



Evidence of the effects of climate change on landbirds in western North America: A review and recommendations for future research

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Abstract: To evaluate the effects of climate change on landbirds in western North America, we reviewed the published literature on changes in avian phenology, geographic distribution, morphology, physiology, and population size that have been linked to climate change in the region. Despite a large literature on the projected effects of climate change, we found surprisingly few published papers that evaluated effects already observed on western North American landbirds. The topic that has received the most attention is the phenology of migration and reproduction. However, researchers have demonstrated consistent patterns of phenological change in fewer than 10 of the region's species. Similarly, shifts in the elevational distribution of birds have not been consistent with the expectation that climate change will cause species to shift upward in elevation. Demonstrable effects of climate change, or in some cases lack thereof, will improve future projections of its effects and efforts toward conservation. Some data from which changes can be evaluated are already available. Our review demonstrates that there is still a very real need to understand how climate change is already affecting landbirds in western North America.

Keywords: breeding, migration, molt, niche, passerines, phenology, physiology

The scientific literature is crowded with papers that project future effects of climate change on birds and the ecosystems in which they live. Although these papers are important, we know that our climate has already changed. Over the last 100 years, global temperatures have increased approximately 1 °C (Jones et al. 2012). The projections agree that climate change will dramatically alter ecological systems, and reports demonstrate that these changes have begun (Root et al. 2003, Burrows et al. 2011). Temperatures in North America have tracked or exceeded the global temperature change, and in parts of California and the Southwest, there is evidence that average temperatures may have risen by up to 2 °C (Polley et al. 2013, Walsh et al. 2014). These changes have been linked to decreasing snow pack, earlier snowmelt, and above-average tree mortality (Mote et al. 2005, Stewart et al. 2005, van Mantgem et al. 2009, Pederson et al. 2011). However, how much evidence do we already have that these changes are affecting ecosystems and the birds within them?

Birds provide a unique opportunity for understanding the ecological consequences of climate change. In part, this is because birds serve as ecological indicators of changing systems (Vos et al. 2000, Gregory and van Srien 2010). Perhaps as important, the popularity of birds as objects of study and recreation means that long-term records are available (e.g., Miller-Rushing et al. 2008). As a result, there have been a number of research efforts to understand how recent climate change has affected bird populations, species, and communities (Crick 2004, Møller et al. 2010, Pearce-Higgins and Green 2014).

Here we review the evidence for effects of climate change on landbirds in western North America, which we define as extending from the Rocky Mountain states to the Pacific states and provinces, including Alaska and Hawai'i, western Texas, and northwestern Mexico. Following Partners in Flight (Rich et al. 2004), we define landbirds as birds that have a primarily terrestrial life cycle. We review published studies that have linked climate change to changes in avian

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phenology, geographic distribution, morphology, physiology, and population size. We limited our review to studies that have attempted to quantitatively or qualitatively associate observed changes in bird populations with climate change forced by anthropogenic emissions of greenhouse gases, and we did not review the large body of literature projecting effects of climate change (e.g., Stralberg et al. 2009, Dybala et al. 2013). We discuss in less detail the vast literature on the responses to year-to-year or decadal variation in weather or climatic conditions (e.g., Skagen and Yackel-Adams 2012). While these types of studies, especially when paired with regional climate projections, offer a wealth of information about the potential effects of climate change on birds, summarizing this information was beyond the scope of this review. However, given the important role of annual and decadal climate variability as a driver of birds' population dynamics, we have noted situations where these patterns may mask or enhance the effects of anthropogenic climate change, or may serve as a proxy for the effects of climate change. Although we focused on birds in western North America, we also considered continent-wide studies that were relevant to species occurring in the West. Finally, we highlight important gaps in our knowledge of how climate change may be affecting bird populations in western North America and suggest directions for future study.

CHANGES IN THE PHENOLOGY OF MIGRATION, REPRODUCTION, AND MOLT

As the climate shifts, there is evidence that the phenology of many plants and animals is shifting to track or otherwise respond to these changes (Parmesan and Yohe 2003, Root et al. 2003). For landbirds, shifts in the phenology of migration have received the most attention (Gordo 2007, Rubolini et al. 2007, Hurlbert and Liang 2012), in part because of the availability of relevant long-term datasets. Evaluating shifts in the timing of nesting (initiation, cessation, incidence of double-brooding, or overall length of breeding season) has also received some attention (Crick and Sparks 1999). Changes in the timing of molt have received less attention (but see Conklin and Battley 2012, Barshep et al. 2013). Shifts in phenology can vary at different trophic levels, causing the uncoupling of peak resources and periods of birds' lives in which they rely on abundant food (Both et al. 2006). Understanding phenological responses to climate change is important because these changes may be closely tied to a species' ability to persist in the face of rapid climate

change (Both and Visser 2001, Møller et al. 2008, Charmantier and Gienapp 2014).

Migration

In recent years, studies based on long-term data have documented shifts in the phenology of migration, particularly in spring; changes are often associated with temperature and climate variables (e.g., Marra et al. 2005, Van Buskirk et al. 2009). In some cases, longer-distance migrants have been found less likely to advance their spring migration with the changing climate than have short-distance migrants (Miller-Rushing et al. 2008, Hurlbert and Liang 2012). Although to date fall migration has received less attention (Gallinat et al. 2015), a few studies have found changes in dates of departure in fall, but direction of those changes has been variable (Cotton 2003, Jenni and Kéry 2003, Mills 2005). Extreme events, and how birds respond to changes in weather or large-scale wind-circulation patterns during migration, can also influence migration phenology (Gill et al. 2014, Senner et al. 2015). Therefore, migratory birds may be vulnerable if conditions during migration become less favorable.

While numerous studies have examined phenological shifts in migration of landbirds, particularly for those that breed in Europe or eastern North America, only a few studies have documented changes in western North American species. In a study of 21 species of migratory landbirds in California, MacMynowski et al. (2007) found significant or near-significant advancement of their spring arrival date in eight; two arrived later, and the change of three differed at different sites. Of the 13 species exhibiting a change in arrival date, the timing of arrival of 10 (77%) was correlated with both temperature and an index of large-scale climate oscillation, indicating an association between arrival time and climate change. In the Colorado Rockies, Inouye et al. (2000) found some evidence for earlier arrival of the American Robin (*Turdus migratorius*) at high elevations, but because the amount of snowfall and date of first bare ground had not changed, they hypothesized that the earlier arrival was driven by changes on the winter grounds at lower elevations. Last, a study of 16 migratory species that breed in northern Alaska documented significant advances in spring arrival dates for all species, including the two landbirds considered, the Snow Bunting (*Plectrophenax nivalis*) and Lapland Longspur (*Calcarius lapponicus*) (Ward et al. 2015). Examining local (e.g., temperature) and regional (Pacific Decadal Oscillation and El

Niño–Southern Oscillation) environmental variables, as well as ecological factors (e.g., migration distance, foraging strategy), Ward et al. (2015) found that mean May temperature, which has been increasing, was the greatest predictor of first arrival date. While documenting changes in the phenology of migration, these studies suggest that not all species are responding to the same cues, and some may be adapting more than others (e.g., Ely et al. 2018).

Landbirds time their migration with resource availability since they rely on stopover sites to refuel during migration, and on resources being sufficient when they arrive at their breeding or wintering grounds. McKinney et al. (2012) found that, although the times of spring arrival of the Broad-tailed Hummingbird (*Selasphorus platycercus*) in Arizona and Colorado had not changed significantly, times of first and peak flowering of early-season nectar sources had advanced at the northern end of the species' breeding range but not at the southern end, resulting in a shorter period between hummingbird arrival and first flowers at the northern location. More recently, on the basis of satellite imagery, Mayor et al. (2017) compared patterns of the greening of North America in spring to times of migratory birds' arrival, estimated from citizen-science data. They reported that arrival times in eastern North America are advancing more rapidly than those in western North America. Furthermore, because spring greening in western North America, especially in the Pacific Northwest, has been shifting later in the year but bird arrival is slowly becoming earlier, a mismatch between the timing of these two events is widening (Mayor et al. 2017).

Breeding

A key response to climate change, as shown in several broad studies across or including North America, is the advancement of laying by some species (Dunn and Winkler 1999, Torti and Dunn 2005, Dunn and Møller 2014), although not all studies have attributed such changes in phenology to climate change. Dunn and Winkler (1999) suggested that the significantly advancing date of breeding of the Tree Swallow (*Tachycineta bicolor*) was most likely due to increases in spring temperature. Dunn and Møller (2014) considered multiple species across Europe and North America and found that the date of laying had advanced and the breeding season had lengthened more in species raising multiple broods than in those raising single broods. In addition, the date of laying had advanced more in herbivorous and predatory

species than in insectivorous birds. These authors also found much variation in patterns within species and no indication that change in timing of migration in response to higher temperatures affected date of laying. Torti and Dunn (2005) found complex and mixed patterns in laying date in six North American species examined; these included overall significant advancement of laying date in western Song Sparrows (*Melospiza melodia*) and Red-winged Blackbirds (*Agelaius phoeniceus*; 7.5 days over 50 years), with the latter also showing a negative relationship between spring temperature and laying date. They also found that American Robins laid earlier in warmer springs but not overall, yet in recent years laid significantly later.

In Idaho, Heath et al. (2012) reported significantly earlier nesting of the American Kestrel (*Falco sparverius*) was linked to warmer winters that allowed the birds to winter farther north and thus arrive at breeding grounds earlier. Brown et al. (1999) reported that in Arizona Mexican Jays (*Aphelocoma wollweberi*) were laying significantly earlier, by about 10 days over 28 years, in response to increasing temperatures. Beyond these examples, we are not aware of other studies that have examined long-term changes in dates of laying by western North American landbirds. As an alternative to dates of laying, Socolar et al. (2017) used bird detections as a proxy for breeding activity to infer that the timing of breeding of California birds has advanced by 5–12 days over the last century. These authors pointed out that this phenological shift could be explained as a means of tracking resources, but it is also possible that it allows birds to track their optimal thermal niche for breeding without shifting their geographic location.

Molt

To our knowledge, there are no studies from the West, or any region, that have directly examined the effects of climate change on the phenology of landbirds' molt (but see Taylor et al. 2018). However, the effects of weather on molt (van den Brink 2000), and the influence of molt on the phenology of migration (Gordo 2007, Végvári et al. 2010), have received some attention and have climate-change implications. Two studies illustrate the potential for plasticity of molt phenology in response to environmental change: Freed and Cann (2012) demonstrated long-term changes in the phenology and extent of molt in native Hawaiian forest birds, driven by factors unrelated to climate change, being related to the abundance

of a competing non-native species. Also, Morrison et al. (2015) revealed flexibility in the duration of molt and intraspecific variability in its timing across regions. However, effects of climate change on molt, and demographic consequences of potential changes in its phenology, remain unknown and virtually unexplored.

CHANGES IN GEOGRAPHIC DISTRIBUTION

A species' distribution is determined by a complex interplay of processes, including environmental, evolutionary, interspecific, and intraspecific (Brown et al. 1996). Changes in species' distributions have been documented globally across taxa over the past half-century, with the predominant trends being movement of species to higher latitudes and higher elevations, providing evidence for a global biological response to climate change (Parmesan and Yohe 2003, Chen et al. 2011).

Changes in birds' distributions are most commonly evaluated by documenting changes in range boundaries over time, or shifts in the center of abundance (Parmesan and Yohe 2003, La Sorte and Thompson 2007). Elevational limits are also an important component, especially in regards to climate change (Brown et al. 1996, Şekercioğlu et al. 2008).

Few studies have evaluated distributional shifts of birds in western North America. Over smaller geographic scales (e.g., states or regions), and possibly even at continental scales, changes in birds' distribution due to climate change can be confounded with changes due to changes in land use or other regional factors (La Sorte and Thompson 2007; but see Zuckerberg et al. 2009).

CHANGES IN LATITUDINAL DISTRIBUTIONS IN WINTER

We are unaware of studies focused on western North America that have evaluated changes in latitudinal distributions of landbirds in winter. However, La Sorte and Thompson (2007) used data from the Christmas Bird Count across North America to document a northward shift in 254 species over three decades. This distributional shift, calculated for all species combined, was evident in the northern boundary, the center of distribution, and the center of abundance. However, examination of distributional changes in species that occur only in western North America reveals that northward shifts are not universal. For example, Lewis's Woodpecker (*Melanerpes lewis*), Acorn Woodpecker (*M. formicivorus*), California Thrasher (*Toxostoma redivivum*), and Abert's

Towhee (*Melospiza aberti*) shifted south in some pattern over the course of the study (Appendix A in La Sorte and Thompson 2007). Climate change may in fact result in multi-directional changes in distribution, reflecting interactions among temperature, precipitation, and species-specific tolerances (VanDerWal et al. 2012).

CHANGES IN BREEDING SEASON LATITUDINAL DISTRIBUTION

Using locality data from museum specimens, eBird, and the Breeding Bird Survey, Billerman et al. (2016) investigated distributional changes in the Red-breasted (*Sphyrapicus ruber*) and Red-naped sapsuckers (*S. nuchalis*) and their hybrids in western North America over the last century. Their models of current breeding distribution showed the probability of occurrence of the Red-breasted is associated with areas with warmer, shorter winters and a wider range of precipitation than for the Red-naped, and that the distribution of these species and their hybrid zone has tracked the shift in these environmental variables resulting from climate change. However, rather than being to the north, the observed shift was an eastward expansion of the Red-breasted Sapsucker's distribution and a contraction of that of the Red-naped Sapsucker. In addition, several studies from eastern North America, and continent-wide, provide evidence of a directional climate signal in changes in species' latitudinal distributions. Hitch and Leberg (2007) used Breeding Bird Survey data to evaluate distributional changes in 56 landbird species east of the Rocky Mountains. Distributions of birds occurring only south of 44° N shifted north at an average rate of 2.35 km/yr over 36 years. There was no evidence of southward expansion in species occurring only north of 34° N. These patterns suggest a northward shift in the distribution of some species rather than overall nondirectional expansion in range. More recently, Huang et al. (2017) used Breeding Bird Survey data to quantify the direction and velocity of shifts in the centroids of abundance of 57 resident birds in North America. They found evidence of shifts in abundance of 36 species. In western North America, the most common direction of movement was to the northwest (Huang et al. 2017).

CHANGES IN ELEVATIONAL DISTRIBUTION

The Grinnell Resurvey Project repeated surveys along elevational gradients in the Sierra Nevada mountains in California almost a century after they were originally done by Joseph Grinnell

between 1911 and 1929 (Tingley et al. 2009, 2012). Of 99 landbird species evaluated, half had a lower range boundary that shifted upslope; however, the elevational distributions of 90% of species surveyed changed in accordance with changes in temperature and/or precipitation, with increases in precipitation correlated with the movement of some species downslope (Tingley et al. 2012). Species' propensities to shift their elevational range varied with their life history (clutch size and status with respect to migration). Patterns of most species differed among the three regions studied (Tingley et al. 2012). In fact, of the 53 species analyzed in all three regions, only four consistently shifted upslope, the Red-breasted Sapsucker, Fox Sparrow (*Passerella iliaca*), Lazuli Bunting (*Passerina amoena*), and Spotted Towhee (*Pipilo maculatus*); only one, the Ash-throated Flycatcher (*Myiarchus cinerascens*), shifted consistently downslope (Tingley et al. 2012). While many climate predictions focus on the effect of increasing temperatures, implying that species should be expected generally to move up in elevation, this work highlights the importance of the combined effects of changes in temperature and precipitation.

Clearly, one of the challenges of an analysis based on two measurements is teasing apart long-term directional change from annual variability reflected by the two points. The studies addressed this concern by using multi-season occupancy estimates generated from several years of data (Tingley and Beissinger 2009). Even without a more complete time series, the combined studies of the Grinnell Resurvey Project provide evidence of birds' response to a century of climate change that can be used to generate hypotheses and guide additional research.

The relevance of change in precipitation as a driver of change in distributions and range boundaries is further emphasized by Bateman et al. (2015). This study used data from the Global Biodiversity Information Facility (GBIF; www.gbif.org) to evaluate changes in the potential breeding distributions of 285 bird species in the United States over 60 years. The models for 190 species were validated with data from the Breeding Bird Survey, a dataset not contained within GBIF. Shifts in distribution are prevailing to the west, northwest, and north; precipitation during the dry season was the second most influential climate variable, following mean temperature (Bateman et al. 2015).

Elevational changes in bird distribution have also been documented in Denali National Park

and Preserve, Alaska (Mizel et al. 2016). In this system, species associated with shrubs have clearly expanded their distribution upslope, which corresponds to a relatively rapid upslope expansion of shrubby vegetation associated with climate change. In contrast, changes in the elevational ranges of birds associated with trees were weaker, reflecting the more gradual rate at which forest structure is changing. These authors suggested that the effects of climate change on the elevational distribution of birds are more likely to be understood in the context of changes in vegetation than simply elevation shifts in temperature or precipitation (Mizel et al. 2016). Similarly, Unitt and Hargrove (2018) concluded that for breeding birds in southern California, habitat modifications are the primary drivers in southward and downslope range expansions.

CHANGES IN MORPHOLOGY AND PHYSIOLOGY

Morphology and physiology are fundamental to how organisms interact with their environment and their ability to adapt to climate change (Somero 2010, Boyles et al. 2011). To date, most morphological and physiological changes discussed for birds have been related to rising temperatures and thermoregulation (McKechnie and Wolf 2010, Boyles et al. 2011). Of these, by far the most commonly investigated change has been in body size. Principles based in energetics, such as Bergmann's rule, have led to the hypothesis that as average temperatures warm, body size should decrease (Yom-Tov and Geffen 2011, van Gils et al. 2016).

In western North America, we are aware of only a single study testing the hypothesis that landbirds' body size should decrease. Goodman et al. (2012) investigated changes in landbirds' body size at two sites of bird banding in California, one with 40 years of data, the other with 27 years. At both sites, they found that wing length, and in many cases body mass, had increased. These results contrasted with those of a similar study in Pennsylvania, which reported body size decreasing across a wide range of species (Van Buskirk et al. 2010). These two contrasting patterns reflect the general recognition that a decrease in body size is not a universal response to climate change (Yom-Tov and Geffen 2011, Salewski et al. 2014). Because a larger body allows a bird to go longer without food (Ashton 2002), Goodman et al. (2012) suggested that increasing body size in western North America could be due to an increase in

the frequency of storms that limit a bird's foraging rather than to an increase in mean temperatures.

CHANGES IN POPULATION SIZE

Ultimately, we expect that all of the changes described above have the potential to affect population sizes. Already, in many parts of the world there is evidence that climate change is depressing populations, especially when a species' phenology becomes mismatched with that of the environment (Both et al. 2006, Møller et al. 2008, Jiguet et al. 2010, Saino et al. 2010). In western North America, the best evidence for the effect of climate change on population size is for the Yellow Warbler (*Setophaga petechia*). Bay et al. (2018) demonstrated that in regions of North America where the Yellow Warbler's genomic vulnerability to climate change is greater—including most of western North America—the Breeding Bird Survey indicates steeper population declines.

Another region where there is evidence for the effects of climate change on bird populations is Hawai'i, where populations of native birds continue to decline, pushing numerous species to the edge of extinction (Paxton et al. 2016). While multiple factors have contributed to these declines, the effect of increasing temperatures on the elevation at which avian malaria can infect birds is believed to be a major driver (Paxton et al. 2016).

RECOMMENDATIONS FOR FUTURE RESEARCH TO ASSESS REALIZED EFFECTS

Despite the considerable body of literature given to the potential future effects of climate change on birds, we found little that pertained to how the terrestrial avifauna of western North America have already been affected by climate change. We suspect this is in part because climate change to date (~ 1 °C of warming) has been modest relative to what is predicted to come in the next 100 years (2–5 °C of warming). Additionally, identifying the long-term effects of climate change with historic data is challenging given that it is a relatively recent endeavor. However, despite these challenges, we believe that there is great opportunity to examine evidence for change with existing long-term monitoring programs, historic data, and museum collections, as well as through new research where the potential to resurvey exists. Developing specific questions will be essential to our ability to assess effects of climate relative to other drivers. We suggest several directions of research that can contribute to this effort.

How Do We Integrate the Effects of Anthropogenic Climate Change with Those Resulting from Other Environmental Change?

Because birds are sensitive to many sources of environmental change, the attribution of change to climate is challenging when many other factors (e.g., land use, pesticide contamination) may be changing concurrently (Hockey et al. 2011, Knudsen et al. 2011). There is a growing body of literature on approaches to attributing ecological change to climate change that can be used to guide future efforts (Parmesan et al. 2013). One recommendation is that the signal of anthropogenic climate change should be considered in the context of other environmental changes, including the possibility of strong interactions between climate change and other environmental change (Parmesan et al. 2013). In the West, this will mean incorporating such other ecologically important changes as those in invasive species (e.g., *Tamarix* in riparian woodlands; Sogge et al. 2013), changes in natural vegetation (e.g., piñon–juniper expansion or die-off; Romme et al. 2009), and urbanization (e.g., Zuckerberg et al. 2011) into our understanding of how climate is affecting birds and their ecosystems. For example, in northeastern North America, Zuckerberg et al. (2011) demonstrated that weather affects bird distribution, but that the effect is modified by the amount of regional urbanization. Extending such an approach to western North America could generate insights into where and under what conditions birds will be most greatly affected by climate change.

How Can We Use Long-term Data to Attribute Changes in Bird Populations to Climate Change?

Over the last century, ornithologists have collected a wealth of data that is stored as specimens (skeletons, tissues, skins) in museums, banding records, locations of occurrence, and more (see Winker 2018). Today, these data can be used to trace the trajectories of species and populations through time, and they are providing valuable insights into the effects of climate change (Porzig et al. 2011, Tingley et al. 2012). There are still many opportunities to learn from historical data. For example, the paucity of published studies on long-term patterns in the phenology of breeding and molt, despite numerous long-term studies of nesting and the massive amount of molt data recorded at banding stations, demonstrates the magnitude of this opportunity. Additionally, these datasets provide opportunities for investigating

the role of cycles in climate on the scale of decades, and for disentangling these effects from those of long-term anthropogenic climate change (e.g., MacMynowski et al. 2007).

How Will the Increasing Severity and Frequency of Drought, Storms, and other Extreme Weather Affect Birds' Migration, Reproductive Success, and Survival?

The effects that the increasing frequency and severity of extreme weather associated with climate change may have on birds and ecosystems are gaining greater appreciation (Jentsch et al. 2007, Van de Pol et al. 2010). The magnitude and direction of these effects may vary dramatically. In some areas, such as the Sonoran Desert of Arizona and California, reduced rainfall will shorten breeding seasons and decrease reproductive success (McCreedy and van Riper 2014). However, in some areas where breeding seasons are constrained by snowfall, or where cold, wet springs delay the onset of the breeding season (Pereyra 2011), droughts may increase reproductive success. Additionally, the plasticity of the phenological response—even within a population—may depend on complex interactions among weather, a bird's age, and its experience with variation in weather (Wilson et al. 2007). Stronger winds or a change in their direction during migration could affect not only survival of migrating birds, but also their phenology of migration and breeding and reproductive output (Drake et al. 2014). Developing a better understanding of how extreme events affect reproductive success and survival, especially at the edges of species' ranges, will improve our understanding of the ability of species to track shifts in climate.

How Are Food Resources Changing Relative to Changes in Avian Phenology?

While change in phenology has received more attention than other aspects of birds' response to climate change, there are still only a handful of such studies from western North America, and even fewer that address the phenology of resources. A three-year study by Kellermann and van Riper (2015) investigated phenological synchrony and overlap between migrating landbirds and tree flowering at stopover sites in various habitats and at various elevations in southeast Arizona. While they found strong overlap, they also uncovered mismatches related to annual variation in climate that differed by habitat type: at high elevation, mismatch was wider under cold and

snowy conditions, whereas mismatches at low-elevation riparian sites increased during dry years (Kellermann and van Riper 2015). Comparing the timing of avian life cycles with that of food resources along latitudinal or elevational gradients would help shed light on these relationships; there is much room for collaboration between ornithologists and other scientists who may have long-term data on phenology of resources, or for long-term ornithological studies to incorporate basic monitoring of plant phenology into their efforts (Kellermann et al. 2015).

How Does Climate Change Affect Molt?

Despite the importance of molt in the life history of birds (Howell 2010), no studies have addressed the effects of climate change on molt in landbirds. However, the results of some studies that have examined related processes (e.g., correlation between breeding phenology and molt phenology, weather and molt, or molt and migration) suggest that these effects may be important. In California, young House Finches (*Haemorhous mexicanus*; Michener and Michener 1940), Northern Mockingbirds (*Mimus polyglottos*; Michener 1953), and Wrentits (*Chamaea fasciata*; Elrod et al. 2011) that hatch later in the breeding season may undergo a less extensive preformative molt, and the phenology of prebasic molt in the White-crowned Sparrow (*Zonotrichia leucophrys*) may be influenced by spring rainfall (Mewaldt and King 1977). Over a five-decade-long assessment (early 1960s to mid-2000s) of molt in the Dunlin (*Calidris alpina*) in northern Alaska, Taylor et al. (2018) found no significant difference in the timing of the initiation of molt, but did find that in the 2000s the completion of flight feather molt was extended by about 25 days more than in the 1960s. In other regions, annual variation in weather variables, such as winter precipitation, has been found to affect the extent (van den Brink et al. 2000) and, perhaps indirectly, the phenology of molt, likely in part because of its effect on food availability. In Hawaii, a study of the effects of food stress on native forest birds, resulting from competition with a non-native species, revealed changes in the phenology, duration, and symmetry of molt, and demonstrated both the adaptive and potentially negative demographic consequences of an altered molt phenology (Freed and Cann 2012). Végvári et al. (2010) found that species molting their flight feathers in winter, preceding their spring migration and breeding, advanced their spring arrival dates significantly

less than species that molt in summer after breeding. Although the influence of climate change on molt has been given less attention than other biological processes, the consequences of climate change for molt, and of the phenology of molt on that of breeding and migration, may influence individuals' condition and species' demographics in complex and critical ways (e.g., through survival, reproductive success, and ability to adapt to changing conditions).

What Species and Regions of the West Will Be Most Affected?

The effects of climate change, and specifically the magnitude of warming, vary across western North America (Wang et al. 2012). Similarly, not all species are expected to be equally vulnerable to climate change (Gardali et al. 2012, Siegel et al. 2014). By using long-term data in a comparative framework across the West, we can begin to build a better understanding of where the effects are greatest and what species are most sensitive.

Do Birds Have the Physiological Capacity to Respond to Climate Change?

Physiological tolerances are recognized as one mechanism limiting birds' ranges (Salt 1952, Jankowski et al. 2013). As a result, physiology is a factor that can be used to predict the vulnerability of birds to climate change (Boyles et al. 2011). In western North America, however, there is very little information on the physiological capacity of birds to respond to climate change (Gardali et al. 2012). Understanding the details of such relationships, especially in extreme environments, will be increasingly important (McKechnie and Wolf 2010).

What Are the Mechanisms by Which Climate Change Affects Bird Population Sizes?

In other regions of the world, mechanistic studies have linked the effects of climate change, such as mismatches between avian phenology and food availability, to long-term population trends (Both et al. 2006, Visser 2008, Saino et al. 2010). In addition to phenological mismatches, habitat change and disease have been hypothesized to be important mechanisms by which climate change can affect bird populations (MacNally et al. 2009, Garamszegi 2011). However, such studies linking long-term population change to specific climate-related demographic mechanisms are lacking in western North America. For example, Hargrove and Rotenberry (2011) compared the demography of the Black-throated Sparrow (*Amphispiza*

bilineata) along an elevational gradient in southern California, finding no evidence of an upslope range expansion during a period of warming temperatures, despite greater reproductive success at higher elevations. Developing a better understanding of these mechanisms in western North America is an important avenue of research.

CONCLUSIONS

Our review reveals a surprising paucity of evidence demonstrating the effects of climate change on landbirds in western North America. Given the scarcity of information, one might conclude that the effects of climate change are relatively modest and may not warrant the attention they receive. While this may be true to date, the magnitude and consequences of projected change must be considered. Over the next century, global temperatures are expected to rise by 2–5 °C, resulting in longer and more frequent heat waves and more intense and frequent extreme storms (IPCC 2014). The potential for these changes to affect ecological systems makes it imperative that we redouble our efforts to understand the ways in which climate change is affecting bird populations and the ecosystems in which they live. From this perspective, our review provides an early snapshot of what we expect will be a rapidly expanding body of literature in which long-term data have been used to develop a sophisticated understanding of how climate change is interacting with other aspects of environmental change.

In this effort, it will be important to pursue and publish cases that test hypothesized effects of climate change. Our understanding of how birds will respond to climate change is at best nascent, and there is no doubt that surprises are ahead. To advance the field, we need to look to the rich historical data on birds in western North America, determine what additional data we should be collecting to better assess these effects, and develop creative approaches to using these data, together with the latest climatological research. This synthesis will both refine our understanding of how climate change is affecting ecosystems and help us prepare for the future.

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