Research Paper

Annual migratory movement, apparent molt-migration, migration schedule, and diffuse migratory connectivity of Hermit Warblers

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ABSTRACT. Quantifying migratory connectivity and annual movement is key to sound conservation planning for migratory species. Hermit Warblers (*Setophaga occidentalis*) are an endemic-breeding species in the Pacific Northwest that winters in Mexico and the Central Americas. This species faces threats from mature forest loss and climate change throughout its range, but we know little about its migration ecology. To understand the annual movements and migratory connectivity of Hermit Warblers, we tracked 22 adult male Hermit Warblers from six breeding sites across the species' breeding range using geolocators to examine migratory connectivity, spatiotemporal patterns, and migration routes. We found a high degree of mixing on the wintering grounds among birds from different breeding locations, indicating low migratory connectivity. However, birds breeding in Yosemite, the southernmost breeding location in our study, wintered farther east and south than birds from more northern breeding locations, providing weak evidence for potential chain migration. All birds showed much shorter and faster movements during spring migration than during fall migration. Birds arrived at breeding grounds from late April to mid-May and left breeding ranges from late June to mid-July. In fall, birds moved slowly from the breeding locations to montane regions in southern Oregon and California, which may indicate post-breeding molt before swiftly migrating to wintering grounds. Low migratory connectivity in this species implies that habitat and climate change across the broad wintering range may affect breeding populations throughout the species' breeding range. A particularly compressed breeding schedule and departure of birds from the breeding grounds in early July may indicate that breeding is limited by a short window of favorable climatic conditions for breeding, which could signal heightened vulnerability under future climatic scenarios.

Mouvements migratoires annuels, possible migration de mue, calendrier de migration et connectivité migratoire diffuse de la Paruline à tête jaune

RÉSUMÉ. La quantification de la connectivité migratoire et des mouvements annuels est essentielle pour une planification rationnelle de la conservation des espèces migratrices. La Paruline à tête jaune (*Setophaga occidentalis*) est une espèce endémique qui se reproduit dans le nord-ouest du Pacifique et qui hiverne au Mexique et en Amérique centrale. Cette espèce est menacée par la disparition des forêts matures et par le changement climatique dans l'ensemble de son aire de répartition, mais nous ne savons que peu de choses sur son écologie migratoire. Pour comprendre les mouvements annuels et la connectivité migratoire de la Paruline à tête jaune, nous avons suivi 22 mâles adultes issus de six sites de nidification différents dans l'aire de reproduction de l'espèce en utilisant des géolocalisateurs afin d'examiner la connectivité migratoire, les schémas spatiotemporels et les routes de migration. Nous avons constaté un degré élevé de mélange des individus sur les sites d'hivernage, quelle que soit leur provenance, ce qui suggère une faible connectivité migratoire. Toutefois, les oiseaux se reproduisant dans le parc national de Yosemite, lieu de reproduction le plus méridional de notre étude, passaient l'hiver plus à l'est et au sud que les oiseaux provenant de sites de reproduction plus septentrionaux, ce qui pourrait suggérer une possible migration en chaîne. Les déplacements de tous les oiseaux étudiés étaient beaucoup plus courts et plus rapides durant la migration de printemps que pendant la migration d'automne. Les oiseaux sont arrivés sur les aires de reproduction de la fin avril à la mi-mai et ont quitté les sites entre la fin de juin et la mi-juillet. En automne, les oiseaux se sont déplacés lentement depuis les sites de reproduction vers les régions montagneuses du sud de l'Oregon et de la Californie, ce qui pourrait indiquer une mue postnuptiale avant une migration rapide vers les aires d'hivernage. La faible connectivité migratoire de cette espèce implique que la perte d'habitat et le changement climatique dans son aire d'hivernage étendue pourraient affecter les populations reproductrices dans l'ensemble de l'aire de reproduction de l'espèce. Un calendrier de reproduction particulièrement serré et le départ des oiseaux des aires de reproduction dès le début de juillet pourraient indiquer que la reproduction est limitée par une courte fenêtre de conditions climatiques favorables à la reproduction, ce qui pourrait présager une vulnérabilité accrue dans les scénarios climatiques futurs.

Key Words: *chain migration; geolocation by light; landbird; migratory connectivity; migration pattern; Pacific Northwest; post-breeding molt*

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INTRODUCTION

Understanding migratory behavior and connectivity throughout the full annual cycle is essential for the conservation of migratory birds (Webster et al. 2002, Kirby et al. 2008, Newton 2008, Faaborg et al. 2010, Marra et al. 2015), because environmental conditions at each stage of the annual cycle can influence individual behavior and fitness and govern species' distributions and population trends (Rushing et al. 2017). For example, habitat degradation and climate change on nonbreeding grounds could increase mortality during the nonbreeding period, and influence spring phenology of migration and breeding, leading to changes in reproductive success (Both et al. 2010, Harrison et al. 2011). Understanding these population linkages is essential for conservation of climate-sensitive migratory species in a time of rapid climate change and habitat loss (Parmesan 2006, Abatzoglou and Williams 2016, Rushing et al. 2016a, Berner et al. 2017, Phalan et al. 2019, Furnas 2020).

The term migratory connectivity describes the linkage and mixture among bird populations at breeding and nonbreeding grounds. When connectivity is strong, populations from different breeding grounds do not intermix on the nonbreeding grounds; if individuals from different breeding grounds do intermix on the nonbreeding grounds, then migratory connectivity is weak (Webster et al. 2002, Cohen et al. 2018, Somveille et al. 2021). Spatial patterns of migratory connectivity in birds are typically grouped into three categories. In chain migration, northern breeding populations migrate to northern parts of the nonbreeding range and southern populations migrate farther south. Alternatively, leapfrog migration occurs when northern breeding populations migrate to the furthest portions of the nonbreeding range, leaping over southern breeding populations that winter in northern portions of the nonbreeding range (Salomonsen 1955, Alerstam and Hedenstrom 1998, Newton 2008, Somveille et al. 2021). Finally, a telescopic migration pattern describes birds from different breeding ranges wintering within the same geographic area, resulting in longer migratory distance for birds breeding farther away (Alerstam and Hedenstrom 1998, Newton 2008). Information on migratory patterns and connectivity of a species can assist conservation decisions by identifying stages of the annual cycle, where environmental changes could affect a population, and direct where conservation efforts can be focused (Kramer et al. 2018). Thus, knowing migratory pattern and connectivity of populations could help reveal annual space use of populations, stressors, and selective pressure that each population might experience throughout the annual cycle (Delmore et al. 2012, Hewson et al. 2016, Ketterson and Nolan 2016, Finch et al. 2017). Theoretical explanations on the mechanisms of evolution of migratory connectivity are still under development. Recent works suggest that species' population spread and mixing between winter and breeding ranges can be explained by energy efficiency, because individuals of species may follow ideal optimal redistribution during migration (Somveille et al. 2021), whereas this may still depend on species' life-history strategy, geographical features on migration route (Somveille et al. 2021), or land availability of the nonbreeding grounds (Finch et al. 2017).

In addition to the spatial pattern of migration, the timing (phenology) of migration plays an essential role in ecology of migratory birds. For many migratory birds, migration phenology closely tracks spatial distribution of food availability (Renfrew et

al. 2013, La Sorte et al. 2016, Helm et al. 2019, Visser and Gienapp 2019). Seasonal climatic cycles are the most common drivers of the timing of peak resource availability (Kharouba et al. 2018, Renner and Zohner 2018), and many small passerine species rely on such pulses of food availability for breeding and migration (Both et al. 2010, Visser et al. 2012, Burgess et al. 2018). To reach breeding and nonbreeding destinations at the right times, many migratory bird species use different migration routes and move at differing rates during pre-breeding versus post-breeding migration (Newton 2008, McKinnon et al. 2013, Morin et al. 2020). Among many factors, wind conditions (Klaassen et al. 2010, Limiñana et al. 2013), resource availability for refueling (Alerstam 2001, Rousseau et al. 2020) or molting (Holmgren and Hedenström 1995, Siegel et al. 2016), and sexual selection (Kokko 1999) are often suggested as key drivers of differential migration rate and route in spring and fall. However, it remains unclear which drivers are most important, or how these drivers are related to differences in migratory routes and rates between pre-breeding and post-breeding migration.

Hermit Warblers (*Setophaga occidentalis*) breed only in montane coniferous forests of the Pacific Northwest region of the United States, where they are a common species in the breeding season (Betts et al. 2018, Furnas 2020, Sauer et al. 2020). As one of the more abundant avian secondary consumers in the canopy food web, the species may provide important ecological functions and services in these forests (Harris et al. 2020). According to North American Breeding Bird Survey (BBS) data, the Hermit Warbler population has declined in recent years (Trend = -0.961, 95% CI = -1.675 - -0.285, in 1993–2019; Sauer et al. 2020). However, this decline was not uniform across their range. Rushing et al. (2016b) and Furnas et al. (2020) demonstrated that populations of Hermit Warblers have identifiable groups across their breeding range based on similarity in demographic parameters and song characteristics. The most recent BBS data suggests that rates of decline vary among regions, with birds in the Sierra Nevada and Washington declining most rapidly during the past two decades (Sauer et al. 2020). The Hermit Warbler is considered a species of concern in the Sierra Nevada Bird Conservation Region by the United States Fish and Wildlife Service (U.S. Fish and Wildlife Service 2021).

Climate change and habitat loss may partly explain variability in Hermit Warbler population trends throughout the breeding range (Betts et al. 2018, Northrup et al. 2019, Phalan et al. 2019). Loss of breeding habitat from increased fire frequency, intensive forest management, and climate change is predicted across the species' breeding range in the future (Bell et al. 2014, Abatzoglou and Williams 2016, Hicke et al. 2016, Berner et al. 2017, Stevens-Rumann and Morgan 2019). Yet, the effects of non-breeding ground climate and land-use change remain uncertain. Hermit Warbler's full annual range extends across a broad latitudinal gradient (Fig. 1), and many aspects of the species' migratory ecology, including connectivity, spatial pattern, phenology, behavior, and routes, are poorly known and thus pose challenges to associating changes in non-breeding ground climate or habitat to particular breeding populations.

Here, we investigated migratory movements of Hermit Warblers throughout the annual cycle, using light-level archival tags (geolocators). We document annual migratory routes, timing, and nonbreeding locations of Hermit Warblers from six locations

 Fig. 1. (A) Location of study sites (black dots) and the number of birds tagged/captured across the Hermit Warbler (*Setophaga occidentalis*) breeding range (green). Yellow and blue shading indicate the known range (modified from NatureServe and BirdLife International 2014) during migration and winter periods, respectively. (B) Adult Hermit Warbler male with geolocator on its back. (C) Mature mixed coniferous forest typical of Hermit Warbler breeding habitat, taken at H. J. Andrews Experimental Forest.
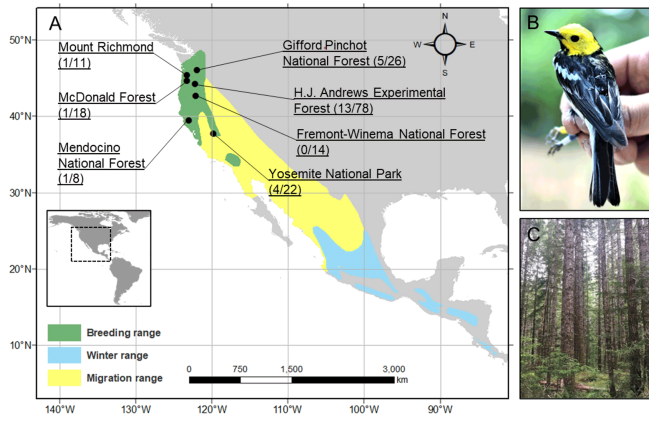
across the breeding range, spanning more than 900 km north-south in the western United States. Through tracking of migratory movement of Hermit Warblers, we aimed to identify potential behavioral characteristics throughout the full annual cycle that could be important for the conservation of this declining species across its breeding range. More specifically, we analyzed (1) migratory connectivity and spatial patterns of migration, to see whether spatial arrangements of breeding grounds are related to wintering locations (core nonbreeding period during boreal winter months, defined in the methods), or vice versa; (2) the timing of migration during pre-breeding and post-breeding periods; and (3) duration of migration and comparison of daily migration rates, in km per day, and routes between post- and pre-breeding migration. In addition, we discuss the timing of flight feather molt during migration based on our observation of migratory behavior from geolocators and a previously known molt schedule of the species. We developed two alternate hypotheses about Hermit Warbler migratory connectivity that are not mutually exclusive: (1) Hermit Warblers may have weak or no migratory connectivity because their breeding range is fairly restricted compared to their winter range across a large expanse of Mexico and Central America; and (2) Hermit Warblers may have strong migratory connectivity, because their specific habitat requirement limits populations to use the most energy-efficient migration routes and nonbreeding grounds, and habitat availability may be limited in the nonbreeding grounds, even though the range is expansive.

METHODS

Study area

We selected seven study sites across the Hermit Warbler's breeding range from Washington to California (Fig. 1). Our sampling locations were selected to represent the breadth of the Hermit

Warbler's breeding range, except for a small discrete population in southern California, extending 8.2 degrees in latitude north-south from southern Washington to California, including the coastal mountain ranges and Cascades-Sierra Nevada geographical provinces. Our sites were 90–580 km apart (Fig. 1), so we assumed each population at these sites were discrete because the distance between sites are much further than usual distance traveled by small songbirds during the breeding season (Cooper and Marra 2020). All our study sites were characterized by montane coniferous forest, but tree species composition varied from pure Douglas-fir (*Pseudotsuga menziesii*) or western-white-fir (*Abies concolor*) stands in plantation forests in Oregon and Washington, to Sierra mixed-conifer forests in California and old growth Douglas-fir western-hemlock (*Tsuga heterophylla*) stands in Oregon and Washington (Table 1). Study sites varied in elevation from 100–2200 m above sea level. We selected local capture locations within each study site based on accessibility and detections of the Hermit Warbler during previous visits. We attempted to sample birds from forests across a broad range of forest types and structural conditions. We recorded the coordinates of capture locations with handheld GPS units (Garmin GPS62, Garmin, USA) with a 3–4 m error range.

Geolocator deployment and retrieval

To track locations of birds across the annual cycle, we attached 177 geolocators to adult, i.e., second year and after second year, male Hermit Warblers. In 2018 birds were tagged only at H. J. Andrews Experimental Forest and MacDonald Research Forest (n = 61) in Oregon, and in 2019 birds were tagged across all seven sites (n = 116; Fig. 1 and Table 1). We captured birds with mist nets, facilitated by plastic decoys and audio lures. Geolocators (Model: ML6340, Lotek Wireless, UK) were deployed on birds using a modified leg-loop harness made with elastic jewelry cord (Rappole and Tipton 1991, Streby et al. 2015). Birds were captured between June and early July in both years. Geolocators weighed 0.38–0.43 g, and were less than 5% of the body mass of individual birds. All birds with geolocators were marked with unique combinations of two or three plastic color bands, and a U.S. Fish and Wildlife Service metal band with a unique number. A year later, we attempted to re-sight and recapture each bird by revisiting initial capture locations and searching areas within an approximately 250-m radius from the initial location. We recaptured birds using the same methods that we used for initial captures, but unlike during initial capture efforts, multiple nets or revisits were often necessary because of vigilant behaviors of birds toward mist nets. Before attaching and after detaching geolocators from each bird, we recorded basic morphometrics, i.e., wing, tarsus, skull length, and body mass, using a wing ruler, calipers, and an electronic scale for future research.

Comparison of return rates between control and geolocator-tagged individuals

We sought to assess the effect of geolocators on return rates without the effects of potential bias from habitat differences or effort on re-sighting and recapture. To control potential habitat differences and effort, we selected a subset of locations at H. J. Andrews, where we released both geolocator-tagged birds (n = 19) and control birds (n = 24) in 2019 for return-rate analysis. At each capture location, observers listened for singing males and used audio lures of conspecific songs to read color-band combinations or capture birds to identify individuals. At these return-rate comparison sites, we made a total of 36 attempts of re-sighting/recapture and 672 minutes of observations and net operation time, from the start of playback

Table 1. The number of birds tagged with geolocators in 2018–2019 and 2019–2020 at each study site, and vegetation description of each site. Note that not all retrieved tags were functional and there we were some birds that we were not able to recapture.

Site	Year	Deployed	Retrieved	Vegetation description
Gifford Pinchot National Forest	2019–2020	26	5	Douglas-fir second growth; Douglas-fir and western hemlock mixed old growth forest
Mount Richmond Forest	2019–2020	11	1	Douglas-fir second growth from young to older uneven-aged mixed forests
MacDonald Research Forest	2018–2019	7	0	Douglas-fir second growth
	2019–2020	11	1	Douglas-fir second growth and older, uneven-aged experimental forests
H. J. Andrews Experimental Forest	2018–2019	54	11	Douglas-fir second growth, old-growth Douglas-fir and western hemlock forests, and high-elevation mixed conifer forest (noble fir *Abies procera*, subalpine fir *Abis lasiocarpa*, mountain hemlock *Tsuga mertensiana*, and more)
	2019–2020	24	2	
Fremont-Winema National Forest	2019–2020	14	0	Western white fir plantation and mixed conifer forest (Douglas-fir *Pseudotsuga menziesii*, sugar pine *Pinus lambertiana*, ponderosa pine *Pinus ponderosa*, incense cedar *Calocedrus decurrens*, and more).
Mendocino National Forest	2019–2020	8	1	Mixed conifer forest (Douglas-fir *Pseudotsuga menziesii*, sugar pine *Pinus lambertiana*, ponderosa pine *Pinus ponderosa*, incense cedar *Calocedrus decurrens*, and more).
Yosemite National Park	2019–2020	22	4	Sierran mixed conifer forest (red fir *Abies magnifica*, western white fir *Abies concolor*, Douglas-fir *Pseudotsuga menziesii*, sugar pine *Pinus lambertiana*, ponderosa pine *Pinus ponderosa*, incense cedar *Calocedrus decurrens*, and more).
Total		177	25	

broadcasting until the end of each attempt. During each attempt, we often detected and identified multiple individual birds with color band combinations and birds without leg bands. We ceased broadcasting after 10 minutes without detecting any Hermit Warblers and moved to the next location. We used Fisher's exact test with the base R function fisher.test to compare proportions of returned individuals between control birds and geolocator-tagged birds (R Core Team 2023).

Location estimation using light data

We followed the general process of geolocator data analysis suggested by Lisvoski et al. (2020). The geolocators recorded light intensity at two-minute intervals. We used the TwGeos package for processing light data (Wotherspoon et al. 2016). We first identified twilight events using the preprocessLight function and automatically filtered out outlier twilight time values to remove effect of shading and artificial lights on estimating twilight times, i.e., those that are greater than 15 minutes from the four-day moving average, with the twilightEdit function (Wotherspoon et al. 2016). Then, we estimated locations between each twilight event, i.e., noon and midnight, by fitting a threshold-based model with estelleMetropolis function in the SGAT package (Sumner et al. 2009, Lisovski and Hahn 2012). We fitted and tuned a series of movement models using Markov Chain Monte Carlo (MCMC) simulations with a set of priors, i.e., probability of stay and migration speed distribution. This model uses raw location estimates, movement speed distribution, error estimations from the calibration process, and a spatial mask that excludes locations from what is clearly not habitat, e.g., oceans. We used a buffered range map to avoid unrealistic movements outside the range, especially northern occurrences during the winter. We buffered range maps to allow for potentially larger movements outside the known range (NatureServe and BirdLife International 2014), at scales of 300 km, i.e., breeding and migration period ranges, and 900 km, i.e., winter range. We used a wider buffer in winter to avoid limiting the predicted movement of individual birds so the model could predict individual locations across all potential land

area in Central America, Mexico, southern Texas, and New Mexico. To confirm that this buffered range matches known records, we overlaid Hermit Warbler records in the eBird database from 2010 to 2020 (http://www.ebird.org), and confirmed that any records from outside these land masks were from vagrant birds, based on the observation notes (Appendix 1). With this buffered range map, we created a spatial mask that allows locations over water and outside the range boundary, but at one-tenth the likelihood of locations within the range boundary (Cooper et al. 2017). Then, we calibrated the timing of twilight from both the breeding and nonbreeding periods. We used the known breeding territory locations, i.e., location of capture as true location, of each tagged bird during the breeding season, i.e., tag deployment to 2 July in the first year and 1 May to the tag retrieval date in the second year, for calibrating geolocator location estimates on the breeding range. This is a conservative window of the stationary period at breeding sites, where we caught and recaptured Hermit Warblers.

Hermit Warblers use different light environments between the breeding season and nonbreeding periods; they breed in dense, closed-canopy conifer stands and winter in relatively open montane mixed conifer-broadleaf forests (Pearson 2020). Thus, we defined the wintering period to a core nonbreeding period from 15 October to 15 March, and calibrated twilight timings using the Hill-Ekstrom method for this period. This approach includes periods influenced by equinoxes, and when the birds are thought to be stationary based on the exploratory location estimates. We limited movement rates to fall within the rate of migration for similar songbirds, i.e., Kirtland's Warbler (Ewert et al. 2012) by using a rate distribution, i.e., km/h (gamma distribution with shape = 2.3, rate = 0.5). We first ran the modified gamma model with 1000 iterations and tuned the model with six chains of each with 1000 iterations. We ran the final model with 3000 MCMC samples, and posterior distribution of location estimates, i.e., longitude and latitudes, were obtained for each twilight event. With these final MCMC samples, we proceeded

with a post-hoc summary and analyses of locations using most probable locations, i.e., median of posterior distribution of daily locations, for each timestamp.

Identification of breeding and winter range, and the timing of arrivals and departures

We used each individual bird's distribution of locations throughout its full annual tracks to create spatial thresholds for identifying breeding and wintering periods. We defined wintering location or wintering ground as representative location or space that hermit warblers use between 15 October and 15 March, i.e., wintering period. First, we set a spatial threshold for classifying wintering and breeding periods for each bird, assuming that the birds will show migratory movements between the wintering and breeding periods. We defined a spatial threshold for the breeding range, as 0.5 degrees latitude and longitude from the location of recapture, and the threshold for winter range at each individual's easternmost 25th percentile longitude of year-round locations. We only used longitude for setting this threshold because latitude was not useful during fall and spring equinoxes, when birds often left or arrived at the wintering locations. After defining spatial boundaries for each individual's breeding and wintering ranges, we used the date of the bird's first passage through the boundary without returning to identify winter and breeding periods. For defining wintering locations, we used the median of the MCMC samples of latitude and longitude when each bird entered the wintering range as point estimate of its winter location.

Migratory connectivity and migration pattern

We used a Mantel correlation test to assess migratory connectivity of birds. The Mantel test calculates the correlation between distances among birds on the breeding grounds and distances among birds on the wintering grounds (Ambrosini et al. 2009, Somveille et al. 2021). Higher Mantel correlation coefficients (rM; closer to 1) indicate strong migratory connectivity, i.e., birds from the same breeding location are clustered together on the wintering grounds. Alternatively, Mantel correlation coefficients near zero indicate a lack of such clustering. We calculated statistical significance of the Mantel correlation using 106 permutations. Mantel correlation was calculated with function mantel in the R package vegan (Oksanen et al. 2022), with distance between points measured on the earth's surface (WGS84 ellipsoid), using the package geosphere (Hijmans 2022). We measured Mantel correlation using three different combinations of sites to see if the Mantel correlation coefficient and its uncertainty draw different conclusion given choice of sites from our study: (1) Gifford Pinchot National Forest and Yosemite National Park, northernmost and southernmost sites that are 930 km apart; (2) Gifford Pinchot, Yosemite, and H. J. Andrews Experimental Forest; (3) birds from 2020 only to remove influence of large sample size from H. J. Andrews in 2019; and (4) all sites with any geolocator retrievals.

We also estimated migratory connectivity (MC) score suggested by Cohen et al. (2018) by setting three distinct geographical regions of target sites in the wintering grounds, i.e., Central Mexico, Gulf Coast and Sierra Madre, and Southern Mexico, and six origin sites in the breeding grounds where we captured and tagged the birds. We calculated relative abundance at sampling locations using the eBird status and trend product's relative abundance during the breeding season (Fink et al. 2022), downloaded through ebirdst package (Strimas-Mackey et al. 2022). The MC index was estimated from estMC function in the MigConnectivity package (Hostetler and Hallworth 2021). Last, to describe population spread and mixing patterns (Finch et al. 2017, Skinner et al. 2022), we calculated the population spread in the wintering grounds in form of median pairwise distance at wintering grounds of individual birds from the same breeding sites, and compared it with geographical spread of individuals, i.e., nonbreeding range spread, from the entire breeding range we sampled using a paired t-test.

We used Bayesian linear mixed-effect models to describe relationships between breeding and winter locations. We set breeding site as a random effect variable, to allow the intercept of each relationship to vary by site and to account for potential similarity among individuals within sites. We standardized location variables, so that regression slopes for each model would be comparable. We used 90% highest density intervals of the posterior probability distribution of standardized coefficients of each variable as credible intervals to describe the strength of statistical support in the relationships. A positive relationship between breeding-ground latitudes and wintering-ground latitudes would describe chain migration, whereas a negative relationship would indicate a leapfrog migration pattern. Also, a positive relationship between breeding and wintering longitudes would indicate longitudinal chain migration, and a negative relationship would indicate a leapfrog migration pattern. Last, because the landmass of southern North America and Central America is oriented diagonally in latitude and longitude (Fig. 1), we expected a diagonal distribution in winter and breeding locations, and hence migration patterns, i.e., diagonal leapfrog, chain migration, and telescopic migration. To describe these potential patterns, we investigated the relationship between breeding latitude and wintering longitude, and breeding longitude and wintering latitude. For both analyses, a negative relationship would indicate chain migration: where birds breeding farther north would migrate to more western wintering grounds, and a positive relationship would indicate a leapfrog migration: where birds breeding further west migrate to more southern wintering grounds. In addition to comparing breeding and wintering locations using coordinates, we looked at correlation between breeding latitude and migration distance, measured as straight distance between breeding and wintering location, i.e., median location from geolocator analysis, to investigate the possibility of telescopic migration; no relationship in breeding ground and wintering locations (both latitude and longitude) but distance is related to latitude or longitude (Skinner et al. 2021).

Migratory phenology and its relationships with locations and subsequent migration phenology

We examined whether breeding or wintering locations of birds are related to the arrival and departure timing to those locations. This is because there could be a spatial gradient in the phenology of primary producers and the arthropod prey that birds rely on for breeding and during wintering periods. For example, birds breeding at more northern breeding grounds would depart later from the wintering grounds and arrive later at the breeding grounds. Next, we assessed whether migration phenology is related to migration phenology of the subsequent stage. Positive correlations would indicate that birds departing earlier arrive earlier, or early arriving birds leave earlier. We predicted migration timing of winter arrival

as function of breeding site departure, breeding arrival as function of wintering site departure, and wintering site departure as function of wintering site arrival. To estimate these relationships, while accounting for potential similarity within sites, we again used the Bayesian linear mixed-effect model with site as a random intercept group. Bayesian linear mixed-effect models were fitted with r package brms and rstan, estimating the posterior probabilities with MCMC sampler program Stan in program R (Bürkner 2021, Stan Development Team 2023). Bayesian slope estimates and 90% credible intervals were presented to describe the strength of support for relationships of interest.

Migration routes and rates between pre-breeding and post-breeding migration

We described migration routes of birds using the path connecting most likely daily locations, i.e., median from posterior distribution, between the day of departure from the breeding range to the day of arrival at the winter range, i.e., fall or post-breeding migration, and the day of departure from the winter range to the day of arrival at the breeding range, i.e., spring or pre-breeding migration, in the following year. Because the latitudinal estimates during an equinox are unreliable (Lisovski et al. 2020), we did not interpret the path during 15 days before and after fall and spring equinoxes. To describe the spatial uncertainty and specific space use during the post-breeding migration, we calculated kernel point-density of posterior locations of three groups of birds during this period: (1) birds from Gifford Pinchot and H. J. Andrews (Cascades); (2) birds from Mt. Richmond, MacDonald Research Forest, and Mendocino (Coast Range); and (3) birds from Yosemite (Sierra Nevada). Because these location estimates are in regular intervals (two per day) across directional movement, higher density areas indicate slower movement and more time spent during fall post-breeding migration, collectively by the birds from each group. For this analysis, we defined the fall post-breeding migration period as between 14 to 90 days after tag deployment for all birds except for birds from Mount Richmond and Mendocino that arrived at wintering locations in early September, for which we defined the post-breeding migration period as two weeks after tag deployment to 60 days. We mapped the contours (10%, 50%, and 75%) of kernel point density of posterior locations of each group's birds during the post-breeding migration on a digital elevation model map of North America from Amazon Terrain Tiles (https://registry.opendata.aws/terrain-tiles) to describe their migratory movements across the geography. Terrain map was accessed through R package elevatr (Hollister et al. 2021), and the kernel point density estimates were calculated with the eks package (Duong 2022).

We calculated daily migration rates (km per day) during average and pre-breeding migration for every five-day interval after departure from the breeding or winter range (Carneiro et al. 2019, Dossman et al. 2023). We compared the duration of migration, i.e., number of days, for post-and pre-breeding migration using a paired t-test for each individual bird. We used the difference between post-and pre-breeding migration duration for each bird as a response variable, with the t.test function in base R program. We used program R, Version 4.0.5. (R Core Team 2023) for all analysis and data preparation in this study.

RESULTS

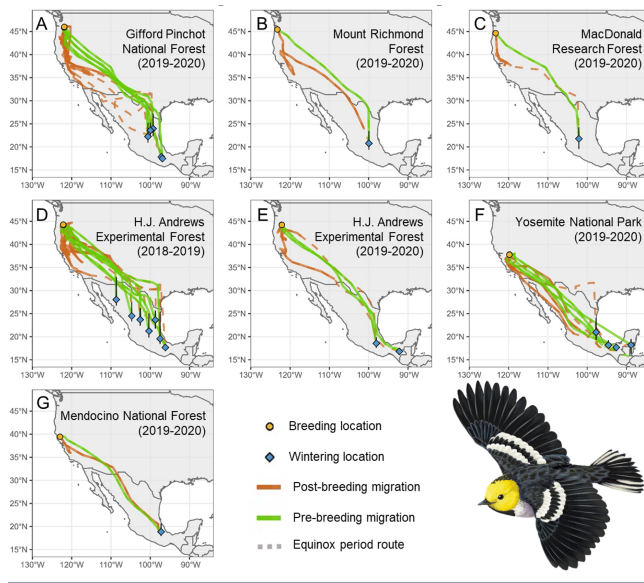## Recapture rates and comparison between control birds and tagged birds

We recaptured 11 and 14 birds with geolocators in 2019 and 2020, respectively. In 2020 we recaptured at least one tagged bird from each of six study sites but failed to retrieve any birds with geolocators at the Fremont-Winema National Forest site (Table 1). Three tags from 2019 malfunctioned and did not record locations from the full annual cycle, and one tag had too many shading events to provide reliable information; we excluded those individuals from the analyses. We were unable to recapture ten additional birds (five birds in each year) that we were nonetheless able to observe and identify based on their unique color-band combinations, yielding overall return rates of 26% in 2018–2019 and 17% in 2019–2020. We compared return rates between control birds and geolocator birds at a subset of locations with both geolocator birds and control birds in H. J. Andrews Experimental Forest. At these locations, the return rate of control birds (three of 24, 12.5%) was lower than that of the geolocator birds (four of 19, 21%) although the difference in proportions was not statistically significant (odds ratio = 1.83, 95% CI of odds ratio = 0.26 - 14.45, p = 0.68).

Wintering locations, migratory connectivity, and migration pattern

Based on the data from retrieved tags, birds wintered across Mexico, from Quintana Roo and Chiapas to Chihuahua and Tamaulipas. Five birds from Gifford Pinchot National Forest wintered in western Tamaulipas (2), central San Luis Potosi (1), and northern Oaxaca (2; Fig. 2A). Two birds from the northern coastal sites (Mount Richmond and MacDonald Research Forest) wintered in Queretaro and Aguascalientes, respectively (Fig. 2B and C). Pooling data across 2018–2019 and 2019–2020, nine birds from H. J. Andrews wintered across a vast region of Mexico, from Chiapas to western Chihuahua (Fig. 2D and E). Four birds from Yosemite National Park wintered in eastern Mexico, across Veracruz, Tabasco, and Quintana Roo (Fig. 2F) and a bird from Mendocino National Forest wintered in western Veracruz (Fig. 2G). Wintering coordinates and their uncertainty are provided in Appendix 2.

The Mantel correlation coefficients from different combinations of sites (all sites: rM = 0.15, p = 0.13; Yosemite-Gifford Pinchot: rM = 0.31, p = 0.06; Yosemite-H. J. Andrews-Gifford Pinchot: rM = 0.15, p = 0.15, 2020 birds only: rM = 0.21, p = 0.05) suggest weak migratory connectivity in this species, even for breeding populations in Yosemite National Park and Gifford Pinchot National Forest that are more than 900 km apart (Fig. 3C). The MC estimate yielded the same conclusion (MC = 0.16, 95% CI = -0.09 - 0.57). In addition to the high level of population mixing in the wintering grounds, the spread of individuals from the same breeding grounds was high; Gifford Pinchot National Forest (median = 444.3 km, SD = 61.9 km), Yosemite National Park (median = 546.4 km, SD = 147.3 km), H. J. Andrews Experimental Forest (median = 644.8 km, SD = 238.7 km). The nonbreeding range spread (as in Skinner et al. 2022) of all individuals from H. J. Andrews, Yosemite National Park, and Gifford Pinchot National Forest (median = 603.1 km, SD = 231.1 km) was not sufficiently different from each population's wintering range spread (t = -1.6, df = 18, p = 0.125).

Fig. 2. Migration routes and winter locations of 21 male Hermit Warblers (*Setophaga occidentalis*) across the study sites. (A) Gifford Pinchot National Forest (2019–2020), (B) Mount Richmond (2019–2020), (C) MacDonald Research Forest (2019–2020), (D) H. J. Andrews birds (2018–2019), (E) H. J. Andrews birds (2019–2020), (F) Yosemite National Park (2019–2020), and (G) Mendocino National Forest (2019–2020). Routes are drawn by connecting median locations for alternating five-day periods. The dotted lines indicate the equinox period when latitudinal estimates are especially poor. Migrating male Hermit Warbler illustration by Lauren Helton.

Fig. 3. Relationship between breeding longitude and winter latitude (A) and longitude (B) of male Hermit Warblers (*Setophaga occidentalis*). Points indicate individual birds' locations, and error bars indicate 50% credible intervals for winter latitude and longitude. Panel (C) shows the distribution of wintering locations of birds from various breeding origin.

Although we observed overlap of wintering locations of birds from different breeding locations, in general the birds breeding in eastern longitudes wintered farther east (slope = 0.502, 90% CI = 0.035 - 0.936; Fig. 3B) and south (slope = -0.518, 90% CI = -1.003 - -0.032; Fig. 3A) than birds from higher latitudes and western longitudes (n = 22; Table 2; Fig. 3A and B). We found no relationship between migration distance and breeding locations (latitude and distance: Pearson's r = 0.05, 95% CI = -0.379 - 0.463; longitude and distance: Pearson's r = 0.005, 95% CI = -0.417 - 0.426),

Migratory phenology and its relationships with locations and subsequent seasonal phenology

In fall, birds departed breeding grounds from late June to late July (mean departure date = July 7, SD = 11.9), arriving at their winter location in late September to early October (mean arrival date = October 3, SD = 16.5). In spring, they left wintering grounds for pre-breeding migration in late March to early April (mean departure date = March 29, SD = 9.6) and arrived at breeding grounds in early May (mean arrival date = May 9, SD = 6.4). Departure dates from breeding grounds in fall were not correlated with wintering or breeding locations, but birds wintering farther south generally arrived at wintering grounds later than birds wintering farther north (slope = -0.459, 90% CI = -0.904 - -0.034). There was weak evidence for a relationship between winter

departure date and breeding ground latitude and longitude (Table 2). For pre-breeding migration, birds wintering farther west departed wintering grounds later than birds wintering farther east (slope = -0.522, 90% CI = -0.845 - -0.198). Also, breeding site arrival was not strongly related to winter locations, but birds breeding north arrived later than birds breeding at lower latitudes (slope = 0.469 90% CI = -0.101 - 0.951; Table 2). This pattern may be due to the leveraging influence of the three birds from Yosemite that wintered in the most eastern and southern locations and started migration from the wintering grounds earlier than other birds (Table 2, Appendix 3). For each subsequent migration phenology date, birds arriving earlier at the breeding sites departed their wintering site earlier than other individuals, indicating possible time constraints for spring pre-breeding migration (slope = 0.497, 90% CI = 0.124 - 0.869). However, neither the timing of departure from breeding grounds and arrival at wintering grounds, nor arrival at wintering grounds and departure from wintering grounds, were strongly related to one another (Table 2).

Migration routes, rate and duration

Most birds from the Cascade mountains (H. J. Andrews and Gifford Pinchot National Forest) moved south to the Klamath mountains and northern California's Sierra Nevada, then to the Central Valley, and finally moved southeast toward Arizona and New Mexico to reach Mexico (Fig. 2A, D, and E). Oregon Coast range birds moved south toward California's Coast ranges then migrated across Nevada and Arizona to Mexico (Fig. 2B and C). Birds from Yosemite National Park and Mendocino National Forest moved to southern California before moving southeast (Fig. 2E and G). Birds arrived at their winter range from September to October, except for one bird from Gifford Pinchot National Forest that arrived in November. Upon leaving the breeding range, birds moved slowly in the early portion of their post-breeding migration, then moved faster as they approached their wintering range (Fig. 4). Our kernel point density analysis shows that during this slow-moving period, birds from the Cascade mountains migrated slowly through the Klamath

Table 2. Standardized beta coefficients from Bayesian linear mixed-effect models showing relationships between migration phenology and locations of Hermit Warblers (*Setophaga occidentalis*; n = 22, from all sites with tag retrieval). Estimates with 90% credible intervals not overlapping with zero are in bold marked with asterisks (*).

	Breeding site departure	Winter site arrival	Winter site departure	Breeding site arrival	Breeding latitude	Breeding longitude
Breeding site departure		-0.025 (-0.426 – 0.377)			-0.035 (-0.692 – 0.625)	0.229 (-0.365 – 0.838)
Winter site arrival			-0.019 (-0.384 – 0.353)		0.283 (-0.457 – 1.031)	0.239 (-0.483 – 0.994)
Winter site departure				**0.497 * (0.124 – 0.869)**	0.474 (-0.028 – 0.961)	-0.428 (-0.885 – 0.061)
Breeding site arrival					0.469 (-0.101 – 0.951)	-0.183 (-0.772 – 0.498)
Winter latitude	0.221 (-0.188 – 0.626)	**-0.459 * (-0.904 – -0.034)**	0.348 (-0.031 – 0.727)	-0.126 (-0.577 – 0.323)	0.330 (-0.189 – 0.844)	**-0.518 * (-1.003 – -0.032)**
Winter longitude	-0.328 (-0.695 – 0.044)	0.241 (-0.153 – 0.638)	**-0.522 * (-0.845 – -0.198)**	0.148 (-0.288 – 0.570)	-0.242 (-0.753 – 0.286)	**0.502 * (0.035 – 0.936)**

mountains and northern Sierra Nevada (Fig. 5A), whereas birds from the Coast range and Yosemite used coastal areas in southern California that include mountain ranges (Fig. 5B and C). During pre-breeding migration (mean = 40.8 days, SD = 8.3 days), birds moved much faster than during post-breeding migration (mean = 87.4 days, SD = 20.2 days), moving north then diagonally northwest toward their breeding range in the Pacific Northwest of the United States. Overall duration of migration was 46.5 days shorter on average (95% CI = 38.242 - 54.776) during pre-breeding migration compared to post-breeding migration (Fig. 4; one-sample t-test, t = 11, p < 0.001). In fall, i.e., post-breeding, migration dates and duration tended to be more variable across individuals than in spring, i.e., pre-breeding (Fig. 4, Appendix 3).

DISCUSSION

We aimed to examine strength of migratory connectivity and spreading pattern of Hermit Warblers across their breeding range. Our results suggest that Hermit Warblers may not have strong migratory connectivity nor exhibit a strong geographical spreading pattern during migration. Using geolocators, we observed that Hermit Warblers migrate slowly during the post-breeding migration in fall as they pass through mountainous regions in California, compared to rapid direct migratory flight from Mexico to the breeding grounds in spring. Based on our tracking data and the known molting cycle of the species, we hypothesize that they may use the Sierra Nevada for post-breeding molt.

Migratory connectivity and pattern

Although limited by small sample sizes at each study location, we did not find evidence for strong migratory connectivity. Birds tagged at H. J. Andrews Experimental Forest, where we had the largest sample size, were distributed widely across Mexico during the winter period, overlapping with birds from other breeding locations and thus supporting a high level of mixing among populations. Yet, individuals from Yosemite National Park, the most southerly breeding site we sampled, wintered in the easternmost locations, in forested areas across Veracruz and Yucatan Peninsula in Southeastern Mexico. Correlations between breeding versus wintering ground latitudes and longitudes suggest some form of chain migration, especially for individuals in the

Sierra Nevada that migrate farther south and east along the Central American landmass. BBS data suggest strong evidence of decline in Hermit Warblers breeding across their range, but the rate of decline is especially pronounced in the Sierra Nevada and Washington during 1993–2019 (Sauer et al. 2020). Whereas warming temperatures and forest loss due to fire have been pervasive across the breeding range in recent years (Abatzoglou et al. 2014, Abatzoglou and Williams 2016), deforestation in southeastern Mexico, where the four tracked birds from Yosemite National Park wintered, has been particularly severe in recent decades (Aide et al. 2013, Bonilla-Moheno and Aide 2020; see also https://www.globalforestwatch.org).

Simulation work of Vickers et al. (2021) showed that for discrete sampling sites, wider spread among sites introduced upward bias in Mantel correlation coefficient values, and also tended to overestimate the mantel correlation coefficient from sampled individuals compared to the population's true migratory connectivity. Spread of winter locations of birds from the same breeding locations in our study was wide, with median distances ranging from 444–644 km across three breeding sites with multiple birds, and was not different from all nonbreeding birds (only considering sites with n > 1), suggesting high-mixing, and high spread of individuals during the wintering period (Finch et al. 2017, Skinner et al. 2022). However, additional sampling sites within the species' range could provide stronger evidence for weak migratory connectivity in this species. Further studies using tracking devices or intrinsic markers such as stable isotopes could focus on the southern portion of the breeding range (e.g., southern Sierra Nevada, San Bernardino Mountains, southern California Coast Range) and Klamath mountains to fill knowledge gaps in these areas (Bowen and West 2019). Although our study covers most of the Hermit Warbler breeding range, expanding future studies to these geographically and acoustically distinct breeding populations (Furnas et al. 2020) would more completely describe the species' complete migration pattern and connectivity. For example, Hermit Warblers occur farther south in Central America than we observed in this study, from Guatemala to Costa Rica during winter months (NatureServe and BirdLife International 2014), but none of our birds wintered farther south than southern Mexico. Furnas (2020) found apparently stable occupancy of Hermit Warblers over a 14-year period in northern California,

Fig. 4. Five-day average rate of migration (km per day) from the onset of migration for fall (brown) and spring (green) migration. Faded bars indicate equinox periods. Numbers on the left-side column are individual bird ID (tag ID).
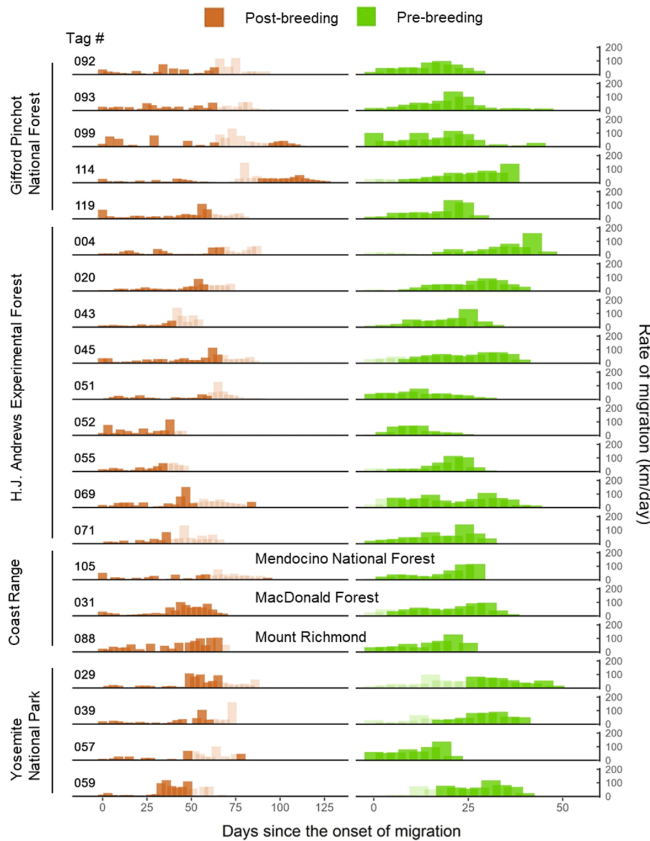
and though lack of change in occupancy does not guarantee stable abundance at locations, it may suggest that populations in the southern Sierra Nevada and Klamath mountains could be declining even faster than other places in California. Additional studies of Hermit Warbler migration that map migratory connectivity and relate local population trends with environmental stressors throughout the annual life cycle across these areas will help identify the drivers of population change in Hermit Warblers.

In general, migratory connectivity could explain the spatial patterns in carry-over effects of stressors from wintering grounds to breeding grounds. This pattern has been observed in Golden-winged Warbler (*Vermivora chrysoptera*), Wood Thrush (*Hylocichla mustelina*), and other species with declining populations showing strong migratory connectivity to wintering grounds that are losing habitat (Newton 2006, Inger et al. 2010, Taylor and Stutchbury 2016, Kramer et al. 2018). However, the lack of strong migratory connectivity in our study supports the notion that local variation in population trends across the breeding range may be more influenced by breeding-ground habitat loss and climate change (Betts et al. 2018, Phalan et al. 2019) rather than stressors in particular locations on the wintering grounds, at least for the northern population of Hermit Warblers. In addition to potential carry-over effects from the wintering

grounds, it is also possible that stressors during migration, especially during post-breeding migration when species seemingly use on-the-ground resources during a longer migration period, can also affect population size and demographics on wintering grounds and breeding grounds in the following year (Tucker et al. 2022). Of course, our conclusions and speculations on entire population-level demographic processes are constrained by the limited sample size of our study.

Migration phenology and schedule

Matching the timing of migration with resource availability is critical for individual survival and reproductive success of migratory birds (Renfrew et al. 2013, Zurell et al. 2018, Visser and Gienapp 2019, Shipley et al. 2020). The phenology and duration of each migration stage recorded by individual tracking data in our study confirm anecdotal field observations on the Hermit Warbler's seasonal movements and annual cycle patterns (Pearson 2020). Across all birds, departure dates from breeding grounds and wintering grounds, and arrival date to the breeding range, were relatively less variable among individuals than timing of arrival at the wintering grounds. The timing of wintering ground departure was positively related to spring arrival timing on the breeding grounds; earlier departing birds arrived earlier at the breeding grounds. The limited window of time for breeding defined by arrival and departure dates, along with an apparent lack of double brooding in this species (Pearson 2020) raises the question of whether Hermit Warblers can show sufficient plasticity to adapt to shifts in timing of food resources resulting from rapid climate change (Visser 2008, Schmaljohann and Both 2017). The capacity of extension or delay of the breeding season into later summer, when spring is delayed, may be limited for Hermit Warblers by drought and excessive summer heat, which are becoming more severe because of anthropogenic climate change (Abatzoglou et al. 2014, Mote et al. 2018). Long-distance Neotropical migrants like Hermit Warblers are known to be less capable than short-distance migrants of advancing spring arrival dates in accordance with warming spring temperatures on the breeding grounds (Furnas and McGrann 2018, Lehikoinen et al. 2019). In a study in western Oregon, the Hermit Warbler's spring arrival date did not advance significantly in the past three decades, whereas some other species showed changes in arrival dates up to two weeks (Robinson et al. 2019). Hermit Warblers may therefore be particularly vulnerable to a shortening in duration of favorable climatic conditions during the breeding season. Finding ecological correlates of migration phenology, especially regional and local microclimate variation driven by topography, elevation, and vegetation type, would be an important next step in understanding how Hermit Warbler's breeding season and migration might be limited under current and future climate change scenarios.

Migration routes, rates and apparent post-breeding molt

During the post-breeding migration period, we found that most birds moved south of their breeding locations to montane regions but remained within the species' known breeding range. Several field observations describe birds migrating to or through higher elevation areas in July and August in the Sierra Nevada and California Coast Range (Pearson 2020). The known molting timing after the breeding season (Jackson et al. 1992) and slow movements in early post-breeding migration (Fig. 5) from our

Fig. 5. Contour lines of kernel density of posterior locations of individual birds during fall migration. Birds from (A) Cascades (H. J. Andrews Experimental Forest and Gifford Pinchot National Forest), (B) Coast Range (Mount Richmond, MacDonald Forest, and Mendocino National Forest), and (C) Yosemite National Park are shown in separate panels. Contour lines show 10% (innermost), 50% (middle, dashed line), and 75% (outermost, dotted line) kernel-density boundaries.
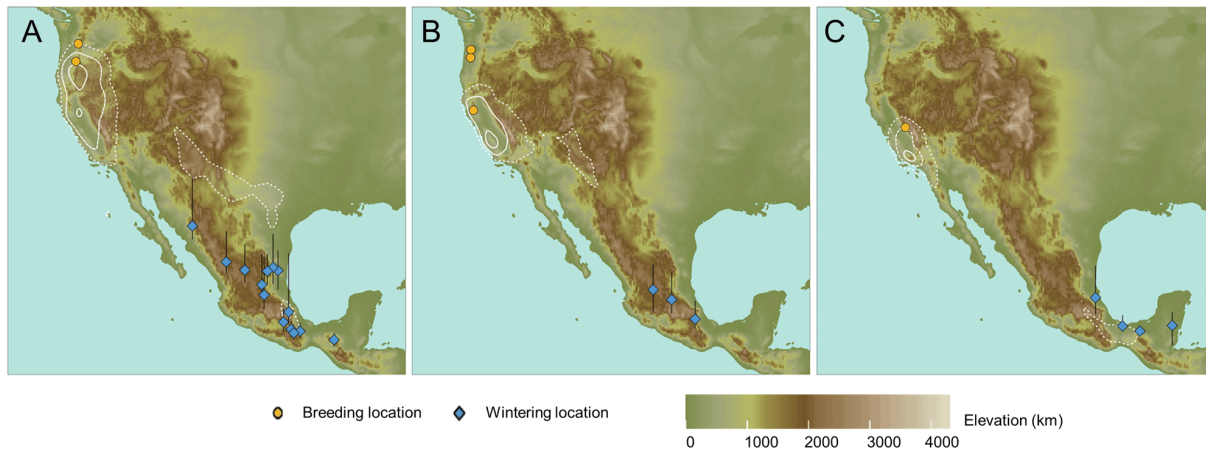
tracking study suggest that Hermit Warblers from Oregon and Washington migrate and presumably molt immediately after leaving their breeding locations in montane regions of Northern California and the Sierra Nevada (Figs. 2, 4, and 5). Knowledge of the exact location during this period is limited by the precision of geolocator location estimates. However, the most likely locations during post-breeding show that the birds move without distinct, extended stopovers, rather than staying for longer periods at more distinguishable staging locations for molting (Figs. 2 and 5). A recent study of Swainson's Thrushes (*Catharus ustulatus*) in eastern North America showed that molting individuals may have extended periods of stopovers during molting, which conforms to the definition of stopover molt-migration, in which birds molt during the migration stopover period (Wiegardt et al. 2017, Tonra and Reudink 2018, Morales et al. 2022). Unlike Swainson's Thrushes, Hermit Warblers seem to move slowly during this apparent molting period, i.e., continuous molt-migration. In the field, when attempting to find and capture geolocator-tagged birds, HKK captured unmarked adult birds (after-hatch-year birds) molting flight feathers (symmetric on both wings) and body feathers in early July, but no birds captured during the earlier breeding season (May–June) showed signs of molting. Given that molting is energy-intensive and reduces flight efficiency (Weimerskirch et al. 1995, Cantarero et al. 2014, Rivers et al. 2017), environmental conditions on molting grounds can be critical for successful migration and survival (Rohwer et al. 2005, Pageau et al. 2020). Changing environmental conditions at higher elevations during July–September could threaten habitat availability for molting Hermit Warblers because rapid climate change is introducing extreme heatwaves and drought that stress plants, reduces ecosystem productivity, and facilitates intense fires (Chmura et al. 2011, Sheehan et al. 2015).

During spring pre-breeding migration, Hermit Warblers moved quickly and did not show any evidence of extended periods of stay between wintering and breeding ranges (Figs. 2 and 4). This short window of migration likely requires much greater energetic

expenditures than protracted post-breeding migration, which would make molting during spring pre-breeding migration too energetically costly. Reports of pre-alternate molt only of face, crown, throat, and chin feathers occurring on wintering grounds (Jackson et al. 1992), also corroborate absence of molt-migration during the pre-breeding migration. In addition, the rapid spring pre-breeding migration of male Hermit Warblers may be driven by sexual selection, wherein males compete for territories to be selected by females for breeding and race to occupy habitat patches (Kokko 1999, Morbey and Ydenberg 2001). Also, at H. J. Andrews Experimental Forest, cooler microclimate areas promoted positive population growth of this species whereas warmer forests produced negative trends (Kim et al. 2022). Individual birds competing for breeding territories in early spring could face greater limitation in cooler forest as breeding season temperatures rise from climate change. However, earlier arrival could be limited by breeding ground conditions in early spring and environmental cues for migration at the wintering range. For instance, high elevation forests in the Pacific Northwest could still have deep snow cover and freezing temperatures when birds arrive in the spring, which could reduce food availability. Together with previous studies that observed limited variability in spring pre-breeding migratory phenology of Hermit Warblers (Mayor et al. 2017, Furnas and McGrann 2018, Robinson et al. 2019), our results on breeding duration and pre-breeding migration characteristics support that Hermit Warblers may have limited adaptive capacity to adjust their migratory phenology to changes in the timing of resource availability.

CONCLUSION

Conservation of this narrow-niched, climate-sensitive species under rapid-climate-change scenarios and continued habitat loss and degradation (Abatzoglou and Williams 2016, Berner et al. 2017, Phalan et al. 2019, Kim et al. 2022) will be challenging without a better understanding of its annual movements (Marra et al. 2015). Our study found weak migratory connectivity and a subtle pattern of chain migration in Hermit Warblers. Weak

migratory connectivity indicates a high level of mixing between individuals from different breeding grounds at the wintering range. This implies local conditions on the breeding grounds are more likely to explain variation in demographics of local populations, rather than carry-over effects from specific wintering grounds, although our work cannot rule out other drivers of demographics throughout the annual life cycle. We also observed weak, overlapping chain migration from the birds in Yosemite National Park that requires further investigation. Future research to further examine migratory connectivity of southern population of the species could supplement limited sample size from northern breeding grounds in California, Oregon, and Washington, and assess the potential effects of habitat and climate change from the species' southern wintering range on the breeding population. Phenology of migration was more similar across birds from different breeding populations in spring, when birds migrated more rapidly and directly toward breeding grounds than in fall, indicating that birds may be limited in their capacity to adapt their pre-breeding migration timing to match the phenology of resources and the thermal environment. Post-breeding, i.e., fall, migration routes and rates indicated that northern breeding Hermit Warblers use montane regions of California and southwestern Oregon during apparent molt-migration, which suggests the additional conservation importance of these areas for Hermit Warblers. Identifying ecological correlates of migration phenology, especially regional and local microclimate, topography, elevation, and vegetation in breeding and wintering ranges would be a valuable next step in understanding how environmental conditions across Hermit Warbler's full annual range affect their population trajectories.

Data Availability:

Raw geolocator archival data, processed location data and codes used for analysis are stored and available at Movebank (Movebank ID:2269303653).

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Appendix 1

eBird record of Hermit Warblers between 2011–2021 (grey dots), with known seasonal range (red, yellow, blue; NatureServe and BirdLife International 2014) and buffer range (green) used as a conservative prior for known distribution.
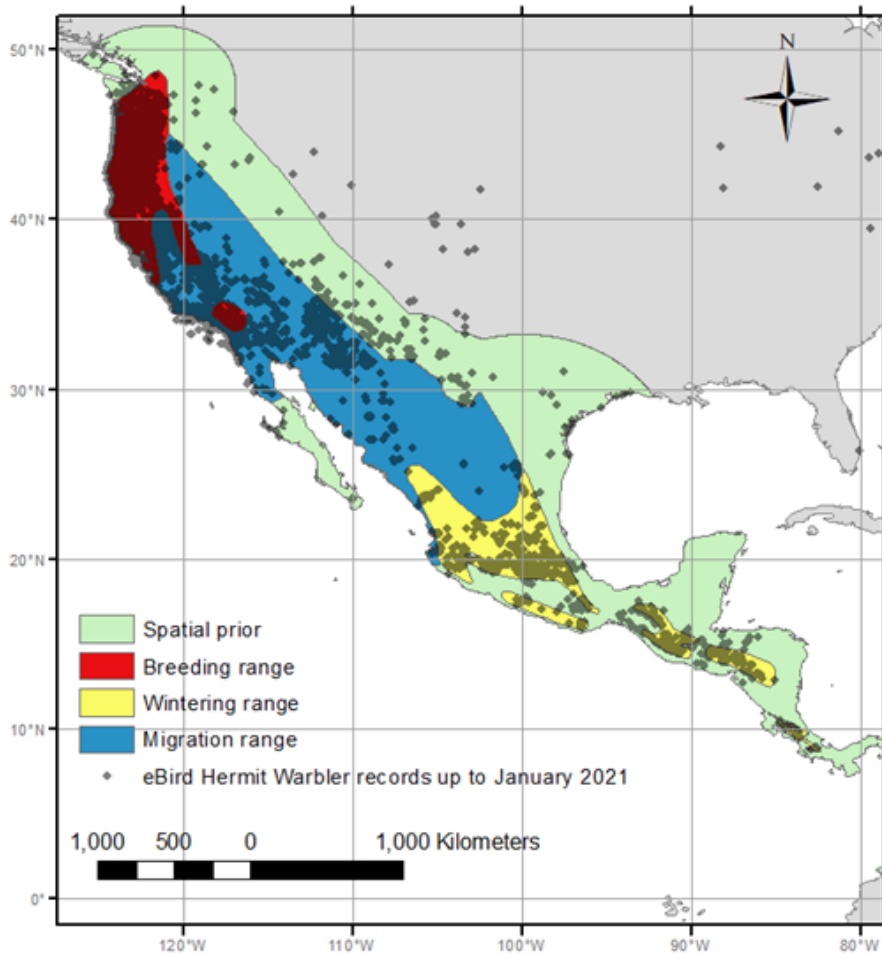
Appendix 2

Breeding and wintering locations of tracked birds. Breeding latitudes and longitudes are taken from handheld GPS units at capture locations, and wintering locations are median and 25% and 75% percentile credible intervals from the geolocator data.

Study site	ID	Year	Breeding latitude	Breeding longitude	Wintering longitude (50% Cl)	Wintering latitude (50% Cl)
H. J. Andrews	4	2019	44.264	-122.184	-98.722 (-99.201 – -98.269)	23.622 (21.751 – 25.637)
	20	2019	44.203	-122.113	-100.341 (-100.984 – -99.668)	21.216 (19.8 – 25.012)
	37	2019	44.273	-122.137	-102.083 (-102.81 – -101.367)	19.942 (18.967 – 22.73)
	43	2019	44.278	-122.141	-97.499 (-98.129 – -96.844)	19.538 (18.373 – 25.347)
	45	2019	44.266	-122.178	-96.174 (-96.743 – -95.617)	17.649 (17.036 – 18.441)
	51	2019	44.277	-122.151	-102.574 (-103.151 – -102.01)	23.671 (22.39 – 26.222)
	52	2019	44.276	-122.159	-108.662 (-109.271 – -108.144)	28.03 (26.705 – 32.889)
	55	2019	44.276	-122.159	-104.731 (-105.201 – -104.247)	24.475 (23.294 – 27.51)
	71	2020	44.251	-122.146	-98.084 (-98.934 – -97.269)	18.552 (17.571 – 19.862)
	69	2020	44.204	-122.118	-92.224 (-92.702 – -91.725)	16.795 (16.098 – 17.46)
Yosemite NP	59	2020	37.755	-119.806	-92.596 (-93.118 – -92.045)	17.654 (17.158 – 18.092)
	29	2020	37.753	-119.807	-88.842 (-89.328 – -88.36)	18.201 (16.245 – 19.504)
	39	2020	37.819	-119.807	-94.609 (-95.586 – -93.73)	18.157 (17.62 – 19.232)
	57	2020	37.755	-119.806	-97.751 (-98.184 – -97.253)	20.956 (19.333 – 24.091)
Gifford Pinchot NF	114	2020	46.001	-121.900	-97.201 (-97.667 – -96.737)	17.828 (17.161 – 18.644)
	119	2020	45.991	-121.914	-99.304 (-99.784 – -98.832)	23.933 (22.282 – 27.217)
	99	2020	45.887	-121.960	-96.901 (-97.396 – -96.417)	17.464 (16.802 – 18.263)
	93	2020	46.008	-121.901	-99.964 (-100.588 – -99.389)	23.572 (22.245 – 25.26)
	92	2020	46.008	-121.901	-100.599 (-101.121 – -100.076)	22.233 (20.913 – 25.277)
Mac-Dunn Research Forest	105	2020	44.635	-123.301	-102.118 (-102.719 – -101.484)	21.741 (19.507 – 24.266)
Mt. Richmond Forest	88	2020	45.425	-123.254	-99.973 (-100.606 – -99.336)	20.761 (19.373 – 23.478)
Mendocino NF	31	2020	39.436	-122.972	-97.246 (-97.796 – -96.722)	18.844 (17.943 – 20.657)

Appendix 3

Arrival and departure dates to and from breeding and wintering range, estimated from geolocator data. Date estimates are mean arrival and departure dates, and 95% credible interval (days) from the MCMC samples were provided as an uncertainty measure.

Study site	ID	Year	Breeding departure (95% CI)	Winter arrival (95% CI)	Winter departure (95% CI)	Breeding arrival (95% CI)
H. J. Andrews	4	2019	2018-06-27 (-5.5,8.1)	2018-09-28 (-1.4,2.1)	2019-03-15 (-15.2,16.3)	2019-05-07 (-3.9,3.7)
	20	2019	2018-07-06 (-11.9,13.5)	2018-09-23 (-2.3,3.7)	2019-03-27 (-20.7,14.3)	2019-05-13 (-3.8,2.2)
	37	2019	2018-07-06 (-14,22)	2018-10-24 (-22.3,39.7)	2019-04-02 (-4.4,6.1)	2019-05-08 (-4.7,3.3)
	43	2019	2018-07-24 (-29.9,26.5)	2018-09-24 (-4.1,11.4)	2019-04-02 (-8.2,7.3)	2019-05-10 (-3.6,1.4)
	45	2019	2018-06-27 (-0.6,1.4)	2018-09-27 (-3,2.5)	2019-03-25 (-5.4,4.1)	2019-05-10 (-2.6,1.4)
	51	2019	2018-07-05 (-8,11.4)	2018-10-06 (-11.7,13.3)	2019-04-10 (-4.4,3.7)	2019-05-17 (-5.4,2.6)
	52	2019	2018-07-25 (-5.6,2.8)	2018-09-12 (-2.9,6.1)	2019-04-04 (-16.3,6.7)	2019-05-04 (-7.7,4.4)
	55	2019	2018-07-29 (-11.1,9.9)	2018-09-19 (-2.8,4.7)	2019-03-30 (-2.5,3.5)	2019-05-05 (-8.8,16.2)
	71	2020	2019-07-26 (-30.1,32.8)	2019-10-08 (-7.8,14.7)	2020-04-10 (-9.8,10.2)	2020-05-18 (-1.4,1.2)
	69	2020	2019-07-12 (-14.3,10.7)	2019-10-15 (-6.5,2.5)	2020-03-26 (-4.2,3.8)	2020-05-15 (-8.5,7.5)
Yosemite NP	59	2020	2019-07-14 (-12.3,6.4)	2019-09-27 (-8.4,12.6)	2020-03-16 (-11.4,7.1)	2020-05-01 (-6.1,6.9)
	29	2020	2019-06-26 (-4.1,10.3)	2019-09-30 (-5.4,4.1)	2020-03-07 (-5.3,4.2)	2020-05-02 (-8.6,12)
	39	2020	2019-07-04 (-11.6,6)	2019-09-26 (-6.7,5.3)	2020-03-13 (-2.7,2.8)	2020-04-28 (-2.5,7.1)
	57	2020	2019-07-17 (-9.7,20.4)	2019-10-09 (-4.2,8.3)	2020-04-11 (-3.1,1.4)	2020-05-07 (-3.3,5.7)
Gifford Pinchot NF	114	2020	2019-07-05 (-1.3,3)	2019-11-16 (-9.8,8.2)	2020-03-22 (-5.4,3.6)	2020-05-06 (-4.2,10.2)
	119	2020	2019-07-04 (-0.4,1)	2019-09-27 (-3.8,4.2)	2020-04-04 (-9.2,6.3)	2020-05-09 (-4.2,7.8)
	99	2020	2019-06-30 (-1.8,4.2)	2019-10-25 (-24.1,12.9)	2020-04-01 (-5.9,6.1)	2020-05-20 (-11.4,3.3)
	93	2020	2019-06-29 (-1.8,3.5)	2019-10-15 (-9.5,8.6)	2020-04-04 (-15.2,7.9)	2020-05-24 (-16.2,4.8)
	92	2020	2019-06-30 (-1.9,1.5)	2019-10-05 (-5.6,4.9)	2020-04-07 (-4.7,3.8)	2020-05-10 (-4.5,13.9)
Mac-Dunn Research Forest	105	2020	2019-07-01 (-0.8,2.6)	2019-10-09 (-4.4,4.6)	2020-03-31 (-16,7)	2020-05-03 (-0.8,0.6)
Mt. Richmond Forest	88	2020	2019-06-26 (-0.9,3.4)	2019-09-08 (-5.3,5.2)	2020-04-08 (-3.4,3.6)	2020-05-07 (-0.6,0.4)
Mendocino NF	31	2020	2019-06-23 (-3.2,4.2)	2019-09-03 (-7.2,8.8)	2020-03-28 (-4.4,2.6)	2020-05-07 (-5.2,8.8)

Appendix 4

Title of the manuscript: Annual migratory movement, apparent molt-migration, migration schedule, and diffuse migratory connectivity of Hermit Warblers

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Appendix 4. Map showing 'target sites' designation required by MigConnectivity package's MC score analysis. Three regions are based on geographic location and environmental conditions. Map drawn from US EPA's Ecoregions of North America. Environmental Protection Agency 2018. Ecoregions of North America. Environmental Protection Agency. https://data.nal.usda.gov/dataset/ecoregions-north-america.