Ecological Release of the Anna's Hummingbird during a Northern Range Expansion

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ABSTRACT: During range expansions, species can experience rapid population growth if changes in climate or interspecific interactions remove limits on growth rates in novel habitats. Here I document a century of range expansion in the Anna's hummingbird (*Calypte anna*) and investigate the causes of its recent abundance through a combination of demographic, climatic, and phenological analyses. Christmas Bird Count records indicate that populations have been growing in California since the early twentieth century. Sites across the Pacific Northwest show striking fits to simple models of exponential growth following colonization in the 1960s and 1970s, and nest records indicate that the species now delays the start of the nesting season by at least 16 days in the north. Although the species now occurs in a much wider range of climates than before the range expansion, the fastest growing populations in the northwest are in regions with minimum breeding season temperatures similar to those occupied by the species in its native range. Range expansions in the Anna's hummingbird thus reflect an ecological release likely caused by a mix of introduced plants, human facilitation, and phenological acclimation that allowed a California native to expand across western North America.

Keywords: range shift, climate, niche, hummingbird, demography.

Introduction

Range shifts are common on evolutionary timescales and are widely predicted to be necessary for species' persistence as climate change alters temperature and precipitation regimes around the world (Keitt et al. 2001; Buckley 2008; Doak and Morris 2010; Chen et al. 2011). When species are introduced to new ranges by humans, they can experience rapid population growth if ecological limits on abundance in the native range—such as predation or interspecific competition—are absent in novel habitats (Veit and Lewis 1996; Tingley et al. 2014). This process of ecological release (Terborgh and Faaborg 1973) can also occur in native species when changes in the biotic or abiotic environment allow increases in population or expansion to new ranges.

In North America, one of the most remarkable range expansions of the twentieth century occurred in the Anna's hummingbird (*Calypte anna*), which is native to California and the Baja Peninsula but now breeds from Arizona to British Columbia (Zimmerman 1973; Greig et al. 2017). This rapid range expansion—particularly into colder regions, such as the Pacific Northwest—suggests that Anna's hummingbirds have escaped historic limits on their range and abundance, but both the timing of population growth across the range and its underlying causes remain poorly understood.

Range shifts are demographic processes occurring over time, so a lag between the initial colonization event and the first observation is inevitable (Kowarik 1995). Small populations may not be dense enough for population growth (Allee 1938; Veit and Lewis 1996) and are particularly vulnerable to extirpation by stochastic events (Lande 1993), creating an initial waiting period in which new regions are intermittently colonized and extirpated until one drifts high enough in abundance to begin growing stably (Levins 1969; Kowarik 1995; Hanski 1998). Once populations are established, the compounding nature of exponential growth and the imperfection of survey data mean that we may not observe a new species in significant numbers until its population has reached what appears to be explosive growth (Crooks 2005).

Because of the time lags inherent in the process of colonization, studies seeking to identify how changes in community composition, climate, or landscape interact with species range shifts require a long historical context. Birds are particularly well suited to this task because of the extensive knowledge of their distributions and availability of historic survey data from programs like the Breeding Bird Survey (Sauer et al. 2017) and the Christmas Bird Count

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(CBC; National Audubon Society 2010). In addition to the Anna's hummingbird, shifts in wintering abundance have been observed in several other species of hummingbird during the twentieth century. These include the nonmigratory subspecies of Allen's hummingbird (*Selasphorus sasin sedentarius*) in southern California (Clark 2017) and rufous hummingbirds (*Selasphorus rufus*) in the southeastern United States (Hill et al. 1998; Bassett and Cubie 2009). The underlying causes are thought to be a mix of direct supplemental feeding, introduced plants, and climate change, but only Greig et al. (2017) have rigorously compared these factors to date.

Here I analyze long-term survey data for the Anna's hummingbird to document the timing and population dynamics of its recent range expansion and assess the evidence for its likely causes. First, I review existing literature on the species' distribution, natural history, and population trends before the availability of survey and museum data starting in the early twentieth century. I then address four questions through analysis of historic survey and climate data: (1) When and where did the range shifts in Anna's hummingbirds begin? (2) Are demographic trends in newly colonized regions different from those within the native range? (3) How much has the species' climatic niche changed over time? (4) Are populations in new areas acclimating to novel conditions by shifting their breeding phenology?

Natural history of the Anna's hummingbird. The Anna's hummingbird is a member of the rapidly diversifying bee hummingbird clade (McGuire et al. 2014) native to western North America. Joseph Grinnell, the early California biogeographer and systematist, described its range in 1915 as chaparral and scrub oak habitats from Baja California to the north end of the Sacramento Valley. The few observations then reported from the north coast or Klamath mountains were "doubtless beyond the regular breeding area of this species" because "in its breeding range and throughout the year . . . the Anna hummingbird adheres with remarkable closeness to the Upper Sonoran life zone" (Grinnell 1915, p. 87). The species is not a typical seasonal migrant but is known to disperse to higher elevations and latitudes after breeding (Clark and Russell 2012).

The nesting season is early in Anna's hummingbirds, running through winter from December to May (Clark and Russell 2012; Williamson 2001). The end of the dry season (late fall) is the low point of nectar availability in most of the native range, and the first significant blooms in the chaparral—particularly manzanita (*Arctostaphylos* sp.) and currant (*Ribes* sp.)—start in November and peak from February to March (Stiles 1973; Jepson 1993), which may explain the early onset of nesting. Anna's hummingbirds are also known to nest twice in a year (Scarfe and Finlay 2001), with two eggs per nest (Stiles 1973), and an early start to the nesting season may leave more time for a second clutch.

By the early twentieth century, birders and naturalists had noticed Anna's hummingbird populations increasing across the range. Robertson (1931) and Grinnell and Miller (1944) both remarked that the mid-nineteenth-century introduction of eucalyptus trees—which bloom from October to April (Jepson 1993)—likely provided the food source that allowed populations to increase. Although the term was not yet in wide use by population biologists, Grinnell and Miller (1944, p. 218) come close to describing the effect as an increase in carrying capacity: "This means that the rigors of a 'minimum food period' in the annual cycle have been abated; a much larger population of wintering hummingbirds can carry over." Although other introduced plants were also likely involved in the species' early increase in California (particularly tree tobacco [*Nictoiana glauca*] in southern California), the scale of eucalyptus planting in the state was exceptional. For example, from 1910 to 1914 the Mahogany Eucalyptus and Land Company planted between 1 and 3 million eucalyptus seedlings in the hills lining the east side of San Francisco Bay (O'Brien 2006), creating a near-monoculture forest that blooms abundantly throughout the breeding season of Anna's hummingbirds and still characterizes much of the region today.

The first accounts of the species in the northwest were recorded in 1944 both in Oregon (Contreras 1999) and on Vancouver Island (Scarfe and Finlay 2001). The first northwestern nest report was in 1958 near Victoria, British Columbia (Scarfe and Finlay 2001). Zimmerman (1973) aggregated reports from birders and breeding bird atlases to document the time of arrivals across the range up to that time, although the species was still considered rare and was not known to regularly breed outside California. Recently, Greig et al. (2017) analyzed a large-scale citizen science data set of backyard bird feeder surveys from 1997 to 2013 and documented a range expansion across the northwest occurring after 1997. They found that Anna's hummingbirds in the expanded northern range are more likely to visit bird feeders and occur in human-modified landscapes than those in California and that changes in climate during the 1990s and 2000s are unlikely to explain the observed shifts. Greig et al. (2017) also document a positive feedback cycle between hummingbirds and humans: people who saw hummingbirds were more likely to hang hummingbird feeders, which could create an upward pressure on carrying capacity as hummingbird populations increase.

Methods

Occurrence Records and Demographic Models

I downloaded records of Anna's hummingbird museum specimens from the Global Biodiversity Information Facility (GBIF 2017) and occurrence records from the CBC (National Audubon Society 2010) and eBird (Sullivan et al. 2009).

eBird records ($n = 744{,}422$) were used only to estimate the nesting season and the range of climates occupied during the nonbreeding season (summer). CBC records ($n = 12{,}444$) and museum data ($n = 3{,}791$) were used to map the wintering range over time and fit demographic models.

To estimate the timing of arrival in regions that currently regularly report Anna's hummingbirds, CBC and museum occurrence records were first subdivided into 10-year time bins from 1940 to 2010. I then estimated pairwise distances between all unique localities and clustered these into groups of localities within approximately 200 km of each other using complete linkage hierarchical clustering, as implemented in the R function hclust (R Development Core Team 2014). This method clusters localities by finding groups in which the distance between clusters is approximately equal to the farthest distance of sites within clusters. Clusters with fewer than 10 reports were then dropped to remove regions with only occasional vagrant records. Last, I estimated minimum concave hull polygons for each cluster using the rgeos (Bivand and Rundel 2013) and concaveman (Gombin et al. 2017) packages in R. This analysis was restricted to the first two-thirds of the breeding season (December–March) to minimize the signal of postbreeding dispersal. Concave hull polygons for each period were buffered by 50 km to account for dispersal from reported sites. In the absence of information on the extent of individual movement during the breeding season, this distance is an arbitrary choice meant to ensure that clusters remain separated by at least 100 km, although records of individuals moving between Arizona and southern California (Clark and Russell 2012) suggest that a 50-km dispersal distance is well within physiological limits.

To estimate growth rates across the range, I fit demographic models to CBC data for the period 1950–2016. CBC data were used for this analysis because the counts occur during the nesting season, the methodology and search areas are standardized, and Anna's hummingbirds are strongly associated with the urban and suburban landscapes typically covered in CBC survey circles (Greig et al. 2017). Site years without effort data were dropped from the analysis. I also removed the highest and lowest abundance index values at each site to minimize the influence of outliers caused by anomalously low effort data in some years (likely representing data entry errors in the CBC data set). Similar to Soykan et al. (2016), I used party hours as a measure of survey effort and analyzed the ratio of *Calypte anna* reports to total survey hours per site/year as an index of abundance. I then subset the data to include only sites with at least 15 years of *C. anna* reports since 1950 and used nonlinear least squares in R to fit models for each site of (1) exponential growth, $n_i = n_0 e^{rt}$; (2) logistic growth, $n_i = Kn_0/[(K - n_0)e^{-rt} + n_0]$; and (3) constant population size, $n_i = n_0$, where n_i is the abundance in year i, n_0 is the starting population size, r is the population growth rate, t is the number of years since the first record at a site, and K is the carrying capacity. Ninety-five percent confidence regions for linear model fits were calculated by generating 100 bootstrap replicates over survey years at each site, fitting a new model to the bootstrapped data, generating predicted abundances under the bootstrap models, and taking the 95% confidence interval (CI) of the predictions. I ranked models for each locality by Akaike information criterion (AIC; Akaike 1974), taking $\Delta\text{AIC} > 2$ as moderately strong evidence in favor of the top model. Geographic trends in growth rates and model fits were plotted using the R packages ggplot2 (Wickham 2016), maps (Becker et al. 2013), and cowplot (Wilke 2016). Data and scripts underlying all analyses have been deposited in the Dryad Digital Repository (https://dx.doi.org/10.5061/dryad.kt06961; Battey 2019).

Climate Niche Analysis

To tests for shifts in the species' climate niche and estimate the role of climate change in facilitating the range expansion, I compared the distribution of climatic conditions at occurrence localities reported in time periods approximating the preexpansion range (1895–1925), the beginning of the range expansion (1945–1975), and the current range (1995–2015). If the species has maintained a constant climate niche over time and has expanded geographically as a result of climate change, I expect modern occurrence records to be within the range of temperature and precipitation conditions in which the species occurred before the expansion and that niche models trained on historic records should predict at least part of the current range.

Interpolated historic climate data for the contiguous United States was downloaded from PRISM (PRISM Climate Group 2018) and summarized by calculating the total precipitation per month and the average daily mean, minimum, and maximum temperatures during the breeding (December–May) and nonbreeding (July–October) seasons. Although these climate variables are highly correlated (average R^2 between temperature variables within time bins is 0.846), I kept all variables separate rather than combining them via principal component analysis to assist with biological interpretation of the results. The climate analysis was limited to the contiguous United States to match the availability of historic climate data, so it likely underestimates the extent of climatic shifts for populations in British Columbia and coastal Alaska.

I first randomly subsampled occurrence records for each time period to equal size ($n = 493$ breeding and 258 nonbreeding reports) to avoid biasing results because of higher survey effort in later years, which is considerable given the use of eBird records in the nonbreeding season. I then used an ANOVA to test for significant differences in means and a Levene test (implemented in the R package car; Fox and

Weisberg 2011) to test for differences in variance across time periods for each climate variable, with P values corrected for multiple comparisons ($n = 8$) with the Holm-Bonferroni method. I also calculated the 2.5% and 97.5% quantiles of variables in each time period and asked whether more recent climate associations were within the range observed during the early twentieth century. This analysis was repeated 10 times using different random subsets to ensure that results were robust to the subsampling procedure.

Last, I compared two strategies for predicting the species' range shift over time on the basis of the climate associations observed before the range shift. First, I fit niche models to breeding season reports for each time period in Maxent (Phillips et al. 2004, 2005) via the R package dismo (Hijmans et al. 2017) and projected all models to 1995–2015 climates. I also used Maxent's built-in permutation test to assess the importance of climate variables in each time period. Second, after observing that minimum breeding season temperatures changed relatively little over time, I plotted regions in which the average minimum temperature during the breeding season was at or above the 2.5% quantile observed before the range expansion.

Nesting Phenology

To test for shifts in breeding phenology, I assembled records of active nests (females on eggs or later) from natural history museums (via http://vertnet.org) and eBird (Sullivan et al. 2009). The data set includes 882 California records, 181 from the southwest interior, and 124 from the northwest. I first used a Wilcoxon test to test for significant differences in the distribution of breeding season days (days since November 1) of nest records across regions. I also calculated differences in the beginning of the breeding season across regions, using the 10% quantile of breeding season days as an estimate of the start of the season. To avoid biases associated with unequal sample sizes across regions, I then randomly sampled 1,000 sets of 124 records from California and compared the differences in the median and 10% quantile of breeding days across native, interior southwest, and northwest ranges in all subsampled replicates. I took the 5% quantile of the resulting distribution of differences in subsampled replicates as a conservative lower bound for shifts in timing between regions. Note that this analysis assumes that the seasonal distribution of survey effort has been approximately equal across regions, which cannot be confirmed because neither museum nor eBird nest records provide direct information on survey effort.

Results

Timing of Range Shifts

Museum and CBC data indicate that Anna's hummingbirds were established in Oregon, Washington, and British Columbia by the early 1970s (figs. 1, S1; figs. S1–S10 are available online). The first Alaska CBC report is in 1974. These dates are consistent with Zimmerman's (1973) study compiling reports from bird atlases but notably later than the first reports by birders on Vancouver island in 1944 (Scarfe and Finlay 2001). This suggests that the initial phase of colonization occurred during the late 1940s through the 1960s, but population densities remained too low to be picked up by standardized surveys. Many early northern records—including the first British Columbia and Alaska reports in this data set—are from CBCs conducted in December, demonstrating that the range expansion was not restricted to warm months.

Specimens as early as 1925 in Arizona and 1936 in east Texas suggest that the species was either occasional in the region before large-scale human development or had already expanded its range by the early twentieth century. However, the first wintering records in the southeast are not until 1937 in Arizona and 1967 in Texas, consistent with earlier reports representing postbreeding dispersal rather than local breeding populations. The species quickly expanded across both states during the 1960s and 1970s, and by the 1980s it was regularly reported across southern Arizona and parts of the Gulf Coast in Texas. The Las Vegas region in Nevada and several sites in New Mexico also reported the species at low frequencies starting in the 1970s. Since 2005, Anna's hummingbirds have been regularly reported in CBCs from southwestern Alaska and have appeared as vagrants as far east as the Atlantic coast of Canada (fig. S1).

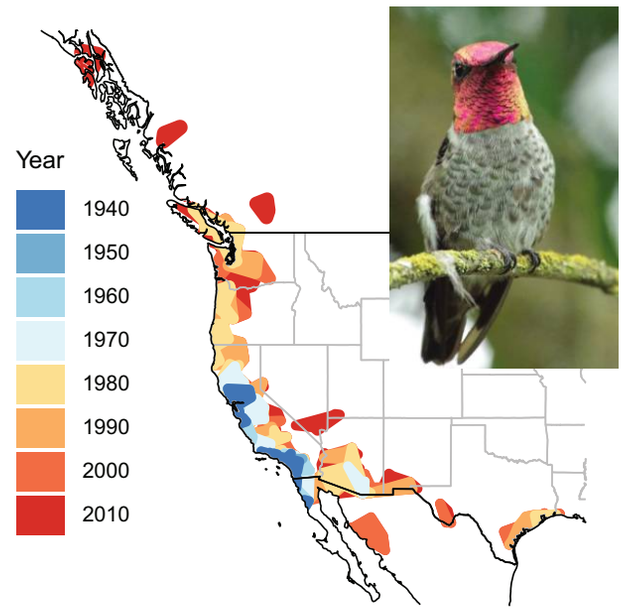

Figure 1: Wintering range (December–March) of Anna's hummingbirds for sites with at least 10 years of Christmas Bird Count records, 1940–2010. *Right*, adult male in Seattle.

Demographic Models

Population growth rates from 1950–2016 range from −0.065 to 0.309 in exponential models (mean: 0.040; 95% quantile: −0.015 to 0.167), with the fastest rates around Puget Sound and the Salish Sea (figs. 2, S2–S7). The mean rate estimated here is slightly lower than the estimates of 4.3%–5.5% annual growth of Soykan et al. (2016; a comprehensive study of CBC records), suggesting that more sophisticated effort corrections may lead to even higher estimates of population growth.

In California and much of the southwest, most populations have been growing steadily since CBC effort data became available, with large variability in abundance estimates between years. Sites in Arizona and Texas report Anna's hummingbirds starting in the 1970s, with moderate growth rates since colonization. In the northwest, populations are consistently reported starting in the mid-1960s but maintained low densities until the late 1990s, followed by rapid growth to the present day. Growth rates in the northwest were significantly higher than in the native range (Wilcoxon test: $P < .01$; 95% CI: 0.08–0.11), but those in the interior southwest were not ($P = .176$; 95% CI: 0–0.02; fig. S8).

Exponential models were most commonly selected in all regions (fig. 2), although model fits were tighter in the Pacific Northwest than elsewhere (figs. S2–S7). Most sites at which constant population models were selected were regions with very low population densities (e.g., sites in the Cascade Mountains, such as Bend and Oakhurst) or regions with relatively large areas of natural habitat in the native range (Santa Cruz, Santa Barbara). Examining growth curves for sites across the range (figs. S2–S7) suggests that most newly colonized sites have not yet reached the logistic phase of population growth. Population densities in northwestern cities (e.g., Seattle: 1.74 birds/party-hour [bph]; Portland: 2.01 bph) have already reached those of cities at the northern half of the historic breeding range (e.g., Oakland: 1.92 bph; San Jose: 1.89 bph). Total populations in the northwest, however, are likely still much lower than those in California because the species is more closely affiliated with human-modified habitats in the north (Greig et al. 2017).

Climate Niche Expansion

The means of occupied climate conditions were significantly different across time periods for all climate variables during the nonbreeding season ($P < .0001$, $df = 2$; all P values in this section are adjusted for $n = 8$ multiple comparisons) but not during the breeding season ($P = 1$, $df = 2$; fig. 3). Variances were significantly different ($P < .01$, $df = 2$) for all variables in both breeding and nonbreeding seasons (in all cases, more recent records had higher variance in climate conditions). The central 95% quantile of 1995–2015 records was larger than that of 1895–1925 records for all climate variables other than nonbreeding mean and minimum temperatures, for which the lower bound was higher after 1925. Although P values shown here are for a single set of subsampled occurrence localities, all replicates returned the same results in terms of statistical significance and very similar results for quantile limits.

Maxent niche models trained on 1895–1925 data fail to predict any newly colonized habitats across the northwest and interior southwest that are currently occupied by expanding breeding populations. However, mapping the regions where minimum breeding season temperatures for each time period were at or above the 2.5% quantile of 1895–1925 localities shows that much of the Willamette Valley and Puget Sound lowlands—regions with the fastest population growth today—were within the historic range of this axis of the species' climate niche before the expansion (fig. 3). The total area in which suitable minimum temperatures occurred increased by approximately 11% between 1895–1925 and 1995–2015, suggesting that climate change may have played a role in expanding northwestern populations after colonization. This analysis was consistent with variable importance rankings from Maxent models, which found that minimum breeding season temperature is the most important climate descriptor of the species' range for 1995–2015 localities (fig. S9).

Nesting Phenology

Nest records show that both the northern and the eastern range expansions created new breeding populations (fig. 4). Differences in median nesting date between interior southwest and California records were not significant ($P = .146$; 95% CI: −2 to 12 days), but the median nest record in the northwest was 11 days later than in California ($P = .009$; 95% CI: 7–27 days). Across randomized equal-sized samples, the middle 95% quantile of differences in median nest days was −5.5 to 20 days for native versus interior southwest ranges and −1.5 to 24 days for native versus northwest ranges. The 95% quantile for differences in the beginning of the nesting season was 6.7–22.1 days for native versus interior southwest ranges and 16.7–32.1 days for northwest versus native ranges (fig. S10). Variation in sample size may thus explain all of the observed difference in median nesting days but not differences in the beginning of the nesting season.

Discussion

Range shifts in the Anna's hummingbird hold two lessons for studies seeking to predict the magnitude and direction of species range shifts. First, observed climatic associations

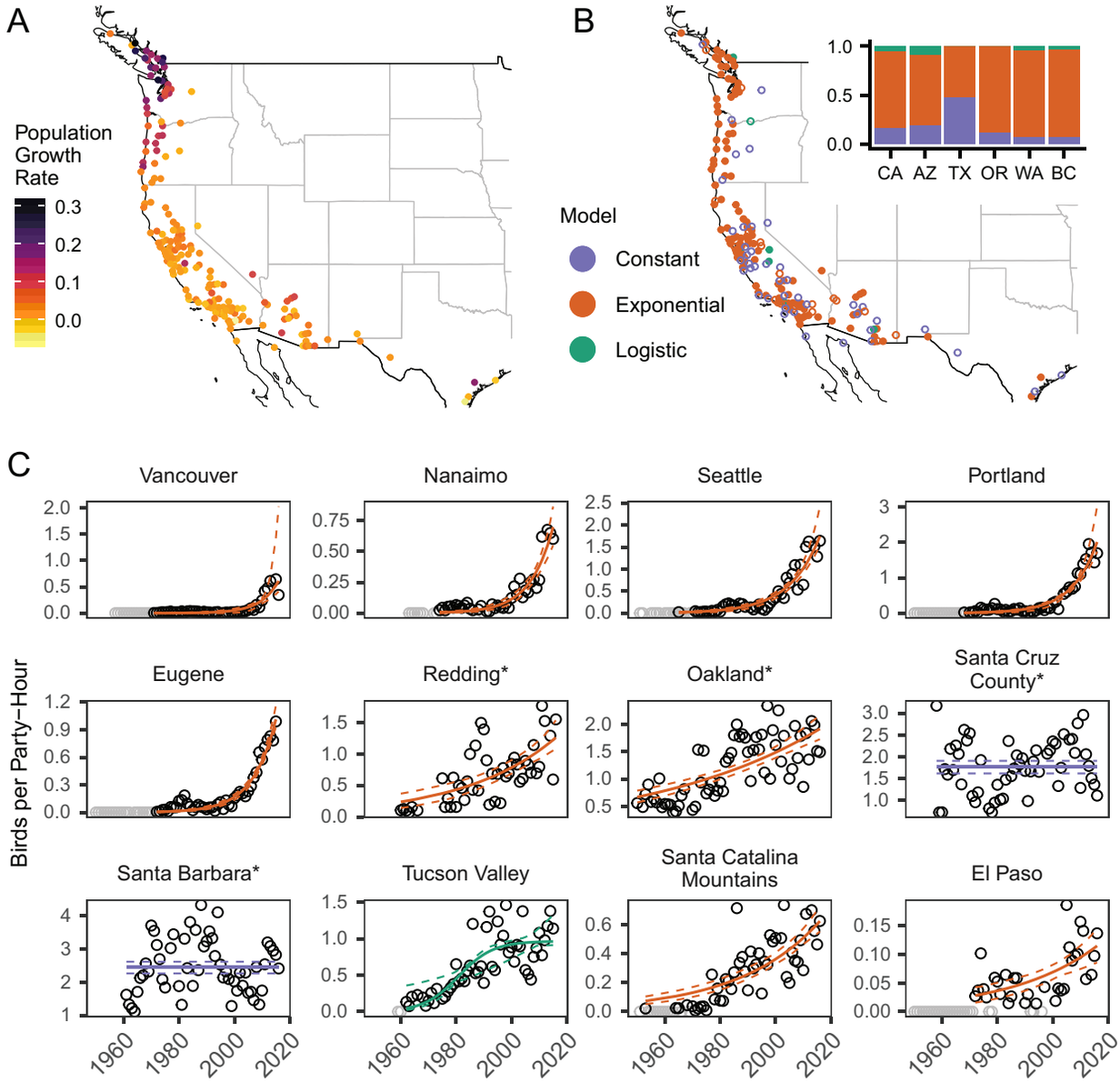

Figure 2: *A*, Growth rate of Anna's hummingbird populations by Christmas Bird Count (CBC). *B*, Akaike information criterion (AIC) model selection by CBC. Filled circles have $\Delta AIC > 2$, and open circles have $\Delta AIC > 2$. Inset bars show the proportion of sites with best fits for each model. *C*, Representative observed and predicted abundance estimates, with model predictions colored by model type. Dashed lines are 95% confidence regions, and gray circles are years with full survey data but no Anna's hummingbird reports. Localities are ordered northwest to southeast. Asterisks indicate localities in the native range.

can be very different from the full niche space in which an organism can live (see also Peterson 2003; Broennimann et al. 2007; Waltari et al. 2007). Correlative niche models trained on early records fail to predict suitable habitat in any part of the Pacific Northwest, and models trained on recent records found that the current range is limited by a different mix of climate variables—in particular, minimum breeding season temperature—than that in the early twentieth century. This suggests that the ecological association with chaparral and scrub oak habitats observed by Grinnell was contingent on the range of habitats available before human landscape modifications of the twentieth century rather than representing intrinsic abiotic limits on the species' range. The current range thus appears to reflect an ecological release made possible by facilitative interaction with humans and introduced plants.

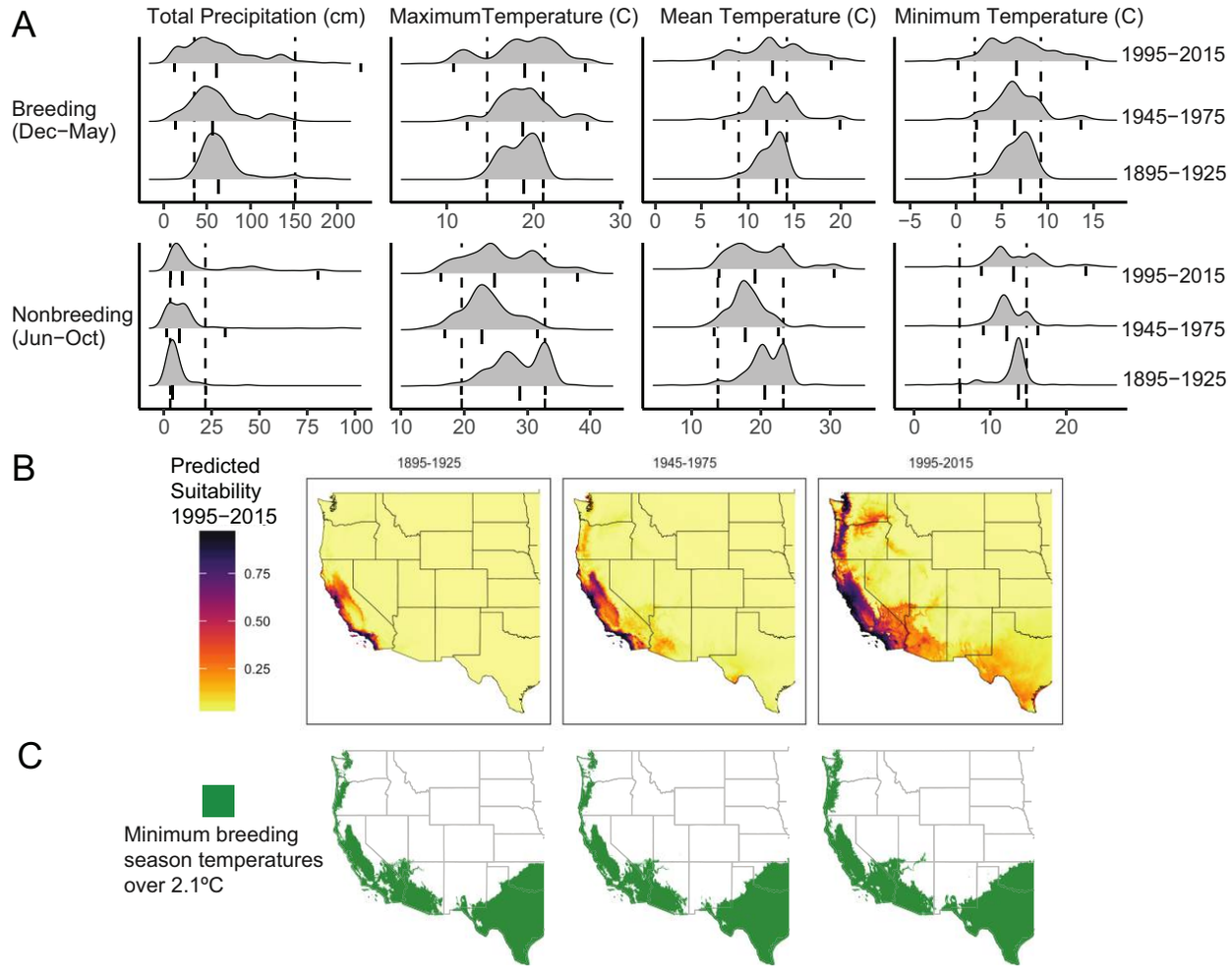

Figure 3: *A*, Climate niche distributions by variable during the breeding and nonbreeding season. Vertical bars are the median, 2.5%, and 97.5% quantiles for each time period, with dashed lines showing the 2.5% and 97.5% quantiles for 1895–1925 records. *B*, Maxent models trained on climate and occurrence records from the time period shown above and projected to 1995–2015 climates. *C*, Green shows regions with minimum breeding season temperatures at or above the 2.5% quantile of preexpansion localities.

Second, when asking whether environmental change explains shifts in range or abundance, we should take time lags and demographic process into account (Kowarik 1995; Crooks 2005; Doak and Morris 2010). In most species, we should expect to observe the largest increases in population size well after the environmental or behavioral shifts that allowed the increase in population. In this case, Anna's hummingbirds were present since at least the early 1970s but remained rare across the Pacific Northwest until the late 1990s. Because of rising populations, many residents of the region began seeing hummingbirds at their feeders after 1997 (Greig et al. 2017), and CBC counts increase rapidly around this time. However, the consistent fit of northwestern survey records to exponential growth models starting in the 1970s shows that observed trends can be explained without any change in growth rates or carrying capacity during the 1990s.

Results of climate analyses here suggest that climate change is unlikely to have played a major role in the early phases of the range expansion, because the current range includes a much wider range of climates than the species occupied in the early twentieth century and niche models fail to predict the modern range. However, regions with the fastest population growth in the Pacific Northwest overlap strongly with sites where minimum breeding season temperatures are similar to the coldest parts of the native range (i.e., the Sierra foothills and northern Sacramento Valley). Because climate change has increased the area in which suitable minimum temperatures occur, it may have assisted in the colonization of some sites in the Pacific

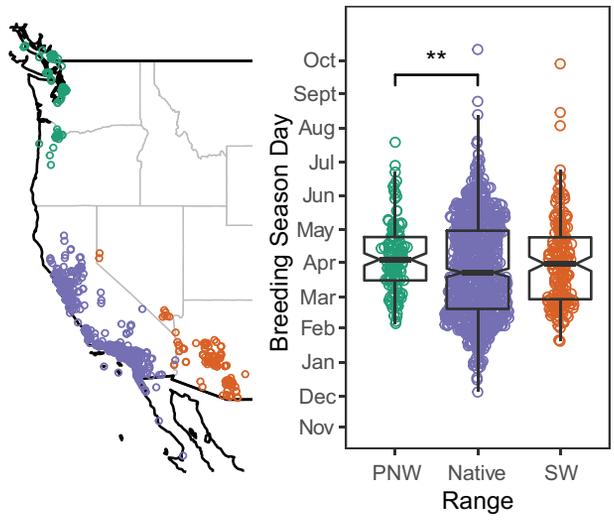

Figure 4: *Left*, map of nest reports colored by region. *Right*, difference in median nest day by region. Asterisks indicate a significant difference ($P < .01$). PNW = Pacific Northwest; SW = southwest.

Northwest after 1970 and will likely play a more prominent role in shaping the species' range in the future. In particular, the Columbia River Gorge east of Portland, Oregon, and parts of the Colorado River stretching into Utah now experience minimum temperatures during the breeding season that are likely within the species' physiological limits and may see the establishment of new populations as climate change continues.

On the basis of historical accounts, niche model results, and the species' unusual nesting phenology, a likely cause of increased abundance up to 1940 is the extensive planting of introduced species, including *Eucalyptus globulus* in California (Robertson 1931; Grinnell and Miller 1944). CBC data show that populations in California have continued growing steadily at least since the 1950s. During the early twentieth century range expansion of house finches (*Carpodacus mexicanus*) across northeastern North America, population growth inside the core introduced area was a strong predictor of rates of colonization of new habitats (Veit and Lewis 1996). Similarly here, I hypothesize that the basic cause of early range expansions was population growth inside the native range. In this case, Anna's hummingbirds were not introduced but appear to have experienced a shift in growth regimes during the early twentieth century that resulted in a larger number of individuals dispersing across the landscape simply as a function of larger populations. This increased population pressure eventually led to colonization of the northwest and interior southwest, where direct supplemental feeding (i.e., hummingbird feeders) combined with ornamental garden plants to support new breeding populations in regions that were unsuitable for the species at the beginning of the twentieth century.

How long will populations continue to grow in the northwest? Because current densities in major urban areas (such as Seattle and Portland) have already reached those found in much of northern California, it is reasonable to expect that growth at these sites will level off over the next several decades. If not, we should ask why urban carrying capacity would be higher outside the native range. Greig et al.'s (2017) finding of an increase in dependency on hummingbird feeders in the north could provide a likely answer. This theory could be tested by comparing isotope ratios from hummingbirds in the northwest and native ranges, particularly because many hummingbird feeders are filled with a sucrose solution made from sugarcane, a grass that should contain the characteristic signal of C4 photosynthesis in its carbon atoms (Von Schirnding et al. 1982). The species is also a promising subject for genetic studies of the impacts of range shifts both because the timing of population growth is relatively well documented and because a high-quality genome already exists as a result of its use as a model system for song learning (Korlach et al. 2017).

The Anna's hummingbird has become a common breeding bird across the lowland Pacific Northwest and parts of Arizona by expanding the range of climates it occupies, shifting its unusual nesting phenology to account for colder and wetter winters and increasing its association with human-modified habitats (Greig et al. 2017). This range expansion appears to be the product of population growth within the native range driven by plant introductions in the late nineteenth century. Since the mid-twentieth century, the colonization and growth dynamics of populations in the northwest have been similar to those of a species introduced to a novel habitat by humans, with abundance growing exponentially and no sign of density-dependent population regulation to date. Whether the dynamics observed in Anna's hummingbirds are typical of range shifts of native species during the twentieth century remains to be seen, in part because many recent studies have been limited to binary presence/absence grids (Parmesan et al. 1999; Tingley et al. 2009; Chen et al. 2011; Greig et al. 2017). As the magnitude of available survey data increases over time, our ability to infer changes in both presence and abundance should increase across many taxa, allowing a more mechanistic view of how—rather than whether—species' ranges change over time.

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Anna's hummingbird (*Calypte anna*) in Seattle. Photo credit: C. J. Battey.