

RESEARCH ARTICLE

The Colorado River Delta and California's Central Valley are critical regions for many migrating North American landbirds

William V. DeLuca,^{1,*} Tim Meehan,² Nat Seavy,³ Andrea Jones,⁴ Jennifer Pitt,² Jill L. Deppe,⁵ and Chad B. Wilsey⁶

¹ National Audubon Society, Amherst, Massachusetts, USA

² National Audubon Society, Boulder, Colorado, USA

³ National Audubon Society, Forestville, California, USA

⁴ National Audubon Society, Sacramento, California, USA

⁵ National Audubon Society, Washington, District of Columbia, USA

⁶ National Audubon Society, San Francisco, California, USA

* Corresponding author: william.deluca@audubon.org

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ABSTRACT

Migration is an important component of some species full annual cycle. California's Central Valley and the Colorado River Delta provide important riparian and wetland habitats for migrating waterbirds in the arid west of North America, but little is known about whether these locations are important at the population level to migrating landbirds. We used eBird Status and Trends abundance data to quantify the importance of the Central Valley and Colorado River Delta to landbirds by estimating the proportion of the breeding population of 112 species that use each site during migration. We found that ~17 million landbirds use the Colorado River Delta in the spring and ~14 million in the fall. Across 4 study regions in the Central Valley, up to ~65 million landbirds migrate through in the spring and up to ~48 million in the fall. In the spring and fall, respectively, up to 37 and up to 30 species had at least 1% of their continental population migrate through the study regions. We also quantified the spatial concentration of each species across latitudinal transects to determine the extent to which study regions were acting as migratory bottlenecks. Landbird abundances were spatially concentrated in study regions 29.4% of all migration weeks, indicating that each study region acts as a migratory bottleneck. This application of eBird data is a powerful approach to quantifying the importance of sites to migrating birds. Our results provide evidence of population-level importance of the Central Valley and Colorado River Delta for many migratory landbirds.

Keywords: bottleneck, concentration, conservation, eBird, migration, population

LAY SUMMARY

- Migratory birds are declining throughout North America, and we must identify places birds need during migration so they can safely move between breeding and winter locations.
- The Colorado River Delta and the Central Valley are known as important landscapes for wildlife, but their importance to migrating landbirds is not well known.
- We used eBird data to measure the importance of the Colorado River Delta and California's Central Valley to birds that migrate through western North America.
- Many species have substantial portions of their populations that depend on these locations during migration.
- Conservation of the Colorado River Delta and Central Valley are important for the entire populations of many breeding landbird species of North America.

El Delta del Río Colorado y el Valle Central de California son regiones críticas para muchas aves terrestres migratorias de Norteamérica

RESUMEN

La migración es un componente importante del ciclo anual completo de algunas especies. El Valle Central de California y el Delta del Río Colorado brindan hábitats ribereños y húmedales importantes para las aves acuáticas migratorias en la parte árida del oeste de Norteamérica, pero se conoce poco si estas localidades son importantes a nivel poblacional para las aves terrestres migratorias. Usamos los datos de abundancia del proyecto eBird Status and Trends para cuantificar la importancia del Valle Central y del Delta del Río Colorado para las aves terrestres mediante la estimación

de la proporción de la población reproductiva de 112 especies que usan cada sitio durante la migración. Encontramos que ~17 millones de aves terrestres usan el Delta del Río Colorado en primavera y ~14 millones en otoño. A lo largo de cuatro regiones de estudio en el Valle Central, hasta ~65 millones de aves terrestres migran en primavera y hasta ~48 millones en otoño. En primavera y otoño, respectivamente, hasta 37 y 30 especies tuvieron al menos el 1% de su población continental migrando a través de las regiones de estudio. También cuantificamos la concentración espacial de cada especie a lo largo de transectas latitudinales para determinar la medida en la que las regiones de estudio estuvieron actuando como cuellos de botella migratorios. Las abundancias de aves terrestres estuvieron espacialmente concentradas en las regiones de estudio el 29.4% de todas las semanas de migración, indicando que cada región de estudio actúa como un cuello de botella migratorio. Esta aplicación de los datos de eBird es un enfoque poderoso para cuantificar la importancia de los sitios para las aves migratorias. Nuestros resultados brindan evidencia de la importancia a nivel poblacional del Valle Central y del Delta del Río Colorado para muchas aves terrestres migratorias.

Palabras clave: concentración, conservación, cuello de botella, eBird, migración, población

INTRODUCTION

Effective conservation of many North American birds requires consideration of more than just the stationary breeding period (Marra et al. 2015). This approach requires understanding the conservation value of bird habitat during breeding, migration, and winter periods. While the breeding ecology of many landbirds is relatively well known, there is much less information available for migration and winter periods (Faaborg et al. 2010). As the conservation community works to address the large-scale declines of migratory birds (Rosenberg et al. 2019), quantifying the importance of areas for migrating landbirds will help prioritize places for the protection of birds across their full annual cycle.

The need for additional information on landbird migration is especially relevant in western North America, where landbird migration remains relatively understudied (Carlisle et al. 2009). Unlike landbirds that migrate through eastern North America, western migrants are not faced with extended overwater flights. Rather, they are faced with the challenge of piecing together suitable stopover sites across a relatively arid landscape (Kelly and Hutto 2005, Azpiroz et al. 2012). In the arid environment of the southwestern United States and northwest Mexico, limited distribution of water influences food and habitat availability for many species passing through this region during migration.

California's Central Valley and the Colorado River Delta are 2 examples of regions in the American West with conservation efforts that focus on water resources and land management to maintain their rich biodiversity throughout the year. In the Central Valley, the Sacramento and San Joaquin Rivers were once the source of extensive riparian ecosystems and wetland complexes, but much of that water is now redirected for anthropogenic purposes and much of the historical floodplain forest has been converted to agriculture. The result has been a reduction in the extent and function of the habitat for migratory birds (Dybala et al. 2017). A similar situation has unfolded in the lower Colorado River Basin. Once a productive biodiversity

hotspot in the otherwise harsh Sonoran Desert, the river's delta is now greatly reduced (Pitt et al. 2000).

As the Central Valley and the Colorado River Delta have become the focus of major restoration efforts, landbird conservation planning has focused on the value of these areas for breeding birds (Hinojosa-Huerta et al. 2004, Dybala et al. 2017), especially their ability to support nesting of species of conservation concern, including Least Bell's Vireo (*Vireo bellii pusillus*), Yellow-billed Cuckoo (*Coccyzus americanus*), and Southwestern Willow Flycatcher (*Empidonax traillii extimus*). During the nonbreeding season, attention has been placed on the conservation value of these areas to migrating and overwintering waterbird and shorebird populations (Shuford et al. 1998, Gomez-Sapiens et al. 2013, Page et al. 2014, Petrie et al. 2016, Hinojosa-Huerta et al. 2013b) with less emphasis on landbirds (but see Hinojosa-Huerta et al. 2004). What is known about landbird migration across these areas has been largely derived from local habitat use studies (van Riper et al. 2008, Cormier et al. 2013, Darrah et al. 2017, Greco and Airola 2018).

One challenge to evaluating the importance of landscapes to migratory species has always been the difficulty in quantifying the passage of migratory birds. However, in recent decades, advances in aggregating observations from community scientists, a more inclusive term for citizen scientists (Meehan et al. 2019), have provided new approaches to understanding bird migration (La Sorte et al. 2014). Range-wide abundance information based on eBird data has been estimated throughout the Western Hemisphere for hundreds of North American breeding bird species (Fink et al. 2020a). These estimates are particularly useful when considering migratory birds because they include weekly estimates of abundance across species' ranges throughout their annual cycle (Johnston et al. 2019, Schuster et al. 2019). Additionally, these estimates are produced at a relatively fine spatial resolution (2.96×2.96 km cell size), allowing for the consideration of site use at relatively local scales. These estimates are a powerful tool that can be used as the basis of spatial prioritizations for conservation efforts in the context of the full annual cycle

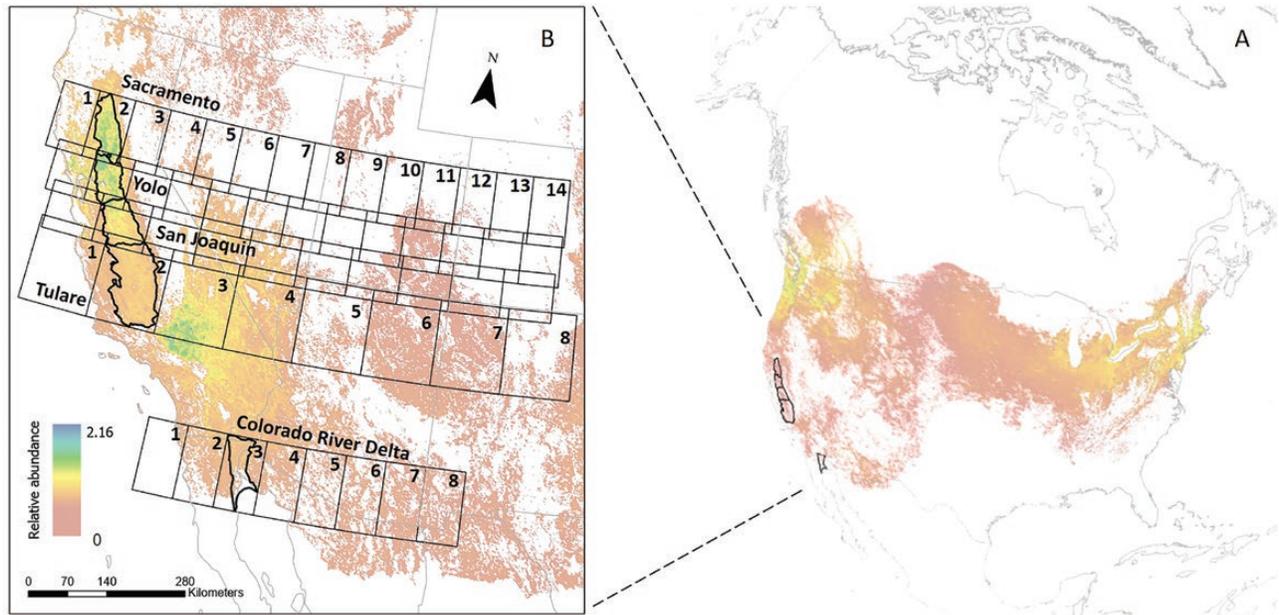


FIGURE 1. (A) eBird abundance estimates averaged across the breeding season throughout the breeding range of Willow Flycatcher. In both (A) and (B), bold black lines define the study regions. (B) eBird abundance data for Willow Flycatcher during a week of fall migration (week 37). The Sacramento, Yolo, San Joaquin, and Tulare are within California's Central Valley. Gray cells comprise each study region's latitudinal transect which stretches from the Pacific Ocean to the Continental Divide. Cells represent a minimum study region containing rectangle, such that the top and bottoms are consistent with parallels and the sides are consistent with meridians. Cells were then repeated latitudinally to complete the transect. Numbered cells along the Sacramento, Tulare, and Colorado River Delta transects correspond to cell numbers in Figure 5.

(Schuster et al. 2019, Wilson et al. 2019, Johnston et al. 2020), as well as offering the potential to quantify the importance of sites to migratory birds.

We used weekly abundance data modeled from eBird (Fink et al. 2020a) to quantify the importance of the Colorado River Delta and California's Central Valley to 112 migratory landbird species during spring and fall migration. We combined abundance data with population estimates to generate weekly estimates of numbers of individuals using the Delta and Valley during migration. We then estimated the proportion of species' continental populations that use each region during each migration season. Finally, we quantified the weekly spatial concentration of each species migrating through the study region along a latitudinal transect from the Pacific Ocean to the Continental Divide to estimate the extent to which the Delta and the Valley may be acting as migratory bottlenecks.

METHODS

Study Regions

We chose 2 study areas that are recognized as important for migratory birds: the Colorado River Delta and California's Central Valley (Figure 1). The Colorado River Delta (hereafter "Delta") study area is ~930,000 ha and is approximately bounded in the north by Interstate 8 in California,

along the west by Route 5 in Mexico, the south by the Gulf of California, and to the east by Routes 40 and 3 in Mexico (Figure 1). Most of this area is within Mexico and is consistent with international planning and conservation efforts (Pitt et al. 2000, Hinojosa-Huerta et al. 2013a). The upland portion of the site is Sonoran Desert and agriculture (Pitt et al. 2000). Along the river, the riparian vegetation was historically dominated by cottonwood and willow (Glenn et al. 2001), but today non-native salt-cedar is dominant outside of habitat restoration sites. At the southern extent of the region, the Delta itself is a broad alluvial plain and is defined by large brackish wetlands and tidal mud flats. Much of the freshwater-dependent habitat is stressed due to the lack of flow from the Colorado River to the sea caused by anthropogenic uses throughout the watershed (Pitt et al. 2017). The general size of the Delta also approximates the smallest extent we felt appropriate to apply our analyses.

California's Central Valley (hereafter "Valley") is generally delineated by the Sierra Nevada to the east and the Coast Ranges to the west. Historically, the Valley contained extensive riparian forests and wetlands but most have been lost due to agriculture, water diversion, and development (Katibah 1984). To maintain consistency with established conservation planning regions and with the analytical spatial extent of analyses applied to the Delta, Valley study

regions are based on 4 planning regions identified by the Central Valley Joint Venture (Figure 1; Dybala et al. 2017). The northern-most region (~1,000,000 ha) is the valley shaped by the Sacramento River (hereafter “Sacramento”); the region immediately south is defined by the Yolo Basin and the delta of the Sacramento and San Joaquin Rivers (~890,000 ha; hereafter “Yolo”); the San Joaquin River Valley (~1,150,000 ha; hereafter “San Joaquin”) is the region just south of the Yolo study region; and the Tulare Basin (hereafter “Tulare”) defines the southernmost sub-region (~2,690,000 ha, Figure 1; Dybala et al. 2017).

Study Species

We identified 112 migratory landbird species (Supplementary Material Table S1) with a reasonable potential to use either the Valley or Delta during migration. We generated this list by using range maps and migratory season dates from eBird Status and Trends (Fink et al. 2020b). We included species that may overwinter or breed at a site as well as migrate through it in addition to species that use the sites solely during migration. The final list includes 25 families of migratory landbirds but did not include raptors. We chose not to include raptors because they have different migratory behavior than most landbirds, often preferring to follow ridgelines (Goodrich and Smith 2008).

Total Landbirds and Population Proportions Migrating through Study Regions

We used the *ebirdst* package (Auer et al. 2020) in Program R 3.6.1 (R Core Team 2019) to access eBird Status and Trends data (Fink et al. 2020b). The following process was applied to each species and study region. First, we summed the relative abundance values across cells (2.96×2.96 km) within a study region per week (Figure 1B) to produce a_w , a “weekly abundance sum,” as $a_w = \sum \alpha_i$, where α_i was the abundance index of the i th cell in the study area. A standard error, s_a , for the sum was estimated by summing errors in quadrature (square root of the sum of squared uncertainty values; Taylor 1997),

$$s_a = \sqrt{\sum \sigma_i^2},$$

where σ_i was the standard error estimate for each α_i , calculated as $\sigma_i = \frac{u_i - l_i}{z}$, where u_i and l_i were the upper and lower 80% confidence limits for α_i , and z was 2.56, a value of the z -distribution for approximating a standard error from an 80% confidence interval. Next, we calculated an analogous weekly sum and standard error, A_w and s_A , but for the entire continent and only for the weeks during the breeding season (as defined by Fink et al. 2020b). This process followed the same equations as above, except that A_w and s_A

were substituted for a_w and s_a , respectively, and i represented each pixel across the continent. After producing a continental sum for each breeding week, we computed an average “breeding season sum,” \bar{A} , and standard error, $s_{\bar{A}}$, as $\bar{A} = \frac{\sum A_w}{W}$ and $s_{\bar{A}} = \sqrt{\sum s_A^2}$. With a weekly abundance sum, a_w , available for a study area, and the average breeding season sum, \bar{A} , available for the continent, we computed the proportion of the continental population that used a study area on a weekly basis. This “weekly continental proportion,” p_w , and its standard error, s_p , were computed as

$$p_w = \frac{a_w}{\bar{A}} \text{ and } s_p = p_w \sqrt{\left(\frac{s_a}{a_w}\right)^2 + \left(\frac{s_{\bar{A}}}{\bar{A}}\right)^2},$$

where fractional errors were summed in quadrature and then scaled to the proportion (Taylor 1997). To convert from relative abundance, a_w , to estimates of numbers of individual birds, N_w , passing through a study area per week, we multiplied the weekly continental proportion, p_w , by Partners in Flight (PIF) continental population estimates, C , for a given species (Stanton et al. 2019), as $N_w = p_w \times C$. The PIF breeding population estimates are the only comprehensive population estimates available for North American breeding birds and are derived from the Breeding Bird Survey. A standard error for N_w was estimated as

$$s_N = \sqrt{\left(\frac{s_p}{p_w}\right)^2 + \left(\frac{s_C}{C}\right)^2},$$

where a standard error for the continental abundance estimate was estimated as $s_C = \frac{u_c - l_c}{z}$, u_c and l_c were the upper and lower 95% confidence limits for C , and z was 3.92, a value of the z -distribution for approximating a standard error from a 95% confidence interval (see Supplementary Material Figure S1 for an illustrated summary of this process).

For species that do not have an overwintering or breeding population within a study region, we calculated the area under the total individuals per week curve for the defined (Fink et al. 2020b) pre- and post-breeding migratory period (Supplementary Material Figure S2A) to estimate the “summed individuals per season” using the study region. When species had either an overwintering or breeding population at a study region, we calculated the area under the curve that was above the maximum of the breeding and overwintering abundance values that occurred during the middle of the 2 seasons (Supplementary Material Figure S2B and C). We chose the chronological medians to account for instances when the predefined seasonal dates (Fink et al. 2020b) were inaccurate for our study regions. Finally, we summed total individuals per season across species for

each season to estimate the total number of migratory landbirds using each study region per season. As before, uncertainty in total individuals per week and season was propagated across sums by summing approximate standard errors in quadrature.

To contextualize the estimate of migrating landbirds passing through the study regions, we calculated the proportion of the continental breeding population (hereafter, “continental breeding proportion”) using the study region during migration. As mentioned above, continental breeding population estimates were taken from North American Partners in Flight estimates (Stanton et al. 2019). The continental breeding proportion was calculated by dividing the summed individuals per season by the continental population estimate per species, season, and study region. Uncertainty was again propagated to this proportion through summing fractional errors and rescaling. In order to put the continental breeding proportions into further conservation context, we compared them to BirdLife International’s criteria A4 for determining important bird areas, which allows study regions to qualify if it is “known or thought to hold congregations of $\geq 1\%$ of the global population of one or more species on a regular or predictable basis” (BirdLife International 2020).

Spatial Concentrations

To determine if species are spatially concentrating at a study region on a weekly basis during migration within western flyways, we established a latitudinal transect for each study region that stretched from the Pacific Ocean to the Continental Divide. We chose to bound this transect at the Continental Divide because most western landbird migration occurs to the west of this major geographic feature (La Sorte et al. 2014). We constructed a minimum bounding rectangle (hereafter “cell”) for each study region such that the tops and bottoms are delineated by parallels, and the sides are delineated by meridians. We repeated this process to create adjacent but non-overlapping rectangles across each transect (Figure 1B). For each week, study region, and species, we estimated the proportional abundance of each cell compared to the complete transect. For species that had breeding or overwintering populations within the study cell, we used the same approach as outlined above to ensure our estimates were focused on migrants. The transect for the Sacramento study region had 14 cells, the Yolo had 13 cells, the San Joaquin had 10 cells, the Tulare study had 8 cells, and the Delta had 8 cells (Figure 1B). Therefore, if abundance was distributed equally across cells within each transect the proportions would be 0.07, 0.08, 0.10, 0.13, and 0.13, respectively. In the absence of knowing exactly what constitutes a meaningful spatial concentration, for each cell containing a study region, we then summarized the number of weeks that each

species had proportional abundance values 1–2, 2–3, and more than 3 times greater than if it was equally distributed across the transect. We then categorized the spatial concentration bins as moderate (1–2 times), high (2–3 times), and extreme (>3 times). For example, if 35% of all abundance values within the latitude transect was found in the cell containing the Delta for week 16, it would get counted in the 2–3 bin and categorized as high spatial concentration, because even distribution across those 8 cells of that transect would be 13%. All values are reported with \pm standard error.

RESULTS

Total Landbirds and Population Proportions Migrating through Study Regions

Of the 112 species considered, 83 used the Delta during migration, 82 used the Sacramento, 79 used the Yolo, 89 used the San Joaquin, and 91 species used the Tulare study regions. Across each of the 5 study regions, landbird abundance peaked during the migratory seasons (Figure 2A–E; Supplementary Material Figure S3). At each of the Central Valley study regions, migrants were more abundant in the fall than in the spring (Figure 2F). The total number of migratory landbirds was relatively similar across migration seasons in the Colorado River Delta (Figure 2F). The Tulare study region, which was the largest study region, had the most migratory landbirds during both fall ($65,229,117 \pm 2,713,517$) and spring ($47,763,101 \pm 736,814$) migration (Figure 2F). In the fall, the Delta had the least number of migrating individuals ($14,329,393 \pm 388,511$), while in the spring the Sacramento study region had the lowest number of migrating landbirds ($14,872,554 \pm 343,184$; Figure 2F). During spring migration, Wilson’s Warbler (*Cardellina pusilla*) was the most abundant landbird in each of the 5 study regions (Supplementary Material Table S1). Wilson’s Warbler was also the most abundant landbird during fall migration in the Sacramento and Yolo study regions. Tree Swallow (*Tachycineta bicolor*) was the most abundant fall migrant in the San Joaquin and Tulare study regions. In the Delta, Orange-crowned Warblers (*Oreothlypis celata*) were the most abundant landbird during fall migration (Supplementary Material Table S1).

Each of the 5 study regions proved to be critically important at the continental population level during one or more of the migration seasons (Figure 3; Supplementary Material Table S1). For spring migration, 79.3% (± 29.1) of the population of Lawrence’s Goldfinch (*Spinus lawrencei*) migrated through the Tulare study region and 37 total species had $\geq 1\%$ of their population migrate through the region (Figure 3; Supplementary Material Table S1). In the Delta, 27.1% (± 1.5) of the Tree Swallow population used the region and 15 other species had $\geq 1\%$

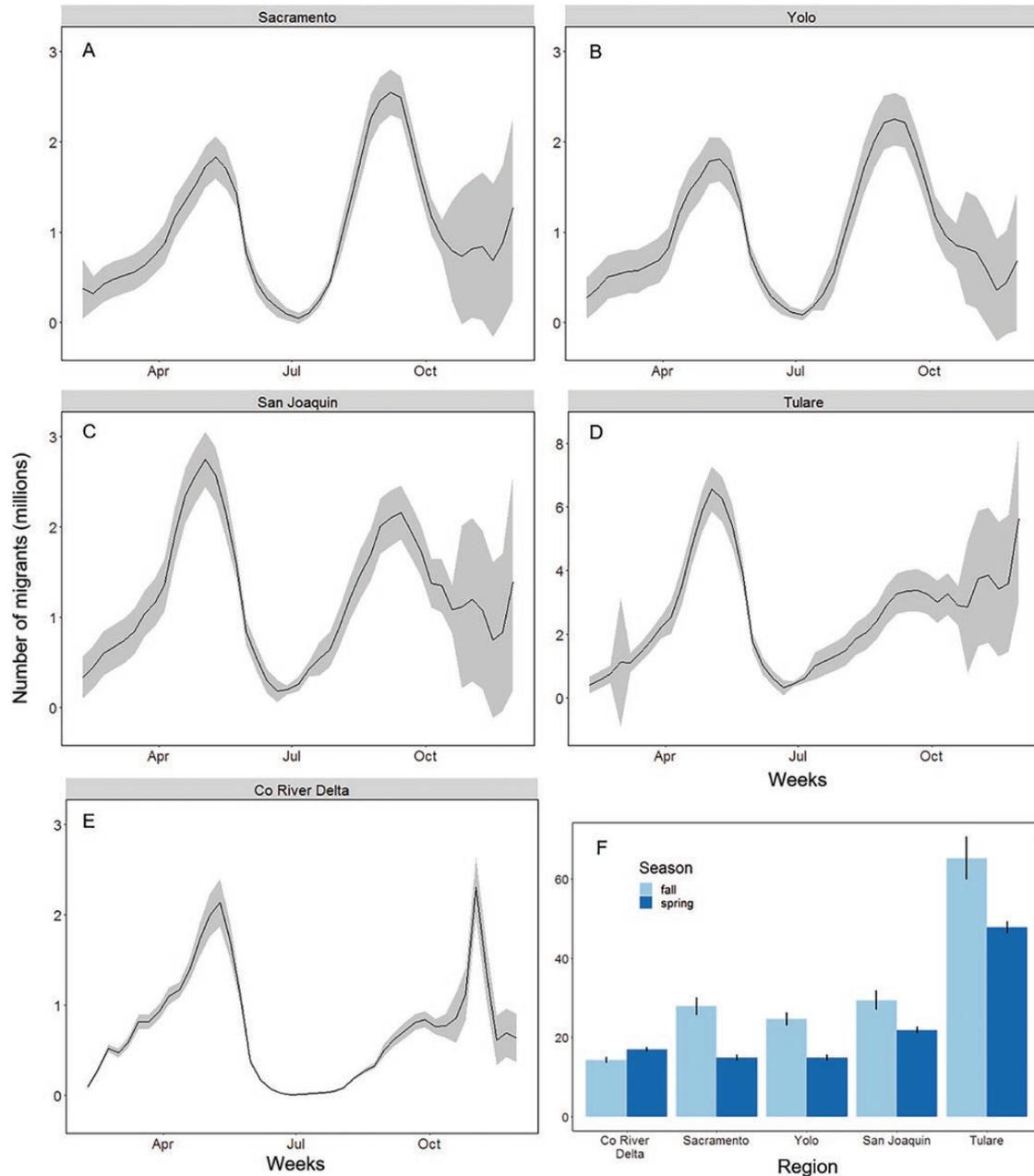


FIGURE 2. Weekly estimates (black lines) and 95% confidence intervals (gray) of a total number of individuals across 112 landbird species using 4 sites in California's Central Valley (A–D) and the Colorado River Delta (E). See [Supplementary Figure S3](#) for individual species plots. (F) Estimates and 95% confidence intervals of a total number of individuals using each site during fall and spring migration across 112 landbird species. Estimates of the total number of individuals were generated using eBird abundance data.

of their population migrate through the Delta ([Figure 3](#); [Supplementary Material Table S1](#)). Marsh Wren (*Cistothorus palustris*) had the highest proportion of its population in the Sacramento, Yolo, and San Joaquin study regions: 17.0% (± 2.9), 14.5% (± 2.5), and 11.6% (± 2.0), respectively. The Sacramento and Yolo study regions had a total of 20 species with $\geq 1\%$ of their population using the regions during spring migration and the

San Joaquin had 29 species ([Figure 3](#); [Supplementary Material Table S1](#)).

Across the 5 study regions, between 11 and 30 species had $\geq 1\%$ of their population occur within a study region during fall migration ([Figure 3](#); [Supplementary Material Table S1](#)). Tree Swallows had the highest proportion of their population occur in the Tulare (58.9% ± 3.2) and San Joaquin (23.6% ± 1.3) study regions. Black-throated Gray

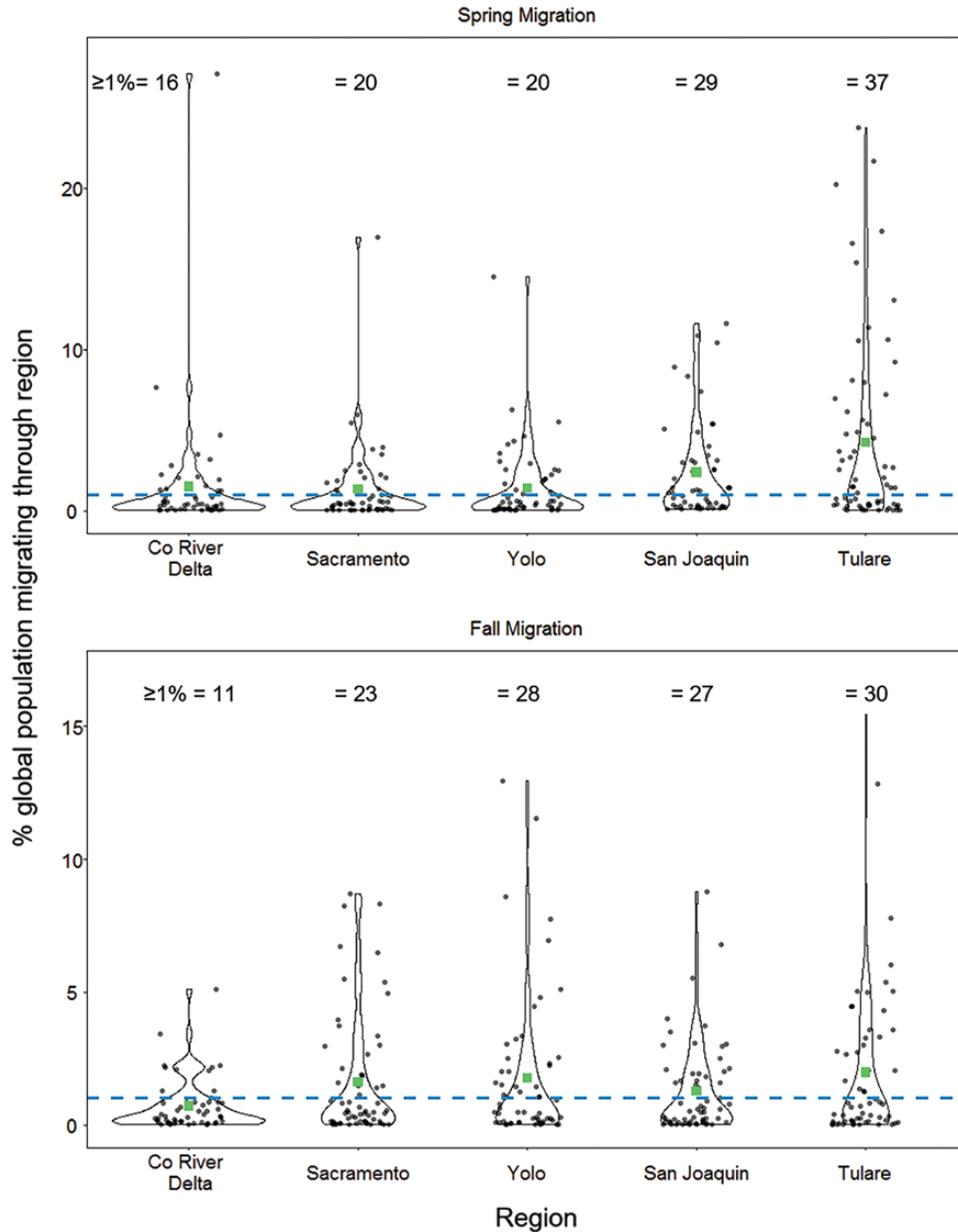


FIGURE 3. Violin plots created from the full species list ($n = 112$) where each dot represents the proportion of a species population that uses a region during spring and fall migration. The green squares show the mean proportion across species within a site and season. The blue dashed line marks the 1% line. Locations meet the criteria as an Important Bird Area when $\geq 1\%$ of a species population consistently and predictably use the location. The total tally of species that meet these criteria is listed along the top. Although all values were included in generating the plot, extreme values in the spring (79.3) and fall (58.9, 38.8, 32.6, 26.5) are not shown in the illustration. Population proportions were generated using eBird abundance data and values for all species are included in [Supplementary Material Table S1](#).

Warblers (*Setophaga nigrescens*) had the highest proportion of their population use the Sacramento ($26.1\% \pm 2.6$), Yolo ($25.9\% \pm 2.6$), and Colorado River Delta ($5.1\% \pm 0.5$) study regions.

Spatial Concentrations

Of the 112 species, 111 had at least 1 week where their abundance during migration was spatially concentrated

(either moderate [$1-2\times$], high [$2-3\times$], or extreme [$>3\times$]) in at least one of the sites and migratory seasons (Figure 4). Within species, spatial concentration in the study region varied across and within migratory seasons (Figure 4; [Supplementary Material Figure S4](#)). Both the Valley and the Delta showed evidence of a migration bottleneck as indicated by the presence of high to extreme spatial concentration within study region

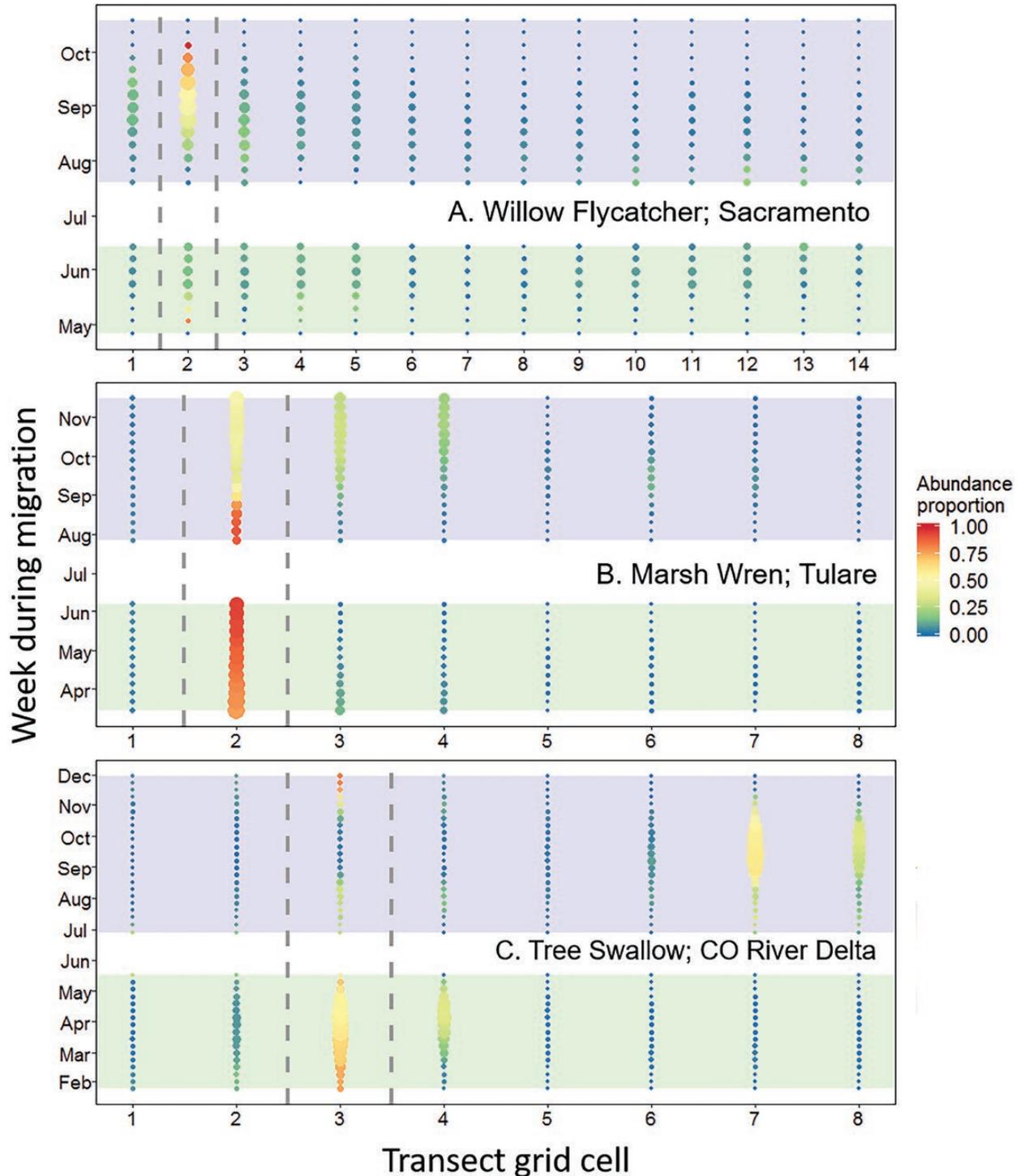


FIGURE 4. Grid plots illustrating the proportional abundance (dot color) in each latitudinal transect grid cell (Figure 1) for each week during fall (blue rectangle) and spring (green rectangle) migration for 3 example species and study regions. Dot size is relative to total abundance for that week and cell, where larger dots are indicative of relatively higher abundance values regardless of their proportional relationships to other cells within the transect. Cells between the dashed gray lines correspond to the cell each study region is located in along the transect illustrated in Figure 1. Examples are (A) Willow Flycatcher for the Sacramento study region transect, (B) Marsh Wren for the Tulare study region transect, and (C) Tree Swallow for the Colorado River Delta study region transect. Figure 1B illustrates the spatial concentration of abundance for Willow Flycatcher in mid-September summarized here (A). See Supplementary Material Figure S4 for plots of each species.

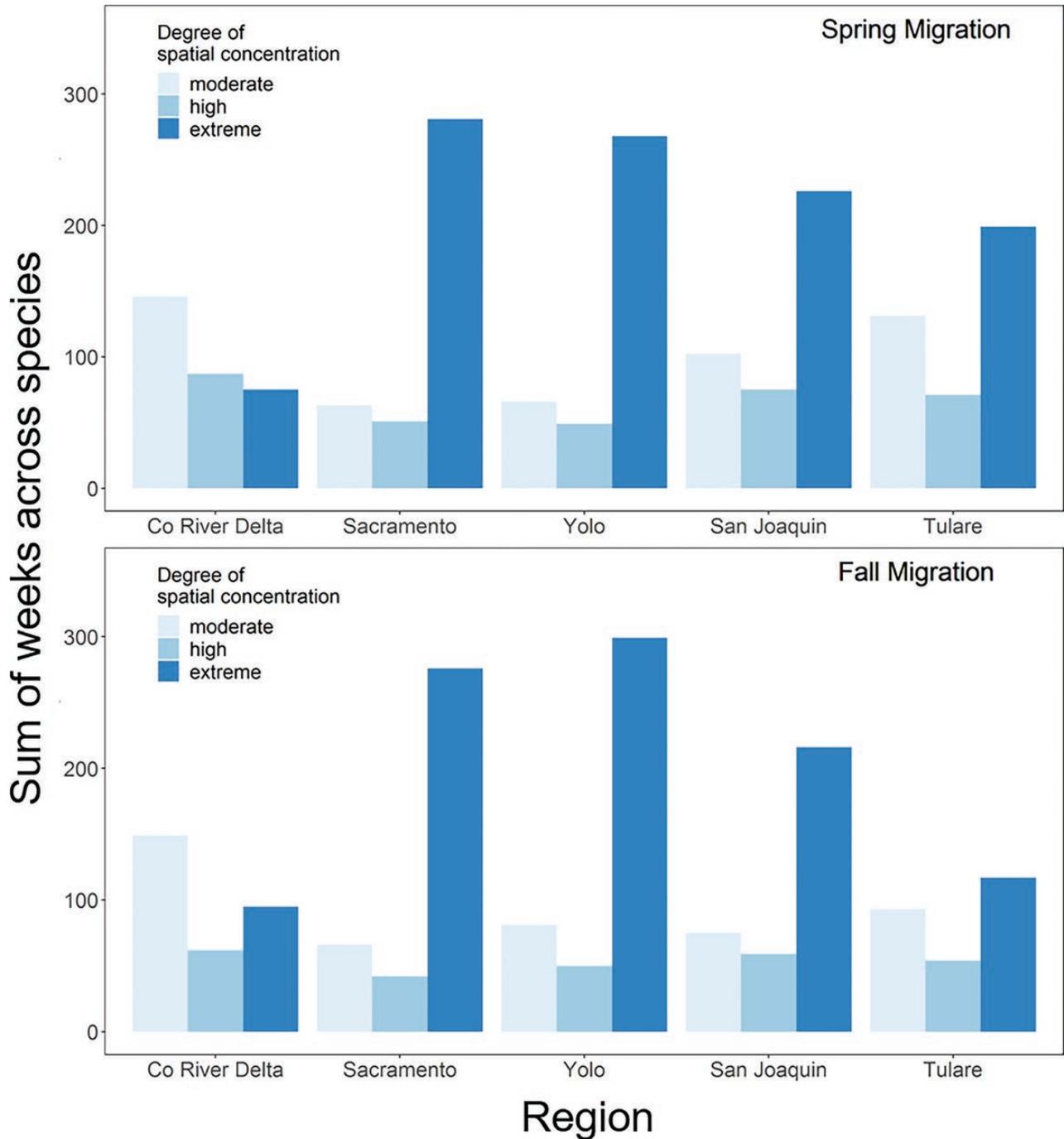


FIGURE 5. Bar plots summarizing the number of weeks that spatial concentration occurred during fall and spring migration across 112 species for each study region. Spatial concentration was assessed by calculating the proportion of total eBird abundance in the study cell compared to the total abundance that was in a latitudinal transect stretching across the Pacific Flyway for each study region (Figure 1). The degree of spatial concentration was classified by first determining the proportion values if abundance was evenly distributed across the latitudinal transect. Spatial concentration was classified as moderate when the proportion values of the study cell were 1 to <2 times the even distribution value; high when proportion values of the study cell were 2 to <3 times the even distribution value; and extreme when proportion values of the study cell were ≥ 3 times the even distribution value. For pre- and post-breeding migration, respectively, the total number of weeks considered during migration across the 112 species were 1,125 and 1,375 for the Colorado River Delta; 1,136 and 1,400 for the Sacramento study region; 1,016 and 1,229 for the Yolo study region; 1,137 and 1,380 for the San Joaquin study region; and 1,150 and 1,399 for the Tulare study region.

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cells compared to the full latitudinal transect (Figure 5). Spatial concentration within a study region cell occurred during 29% (range across regions: 24.6–36.2%) of all migration weeks across species (Supplementary Material Table S2). On average, extreme spatial concentration within a study region cell occurred during 16.8% (range across regions: 6.8–25.3%) of all migration weeks (Figure 5; Supplementary Material Table S2). Migratory spatial concentration was more evident in study region cells in spring, with an average across sites of 34.0% (range: 27.4–37.7%) of migration weeks with spatial concentration, compared to the fall (average across study regions: 25.6%; range across regions: 18.0–35.0%; Figure 5; Supplementary Material Table S2).

DISCUSSION

We showed that each of the 5 study regions is crucial to the population-level conservation of several landbird species (Figure 3) because they host significant proportions ($\geq 1\%$) of species' populations during migration. Our study used community science-based, weekly eBird abundance estimates to provide a comprehensive quantification of the use of 2 critical regions of conservation concern in the western United States, the Colorado River Delta and the Central Valley of California, by 112 migrating landbird species. Here we developed and applied an approach to estimate the population-level importance of specific locations during migration to breeding landbird populations and to quantify the degree to which species weekly abundances are spatially concentrated and, thus, may be considered a migratory bottleneck. We show that across species, there are hundreds of weeks when species' abundance is concentrated within study regions (Figure 5). This work offers a novel, multifaceted approach of quantifying spatial use of migrating landbirds using community-based, eBird abundance data.

Total Landbirds and Population Proportions Migrating through Study Regions

We estimated that a total of ~ 14 (spring) and ~ 17 (fall) million landbirds migrated through the Colorado River Delta and at least ~ 65 (spring) and ~ 48 (fall) million landbirds migrated through the Central Valley (Figure 2). There are several examples of species for whom some study regions are important at the population level. One such example is Tree Swallow, a declining aerial insectivore whose breeding population is distributed across North America (Rosenberg et al. 2019); 27.1% (± 0.02) of their population uses the Colorado River Delta in the spring and 58.9% (± 0.03) of their population uses the Tulare of the Central Valley in the fall. Tree Swallows have previously been identified as the Colorado River Delta's most numerous migrant with

estimates of "several million" individuals passing through each season (Rosenberg 1991). Our results not only refine these estimates but place them in population-level context. Other examples include Black-throated Gray Warbler which has 26.0% of its population migrating through the Sacramento study region in the fall and Marsh Wren which has 14.5% of its population migrating through the Yolo study region in the spring (Supplementary Material Table S1). Our results suggest that the Colorado River Delta and California's Central Valley are important regions for maintaining populations of many migratory landbirds with ranges that are not only limited to the west but that span across North America.

Our approach to use eBird abundance models to generate estimates of total individuals using a defined geography offers a new tool for assessing space use by migrating birds. Other approaches that have quantified broad-scale use of space by migrating passerines in North America include methods that use radar to estimate the number of birds passing latitudinal transects at the northern and southern extents of the United States during spring and fall (Dokter et al. 2018). Radar-derived estimates have proved vitally useful in identifying seasonal (Dokter et al. 2018) and long-term (Rosenberg et al. 2019) population changes; however, radar technology cannot identify species and therefore results in conclusions spanning all avifauna. For species such as shorebirds that regularly congregate in habitats that make broad-scale, field-based surveys feasible, counts of total individuals, similar to those presented in our study, have been made for sites like the Delaware Bay which report daily counts up to 426,162 total shorebirds (Clark et al. 1993). Survey-based estimates of site use during migration can offer fine temporal resolution and reasonably accurate estimates by species (Kwon et al. 2018) but this usually comes with significant time and financial investments. eBird currently has weekly abundance estimates for 610 species, enabling the possibility of applying our approach to other species and locations at minimal costs.

To understand the population-level importance of a location to a species during migration, we determined the proportion of each species' population that uses each study region during spring and fall migration. There is no clear threshold for determining whether a specific population proportion value is critical from a conservation perspective, and it is likely that values vary by species depending on population size and trend. However, we used BirdLife International's Global Important Bird Area criteria A4, which allows a site to qualify as globally significant if it regularly holds congregations of $\geq 1\%$ of the global population of one or more species (BirdLife International 2020). We used the $\geq 1\%$ threshold only to provide context for the population proportions calculated for each site and species. Therefore, we interpret values that meet this threshold

(Figure 3) as the study region having population-level importance for a given species. We recognize that despite the use of this threshold, interpretation of these data does not necessarily mean that a value below the threshold is not important for a species. Consequently, we provide total population proportion values for each species, study region, and migratory season (Figure 3 and Supplementary Material Table S1).

Spatial Concentrations

Migratory bottlenecks are “passage points where geography constrains migration, leading to significant concentrations of populations that could elevate threats or risks” (Bayly et al. 2018). We found that each study region had hundreds of weeks where bird abundance estimates were concentrated in study regions. Regions in the Central Valley, in particular, showed evidence of migratory bottlenecks; most had well over 400 weeks during migration (16.8% of all weeks during migration across species) when abundances were concentrated compared to the rest of the latitudinal transect (Figure 5). These results suggest that when landbirds are migrating through western flyways of North America, they are often funneled through the Central Valley and Colorado River Delta.

The temporal resolution of the data (weekly) enabled us to detect variations in the spatial concentration within and between migratory seasons, suggesting that regions may act as a migratory bottleneck during either spring or fall but often not both (Figure 4). Furthermore, within a migratory season, the distribution of landbird abundance across space can either remain relatively constant throughout a migratory season (Figure 4B) or the concentration abundance can vary as a migratory season progresses (Figure 4C). The temporally dynamic nature of migratory bottlenecks is often only detected with labor-intensive surveys (Farmer et al. 2007, Stępniewska et al. 2013). When locations are quantified as migratory bottlenecks, they frequently depend solely on surveys conducted at a site and lack a comparison across space to confirm disparate abundance across the flyway. Our approach offers the flexibility of using readily available community science-based data (Fink et al. 2020a) and can be applied to any region of conservation concern in the context of any flyway. Locations with on-the-ground migratory abundance surveys, coupled with a spatial concentration analysis like the one highlighted here, would offer a comprehensive examination of space use by migrants at both the site and flyway scales.

Limitations and Assumptions

The eBird Status and Trends weekly estimates of abundance are a powerful tool for conservation (Schuster et al. 2019, Wilson et al. 2019), but it is important to understand

the limitations of the data and how they are applied. We recognize that eBird abundance estimates vary in predictive ability across species and within species, across their range throughout the year. For example, our results (Figure 2) reflect a decrease in eBird abundance model performance during the overwintering season, which is a common signature in eBird relative abundance models (Fink et al. 2020b). eBird data, upon which the abundance models are dependent, are not randomly sampled across space, and the observations not necessarily independent, particularly when they are entered as complete checklists. It is possible that the abundance models across species could exaggerate consistency in the response of species to their environmental predictors. Our results would then reflect that potentially misleading consistency across species. Furthermore, the accuracy of the PIF population estimates also has many sources of error that vary across species (Stanton et al. 2019). Therefore, our estimates of study region use by migrating landbirds incorporate this variation in predictive ability over time, space, and species.

Our approach depends on several assumptions and the extent to which they are violated introduces new sources of error. One assumption that our analysis makes is that once an individual passes through the region, it does not reenter the region. For example, during the spring migration, a bird would not travel north through the site and then return south, reentering the site. We believe that this assumption is likely not violated to the extent that it would influence our results. In addition to being sensitive to the abundance models, our results, like previous efforts to quantify the number of migratory birds (Hahn et al. 2009), are dependent on the accuracy of continental estimates of the size of breeding populations. A second assumption our approach uses is that individuals do not linger within the study region for prolonged periods of time (i.e. longer than 1 week, the temporal resolution of the eBird abundance models). The extent to which this assumption is violated could inflate our estimates of total individuals using the region and the extent to which individuals stay in the region for less than a week, we could be underestimating the number of individuals using the study region. For example, Rosenberg (1991) states that Tree Swallows may “take up temporary residence in roosts” at specific locations in the Colorado River Delta region. Examples like this could result in our counting temporary residents across multiple weeks when our approach assumes new individuals each week.

The population estimates we used have been carefully developed by Partners in Flight (Stanton et al. 2019) and have been used to quantify the magnitude of broad-scale changes in the number of migratory birds over time (Rosenberg et al. 2019). As estimates of breeding populations become more accurate, so will our ability to use eBird

abundance models to quantify the numbers of migrating birds. In the meantime, on-the-ground counts of migrating birds will remain an important component of validating these modeled results. These assumptions highlight the importance of maintaining a measure of uncertainty and were the motivation that we used the delta method, as described above, to propagate error through all the estimates generated in these analyses.

Within the study regions in which we quantified migrant abundance, there may be significant variation across habitats is not recognized by our coarse-filter approach. For example, Humple and Geupel (2002) found that Orange-crowned Warblers, Yellow Warbler (*Setophaga petechia*), and Ruby-crowned Kinglet (*Regulus calendula*) were common migrants in remnant riparian forests along the Sacramento, San Joaquin, and Cosumnes Rivers. However, in an independent study in urban areas of the northern Central Valley, Greco and Airola (2018) reported that the most abundant migrants were 4 species of wood warblers, Black-throated Gray, Wilson's, Orange-crowned, and Yellow Warblers. Similarly, in the southwestern United States, migrating landbirds use both riparian and upland areas, and the year-to-year preference for these sites may depend on annual weather conditions (Kellermann and van Riper 2015). Because our analysis was based on eBird abundance models that average across multiple years, they cannot be used to evaluate whether migrating birds may be more abundant along these major rivers during dry years, nor can they be used to evaluate whether some vegetation types may be used preferentially over others. However, as these models become available at finer spatial and temporal resolutions, the application to these types of questions will improve.

Conservation and Management Implications

Our results demonstrate that the protection and restoration of ecosystems in the Central Valley and the Colorado River Delta have the potential to contribute to the conservation not just of birds that breed or winter within these regions, but also to the conservation of millions of birds that breed across North America but migrate through this region. Incorporating this information into conservation planning has the potential to extend the value of ecosystem restoration beyond the local footprint of the Colorado River Delta and Central Valley. For example, analytical approaches have been developed to use the information on migratory species movements to quantify the flow of ecosystem services between breeding and nonbreeding regions (Semmens et al. 2011). If migratory birds generate significant economic value on their breeding grounds (e.g., through recreational bird watching), this approach could be used to quantify the degree to which the habitat used

during migration subsidizes the values generated during the breeding season (Semmens et al. 2018). Quantifying the value of these subsidies to other regions could provide additional funding for large-scale river restoration programs. The regional and population-level importance of these sites underlines the significance of maintaining local habitat quality, not only for breeding birds, but also for those that are passing through on migration. For example, in the Colorado River Delta, native riparian willow (*Salix gooddingii*) habitat provides the most efficient foraging for spring migrating Wilson's Warbler (Darrah et al. 2017) and is sensitive to Colorado River flow reductions (Hinojosa-Huerta et al. 2013a). Likewise, in urban areas in the Central Valley, the abundance of migrating wood warblers is positively correlated with the cover of native oaks (*Quercus lobata*; Greco and Airola 2018). Both examples illustrate how fine-scale vegetation characteristics may be important to maintaining habitat quality for migratory birds within and beyond the boundaries of the site. Our approach can identify which migrants are most abundant across large areas but maintaining the habitat quality within these areas will depend on more detailed studies of bird behavior and their habitat preferences during migration.

One of the challenges to understanding migratory birds across their full annual cycle is that their annual migratory movements cover long distances, are spread across vast areas, and their presence in any one location is typically fleeting. This analysis illustrates the tremendous value of applying models generated from data collected by community scientists to address questions about bird migration at appropriate spatial scales and at population levels (La Sorte et al. 2014). The application of this analysis framework across broader spatial extents could help identify important stopover regions not previously identified and in addition, when applied to other known areas of conservation importance, could help illuminate temporal shifts of avian use throughout the year. Further analyses that address similar questions at finer spatial and temporal resolutions and in more remote regions will depend on the continued engagement of community scientists.

SUPPLEMENTARY MATERIAL

Supplementary material is available at *Ornithological Applications* online.

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Data availability: Analyses reported in this article can be reproduced using the data and code provided by https://github.com/audubongit/western_landbird_migration. **Supplementary Material Figures S3 and S4** are located at <https://doi.org/10.5061/dryad.3j9kd51gc>.

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