RESEARCH ARTICLE

Utilizing high-resolution genetic markers to track population-level exposure of migratory birds to renewable energy development

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Abstract

With new motivation to increase the proportion of energy demands met by zero-carbon sources, there is a greater focus on efforts to assess and mitigate the impacts of renewable energy development on sensitive ecosystems and wildlife, of which birds are of particular interest. One challenge for researchers, due in part to a lack of appropriate tools, has been estimating the effects from such development on individual breeding populations of migratory birds. To help address this, we utilize a newly developed, high-resolution genetic tagging method to rapidly identify the breeding population of origin of carcasses recovered from renewable energy facilities and combine them with maps of genetic variation across geographic space (called 'genoscapes') for five species of migratory birds known to be exposed to energy development, to assess the extent of population-level effects on migratory birds. We demonstrate that most avian remains collected were from the largest populations of a given species. In contrast, those remains from smaller, declining populations made up a smaller percentage of the total number of birds assayed. Results suggest that application of this genetic tagging method can successfully define population-level exposure to renewable energy development and may be a powerful tool to inform future siting and mitigation activities associated with renewable energy programs.

Author summary

Increased demand for renewable energy, sparked by both public and government awareness of impending changes to the planet, can act as an additional impetus to understand the effects that renewable development might have on wildlife populations. Birds, in particular, may be exposed to industry activity during portions of their full migratory life

cycle, but understanding how this exposure might affect distinct populations has been difficult to ascertain in the past. Here, we utilize newly-developed methods to assign individuals from five species of migratory birds to genetically distinct populations, and combine these with mortality data from renewable energy facilities (both wind and solar) and banding station data in the West and Desert Southwest of the United States, to determine the impacts that these facilities might have on populations. We found that individuals most often exposed to renewable development were from the largest populations, and that rarer populations were exposed less often, despite their closer geographic proximity to anthropogenic activities in some cases. We present this work not only as a preliminary analysis that identifies potential exposure to renewable energy development for migratory species, but also as a template to allow future work to quantitatively assess this exposure risk as compared to other natural or anthropogenic changes.

Introduction

The increased environmental impact of fossil fuel consumption and recent government mandates to reduce CO_2 emissions to slow the pace of climate change have stimulated a considerable rise in renewable energy development [1]. According to the U.S. Energy Information Association, annual energy production from utility-scale solar facilities in the country increased from less than 1 million megawatt-hours (MWh) in 2008 to over 100 million MWh in 2021 [2]. Similarly, energy production from wind facilities has increased nationally 60-fold since 2001, reaching 380 MWh in 2021 [2]. A desire to reduce carbon emissions combined with technology innovations has allowed for the rapid scaling, growth, and deployment of wind and solar installations across the U.S., particularly in California [3]. For instance, the expansion of wind and solar energy production in the state has led to their emergence as the largest sources of renewable energy, together comprising over 75% of renewable energy produced [4]. Further, to meet growing energy needs while addressing climate change, California aims to increase such renewable energy production to meet the goal of 100% clean (zero-carbon) electricity to consumers by 2045 [5].

While such shifts to renewable energy are intended to reduce carbon emissions and ultimately changes to climate, minimizing the adverse effects to all wildlife, and particularly to groups more susceptible to interactions with infrastructure such as birds, is essential [6]. For example, hundreds of thousands of birds are estimated to be killed yearly in collisions with wind turbines [7,8]. Bird mortality caused by collisions with monopole wind turbines alone in the contiguous United States may be between 180,000–200,000 annually [9,10], occurring in over 300 species of birds in North America, and seasonally distributed concomitant with migratory patterns for particular groups [11]. In contrast, due to the technology's more recent adoption, the nature and extent of avian mortality due to solar photovoltaic (PV) and concentrating solar power (CSP) generating facilities are not well understood, but are still considered a conservation concern [12–14]. It is clear that these technologies, despite falling under the umbrella of "renewable", are likely to affect wildlife populations in different ways, and developing a method that could be used ubiquitously across each would allow for a better understanding of their relative impacts to populations. California can serve here as a suitable testbed for such an application, due to its relatively widespread adoption of a variety of renewable energy technologies, its habitats that are utilized by nearly 650 species of birds, and its coastline and interior habitats serving as vital migration corridors for avian populations across the United States and Canada [15–18].

It is widely accepted that both pre- and post-construction monitoring of avian wildlife is critical to understand the impacts that renewable energy may have on bird species [19–21]. A central challenge for these monitoring efforts, however, is the lack of precise knowledge about when, and to what extent, different breeding populations of a species (that are often genetically distinct from one another) may be exposed to facilities during migration, and whether observed mortality at renewable energy facilities will have effects on these distinct populations. For example, when avian samples are recovered at renewable energy facilities, knowledge of whether individuals came from stable or declining population segments (or conservation units, depending on goals) could have very different implications for possible conservation and mitigation strategies.

Efforts to understand population-specific bird migration patterns, however, have been met with numerous limitations and technological hurdles over the last century. Past attempts to map population-specific bird migration patterns relied either on the recovery of individual birds previous captured and tagged with bird bands, an approach that has had limited success in part because recapture rates of birds are generally very low [22], or on light-level geolocators, that do provide new information on migratory pathways of songbirds [23], but may be deployed only on relatively large birds, are expensive if deployed widely, and still require recovery of individuals [24,25]. These limitations can be overcome by utilizing genetic and isotopic markers to estimate an individual's population of origin. Such markers are an attractive alternative to previous standards, as they are noninvasive, require no re-capture, and are increasingly cost-effective [26–28]. However, until recently these methods yielded insufficiently resolved data (e.g. individuals assigned to broad geographic ranges and/or assigned with relatively low probabilities of membership) and could be limited by technical issues [29–31].

Here we utilize a high-resolution genetic tagging method for identifying the population-specific exposure of renewable energy development on migratory birds in California that provides a significant advantage over previous tracking methods [32]. We test our methodology on five species of migratory birds with diverse life histories, specifically of interest with regards to their interactions with renewable energy installations: the American Kestrel (*Falco sparverius*), Common Loon (*Gavia immer*), Common Yellowthroat (*Geothlypis trichas*), Wilson's Warbler (*Cardellina pusilla*), and Yellow Warbler (*Setophaga petechia*). We begin with genoscape maps that define genetically distinct populations (i.e., conservation units, see below for definition) at regional spatial scales [33–36]. We then use genomic information contained within feathers collected outside of breeding regions (specifically at energy facilities, as well as adjacent banding stations) to identify the breeding origin of those individuals. As a result, feathers collected from a carcass or living bird can be used to make essential links between where that bird was collected and which breeding population it came from [36,37]. Our objective is that these newly developed assignment methods can be used across species, technologies, and geographic locations to determine the genetically distinct breeding populations that individuals recovered from renewable energy facilities came from. Once identified, the status of those origin populations can be assessed, via demographic tools or models, to inform future management strategies. Such applications can also allow for the potential exposure to facilities along the full migratory pathway of individual birds to be quantified and, perhaps more importantly, compared to other looming risks to populations that include predation, habitat loss/conversion, and climate change.

Results

Sampling and DNA isolation

Samples were collected from either the carcasses of morphologically identified species in the field, or "feather spots" that were identified using genetic methods [38] from both wind or
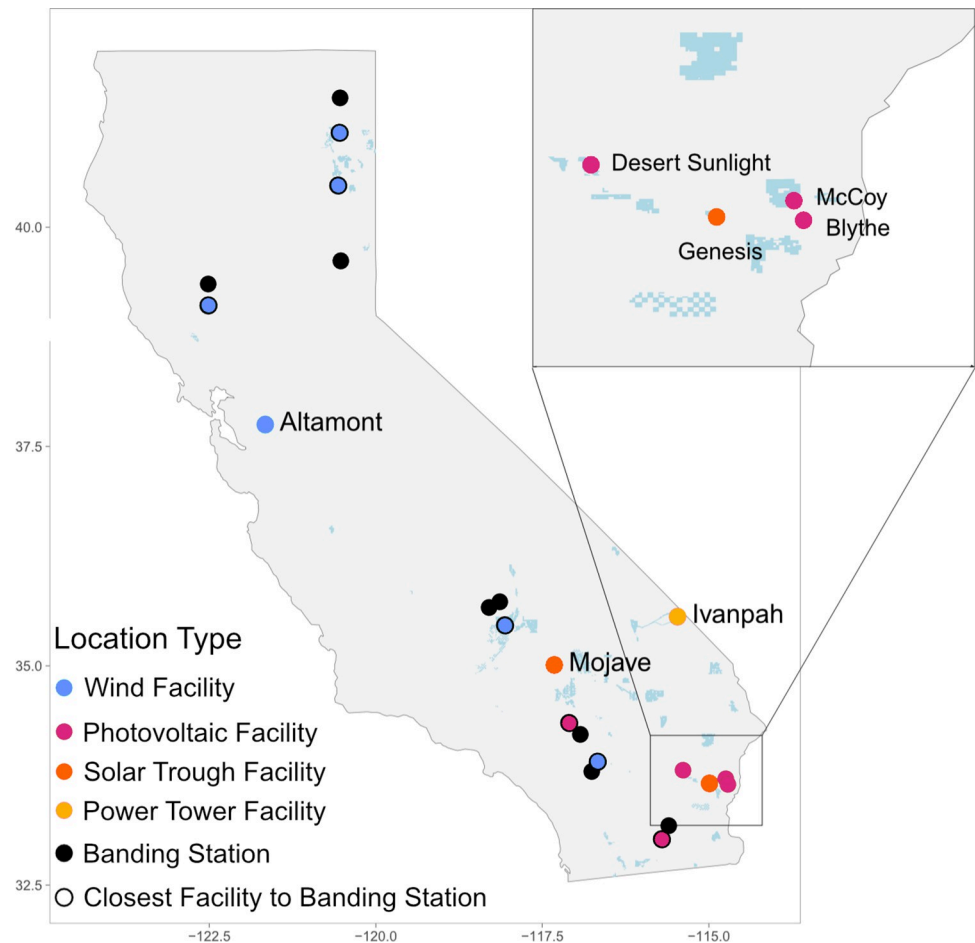
Fig 1. Solar and wind facilities that collected bird carcasses, as well as distribution of Wilson's Warbler and American Kestrel feathers collected at banding stations (black circles) near solar/wind facilities (outlined in black) that were genotyped to determine individuals from populations that may utilize flyways that are in close proximity to renewable facilities. Basemap downloaded from data.ca.gov.

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solar facilities (Fig 1). DNA extracts of 200 American Kestrels, 20 Common Loons, 33 Common Yellowthroats, 303 Yellow Warblers, and 178 Wilson's Warblers (Table 1) were amplified (see Methods for details) and genotyped by screening for up to 186 species-specific, diagnostic SNPs to assign individuals to conservation units (see below). American Kestrels had the highest genotyping success rate (i.e., when > 80% of variants were successfully called for an individual), with 89.5% of individuals successfully genotyped, followed by Wilson's Warbler (88.8%), Yellow Warbler (88.1%), Common Yellowthroat (75.8%), and Common Loon (75%, Table 1).

SNP genotyping

To understand the population-level exposure of migratory birds to renewable energy facilities, we combined genoscape methods with individual assignments at several solar and wind energy facilities, as well as several banding stations close to energy facilities, across California for five species: Yellow Warbler, Common Loon, Wilson's Warbler, American Kestrel and Common Yellowthroat. Briefly, a genoscape is a spatially explicit map of genetic variation across the geographic extent of the breeding range [32], which can be used as a baseline for assigning

Table 1. Priority taxa samples collected and genotyped from 2014–2021 from solar and wind facilities (colors as depicted in Fig 1). Numbers in parentheses reflect the number of birds genotyped (i.e. each individual had >80% of variants successfully called), but does not necessarily imply that individuals were assigned to a breeding population with certainty.

Technology Type	Wind	PV	PV	Trough	Tower	PV	Trough	
Species	Altamont	Blythe	D. Sunlight	Genesis	Ivanpah	McCoy	Mojave	Total
Common Loon		4 (2)	11 (8)	4 (4)		1 (1)		20
American Kestrel	170 (162)			9 (4)	21 (13)			200
Common Yellowthroat		9 (6)	4 (4)	4 (3)	3 (2)	4 (3)	9 (7)	33
Yellow Warbler	1 (0)	6 (3)	2 (1)	5 (3)	286 (258)	2 (2)	1 (0)	303
Wilson's Warbler	5 (4)	20 (19)	6 (3)	1 (1)	126 (114)	20 (17)		178
Total	176	39	23	23	436	27	10	734

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individuals from nonbreeding and, in this case, renewable energy sites to their most likely breeding population and region. From initial reduced representation sequencing, RAD-seq, in the American Kestrel [39], Common Loon [35], Yellow Warbler [33], Wilson's Warbler [34], and a new low coverage whole genome sequencing protocol for the Common Yellowthroat [40], we used custom R scripts to identify 96–192 highly divergent population-specific SNPs and to convert this panel into a SNP-type Assay (Fluidigm Inc.) following the methods of [32]. The SNP-type assays designed for each species were then used to screen birds collected at renewable energy sites to assign them back to breeding population of origin using the program RUBIAS [41], a program which infers individual posterior probabilities of assignment through Markov-chain Monte Carlo conditioned on the reference allele frequencies of known individuals (Dryad Accession doi:10.5061/dryad.h44j0zprq, [42]).

Defining baseline conservation units and accuracy of assignment

Conservation units (hereafter *units*) were defined by using developed genoscapes for each target taxon:

American Kestrel–The American Kestrel genoscape was comprised of genetic sampling of 573 kestrels from 36 locations and identified 5 genetically distinct units (e.g., Alaska, East, Florida, Texas and West; [36]). American Kestrels of known origin were assessed for assignment accuracy using two data subsets–one with 501 individuals that were included in the assay, and another with 329 individuals that were omitted during assay design (hereafter Training and Testing, respectively, S5 Table). All breeding individuals of this species were assigned to one of the five genetically distinct units in RUBIAS. The proportion of correct assignment for the first set of samples ranged from 71% (Alaska) to 92% (Texas), with a few notable misassignments. Breeding birds from Alaska were misassigned to the West unit 24% of the time, and 5% of the time to the Texas unit; while birds from Florida were misassigned to the East unit 23% of the time.

The self-assessment of American Kestrel breeding individuals from the Testing subset had a lower accuracy of assignment, especially for the Alaska genetic unit. Of the six additional breeding birds collected from Alaska that were not used to design assays for the target variants, the proportion of correct assignment to Alaska was only 17%; rather birds from Alaska were more likely to be misassigned to the West unit (83%). Breeding kestrels from Florida showed 50% assignment to Florida and 50% misassignment to the East unit. Assignment to the East and West showed higher accuracy with an 84% and 91% correct assignment, respectively. Birds from the East unit, Texas and West showed >0.80 posterior probability of assignment to the correct unit.

Common Loon–The Common Loon genoscape was comprised of 300 individuals sampled from 23 sites across their breeding range that were clustered into six distinct genetic units (e.g., Alaska, Pacific Northwest, North Central, Midwest, Eastern Canada and New England; [35]). Approximately 97% of Common Loon breeding individuals were assigned with certainty to one of these six genetically distinct units, with assignment accuracy ranging from 84% (North Central) to 100% (eastern Canada; S6 Table). The self-assessment of Common Loon breeding individuals from the Testing subset had a similarly high accuracy of assignment. We calculated 98% correct assignment to the New England unit, 82% accuracy for North Central, 96% accuracy for Alaska, 94% for Pacific Northwest and 92% for Midwest units (S5 Table). We did not have enough newly genotyped individuals to test the accuracy of the East Canada unit without assignment bias.

Common Yellowthroat–The Common Yellowthroat genoscape was generated from 271 breeding birds sampled from 37 sites across the breeding range [40] and five genetically distinct units were identified (e.g. northern California, West, Southwest, Midwest and Atlantic Coast; [40]). Cross validation assignment of the known Common Yellowthroat breeding individuals indicated the ability to correctly assign individuals to five genetically distinct units was high, ranging from 71% (California) to 94% (West; S7 Table). The greatest proportion of incorrect assignments was between the Midwest and Atlantic Coast units (19%) and did not impact assignment of unknown origin birds in California.

Yellow Warbler–Early genoscape analyses identified five genetically distinct units (e.g., Alaska, Western Boreal, Southwest, Central, and East) using 419 breeding birds sampled from 50 sites across the breeding range [33]. Cross validation of assignment in the Yellow Warbler illustrated the ability to correctly assign individuals to five units was slightly lower than for Wilson's Warbler (see below), ranging from 69% correct assignment for the Central unit to 93% for Western Boreal and Eastern units (S8 Table). Yellow Warbler individuals from the Central unit showed 24% probability of misassignment to the Eastern unit, and 7% to the Western Boreal unit.

Wilson's Warbler–The Wilson's Warbler genoscape was generated from 393 breeding individuals sampled from 33 sites across the breeding range and is comprised of six genetically distinct units (e.g., Western Boreal, Pacific Northwest, Coastal California, California Sierra, Basin Rockies and Eastern Boreal; [32,43]). Cross validation assignment of Wilson's Warbler indicated the ability to correctly assign individuals to six genetically distinct units was high, ranging from 80% (California Coastal) to 100% (Eastern Boreal unit; Table not shown but see [32]). The majority of incorrect assignments was between the California Coastal, Sierra and Pacific Northwest groups.

Assignment of unknown origin individuals

American Kestrel–Most of the American Kestrel carcasses collected at the wind and solar facilities were assigned to the West unit, with a few also assigned to the Texas unit (Fig 2). All of the carcasses at Ivanpah and almost all at Altamont were assigned to the West unit, whereas carcasses at Genesis were assigned to either Texas or West units. Altamont also had a higher proportion of carcasses assigned with certainty to specific units (n = 151) as compared to Ivanpah (n = 13) and Genesis (n = 4) (Fig 2). In addition to genotyping carcasses found at the renewable energy stations above, we also genotyped feather samples for American Kestrels collected at a migratory bird banding station that was located in close proximity to the Sunpeak Solar Energy facility (S4 Table). For this species, all 11 of these samples were assigned to the West unit (Fig 2).

Common Loon–The majority of the Common Loon carcasses collected at solar facilities were assigned to the North Central unit, with the remainder assigned to the Midwest (Fig 3). The carcasses collected at McCoy and Blythe were assigned to the North Central unit, whereas
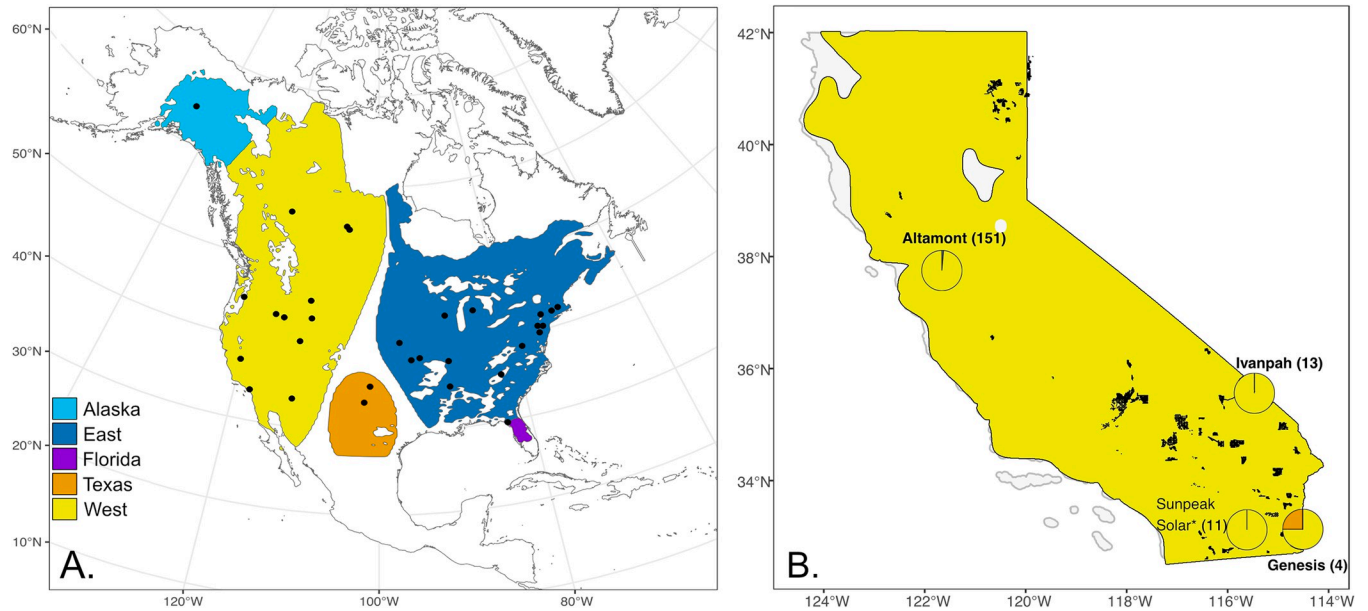
Fig 2. American Kestrel genoscape (A) and population-specific assignment of American Kestrels collected at renewable energy sites in California (B, bold) and birds collected near renewable energy facilities (B, *). Black circles in (A) indicate locations of samples used to construct the genoscape. Numbers reflect individuals that were assigned with certainty to a breeding population as identified by the genoscape in (A). Two kestrels found at the Altamont wind facility were assigned to the East unit (small sliver in pie chart at that location). Basemap in (A) downloaded and modified from sciencebase.gov [56], basemap in (B) downloaded from data.ca.gov.

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two out of four carcasses at Genesis and one out of eight carcasses at Desert Sunlight were assigned to the Midwest unit. Desert Sunlight Solar Farm had the highest number of Common Loon carcasses assigned with certainty to units (n = 8) as compared to the southern solar facilities McCoy (n = 1), Blythe (n = 1) and Genesis (n = 4) (Table 1).

Fig 3. Common Loon genoscape (A) and population-specific assignment of Common Loon fatalities collected at renewable energy sites in California (B). Black circles in (A) indicate locations of samples used to construct the genoscape. Numbers reflect individuals that were assigned with certainty to a breeding population as identified by the genoscape in (A). Basemap in (A) downloaded and modified from sciencebase.gov [56], basemap in (B) downloaded from data.ca.gov.

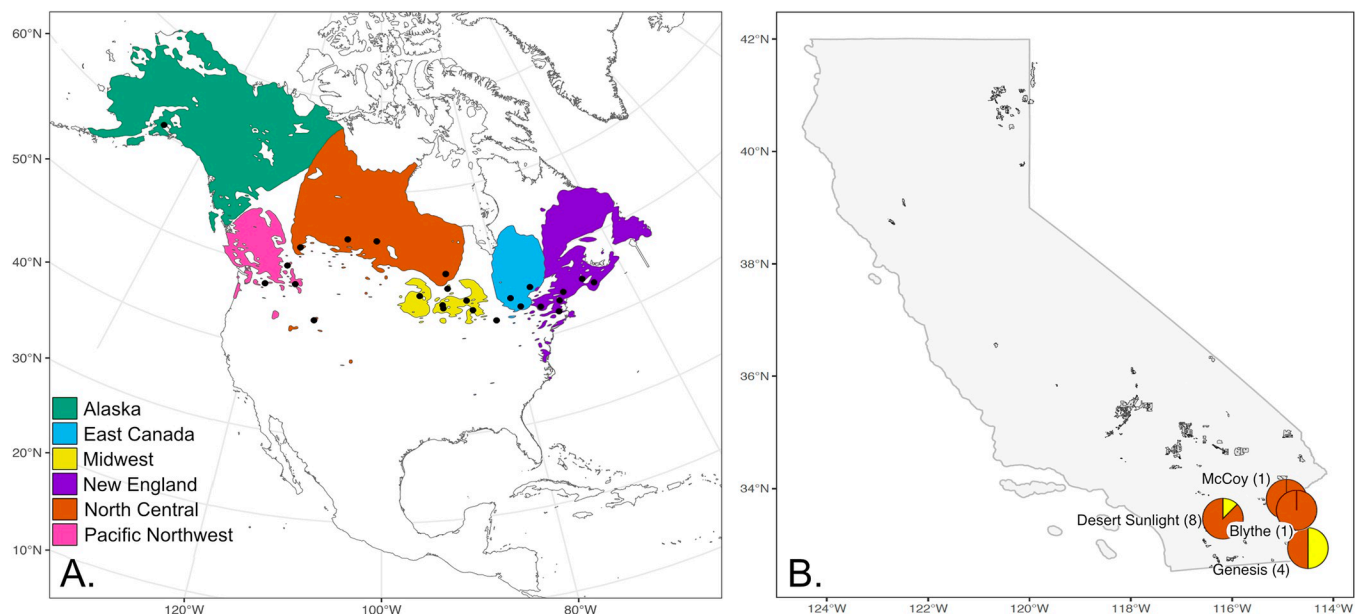https://doi.org/10.1371/journal.pstr.0000088.g003

Fig 4. Common Yellowthroat genoscape (A) and population-specific assignment of Common Yellowthroat fatalities collected at renewable energy sites in California (B). Black circles in (A) indicate locations of samples used to construct the genoscape. Numbers reflect individuals that were assigned with certainty to a breeding population as identified by the genoscape in (A). Basemap in (A) downloaded and modified from sciencebase.gov [56], basemap in (B) downloaded from data.ca.gov.
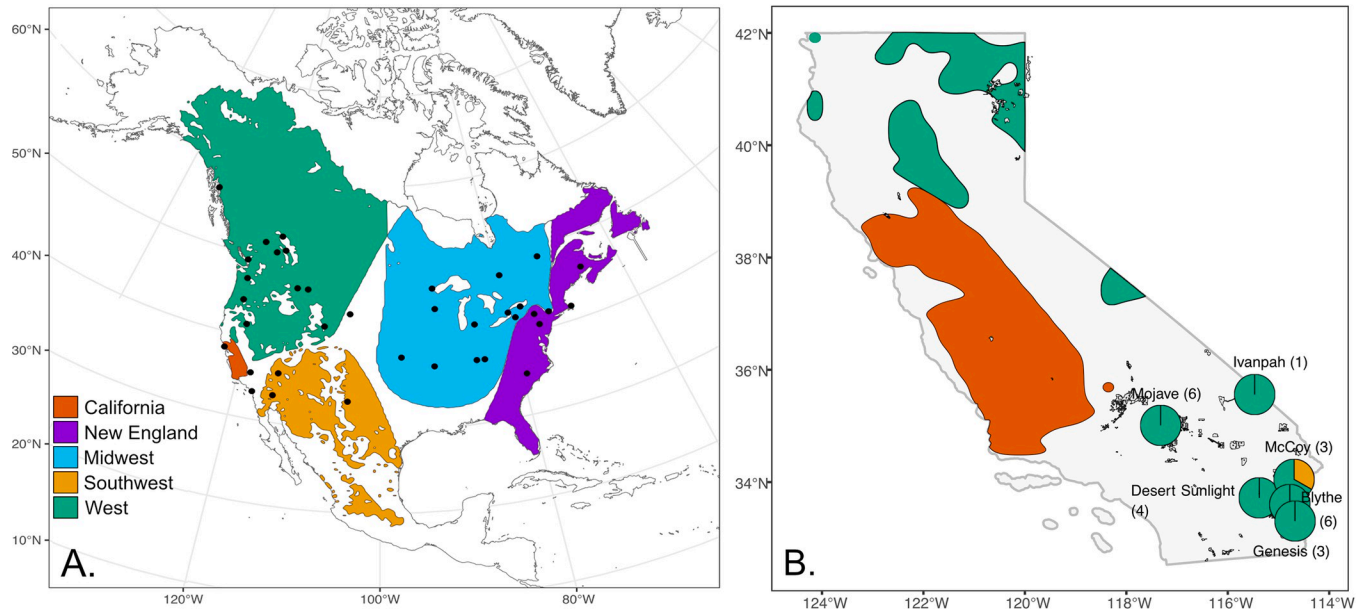
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Common Yellowthroat–The majority of the Common Yellowthroat carcasses collected at seven solar facilities were assigned to the West unit (Fig 4). Mojave Solar and Blythe had the highest number of Common Yellowthroat carcasses assigned with certainty to the West (n = 6 each), followed by Genesis (n = 3), and then Desert Sunlight and McCoy (n = 4 and 3, respectively). McCoy also had one sample assigned to the Southwest unit with certainty.

Yellow Warbler–Most of the Yellow Warbler carcasses collected at the solar facilities in this study were assigned to the Pacific Northwest, followed by Coastal Western and East units (Fig 5). A higher number of Yellow Warbler carcasses were collected and assigned with certainty at the Ivanpah facility (n = 223) than four other facilities (Blythe, Desert Center, Genesis, and McCoy) that had three or fewer that were successfully genotyped and assigned with high posterior probability.

Wilson's Warbler–The majority of Wilson's Warbler individuals collected at renewable energy sites in California were assigned to the Western Boreal unit; however, carcasses of individuals from Pacific Northwest, and two of the smaller populations, California Coastal and Sierra, were also found at some of these facilities (Fig 6). While most facilities had carcasses assigned to only one (Desert Sunlight and Desert Center) or two (Altamont) units, McCoy, Ivanpah and Blythe had carcasses assigned to at least three separate units. In addition to genotyping carcasses found at the wind and solar sites involved in this study, we also genotyped feather samples collected at migratory bird banding stations that were located in close proximity to a wind or solar facility (S4 Table). These additional sites show a similar pattern, with most individuals assigned to the Western Boreal unit (i.e. Padoma Wind Power, East Park Reservoir, Tehachapi Wind Energy, FPL Energy and Sunpeak Solar LLC). Wilson's Warblers caught at stations near the Horizon Wind Energy and Tehachapi Wind Energy were assigned to three units (Western Boreal, Pacific Northwest, and Sierra), whereas those banded near Airtricity were assigned to either Pacific Northwest, Sierra or California Coastal units.
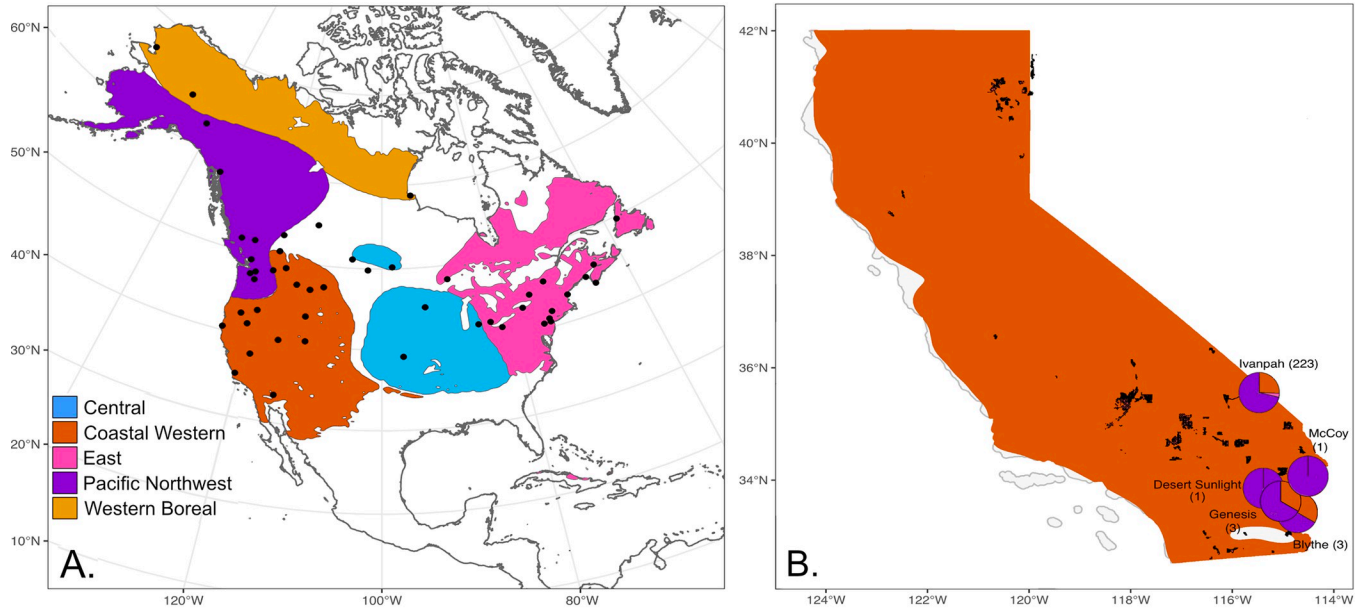
Fig 5. Yellow Warbler genoscape (A) and assignment of Yellow Warbler individual carcasses collected at renewable energy sites in California to genetically distinct populations (B). Black circles in (A) indicate locations of samples used to construct the genoscape. Numbers reflect individuals that were assigned with certainty to a breeding population as identified by the genoscape in (A). Basemap in (A) downloaded and modified from sciencebase.gov [56], basemap in (B) downloaded from data.ca.gov.

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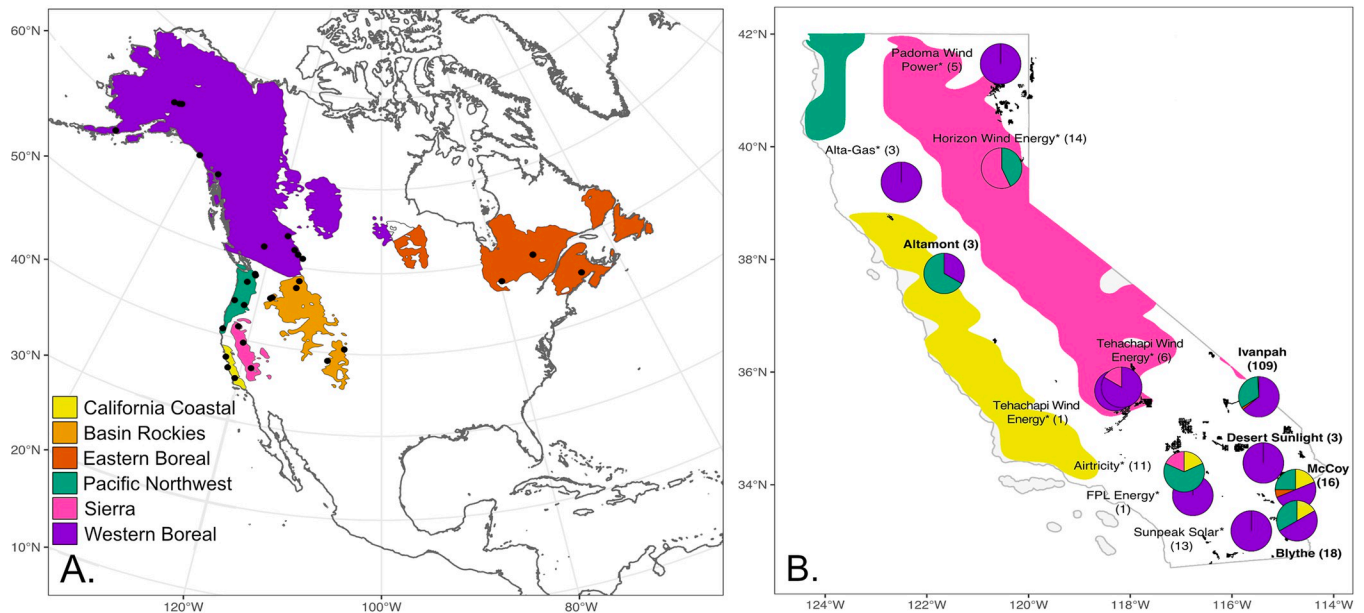
Fig 6. Wilson's Warbler genoscape (A) and assignment of Wilson's Warbler individuals collected at renewable energy sites in California to genetically distinct breeding populations (B, bold) and birds collected near renewable energy facilities (B, *). Black circles in (A) indicate locations of samples used to construct the genoscape. Numbers reflect individuals that were assigned with certainty to a breeding population as identified by the genoscape in (A). Basemap in (A) downloaded and modified from sciencebase.gov [56], basemap in (B) downloaded from data.ca.gov.

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Discussion and conclusions

Here we illustrate the utility of genoscape maps [32] to assign bird remains or feathers collected at solar and wind facilities and banding stations to genetically and geographically distinct breeding populations. Our method helps fill an important gap in estimating the effects of renewable energy development on bird populations, and can contribute valuable data to assist assessments of the impacts of such development as compared to other anthropogenic changes to both climate and habitat [44]. Below we discuss the efficacy of our method for assigning birds to distinct populations as well as the utility of these results for managing migratory birds in California and beyond, under conditions that will include increased reliance on renewable energy sources.

Population-specific exposure by species relative to trends and abundance

The development of high-resolution genetic tags for each species allowed us to better understand the population-specific exposure to renewable energy on migratory birds for five taxa of birds and four renewable energy technology types (1 wind, 3 solar) across California. In contrast to previous work which used isotopic methods to distinguish between local and non-local birds [14], here we use genetic tools to identify birds to conservation units. The units identified here are analogous to a catchment area [45] of energy development impacts (the area from which birds impacted by energy development are drawn). Despite this analogy, however, the spatial resolution of the genetic units was higher than the catchment areas defined using hydrogen isotopes alone, thereby providing additional geographic resolution on the scale at which population level impacts are dispersed. Future refinement of this scale of catchment areas may be attained by combining genetic and isotopic signatures into a joint assignment, as has been shown for other species [27,28].

Broadly, the majority of individuals exposed to renewable energy development were from the largest identified units within each species, while those from rare, declining, or more geographically distant populations made up a smaller percentage of the total number of birds sampled. We interpret these results in the context of population density and trend estimates from the North American Breeding Bird Survey [46], while recognizing that these estimates can vary in accuracy [47]. We avoid speculating on absolute estimates of mortality or impacts to populations, as raw mortality data available from these renewable energy sites do not account for detection biases, search effort, or local population sizes (for unique genetically distinct units), and because the renewable energy technologies represented here may impact populations in different ways or to different extents. Additionally, while determining the cause of mortality may be less important for demographic analyses, it should be considered a critical component when quantifying for management and monitoring purposes.

All of the American Kestrel carcasses from Ivanpah, and the majority from Altamont and Genesis, were assigned to the most widespread unit for this species, the West unit, except for two Altamont carcass assigned to the East unit and one individual from Genesis assigned to Texas (Fig 2). We did not identify any birds assigned to the Alaska unit, however this may be due to the inherent bias of our assays. Given the fact that there was lower accuracy of the Alaska assays (e.g. high misassignment to the West), our analyses are potentially assigning a greater number of individuals to the West population due in part to our ability to better differentiate this unit. This West unit, however, covers the largest geographic area of any kestrel unit, spanning from coastal to central United States and Canada. As this unit is so widespread, the genetic resolution of our markers was lower than that of Conkling et al. [14], who were able to distinguish between local and non-local individuals. While BBS data suggest that breeders in this region vary in population density and overall may be declining (1966–2019 Average

BBS Trend = -1.78, 95% CI = −3.00, −0.505; [46]), the population level impacts for birds in the West unit would theoretically be dispersed across a comparatively large population. In contrast, the Texas group shows a slower population decline (BBS Trend = -0.642, 95% CI = −2.13, 0.91), but given how geographically narrow this population's range is [46], any exposure to renewable energy facilities in California may have a disproportionately larger relative population effect.

Common Loon carcasses were assigned mostly to the North Central unit, with a smaller proportion assigned to the Midwest unit (Fig 3). Interestingly, no birds were identified from the two western units, Alaska and the Pacific Northwest, despite their geographic proximity to the study area, suggesting that individuals from these populations may not utilize land-based routes within the Pacific Flyway. Both the North Central and Midwest units show an increasing population trend (average BBS Trend = 0.665 (-0.37,1.855) and 0.63 (-0.39,1.81) respectively, [46]), supporting the idea that energy development may not be impacting the most vulnerable groups of this species. It is important to note, that the BBS data for loons in particular must be interpreted with caution, as loons are unlikely to be well counted by traditional BBS approaches [48].

The majority of Common Yellowthroat carcasses were assigned to a large West unit, similar to American Kestrels (Fig 4). While BBS estimates in this region show an increasing trend (average BBS Trend = 1.024 (-0.691, 3.067), the density maps suggest a relatively low abundance [46]. In contrast to loons, this species is more likely to be better surveyed by BBS estimates. While a smaller genetic unit was identified by our genoscapes in the central coast of California, none of the samples assayed in our study were drawn from this geographically restricted unit. This may be due to low sample sizes or the fact that the California genetic unit is thought to be made up of resident birds that may not be impacted by threats outside their relatively restricted range. Nevertheless, it is notable that despite the geographic proximity of these areas to the renewable facilities we considered, these subpopulations do not appear to be affected by those facilities. Overall, our results suggest that for this species, the impact of energy development is likely dispersed across a wide-ranging population with high gene flow across the unit. Thus, even if all impacted birds were from one smaller geographic region contained within the West unit, gene flow from neighboring regions within the same genetically distinct population is likely to help maintain healthy populations.

The Yellow Warbler genoscape and resulting genetic assignments revealed that the majority of carcasses were drawn from the Pacific Northwest unit, followed by the Coastal Western unit (Fig 5). While BBS data for the Pacific Northwest region suggest that Yellow Warblers are relatively abundant and most populations are experiencing only moderate declines (average BBS Trend = -0.75 (-1.7, 0.24); [46]), BBS data for the Coastal Western unit suggest that birds are comparatively less abundant in this unit (BBS Relative Abundance = 3.9 vs. 5.78; [46]). Thus, despite the lower number of individuals assigned to the Coastal Western unit, the population level effects of renewable energy on birds breeding in this region are likely to be greater than for birds breeding in the Pacific Northwest. When combined with other recent work suggesting that birds within the Coastal Western may experience the most difficulty adapting to changing climate [33], our results suggest the impacts of energy development on birds in this region may be more critical to monitor as compared to other regions.

In contrast to the other 4 species in our study, identification of vulnerability status in the Wilson's Warbler is made possible by previous work combining habitat-suitability derived estimates of population size and demographic trends stratified by genetic unit to assign groups to risk categories [43]. This work categorized Coastal California, Sierra Nevada, and Basin Rockies as highly vulnerable to local extinction, Pacific Northwest and East as elevated vulnerability, and Western Boreal as low vulnerability [43]. These categories are supported by BBS

data that suggest that Coastal California, Sierra, and Basin Rockies units are all experiencing moderate to significant downward population trends (average BBS trends = -0.28 (-1.18,0.49), -2.05 (-3.8, -0.16), and -2.31 (-3.62,-1.01), respectively [46]. Here we show that most remains collected at energy facilities were drawn from the largest and least vulnerable Western Boreal unit, suggesting that the population-level impacts may be less severe (Fig 6). Alternatively, the next most frequently impacted unit was the Pacific Northwest unit which spans a smaller geographic area and is closer to the renewable energy sites we considered. In addition, samples collected at sights adjacent to facilities originated from the more local Coastal California and Sierra Nevada units, both of which are small in spatial scale and considered highly vulnerable to future local extinction. Thus, while most Wilson's Warblers impacted are drawn from the biggest and least vulnerable genetic unit, there are existing and potential threats to several of the smaller more vulnerable units where population level impacts would be elevated. These results are consistent with Conkling et al. [14], who found evidence to suggest that Wilson's Warblers were highly vulnerable to impacts by renewable energy facilities in California. Future work will focus on combining demographic, genetic and habitat suitability modeling to assign threat status to genetic groups in order to more confidently assess the population-specific threats posed by renewable energy development.

Efficacy of High-Resolution markers for genotyping samples from carcasses

While our genoscape maps for each species allow for most samples to be resolved to at least the population level, the probability and confidence of these assignments largely depend on the resolution of the developed markers for each species. In general, the more genomic differentiation observed between populations within a species, the more confidence (i.e. higher probability of membership) we can ascribe to individual assignments. For example, we can define six genetically distinct populations of Wilson's Warbler, four of which are from the western region, with pairwise F_{ST} at outlier loci (a measure of the extent of population structure, with 1 = complete differentiation and 0 = panmixia) between these units ranging from 0 to 0.68 [32]. The strongest genomic differentiation is observed between eastern and western groups with strong differentiation also seen between the Southern Rockies and Colorado Plateau and all other groups. These relatively deep genomic splits allow for a multitude of diagnostic SNPs and/or SNP frequencies to evolve in each population, which then can help assign unknown individuals with relatively high probabilities. For the American Kestrel, in contrast, a greater number of SNP variants (n = 186) are required to assign individuals to populations, and these assignments are made with lower probabilities, due to overall lower genome-wide differentiation between populations. While two of the five units for this species are identified in the west (West and Alaska), low population differentiation between these groups (F_{ST} = 0.023–0.033) leads to lower assignment probabilities and a larger proportion of incorrect assignments. Additionally, the high misassignment of the Alaska genetic unit to the West genetic unit may inherently bias our results toward the Western population, which is better differentiated and has a higher assignment accuracy. Fortunately, these kinds of species-specific limitations will assuredly be reduced in the future, particularly as additional genomic resources, SNPs, and samples become available, and as a larger percentage of the genome is sequenced per individual and species. Future monitoring of bird activity and collection of both identified and unidentified [38] remains at facilities across the breeding ranges of these species will help further define population boundaries, allow for better estimates of the number of fatalities actually caused by facilities or facility activities [49], and could better estimate variation in effects across the different technology types we surveyed.

Utility of feathers for population assignment

The ability to assign carcasses to conservation units using our approach varied with the species-specific technical details associated with extracting DNA from feathers. The larger American Kestrel feathers yielded almost twice the amount of DNA as the smaller Wilson's Warbler and Yellow Warbler feathers did (average DNA = 5.67 ng/ul for American Kestrel versus 2.45 ng/ul for Yellow Warbler and 2.67 ng/ul for Wilson's Warbler), which could in part help explain the higher genotyping success rate for American Kestrel carcasses. In general, the genotyping success rate on DNA extracted from samples collected at facilities is lower than that of fresh feather DNA. For example, in previous work using identical extraction protocols, American Kestrel DNA from fresh feathers was extracted with a 93.6% success rate [36]; Wilson's Warbler DNA at a 96% success rate [32]; and Yellow Warbler DNA at a 98.3% success rate [33]. In contrast, in this study, our success rates for DNA amplification and genotyping for these three species are 91%, 84%, and 80%, respectively (Table 1). Hogan et al. [50] found that DNA amplification success was significantly influenced by the quality of feathers, which explains the lower genotyping success rate for feathers from carcasses relative to feathers from live birds, given that carcass feathers may be exposed to ultra-violet light, high temperatures, and other exposure conditions that lead to lower DNA quality or quantity as compared to fresh feathers. This finding suggests the value of timely and routine monitoring for, and collection of, carcasses at renewable energy facilities, to ensure the highest likelihood that such samples can be used in downstream analyses.

We chose to utilize data collected from renewable energy facilities, as well as banding stations in close proximity to operations in order to sample as thoroughly as possible across our target taxa and study region. These data sources, together with the ability to assign individuals to established genoscapes, provide a new opportunity to address research questions that would previously have been difficult to ascertain. Comparison of pools of samples collected from each of these independent data sources, for instance, would allow for quantitative assessments of not only those populations that were most likely exposed to renewable energy development, but might also reveal populations or individuals that were less likely to be impacted (e.g. individuals from particular populations that were only observed at banding stations near renewable energy facilities, but were not recovered from the renewable energy facilities themselves). In addition, such combinations of data may allow for temporal resolution of exposure risk, for example by allowing for the detection of any mismatches between when birds may be utilizing the region as part of a migratory pathway (obtained from banding station records) and when they may be most exposed to renewable energy facilities (obtained from samples collected at facilities). Finally, these types of quantitative analyses, when combined with other sources of mortality for bird populations such as predation, wintering range land-use changes, or loss of stopover sites, can allow for the relative impacts of renewable energy development on populations to be assessed. The possibility of addressing these conservation concerns in a spatiotemporally explicit manner is an exciting avenue for future research, and should underscore the importance of monitoring and collecting avian data at both banding stations and renewable energy facilities, across the full life cycle routes of these species.

Conclusions

Here we present the results of a multi-organization collaborative effort to assess the population-level exposure to renewable energy development on migratory birds in California. The development of high-resolution genetic markers for five species of birds provides us new ability to test these methods, and their application for assessing the population-specific effects on migratory birds in a region with greater resolution than previous methods could have allowed.

Interpretation of the potential impact of renewable energy development on populations is improved via a priori analyses assigning impact status to units, so as to better understand the relative impacts to (genetically unique) populations within a species. While the number of individuals, markers, species, and our ability to better estimate a number of biases currently in the data are all likely to increase in the future, the methods developed here can readily be applied to data as it is acquired to help understand the impacts of renewable energy at a resolution beyond that of the species. Future work could also emphasize combined analyses to assess vulnerability status by genetic unit, as well as the relative threat imposed by renewable energy development as compared to other natural and anthropogenic stressors across species. Ultimately, it is our hope that these methods can be integrated into informed strategies to track population-level effects of renewable energy development, in a manner that is bespoke to region, ecology/wildlife composition, and anthropogenic activities present.

Methods and materials

Sampling and DNA isolation

To understand the population-level exposure of migratory birds to renewable energy facilities, we coordinated with the United States Fish and Wildlife Service in the Pacific Southwest Region (USFWS) and the United States Geological Survey's (USGS) Forest & Rangeland Ecosystem Science Center to process carcasses and "feather spots" collected by authorized personnel with a SPUT (Special Purpose Utility Permit) during routine surveys and incidentally from 2014–2021 across all seasons at one wind and six solar facilities (Fig 1, S1 and S2 Tables) in California. The technologies represented across the solar facilities (photovoltaic, concentrated solar trough, and concentrated power tower), and between wind and solar facilities, are vastly different from one another, and likely to affect avian populations and species in different ways from a siting and operating perspective. Despite this, we integrated data from these sites for the purpose of this study to arrive at a broad sense of trends represented in the region, as each of these technologies might contribute to total wildlife impacts.

As a result of this collaborative effort we were able to obtain samples from 5,137 carcasses (S1 and S3 Tables), 734 of which were identified as from target taxa (either in the field or through molecular methods [38], Table 1). In addition, 69 feathers from birds (Wilson's Warblers and American Kestrels) banded within 30 miles of seven facilities were also analyzed to identify the populations that use flyways proximate to energy facilities (Fig 1, S4 Table). The five target migratory birds: the American Kestrel (*Falco sparverius*), Common Loon (*Gavia immer*), Common Yellowthroat (*Geothlypis trichas*), Wilson's Warbler, (*Cardellina pusilla*), and Yellow Warbler (*Setophaga petechia*) were specifically chosen based on consultation with federal and state agencies, wildlife organizations, and industry leaders, as those that were found regularly at either wind and/or solar energy facilities, and were of concern for conservation, at either a regional or national scale.

Remains collected and identified to species at the seven renewable energy facilities (S1 Table, and named on Fig 1), were temporarily held in freezers on site. These were then either shipped to USGS, the University of California Los Angeles (UCLA), or Colorado State University (CSU) for sampling, or sampled directly on site by USFWS, USGS and/or UCLA/CSU staff. Carcass quality varied significantly–some carcasses were intact, some were scavenged and/or degraded to varying degrees, and some only consisted of feathers (i.e. feather spots). All of the samples used in this study were identified to species either via morphology in the field or via genetics in the laboratory [38]. From each carcass, a minimum of two feathers were sampled and transferred to long-term storage envelopes with associated information on species, site, and collection date. Finally, all feather samples were sent to either UCLA or CSU

where they were stored in -20˚C freezers. Additional summary information for these samples, including proportions of species and guilds found at each location, are provided in the Supplemental Information (S1–S4 Tables, S1 Fig).

We used Qiagen DNeasy 96 blood and tissue kits (Qiagen Inc., Valencia, CA, USA) to extract DNA from each feather sample (one calamus from a wing/tail feather or 5 tips for body feathers), and negative controls were included in each step of the extraction process. We followed manufacturer's instructions with minor modifications to optimize the final DNA yield. Specific protocols for feather extractions can be found in earlier manuscripts [32,33,36].

SNP Genotyping

From initial RAD sequencing and genome assembly for four species ([32,33,35,36], Common Yellowthroat (COYE) in review), and a new low coverage whole genome sequencing protocol for the Common Yellowthroat [40], we used custom R scripts to identify 96–192 population-specific differentiated SNPs and to convert these panels into species-specific SNP Type™ Assays (Fluidigm Inc.) following the methods of [32]. The solar, wind, and banding station samples, along with negative controls, from each of our target taxa were screened for each selected SNP leveraging a fluorescence-based competitive allele-specific PCR (also known as KASP genotyping). SNP genotyping results were imaged on an EP1™ Array Fluorescence Reader. Fluidigm's automated Genotyping Analysis software (Fluidigm Inc.) was used to identify genotypes for each individual with a confidence threshold of 90%. In addition, all SNP calls were visually inspected and any calls that did not fall clearly into either the heterozygote or one of the homozygote clusters were removed from the analysis. As DNA quality can affect call accuracy, a stringent quality filter was employed and loci with > 80% missing calls across samples were filtered out. The final variant species-specific sets used to assign an individual to a given breeding population of origin included: 186 SNPs genotyped for American Kestrel individuals, 158 for Common Loons, and 96 each for Common Yellowthroat, Yellow Warbler, and Wilson's Warbler individuals (Dryad Accession doi:10.5061/dryad.h44j0zprq, [42]).

Baseline reporting groups and accuracy of assignment

Conservation units (hereafter *units*, i.e., populations for assignment purposes as defined in [51,52]) were defined based on genetic variation of breeding individuals within each species. For each species, the genetic variation was assessed with the SNP-type assays using population structure analyses in *structure* [53] and *admixture* [54]. This provides the baseline genetic structure of a species mapped across the full breeding range of each species to provide geographic boundaries for each unit, as part of the completed "genoscape" of a species [32–37]. Accuracy of individual assignment analysis to these units were evaluated using self-assessment testing in RUBIAS [41,55]. This function in RUBIAS tests the accuracy of assignment by assigning individuals back to the collections in the reference using a leave-one-out cross validation approach. Based on species sample sizes, assignment accuracies were assessed for either all individuals (including those used in assay design), or separated into two groups, those individuals used in assay design and those that were not included, to reduce training biases (see S1 Text for more details). Accuracy is the proportion of individuals from known units that are assigned back to the correct unit. For each specimen, the probability of assignment to a specific unit was calculated and significant assignment was made when there was > 0.8 posterior probability of assignment to the inferred collection. Assignments with a posterior probability < 0.8 were designated as uncertain (i.e. could not be reliably assigned back to their correct population), and these individuals were filtered from final reporting.

Assignment of unknown individuals found at renewable energy facilities

Individuals of known species but unknown breeding origin collected from renewable energy locations (hereafter called "unknown origin") were assigned to units defined in the completed genoscape using RUBIAS [41]. While we knew the species identification of the unknown origin bird carcasses or feather spots (through either morphological or genetic identification) collected at, and of the living birds banded near, renewable energy facilities, we did not know the breeding unit these birds would be assigned to, therefore we initially grouped them by site location collection (i.e. where collection occurred), and treated them as a separate group during processing. Once assignments were made, we then report the proportion of certain assignment (individuals with a posterior probability > 0.8) to each known breeding population (Figs 2–6, S5–S8 Tables) at each renewable energy collection site (Dryad Accession doi:10.5061/dryad.h44j0zprq, [42]).

Supporting information

S1 Text. Carcass collection and proportion of species found at each facility.
(DOCX)

S1 Table. Summary of bird carcasses collected from each solar and facility.
(DOCX)

S2 Table. Carcasses sampled at solar and wind facilities by guild.
(DOCX)

S3 Table. Samples shipped per collection date.
(DOCX)

S4 Table. Wilson's Warbler (WIWA) and American Kestrel (AMKE) feathers collected at banding stations near solar/wind facilities.
(DOCX)

S5 Table. Assignment accuracy of American Kestrel breeding individuals using 186 SNPs.
(DOCX)

S6 Table. Assignment accuracy of Common Loon breeding individuals using 158 SNPs.
(DOCX)

S7 Table. Assignment accuracy of Common Yellowthroat breeding individuals using 96 SNPs.
(DOCX)

S8 Table. Assignment accuracy of Yellow Warbler breeding individuals using 96 SNPs.
(DOCX)

S1 Fig. Sample composition by guild at each facility.
(DOCX)

Acknowledgments

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References

1. Allison TD, Root TL, Frumhoff PC. Thinking globally and siting locally–renewable energy and biodiversity in a rapidly warming world. Climate Change. 2014; 126:1–6.

2. United States Energy Information Administration (US EIA, 2022, https://www.eia.gov).

3. Shaker H, Zareipour H, Wood D. Impacts of large-scale wind and solar power integration on California's net electrical load. Renewable and Sustainable Energy Reviews. 2016; 58:761–774. https://doi.org/10.1016/j.rser.2015.12.287

4. California Energy Commission. 2021;Sacramento, CA, https://www.energy.ca.gov).

5. Gill L, Gutierrez A, Weeks T. SB 100 Joint Agency Report, Achieving 100 Percent Clean Electricity in California: An Initial Assessment. 2021, CEC-200-2021-001.

6. Strickland MD, Arnett EB, Erickson WP, Johnson DH, Johnson GD, Morrison ML, Shaffer JA, Warren-Hicks W. Comprehensive guide to studying wind energy/wildlife interactions. 2011; Prepared for the National Wind Coordinating Collaborative, Washington, D.C., USA.

7. Kuvlesky WP, Brennan LA Jr., Morrison ML, Boydston KK, Ballard BM, Bryant FC. Wind energy development and wildlife conservation: Challenges and opportunities. Journal of Wildlife Management. 2007; 71:2487–2498.

8. Smallwood KS. Comparing bird and bat fatality-rate estimates among North American wind-energy projects. Wildlife Society Bulletin. 2013; 37:19–33.

9. American Wind Wildlife Institute (AWWI). Summary of Bird Fatality Monitoring Data Contained in AWWIC (2nd Edition). 2020; Washington, DC. Available at www.awwi.org. © 2020 American Wind Wildlife Institute.

10. Loss SR, Will T, Marra PP. Estimates of bird collision mortality at wind facilities in the contiguous United States. Biological Conservation. 2013; 168:201–209.

11. Lloyd JD, Butryn R, Pearman-Gillman S, Allison TD. Seasonal patterns of bird and bat collision fatalities at wind turbines. PLOS ONE. 2023; 18(5): e0284778. https://doi.org/10.1371/journal.pone.0284778 PMID: 37163474

12. Erickson WP, Wolfe WM, Bay KJ, Johnson DH, Gehring JL. A comprehensive analysis of small-passerine fatalities from collision with turbines at wind energy facilities. PLOS ONE. 2014; 9:e107491. https://doi.org/10.1371/journal.pone.0107491 PMID: 25222738

13. Smallwood KS. Utility-scale solar impacts to volant wildlife. The Journal of Wildlife Management. 2022; 86(4);Article e22216. https://doi.org/10.1002/jwmg.22216

14. Conkling TJ, et al. Vulnerability of avian populations to renewable energy production. R. Soc. Open Sci. 2022; 9:211558. https://doi.org/10.1098/rsos.211558 PMID: 35360356

15. Cryan PM. Seasonal distribution of migratory tree bats (Lasiurus and Lasionycteris) in North America. Journal of Mammalogy. 2003; 84:579–593.

16. Cryan P, Brown A. Migration of bats past a remote island offers clues toward the problem of bat fatalities at wind turbines. Biological Conservation. 2007; 139:1–11.

17. Kays RW, Wilson D. Mammals of North America. 2009; Second Edition. Princeton University Press.

18. DeSante DF. Annual variability in the abundance of migrant landbirds on Southeast Farallon Island, California. The Auk. 1983; 100:826–852.

19. United States Fish and Wildlife Service (USFWS). U.S. Fish and Wildlife Service Land-Based Wind Energy Guidelines. 2012; Report by US Fish and Wildlife Service (USFWS).

20. Renewable Energy Wildlife Institute. Guide to Wind Energy and Wildlife. REWI, Washington, DC, 2022, https://rewi.org/guide/.

21. American Bird Conservancy. Wind Energy: Bird-Smart Strategies. American Bird Conservancy, The Plains, Virginia, 2015.

22. Faaborg J, Holmes RT, Anders AD, Bildstein KL, Dugger KM, Gauthreaux SA Jr, et al. Conserving migratory land birds in the New World: Do we know enough?. Ecological Applications. 2010; 20: 398–418. https://doi.org/10.1890/09-0397.1 PMID: 20405795

23. Stutchbury BJ, Tarof SA, Done T, Gow E, Kramer PM, Tautin J, et al. Tracking long-distance songbird migration by using geolocators. Science. 2009; 323: 896. https://doi.org/10.1126/science.1166664 PMID: 19213909

24. Arlt D, Low M, and Part T. Effect of geolocators on migration and subsequent breeding performance of a long-distance passerine migrant. PLOS ONE. 2013; 8:e82316. https://doi.org/10.1371/journal.pone.0082316 PMID: 24324770

25. Bridge ES, Kelly JF, Contina A, Gabrielson RM, MacCurdy RB, Winkler DW. Advances in tracking small migratory birds: a technical review of light-level geolocation. Journal of Field Ornithology. 2013; 84:121–137.

26. Rubenstein DR, Chamberlain CP, Holmes RT, Ayres MP, Waldbauer JR, Graves GR, et al. Linking breeding and wintering ranges of a migratory songbird using stable isotopes. Science. 2002; 295:1062–1065. https://doi.org/10.1126/science.1067124 PMID: 11834833

27. Kelly JF, Ruegg KC, Smith TB. Combining isotopic and genetic markers to identify breeding origins of migrant birds. Ecological Applications. 2005; 15:1487–1497.

28. Rundel CW, Wunder MB, Alvarado AH, Ruegg KC, Harrigan RJ, Schuh A, et al. Novel statistical methods for integrating genetic and stable isotope data to infer individual-level migratory connectivity. Molecular Ecology. 2013; 22:4163–4176. https://doi.org/10.1111/mec.12393 PMID: 23906339

29. Wunder MB, Kester CL, Knopf FL, Rye RO. A test of geographic assignment using isotope tracers in feathers of known origin. Oecologia. 2005; 144:607–617. https://doi.org/10.1007/s00442-005-0071-y PMID: 15891836

30. Lovette IJ, Clegg SM, Smith TB. Limited utility of mtDNA markers for determining connectivity among breeding and overwintering locations in three neotropical migrant birds. Conservation Biology. 2004; 18:156–166.

31. Segelbacher G. Noninvasive genetic analysis in birds: testing reliability of feather samples. Molecular Ecology Notes. 2002; 2:367–369.

32. Ruegg KC, Anderson EC, Paxton KL, Apkenas V, Lao S, Siegel RB, et al. Mapping migration in a songbird using high-resolution genetic markers. Molecular Ecology. 2014; 23(23),5726–5739. https://doi.org/10.1111/mec.12977 PMID: 25346105

33. Bay RA, Harrigan RJ, Le Underwood V, Lisle Gibbs H, Smith TB, Ruegg K. Genomic signals of selection predict climate-driven population declines in a migratory bird. Science. 2018; 359(6371),83–86. https://doi.org/10.1126/science.aan4380 PMID: 29302012

34. Ruegg KC, Bossu CM, Rajbhandary J, Fuller T, Harrigan RJ, Smith TB. University of California, Los Angeles. A Genoscape Framework for Assessing the Population-level Impacts of Renewable Energy

Development on Migratory Bird Species in California. California Energy Commission. 2019;Publication Number: CEC-500-2020-036.

35. Larison B, Lindsay AR, Bossu C, Sorenson MD, Kaplan JD, Evers DC, et al. 2021. Leveraging Genomics to Understand Threats to migratory birds. Evolutionary Applications. 2021; 14(6):1646–1658. https://doi.org/10.1111/eva.13231 PMID: 34178110

36. Ruegg KC, Brinkmeyer M, Bossu CM, Bay R, Anderson EC, Boal CW, et al. The American Kestrel Genoscape (Falco sparverius): Implications for Monitoring, Management, and Subspecies Boundaries. Ornithology. 2021a; 138:1–14. https://doi.org/10.1093/auk/ukaa051

37. Ruegg K, Bay RA, Anderson EC, Saracco JF, Harrigan RJ, Whitefield M, et al. Ecological genomics predicts climate vulnerability in an endangered southwestern songbird. Ecology Letters. 2018; 21(7),1085–1096. https://doi.org/10.1111/ele.12977 PMID: 29745027

38. Gruppi C, Sanzenbacher P, Balekjian K, Hagar R, Hagen S, Rayne C, et al. Genetic identification of avian samples recovered from solar energy installations. 2023, PLOS ONE, https://doi.org/10.1371/journal.pone.0289949 PMID: 37672506

39. Ruegg KC, Anderson EC, Somveille M, Bay RA, Whitfield M, Paxton EH, et al. Linking climate niches across seasons to assess population vulnerability in a migratory bird. Global Change Biology. 2021b; 27(15),3519–3531. https://doi.org/10.1111/gcb.15639 PMID: 33844878

40. Bobowski TJ, Bossu CM, Hernández RR, Schweizer T, Tello-Lopez I, Smith TB, et al. Ultimate factors underlying migratory timing in a seasonally migratory bird. In review. American Naturalist.

41. Anderson EC, Moran B. rubias: Bayesian Inference from the Conditional Genetic Stock Identification Model. 2022;https://github.com/eriqande/rubias

42. Harrigan R, Rajbhandary J, Bossu C, Sanzenbacher P, Dietsch T, Gruppi C, et al. Dataset as Analyzed and Presented in "Utilizing High-Resolution Genetic Markers to Track Population-Level Exposure of Migratory Birds to Renewable Energy Development", 2023;Dryad, Dataset, https://doi.org/10.5061/dryad.h44j0zprq

43. Ruegg KC, Harrigan RJ, Saracco JF, Smith TB, Taylor CM. A genoscape-network model for conservation prioritization in a migratory bird. Conservation Biology. 2020; 34(6),1482–1491. https://doi.org/10.1111/cobi.13536 PMID: 32391608

44. Katzner TE, Allison TD, Diffendorfer JE, Hale AM, Lantz EJ, Veers PS. Counterfactuals to Assess Effects to Species and Systems from Renewable Energy Development. Frontiers in Conservation Science. 2022; 10, https://doi.org/10.3389/fcosc.2022.844286

45. Voigt CC, Popa-Lisseanu AG, Niermann I, Kramer-Schadt S. The catchment area of wind farms for European bats: a plea for international regulations. Biological Conservation. 2012; 153:80–86.

46. Sauer JR, Link WA, and Hines JE. The North American Breeding Bird Survey, Analysis Results 1966–2019. 2019; USGS Patuxent Wildlife Research Center, Laurel, MD, https://doi.org/10.5066/P96A7675

47. Ankori-Karlinsky R, Kalyuzhny M, Barnes KF, Wilson AM, Flather C, Renfrew R, et al. "North American Breeding Bird Survey Underestimates Regional Bird Richness Compared to Breeding Bird Atlases." Ecosphere. 2022; 13(2): e3925. https://doi.org/10.1002/ecs2.3925

48. Paruk JD, Evers DC, McIntyre JW, Barr JF, Mager J, Piper WH. Birds of the World, Version: 2.0—Published March 12, 2021.

49. Kosciuch K, Riser-Espinoza D, Gerringer M, Erickson W. A summary of bird mortality at photovoltaic utility scale solar facilities in the Southwestern U.S. PLOS ONE. 2020; 15(4):e0232034. https://doi.org/10.1371/journal.pone.0232034 PMID: 32330207

50. Hogan FE, Cooke R, Burridge CP, Norman JA. 2008. Optimizing the use of shed feathers for genetic analysis. Molecular Ecology Resources. 2008; 8 (3):561–567.

51. Kalinowski ST, Manlove KR, Taper ML. ONCOR: Software for genetic stock identification. 2007; Bozeman, MT: Montana State University.

52. Bradbury IR, Wringe BF, Watson B, Paterson I, Horne J, Beiko R, et al. Genotyping-by-sequencing of genome-wide microsatellite loci reveals fine-scale harvest composition in a coastal Atlantic salmon fishery. Evolutionary Applications. 2018; 11(6):918–930. https://doi.org/10.1111/eva.12606 PMID: 29928300

53. Pritchard JK, Stephens M, Donnelly P. Inference of population structure using multilocus genotype data. Genetics. 2000; 155, 945–959. https://doi.org/10.1093/genetics/155.2.945 PMID: 10835412

54. Alexander DH, Novembre J, Lange K. Fast model-based estimation of ancestry in unrelated individuals. Genome Research. 2009; 19,1655–1664. https://doi.org/10.1101/gr.094052.109 PMID: 19648217

55. Anderson EC, Waples RS, Kalinowski ST. An improved method for predicting the accuracy of genetic stock identification. Canadian Journal of Fisheries and Aquatic Sciences. 2008; 65:1475–1486.

56. United States Geological Survey (USGS). North American Atlas–Political Boundaries. 2010. https://www.sciencebase.gov.