in north-western California. This suggests that Calliope Hummingbirds may prefer shrubby habitats in early succession (8 to 15 years postfire) for nesting. Results from fire and avian ecology studies in the Sierra Nevada also indicate that Calliope Hummingbirds prefer shrubby, early successional postfire habitats for nesting (Burnett et al. 2011; Raphael et al. 1987).

Studies of avian ecology and wildfire in the northern Rockies indicate that wildfire, including high-severity fire, is beneficial for many birds, and that a range of fire severities and frequencies across the landscape provide for a diversity of bird species (Hutto 1995; Kotliar et al. 2002; Saab and Powell 2005; Smucker et al. 2005; Taylor and Barmore 1980). Smucker et al. (2005) demonstrated that avian responses to fire can vary significantly with fire severity and that postfire bird communities after high-severity fire were unique. Hutto (1995) also found that bird communities after high-severity fire were unique, with seed-eating, timber-drilling, and insectivorous birds being most abundant.

While detections of hummingbirds in fire and avian ecology studies in the northern Rockies are low, available data indicate that Calliope Hummingbirds increase in abundance in early successional postfire forests, especially in forests that burned at moderate to high severities (Hutto 1995; Smucker et al. 2005). Smucker et al. (2005) studied avian responses to

a 125,000-hectare wildfire in mixed-conifer forests that burned at variety of severities across the Bitterroot National Forest in Montana in 2000. In this study, nearly twice as many bird species increased as decreased in response to fire. Rufous Hummingbirds declined slightly postfire at unburned points and were not detected at burned points before or after the fire. Calliope Hummingbirds increased in abundance postfire at both previously burned and previously unburned points, although the increase was greater at previously unburned points. Slightly more Calliope Hummingbirds were detected at points that burned at moderate to high severities than at points that burned at low severity or did not burn. Rufous Hummingbirds declined slightly postfire at unburned points and were not detected at burned points before or after the fire. These results are similar to those of fire and avian ecology studies in the Pacific Northwest, which indicate that Calliope Hummingbirds prefer early successional forests for nesting, while Rufous Hummingbirds may decline after fire (Marcot 1984; Meslow and Wight 1975). Caution is needed in interpreting these results, however, as detection rates were low.

In a study of bird community composition following a series of wildfires in northern Wyoming and western Montana, Hutto (1995) detected Calliope Hummingbirds at six burned sites and Rufous Hummingbirds at four burned sites. These detection rates are too low to draw meaningful conclusions; however, combining these data with bird survey data from throughout the northern Rockies, Hutto (1995) found that Calliope Hummingbirds were most abundant 10 to 40 years postfire. Saab et al. (2005) cited a study from Harris (1982) indicating that Calliope Hummingbirds had a positive response to wildfire from 1 to 4 years after a 120,480-hectare fire in a mixed-conifer forest in the northern Rockies. Bird species including Calliope Hummingbird benefit from high-severity fire, even though the positive response may not be detected for 10–30 years (Hutto and Patterson 2016). Overall, results from fire and avian ecology studies in the northern Rockies indicate that Calliope Hummingbirds prefer early successional postfire habitats for nesting, while Rufous Hummingbirds possibly decline or have variable responses to fire.

Restoration and Hummingbirds

Several studies from Pacific Northwest forests indicate that Rufous Hummingbirds increase in abundance in managed stands immediately after logging and prescribed fire. Bettinger (1996) studied bird communities in Douglas fir forests in western Oregon that had been managed through logging and prescribed fire. Rufous Hummingbirds were significantly more abundant in managed, open-canopy stands, although no habitat variables were significantly associated with their abundance. Morrison and Meslow (1983) found similar results in a study of bird communities after logging and prescribed fire in western Oregon. In this study Rufous Hummingbirds were one of the most abundant species on early clearcuts, and their presence was associated with a low shrub-herb layer and low deciduous tree cover. Rufous Hummingbirds decreased in abundance with increasing stand age in this study.

Betts et al. (2010) noted that Rufous Hummingbirds are positively associated with early seral mixed conifer-hardwood forests in the Pacific Northwest. These results conflict some-what with those fire and avian ecology studies, which indicate that Rufous Hummingbirds may decline after fire and that they may prefer forests from 16 to 20 years into secondary succession as well as mature forests for nesting (Huff 1985; Meslow and Wight 1975). It is possible that Rufous Hummingbirds use early clearcuts and burned habitats for foraging, while they nest primarily in mid-successional to mature forested habitats with slightly more canopy cover in

the Pacific Northwest. Rufous Hummingbirds have been observed in large numbers in postfire habitats in the Sierra Nevada during migration (Burnett et al. 2011), indicating that these habitats are likely important to the species for foraging as well as during migration. Therefore, it is possible that both early to mid-successional forests as well as mature forests are important for Rufous Hummingbirds.

The majority of studies of the effects of management practices on birds in the northern Rockies focus on silvicultural treatments, and few have examined the effects of prescribed fire. In a review of the effects of silvicultural treatments on birds in the Rocky Mountains, Hejl et al. (1995) compared bird abundances in unlogged forests with early successional forests after clearcutting. In this synthesis, Calliope Hummingbirds were always more abundant in partially logged forests than in unlogged forests. Rufous Hummingbirds were associated with "tall shrub" clearcuts, but the species was equally abundant in recent clearcuts and unlogged forests. These results align with wildfire studies indicating that Calliope Hummingbirds consistently prefer open habitats while Rufous Hummingbirds are more variable in their habitat selection. In this study Broad-tailed Hummingbirds were most abundant in tall-shrub clearcuts, a result that aligns with those of fire, restoration, and avian ecology studies in the southern Rockies, where they primarily breed.

Management Implications

Rufous and Calliope Hummingbirds use early to mid-successional forests for nesting and foraging in the Pacific Northwest (Calder 1993; Calder and Calder 1994). In inland montane and mixed-conifer/hardwood forests of the Pacific Northwest, fire suppression and other management practices have altered forest structure and reduced the amount of hardwoods and early successional habitat across the region (Agee 1993). The loss of these habitats, as well as increases in forest stand densities, has likely had detrimental effects on both the Rufous and Calliope Hummingbird (Huff et al. 2005). Restoration efforts that increase the amount of early and mid-successional forest habitats and encourage the regeneration of hardwoods are likely to benefit these species. Early successional forest habitat availability following timber harvest may provide habitat for Rufous Hummingbirds, but in a study of herbicide treatments in early seral forests, Rufous hummingbirds were significantly sensitive to intensive management herbicide treatments (Betts et al. 2013). More research is needed to determine how timber management practices may alter important habitat characteristics in early seral forests for Rufous hummingbirds.

In inland montane forests, the restoration of a mixed-severity fire regime as was characteristic historically, with a fire return interval of 5 to 75 years, will likely benefit both Rufous and Calliope Hummingbird by increasing the amount of early successional habitats. In habitats that were historically characterized by mixed-conifer/hardwood forest types, the restoration of a mixed-severity fire regime that incorporates high-severity fires will likely benefit Rufous Hummingbirds and other birds that use these forest types (Fontaine et al. 2009; Swetnam et al. 1999). Prescribed fire can be used as a management strategy to increase the amount of early to mid- successional habitat and to encourage the regeneration of hardwoods, and will be beneficial for hummingbirds through encouraging the regeneration of flowering plants. Both Rufous and Calliope Hummingbird use open, shrubby habitats created through fire and logging; therefore, both of these species should be able to tolerate some forest harvest in the context of larger restoration objectives. Because these species use open habitats for

foraging, management that promotes the restoration and maintenance of natural forest openings like meadows across the landscape will be beneficial (Hagar and Stern 2001; Huff et al. 2005).

Wildfire and avian ecology studies indicate that fire, at a variety of frequencies, scales, and severities, is critical to maintaining avian diversity and abundance, as well as vegetative diversity, in northern Rockies forests (Agee 1993; Hutto 1995; Hutto et al. 2008; Kotliar et al. 2002). In this region, burned habitats, including those that burned at high severities, support a high diversity of bird species and unique bird communities (Saab et al. 2005). Many flowering plants in the northern Rockies, including heartleaf arnica (*Arnica cordifolia*), broadleaf arnica (*Arnica latifolia*), showy aster (*Eurybia conspicua*), and fireweed (*Chamaenerion* spp.), are adapted to resprout after fire (Frye 1934; Moss 1936). In the northern Rockies, Calliope Hummingbirds demonstrate a clear preference for the open, shrubby habitats characteristic of early postfire habitats. Rufous Hummingbirds demonstrate a mixed response to fire. Management that aims to restore historic fire regimes and promote the development of a mosaic of successional stages across the landscape will likely benefit both Calliope and Rufous Hummingbird. These goals can be achieved through the reintroduction of frequent, low- to- mixed-severity fire at lower elevations and infrequent, stand-replacing fire at higher elevations (Hejl et al. 1995; Hutto 1995; Saab et al. 2005; Smucker et al. 2005). Based on limited information, both species appear to be tolerant of some forest harvest in the context of these management objectives. The effects of prescribed fire on hummingbirds in northern Rockies habitats are unknown but are likely to be comparable to the effects of wildfire.

Southern Rockies/Colorado Plateau

Habitats and Fire Regimes

The Southern Rockies /Colorado Plateau region (BCR 16) extends through southern Wyoming, central and western Colorado, eastern Utah, and northern Arizona and New México. It includes the Wasatch and Uinta mountains to the west and the southern Rocky Mountains to the east, separated by the tableland of the Colorado Plateau (NABCI 2012). Engelmann spruce, subalpine fire, and lodgepole pine forests dominate the higher elevations, while pinyon-juniper woodlands are found at lower elevations. Ponderosa pine forests dominate higher elevations of the Colorado Plateau above 6,000 ft, as well as much of northern Arizona, New México, eastern Utah, and western Colorado. It is thought that mid- to high-elevation mixed-conifer forests of the southern Rockies historically experienced infrequent, high-severity fires, while ponderosa pine forests of the Colorado Plateau, Arizona, and New México historically experienced frequent, low- to mid-severity fires (Brown and Kapler Smith 2000; Fischer and Bradley 1987; Shinneman and Baker 1997).

Fire suppression is thought to have altered forest composition in the southern Rockies. While historically ponderosa pine forests in this region were open and parklike, with a low accumulation of fuels, many of these forests are now crowded, with large accumulations of fuel (Brown and Davis 1973). Fire suppression at higher elevations may have also led to accumulations of fuel and to even-aged, decadent forest stands at risk for uncharacteristically severe fire (Barrett et al. 1991). Population estimates for hummingbirds in BCR 16 are presented in table 9.

Table 9—Western hummingbird percent global population and population estimates for BCR 16: Southern Rockies/ Colorado Plateau.

Species	% Global population	Population estimate
Black-chinned Hummingbird	17.7	800,000
Broad-tailed Hummingbird	48.4	4,700,000
Anna's Hummingbird	0.9	30,000
Total		5,530,000

Source: Partners in Flight Landbird Population Estimates Database, http://pif.birdconservancy.org/PopEstimates/Database.aspx.

Wildfire and Hummingbirds

Studies of avian ecology and wildfire in the southern Rockies indicate that many avian species do not change in abundance after low to moderate-severity fire, but that high-severity fire may affect bird abundance and community composition. For example, Kotliar et al. (2007) found that after wildfire in a mixed-conifer forest in New México, pre- and postfire bird communities were similar except in areas of high-severity fire, and species richness was similar pre- and postfire across all fire severities. Four species demonstrated significant effects of fire severity, and their densities were all higher in burned compared to unburned forests. A comparison study of bird responses to fire severity in Arizona (with historical low-severity fire regime) and Idaho (with historical mixed-severity fire regime) found that more species responded negatively to wildfire in Arizona and positively to wildfire in Idaho. The study highlighted the importance of considering individual species life history and regional differences in historical fire regimes when predicting bird responses to mixed-severity fires (Latif et al. 2016).

Broad-tailed Hummingbirds demonstrate a positive response to moderate and high-severity fire in the southern Rockies. In Kotliar et al.'s (2007) study, Broad-tailed Hummingbird densities were slightly lower postfire, except at the high-severity burn level, where their densities were higher postfire. Broad-tailed Hummingbirds' mean densities were highest on high-severity plots both one and two years after fire. The authors attributed these high densities to an increase in flowering plants in areas that burned at high severities (Kotliar et al. 2007). In a review of avian responses to fire in the southwestern United States, Bock and Block (2005) indicated that Broad-tailed Hummingbirds showed a positive response 3 years after moderate-severity wildfire in a ponderosa pine forest in Arizona.

Restoration and Hummingbirds

Studies indicate that many birds are tolerant of low- to moderate-severity prescribed fire, as well as thinning practices, in ponderosa pine forests of the southern Rockies. In a study of avian responses to prescribed fire in ponderosa pine forests of Arizona and New México, Dickson et al. (2009) found most breeding birds to be tolerant of low- to moderate-severity fire. Bagne and Finch (2005) studied avian responses to thinning in ponderosa pine forests in

New México. The study found that avian responses generally only lasted 1 or 2 years, and that many species had no response to the treatments. In a study of bird responses to thinning treatments in ponderosa pine forests in Arizona, occupancy for several songbird species and species richness was generally higher in sites with larger trees and higher snag density, and lower in sites with greater canopy cover (Kalies and Rosenstock 2013).

Several studies indicate that the Broad-tailed Hummingbird responds positively to logging, thinning, or other treatments that create open habitats in the southern Rockies. Blake (1982) studied bird communities on burned and unburned plots in ponderosa pine forests in northern Arizona in 1973 and 1974. Logging had occurred on two burned and two unburned plots. In this study, 14 species had positive responses to thinning, five had negative responses, seven had no responses, and one had a mixed response. Broad-tailed Hummingbirds were most abundant on sites that were burned and clearcut and were not detected on unburned, uncut sites. In a synthesis of studies comparing bird abundances in unlogged forests with early successional forests after clearcutting in the Rocky Mountains, Hejl et al. (1995) found that Broad-tailed Hummingbirds were generally more abundant in clearcuts than in unlogged areas. Szaro and Balda (1982, 1986) found that in southwestern ponderosa pine forests, Broad-tailed Humming-birds preferred moderately to heavily disturbed areas, and that the species reached its highest population densities on treated plots.

Management Implications

Studies of avian responses to fire and restoration in the southern Rockies indicate Broad-tailed Hummingbirds increase in abundance after high-severity fire. These increases are likely due to the profusion of flowering plants in these postfire habitats (Kotliar et al. 2007). Broad-tailed Hummingbirds are also thought to prefer nesting in open and shrubby habitats that are prevalent after fire (Calder 1992). Hejl (1994) suggested that declines in the Broad-tailed Hummingbird may be due to decreases in the prevalence of burned forests. Therefore, Broad-tailed Hummingbirds are likely to benefit from treatments that increase the amount of early successional postfire habitats in the southern Rockies, including areas that burned at high severities (Block and Finch (1997). Broad-tailed Hummingbirds are also likely compatible with some degree of timber harvest and/or thinning in the southern Rockies (Blake 1982; Hejl et al. 1995).

The application of low to moderate-severity prescribed fire in ponderosa pine forests of the southern Rockies is likely to benefit Broad-tailed Hummingbirds through increasing the amount of early successional habitat and flowering plants. Due to a long history of fire suppression in these habitats, it is thought that prescribed fire efforts will have to be scaled up significantly in order to restore southwestern ponderosa pine forests to historic conditions (Finch et al. 2007). However, it will be important to ensure that fire, both wild and prescribed, remain within the range of historical variation, both in frequency and intensity. In a study of understory plant responses to restoration treatments (including no treatment, thinning, thinning and prescribed fire, prescribed fire, and wildfire of varying intensity) in northern Arizona ponderosa pine forests, Griffis et al. (2001) found that exotic plants increased in richness and abundance with treatment intensity, while the abundance of native shrub species decreased with treatment intensity, especially after wildfire. To prevent the spread of exotic shrubs, techniques like prefire forest thinning may be required to reintroduce fire to areas where it has been excluded for long periods of time (Covington et al. 1997).

In mixed-conifer forests of the southern Rockies, the restoration of a mixed-severity fire regime with areas of high-severity fire will create landscape-scale heterogeneity as well as provide habitat for species dependent on heavily disturbed habitats, including the Broad-tailed Hummingbird. Restoring high-severity fire to mixed-conifer forests of the southern Rockies may help to reverse declines in Broad-tailed Hummingbird and other species dependent on these habitats (Brawn and Balda 1988; Hejl 1994).

Conclusion

Disturbance is a major driver of biological and structural diversity at habitat, stand, and landscape scales (Brawn et al. 2001). Fire is a natural disturbance that has shaped the ecosystems of western North America for millennia. Policies of fire suppression throughout much of the 20th century are thought to have led to increased fuel loads and shifts in forest stand composition, leading to more frequent, large-scale, and higher severity wildfires that are damaging to human communities as well as forest health and wildlife populations (Schoennagel et al. 2004). The combined effects of fire suppression and the introduction of exotic grasses in arid habitats of the western United States are thought to be altering habitat structure and increasing fire frequencies in these habitats. Trends toward a warmer, drier climate are also thought to be influencing the pattern and scale of wildfires, with a trend toward more frequent and severe fires (Trouet et al. 2010). These changes have caused concern among land managers charged with maintaining forest and ecosystem health, as well as among scientists, landowners, and the public.

As land managers design, implement, and scale up restoration projects that aim to improve forest and aridland health and increase the resilience of western ecosystems to a changing climate, it is important to understand the impacts of fire and fire-adapted ecosystem restoration on wildlife populations. The literature presented in this review suggests that, while hummingbirds face a variety of potential challenges on their breeding grounds in the western United States, their persistence is compatible with many fire-adapted ecosystem restoration efforts. Hummingbirds evolved in the context of wildfire, and are adapted to feeding on nectar from flowering plants, which flourish in open, disturbed areas, especially after fire (Brown and Kapler Smith 2000); hummingbirds can quickly take advantage of new food resources from disturbances following fire. Many flowering plants are adapted to resprout or germinate after fire.

In southwestern desert scrub and riparian habitats, the control of exotic plants is a critical management issue and is likely to pose a continued challenge under climate warming scenarios (Smith et al. 2000). The invasion of buffelgrass and the subsequent conversion of southwestern desert scrub habitats to homogenous grassland has potentially serious implications for hummingbirds that nest in desert scrub, including the Costa's and Black-chinned Hummingbird, as well as for hummingbirds that use these habitats during migration. In southwestern riparian habitats, the spread of tamarisk and the subsequent increased risk of catastrophic fire pose a serious threat to breeding birds that use these habitats, including the Black-chinned Hummingbird. While prescribed fire is not advised in desert scrub, it may have a role in riparian restoration in the Southwest when used in careful combination with mechanical treatment, herbicide application, and the replanting of native species. In desert scrub,

manual and mechanical treatments to remove buffelgrass, along with herbicide application, should continue on an experimental scale, with monitoring to ensure the successful reduction or eradication of exotics.

In California coastal scrub and chaparral habitats, the Costa's Hummingbird is thought to use postfire habitats, although data are limited, and Anna's Hummingbirds appear to decline immediately after fire. Unfortunately, virtually nothing is known about Allen's Hummingbirds' response to fire or restoration, but their restricted range and specific habitat requirements indicate that this species is highly sensitive to habitat fragmentation. Costa's Hummingbirds are also thought to be highly sensitive to habitat fragmentation; therefore, the preservation of existing large, undisturbed stands of coastal scrub and chaparral is likely of critical importance to both the Allen's and Costa's Hummingbirds, both species of conservation concern. Management efforts in intact coastal scrub and chaparral stands should focus, as much as possible, on allowing natural fires to burn and on restoring a diversity of successional stages to maximize bird abundance and diversity (CalPIF 2004; Westman 1987). In habitats that are fragmented or degraded, management efforts should focus on the removal of exotics and on the development of intact corridors between habitats as well as buffers between habitat patches and developed areas (Eliason and Allen 1997; Allen et al. 2000).

In forested ecosystems of the western United States, several hummingbird species, including Rufous, Calliope, and Broad-tailed Hummingbird, show a clear preference for the open, disturbed, early successional habitats created through fire (Wethington and Finley 2009). Broad-tailed Hummingbirds' abundance has been positively correlated to areas of high-severity fire, and Calliope Hummingbirds are consistently more abundant in habitats that have been disturbed through fire (Bock and Block 2005; Kotliar 2007; Smucker et al. 2005). Rufous Hummingbirds are also known to use postfire and clearcut habitats, although they may prefer mature forests for nesting (Huff 1985; Meslow and Wight 1975; Morrison and Meslow 1983). Studies of avian ecology and fire indicate that wildfire benefits aerial foraging and insectivorous birds, which share similar foraging strategies to hummingbirds (Bagne and Purcell 2011; Hutto 1995). Therefore, restoration efforts that aim to increase the amount of early and mid-seral habitat in forested ecosystems in the western United States are likely to benefit hummingbirds as well as other birds that use these habitats. Whenever possible, prescribed fire, alone or in combination with thinning or mechanical treatments, is preferred to logging or thinning alone in forested habitats. Prescribed fire stimulates germination and growth in flowering plants and creates spatial heterogeneity (Imbeau et al. 1999).

As land managers move forward with planned restoration projects, there are many opportunities to continue to broaden our understanding of hummingbirds' habitat selection, movements, and responses to fire and fire-adapted ecosystem restoration efforts. While more research is needed and warranted, the existing fire and avian ecology literature provides a strong conceptual framework from which to move forward with needed restoration efforts, despite uncertainty. Land managers should strive to integrate bird monitoring into restoration projects in the early planning stages with a Before, After Control Impact approach. As fire and avian ecology research methodologies and hummingbird monitoring techniques continue to improve, so will our ability to draw inferences about the factors limiting hummingbird populations and the potential effects of planned restoration efforts. Close cooperation between land managers and the scientific community will be key to developing and prioritizing management actions that will benefit western hummingbirds throughout their migratory ranges.

Research, Inventory, and Monitoring Priorities

There is a need for Before, After Control Impact approach studies to understand the impact of fire on hummingbird populations. Long-term monitoring of hummingbird population trends are available through North American Breeding Bird Surveys (Rosenberg et al. 2017). Trends in occurrence and inventory of some North American species can be acquired through Christmas Bird Counts (National Audubon Society 2010) or eBird (https://ebird.org/). Still, there are limits to those methodologies for studying hummingbirds due to the timing of the migration polygynous mating system and other unique life history traits.

The following research, inventory, and monitoring priorities were identified through this review. Many align with those set forth in the Western Hummingbird Partnership Action Plan (Contreras-Martínez 2015; Contreras-Martínez et al. 2017; Wethington et al. 2010). Bird monitoring should be incorporated into land management and restoration efforts before, during, and after the treatments to assure that the ecological objectives of restoration are being met.

Improve Hummingbird Monitoring and Data Sharing Techniques

There is a critical need to improve and expand upon existing hummingbird population monitoring techniques, as well as to encourage and facilitate the sharing of data among cooperators. Improvement in monitoring techniques are needed to determine hummingbird responses to fire effects and postfire restoration. The following steps are recommended:

1. *Expand hummingbird banding locations to replicate sites and sample a broader range of ecotypes.*
   The expansion of hummingbird banding efforts is valuable for understanding hummingbird demographics, population trends, migration routes, and timing. However, there is a need to establish banding locations that have replicated sites that are representative of a spectrum of habitats within ecozones and conditions (e.g., exposed vs. not exposed to fire; fragmented vs. unfragmented; forested vs. meadow; a spectrum of successional habitat and altitudinal variation; migration versus breeding locations). Training and support should be provided for existing and new hummingbird banding efforts, and existing bird banding stations should be provided with the training and resources necessary to accurately identify, age, and band hummingbirds.

2. *Explore new monitoring methods for hummingbirds.*
   When typical breeding bird survey techniques are applied, hummingbirds are challenging to monitor compared to passerines (for which many survey methods have been developed). Field identification requires specialized training due to the unique vocalizations, timing of breeding, and polygynous mating systems of hummingbirds. Existing monitoring techniques should be refined or improved, or new monitoring strategies should be developed, to improve hummingbird monitoring data collection, particularly adjusting the timing of surveys to identify migration phenology and breeding densities.

3. *Streamline hummingbird monitoring, data collection, and reporting techniques among cooperators.*

4. Encourage the sharing of hummingbird data among cooperators through the use of data sharing portals, e.g., the Avian Knowledge Network.

Address Information Gaps Regarding Hummingbird Biology and Life History

Basic information gaps remain in our understanding of hummingbird movements, populations, and habitat selection. The following are key areas requiring study:
1. Abundance and distribution at landscape and regional scales
2. Habitat selection and specific habitat requirements
3. Migration and seasonal movement patterns
4. Site fidelity and adult dispersal
5. Reproductive strategies

Understand Hummingbird Demographics and Factors Limiting Populations

There are many gaps in our understanding of the factors limiting hummingbird populations, including:
1. Population trends
2. Estimates of population size
3. Where populations are limited
4. Reproductive success, including factors related to nesting success
5. Estimates of adult and juvenile survivorship
6. Source/sink dynamics, dispersal, and recruitment

Synthesize Predicted Climate Change Impacts on Phenology of Key Plant Species for Hummingbirds

There is a critical need to understand the potential impacts of climate change on the phenology of flowering plants, especially those plants that are key nectar sources for hummingbirds. Variations in precipitation, snowpack, timing of snowmelt, and drought cycles are likely to seriously impact flowering plant phenology and, in turn, hummingbirds. As a starting point, we recommend the development of a matrix of key flowering plants for western hummingbirds on their breeding, migration, and wintering grounds, accompanied by a synthesis of known or anticipated climate change impacts on these plants.

Study the Effects of Changing Fire Frequencies and Severities on Hummingbirds' Food Sources

Fire suppression and climate change are likely leading to alterations in historic fire regimes and forest stand structures, leading to fire frequencies and intensities that are outside of the range of historic variation. There is a need to understand how these changes are affecting hummingbird food sources. For example, Keeley and Zedler (1978) suggested that shorter fire frequencies may, over time, favor resprouting plant species over reseeding species. Carpenter and Recher (1979) noted that resprouting species generally produce fewer and smaller flowers that produce less nectar and are less fragrant than reseeding species, which allocate more

resources to flower production and pollination (Fulton and Carpenter 1979). Resprouting species also tend to grow more slowly and reach smaller sizes during the first 10 to 20 years after fire (Carpenter and Recher 1979). Furthermore, very intense fires may kill the regenerative structures of resprouting plants, even those that are adapted to fire. How hummingbirds will be affected by these potential changes is unknown.

Assess the Long-Term Impacts of Restoration on Hummingbird Populations

Most of the studies in this review assess the short-term (1 to 5 years) impacts of fire and restoration. In general, avian responses to fire are complex due to variation in ecological conditions, fire severity, and time since fire, making species and context-specific studies important for assessing management and restoration impacts (Hutto et al. 2015). It is recommended that restoration efforts, when possible, incorporate monitoring prior to fire events and thereafter for 5 to 10 years, to control for variation in hummingbird movements and site selection from year to year and to assess the medium to long-term impacts of restoration.

Assess Seasonal Timing of Prescribed Fire in Relation to Hummingbirds

It is generally recommended that managers avoid burning during the nesting season for migratory birds. For hummingbirds in North America, this period can extend from February through July. Therefore, to minimize impacts to nesting hummingbirds, fall burning is recommended, although prescribed burning in the spring may help promote the growth of flowering plants, which could possibly benefit hummingbirds (Allen et al. 2000; Huff et al. 2005; Thies et al. 2005). More study is needed in this area.

Study the Effects of Herbicide Application on Hummingbirds in Southwestern Desert Scrub and Riparian Habitats

Herbicide application to control exotics in southwestern desert scrub and riparian habitats has found some success experimentally, but the short or long-term effects of herbicide application on hummingbirds as well as other birds is unknown.

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