

FINAL REPORT

Using Remotely-sensed Data and Light-level Geolocator Technology to Inform Off-Post Landscape-Scale Conservation Planning for a Migratory Species

Ashley Long
Melanie Colón
Jane Kunberger
Michael Gamble
Louisiana State University

John Macey
USACE Regional Planning & Environmental Center/Fort Cavazos Military Installation

Nathan Grigsby
University of Illinois at Urbana-Champaign

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14. ABSTRACT Identifying focus areas for multi-agency conservation efforts on landscapes that include Department of Defense facilities is essential to protect military readiness and maintain populations of threatened and endangered species. Achieving this goal requires that we know where species occur, when they move, and how their habitats might change over time. We lack this information for most migratory songbirds, many of which have experienced significant population declines over the past century and are often too small to track with devices that record their movements across broad spatial and temporal scales. We used miniaturized light-level geolocators to examine the migratory behavior of a small (~10 g) endangered songbird, the golden-cheeked warbler (<i>Setophaga chrysoparia</i> , hereafter warbler). We also used remotely sensed data to develop an updated winter habitat model for the warbler and to identify areas of highest risk of habitat conversion on the warblers breeding and wintering grounds. In addition, we created a web-based application that allows users to visualize our results and could help inform conservation planning during all stages of the species' annual cycle.					
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List of Acronyms

ΔAIC_c	delta Akaike Information Criteria corrected for small sample sizes
AIC_c	Akaike Information Criteria corrected for small sample sizes
ANOSIM	Analysis of Similarity
ANOVA	Analysis of Variance
AOI	Area of Interest
ASY	After Second Year
BBL	U.S. Geological Survey Bird Banding Lab
BCNWR	Balcones Canyonlands National Wildlife Refuge
BRT	Boosted Regression Tree
CART	Classification and Regression Tree
CB	U.S. Air Force's Joint Base San Antonio-Camp Bullis
CI	Confidence Interval
CMIP5	Coupled Model Intercomparison Project fifth phase
CONUS FORE-SCE	Conterminous United States Forecasting Scenarios
CTT	Cellular Tracking Technologies
DoD	Department of Defense
DVSP	Dinosaur Valley State Park
EPA	U.S. Environmental Protection Agency
ESA	Endangered Species Act
EVI	Enhanced Vegetation Index
FCMI	U.S. Army's Fort Cavazos Military Installation
FIO-ESM	First Institute of Oceanography-Earth System Model
GAM	Generalized Additive Model
GCM	General Circulation Model
GEE	Google Earth Engine
GIS	Geographic Information System
GLM	Generalized Linear Model
GPS	Global Positioning Systems
HadGEM2-AO	Hadley Global Environment Model 2 Atmosphere-Ocean
HSD	Honestly Significant Difference
HY	Hatch Year
ICLUS	Integrated Climate and Land Use Scenarios
IPCC	Intergovernmental Panel on Climate Change
IUCN	International Union for Conservation of Nature
KWMA	Kerr Wildlife Management Area
LRMP	Legacy Resource Management Plan
LST	Land Surface Temperature
LULC	Land Use and Land Cover
MARS	Multivariate Adaptive Regression Splines
MODIS	Moderate Resolution Imaging Spectroradiometer
PARC	Partners in Amphibian and Reptile Conservation

PIF	Partners in Flight
RCP	Representative Concentration Pathway
REPI	Readiness and Environmental Protection Integration Program
RF	Random Forest
RSS	Received Signal Strength
SGCN	Species of Greatest Conservation Need
SDM	Species Distribution Model
SERDP	Strategic Environmental Research and Development Program
SVM	Support Vector Machine
SY	Second Year
T&E	Threatened and Endangered
U.S.	United States
TPWD	Texas Parks and Wildlife Department
UD	Utilization Distributions
USAF	U.S. Air Force
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
UTM	Universal Transverse Mercator
VHF	Very High Frequency

List of Abbreviations

%	percent
~	approximately
Apr	April
AUC	area under the receiver operating curve
Aug	August
C	Celsius
cm	centimeter
d	days
dB	decibel
Dec	December
e.g.	exempli gratia (for example)
et al.	et alia (and others)
<i>F</i>	F-statistic
Feb	February
Fig.	figure
FL	Florida
g	gram
ha	hectare
i.e.	id est (that is)
Jan	January
Jul	July
km	kilometer
LST	average annual mean land surface temperature
m	meter
Mar	March
masl	meters above sea level
MaxEnt	maximum entropy
<i>MC</i>	migratory connectivity
min	minute
mm	millimeter
<i>n</i>	sample size
N	north
NM	New Mexico
NP	National Park
NWR	National Wildlife Refuge
Oct	October
OK	Oklahoma
P	P value
pers. comm.	personal communication
<i>r</i>	Pearson correlation coefficient
R	range

R^2	coefficient of determination
r_M	Mantel's correlation coefficient
SD	standard deviation
SE	standard error
sec	second
Sep	September
t	t-statistic
TSS	true test statistic
TX	Texas
VIF	variance inflation factor
vs	verses
W	west
w_i	model weight
$\bar{x}$	mean
Y/N	yes/no

Keywords

climate change, conservation planning, golden-cheeked warbler, habitat conversion, light-level geolocator, migration, migratory connectivity, *Setophaga chrysoparia*, songbird, species distribution models, tracking

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1. Abstract

INTRODUCTION AND OBJECTIVES: Identifying focus areas for multi-agency conservation efforts on landscapes that include Department of Defense (DoD) facilities is essential to protect military readiness and maintain populations of threatened and endangered (T&E) species. Achieving this goal requires that we know where species occur, when they move, and how their habitats might change over time. We lack this information for most migratory songbirds, many of which have experienced significant population declines over the past century and are often too small to track with devices that record their movements across broad spatial and temporal scales. These data are critical because threats that impact any one part of a migratory species' annual cycle can affect the entire population. We responded to a Statement of Need from the Strategic Environmental Research and Development Program that requested advanced approaches for management of species and ecosystems in a non-stationary world. Our goal was to demonstrate how remotely sensed data and miniaturized light-level geolocator technology (hereafter geolocator) could be used to help inform off-post landscape-scale conservation planning for small migratory songbirds that occur on DoD lands.

TECHNICAL APPROACH: We used 0.41 g geolocators to examine the migratory behavior of a small (~10 g) endangered songbird, the golden-cheeked warbler (*Setophaga chrysoparia*, hereafter warbler). We also used remotely sensed data to develop an updated winter habitat model for the warbler and to identify areas of highest risk of habitat conversion on the warblers breeding and wintering grounds. In addition, we created a web-based application that allows users to visualize our results and could help inform conservation planning during all stages of the species' annual cycle.

RESULTS: We deployed 309 geolocators at five study sites across the warbler's breeding range and used data recovered from 61 devices to examine the migratory movements of warblers. Eighty percent of warblers migrated from their breeding grounds in Texas and along the Sierra Madres to wintering grounds in southern Mexico and Central America, but 20% migrated over the Gulf of Mexico or traveled further east before arriving on their wintering grounds. We identified several areas along the warbler's migration route and on their wintering grounds that were used by most birds we tracked. We also found locations outside the known winter range where warblers may occur. Our results suggested that warblers exhibit weak migratory connectivity, but given their relatively small winter range (~104,000 km²) and habitat losses forecasted to occur under optimistic climate change scenarios (~43,000 km²), continued and increased conservation along the warbler's migration route and on the wintering grounds are necessary to ensure population persistence and would simultaneously help protect co-occurring species of conservation concern. The web-based application we developed includes movement data, habitat models, locations of formally protected areas, and projections for habitat loss.

BENEFITS: Our project filled critical knowledge gaps for an endangered species that occurs on DoD lands. Our results could help inform future conservation efforts on the warbler's breeding and wintering grounds, which is necessary to ensure population persistence and protect on-post training capabilities. We also demonstrated the use of miniaturized tracking technologies to study movements of small long-distance migrants. Such data are essential to slow and reverse continental-scale population declines of migratory songbirds, including several DoD mission sensitive species.

2. Executive Summary

INTRODUCTION: Identifying focus areas for multi-agency conservation efforts on landscapes that include Department of Defense (DoD) facilities is essential to protect military readiness and maintain populations of threatened and endangered (T&E) species. Achieving this goal requires that we know where species occur, when they move, and how their habitats might change over time. We lack this information for most migratory songbirds, many of which have experienced significant population declines over the past century and are often too small to track with devices that record their movements across broad spatial and temporal scales. These data are critical because threats that impact any part of a migratory species' annual cycle can affect the entire population. We responded to a Statement of Need from the Strategic Environmental Research and Development Program that requested advanced approaches for management of species and ecosystems in a non-stationary world. Our goal was to demonstrate how remotely sensed data and miniaturized light-level geolocator technology (hereafter geolocator) could be used to help inform off-post landscape-scale conservation planning for small migratory songbirds that occur on DoD lands.

The golden-cheeked warbler (*Setophaga chrysoparia*; hereafter warbler) is an endangered songbird that breeds exclusively in mature oak-juniper (*Quercus-Juniperus*) woodlands of central Texas and winters in montane pine-oak forests of southern Mexico, Guatemala, El Salvador, Honduras, and Nicaragua (Ladd and Gass 2020) (Fig. 1). The warbler's breeding habitat is well-defined (e.g., Collier et al. 2012, Mueller et al. 2022) and includes the U.S. Army's Fort Cavazos Military Installation (formerly named Fort Hood Military Installation), the U.S. Air Force's Joint Base San Antonio-Camp Bullis (hereafter Camp Bullis), and the U.S. Army's Camp Stanley (hereafter Camp Stanley) (Fig. 2). As with all migratory species, warbler recovery, and thus minimization of potential impacts to the military mission (e.g., training restrictions, changes to existing infrastructure, increased financial investment, disproportionate responsibility of DoD to conserve T&E species habitat), depends on our ability to identify and manage potential risks during all stages of the species' annual cycle.

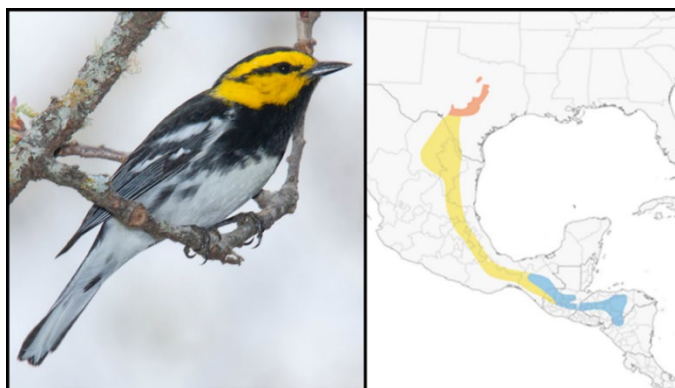


Figure 1. Left: photo of a male golden-cheeked warbler (*Setophaga chrysoparia*) taken by Jill Wussow. Right: map of the golden-cheeked warbler's breeding range (orange), migration route (yellow), and winter range (blue) as identified by Ladd and Gass (2020).

Habitat loss and fragmentation are the biggest threats to warbler population persistence (USFWS 2014). On the breeding grounds, warbler habitat loss most often occurs via urbanization along the Interstate 35 corridor where Fort Cavazos, Camp Bullis, and Camp

Stanley are located (Fig. 2). Similar to the breeding grounds, the greatest threats to warblers on their proposed migration route and on their wintering range are habitat loss and fragmentation (Fig. 1; Perez et al. 2008, USFWS 2014). However, models of warbler wintering habitat are limited, and we lack predictive models to forecast habitat conversion risk on the warbler's breeding and non-breeding grounds, which could aid development of a more effective conservation prioritization strategy for this species (Guisan et al. 2013).

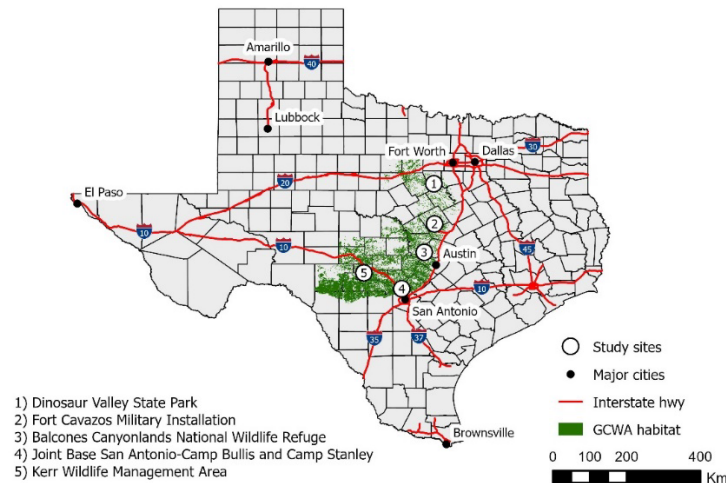


Figure 2. Map of study sites we used from 2017–2023 to examine movements of golden-cheeked warblers (*Setophaga chrysoparia*) and the distribution of golden-cheeked warbler breeding habitat in Texas (Mueller et al. 2022).

OBJECTIVES: We (1) used geolocators to examine the migratory behavior of a small (~10 g) endangered songbird, the golden-cheeked warbler; (2) used remotely sensed data to develop an updated winter habitat model for the warbler and to identify areas of highest risk of habitat conversion on the warblers breeding and wintering grounds, and (3) created tools that could help inform conservation planning during all stages of the species' annual cycle.

TECHNICAL APPROACH: To identify the warbler's migration route and winter habitat and to quantify migratory connectivity (i.e., the degree to which breeding and non-breeding populations of a migratory species are linked; Webster et al. 2002, Marra et al. 2006), we deployed and retrieved geolocators (Migrate Technology Intigeo P30Z11-7 Dip with a 5-mm light stalk) on male warblers at five study sites separated by 51–110 km across the warbler's breeding range in Texas (2017–2021) (Fig. 3). North-to-south, our study sites included Dinosaur Valley State Park (DVSP), Fort Cavazos Military Installation (FCMI), Balcones Canyonlands National Wildlife Refuge (BCNWR), Joint Base San Antonio-Camp Bullis (CB), and Kerr Wildlife Management Area (KWMA) (Fig. 2). During our study, we mapped and monitored the territories of warblers with and without geolocators on three plots at FCMI and three plots at CB to concurrently examine the potential impacts of geolocators on aspects of warbler breeding ecology and behavior.



Figure 3. Left: Geolocator with a 5-mm light stalk and leg-loop harness (0.41 g). Center: Geolocator attached to male golden-cheeked warbler (*Setophaga chrysoparia*). Right: Geolocator retrieved from a male golden-cheeked warbler the year after it was attached.

When we began our research in 2017, geolocators represented the only low-cost, lightweight option for tracking long-distance movements of small (<50 g) migratory species (Bridge et al. 2013, McKinnon et al. 2013), but by 2021, companies had developed radio transmitters that were small enough to deploy on warblers and worked in conjunction with automated telemetry technologies (i.e., towers installed as part of the Motus Wildlife Tracking network that allow researchers to collect broad-scale movement data and mini-base stations called “nodes” that allow researchers to collect fine-scale movement data). Thus, in 2022 and 2023, we deployed radio transmitters (PowerTags and LifeTags manufactured by CTT) on male and female warblers and installed automated telemetry stations at KWMA (Fig. 4). As described for the geolocator aspect of our project, we monitored birds with and without radio transmitters to examine the potential impacts of these devices on warbler breeding ecology and behavior. In 2023, we additionally attached a small number of NanoTags (Lotek Wireless, Inc) to male warblers at KWMA and FCMI. NanoTags do not work in conjunction with the nodes, but they could be detected by Motus towers located along the warbler’s migration route or on their wintering grounds.

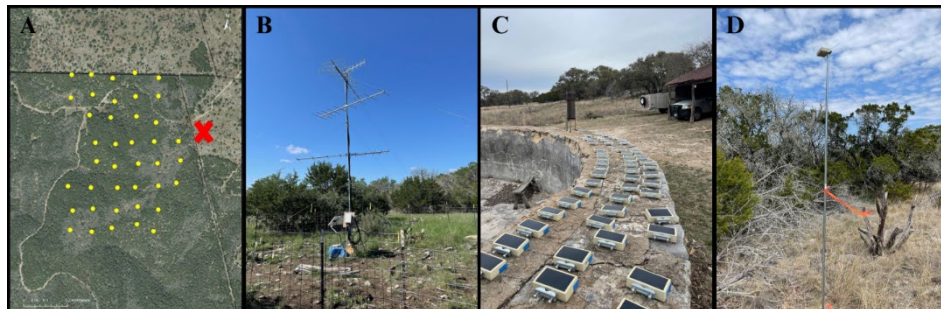


Figure 4. A: Map of Motus station (red X) and grid of automated telemetry nodes (yellow dots) at Kerr Wildlife Management Area in Texas. B: Motus tower. C: Nodes charging prior to installation. D: Node at a grid point. Photos by Michael Gamble.

We used an ensemble model approach to predict the wintering distribution of warblers under current and projected climate conditions and identified locations that may be key to the species’ continued survival under climate change. We also classified Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper Plus, and Landsat 8 Operational Land Imager Tier 1 Surface Reflectance imagery for the years 2000, 2010, and 2020 to examine land cover

change for classes that best aligned with warbler breeding habitat. We additionally summarized projected land use and land cover change within the spatial extent of the warbler breeding habitat model (Mueller et al. 2022) for the years 2050 and 2070 using data from the U.S. Geological Survey's CONUS FORE-SCE model (Sohl et al. 2018) and the Environmental Protection Agency's ICLUS project (EPA 2020). Last, we used data from our project and others to create an interactive web-based tool (i.e., the Golden-cheeked Warbler Habitat Explorer) that can be used to support strategic conservation planning for the warbler and demonstrated a mapping application that could enhance decision-making for other listed or at-risk species that occur on DoD lands.

RESULTS AND DISCUSSION: We deployed 309 geolocators and used data recovered from 61 devices to examine the migratory and winter movements of warblers (example in Fig. 5). Eighty percent of warblers migrated from their breeding grounds in Texas and along the Sierra Madres to wintering grounds in southern Mexico and Central America, but 20% migrated over the Gulf of Mexico or traveled further east before arriving on their wintering grounds (Fig. 6, 7). We identified several areas along the warbler's migration route and on their wintering grounds that were used by most birds we tracked (Fig. 6, 7). We also found locations outside the known winter range where warblers may occur (Fig. 7). Our results suggested that warblers exhibit weak migratory connectivity ($rM = 0.04 \pm 0.06$) but given their relatively small winter range ($\sim 104,000 \text{ km}^2$; see below) and habitat losses forecasted to occur under optimistic climate change scenarios ($\sim 43,000 \text{ km}^2$; see below), continued and increased conservation along the warbler's migration route and on the wintering grounds are necessary to ensure population persistence and would simultaneously help protect co-occurring species of conservation concern.

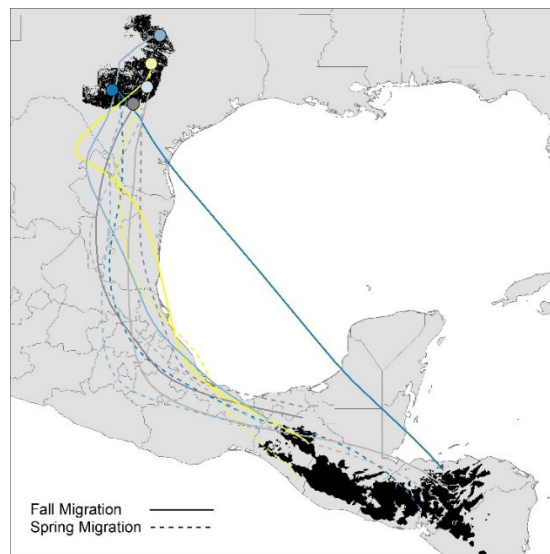


Figure 5. Example migration paths for one golden-cheeked warbler (*Setophaga chrysoparia*) per study site based on data from light-level geolocators.

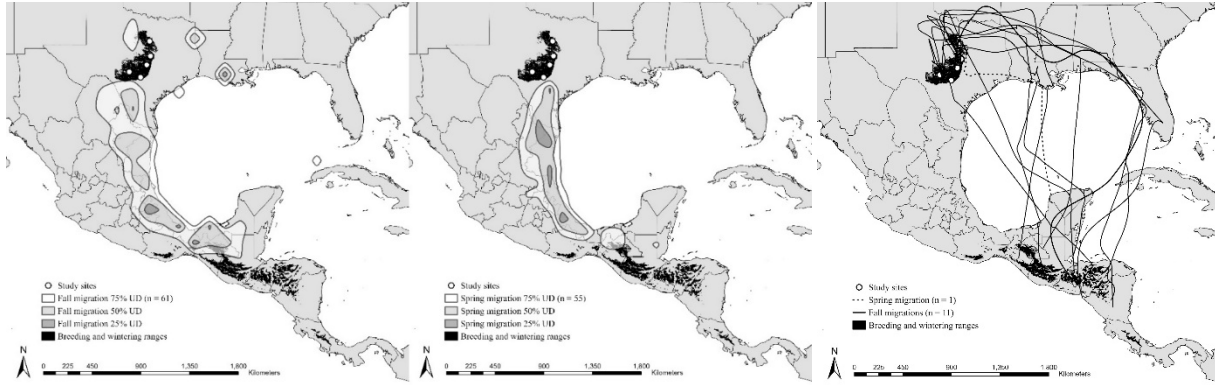


Figure 6. Utilization distributions for fall (left) and spring (middle) migration and trans-gulf migration routes of male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021).

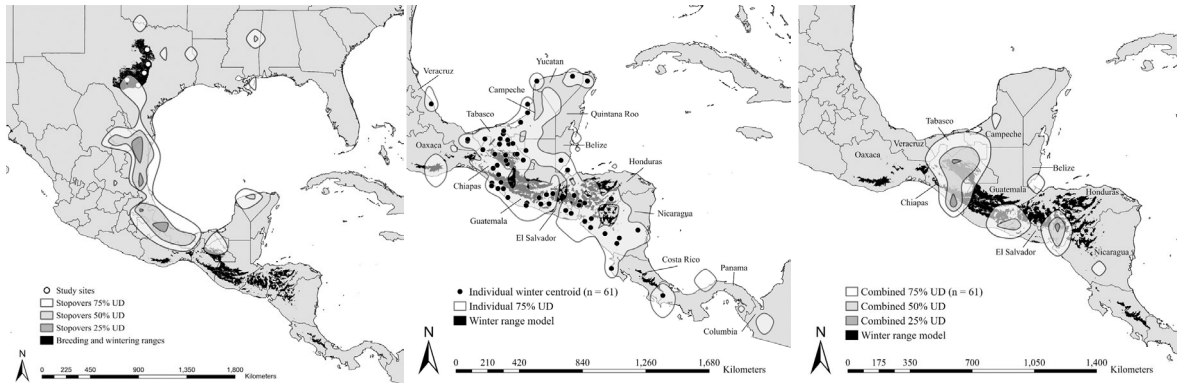


Figure 7. Utilization distributions of stopover locations during migration (left), centroid for overwintering locations and 75% utilization distributions (middle), and utilization distributions for combined overwintering locations of male golden-cheeked warblers (*Setophaga chrysoparia*) based on data we obtained from 61 light-level geolocators (2017–2021).

We found minimal impacts of geolocators on warbler pairing success, fledgling success, return rates, and body mass. Return rates were considerably lower for second year (SY) warblers with geolocators compared to after second year (ASY) birds without geolocators at CB. However, our sample size for SY warblers with geolocators at CB was low and return rates for SY warblers without geolocators at CB was unusually high. Overall, our results support further use of geolocators to obtain critical broad-scale movement data on songbirds, including species weighing <12 g. However, we urge continued research on the potential impacts of geolocators on very small songbirds to help scientists identify the most ethical methods for their questions and to help governing bodies (e.g., USGS Bird Banding Lab) make research permitting decisions.

In 2022, we attached radio transmitters to 26 warblers within our grid of 40 automated telemetry nodes that we set up across our study site at KWMA prior to the breeding season: 15 males and 11 females. All birds resumed normal activities after we attached the tags, and we recorded signals through the nodes or with a handheld antenna from all 26 transmitters ≥ 1 d after we attached the units. Pairing success was 91% and fledging success was 30% for male warblers with tags, which is similar to other studies on warblers, but lower than pairing success (100%) and fledging success (79%) we observed for 14 males without tags that we monitored at KWMA

during the 2022 breeding season. In 2022, the node grid collected 160,211 total location points we could use for analyses, which included 124,304 male and 35,907 female location points (examples in Fig. 8). The warblers we tagged in 2022 were not detected by any other Motus towers along the warbler's route or on their wintering grounds. However, some radio transmitters we attached to the warblers should remain active for several months following the 2023 breeding season while others should remain active for the life of the birds. Migration data recorded by the Motus towers could supplement the migration route, timing, and location data we obtained from the geolocators. Beyond warblers, the Motus tower we installed at KWMA has and will continue to detect movements of wildlife tagged by other researchers, and the knowledge we gain from installing nodes for high-resolution tracking of warblers will contribute to overall testing of automated tracking technologies for wildlife.

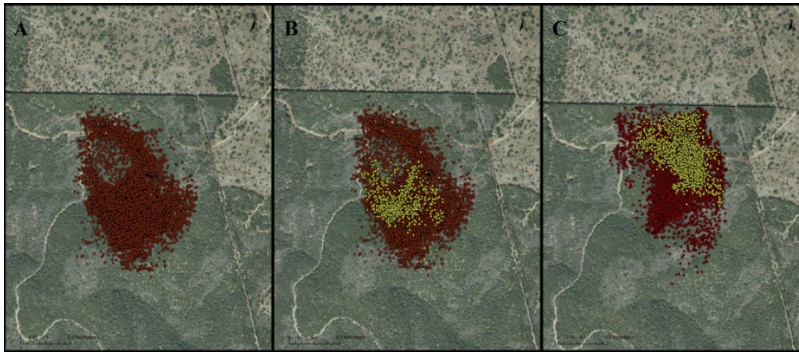


Figure 8. A: Localizations from a male golden-cheeked warbler (*Setophaga chrysoparia*) (50 days, 25,644 red points). B) Localizations from the male golden-cheeked warbler presented in A and from a female golden-cheeked warbler (5 days, 1,934 yellow points). Individuals were paired during the breeding season. C) Localizations from an adjacent pair of golden-cheeked warblers (male: 45 days, 24,592 red points and female: 10 days, 4,263 yellow points).

Our ensemble model predicted ~104,000 km² of potentially suitable wintering habitat for warblers across the study area (Fig 9). More than 80% of the predicted habitat occurred in Honduras, Guatemala, and Chiapas, and our geolocator data supported relatively high use of these areas compared to other portions of the predicted range. From 2000–2019, forest cover loss and the mean annual rate of forest loss within the predicted winter range of warblers was highest in Honduras compared to other regions and forecasted winter habitat loss was 44% under the most optimistic climate scenario (Fig. 10). Forecasted losses were even higher in Guatemala and Chiapas (59% and 72% loss of winter habitat under the most optimistic climate scenario, respectively), and these losses will likely be exacerbated by continued land use pressures in the regions. Existing protected areas cover ~20% of the current winter habitat in both Honduras and Chiapas, and ~14% of the current winter habitat in Guatemala, but protected areas are not impenetrable to change. In Honduras and Guatemala, the level of forest loss within protected areas Guatemala was similar (within 1–2%) to rates of loss we observed across predicted habitat in each country, whereas loss of forested habitat in protected areas in Chiapas was slightly better at 5% lower than that seen across the state. Given the high use of these core areas by warblers and the continued loss of habitat that is expected to occur within the next several decades (~43,000 km² under optimistic climate scenarios according to our model), increased conservation in and outside of currently protected areas may be critical to maintaining warbler populations.

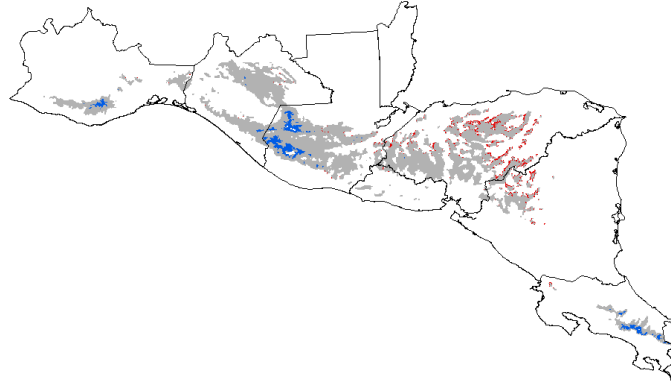


Figure 9. Predicted golden-cheeked warbler (*Setophaga chrysoparia*) wintering distribution under current climate conditions, with core elevation zone of 800 to 2,600 meters above sea level in gray and areas above and below that range in blue and red, respectively.

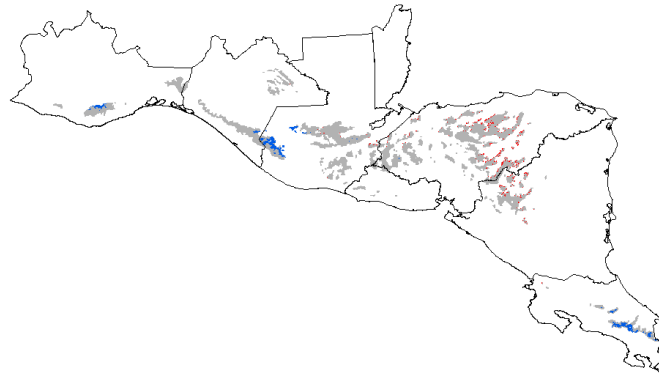


Figure 10. Forecasts of golden-cheeked warbler (*Setophaga chrysoparia*) wintering habitat distribution for 2050 under the most optimistic Representative Concentration Pathway scenario.

The total amount of forest cover across the warbler's breeding range was similar in 2000 and 2020, reflecting a total loss over the 20-year period of ~1%. However, excluding forest gains from consideration, we estimated a 28% rangewide loss in forest cover between 2000 and 2020, with the highest percent loss of forest cover occurring in the central portion of the warbler's breeding range (Fig. 11). On average, the most optimistic CONUS FORE-SCE scenarios (i.e., B1 and B2) projected a 25% and 37% increase in the amount of developed cover within the boundaries of the warbler breeding habitat model by 2050 and 2070, respectively, and the most pessimistic CONUS FORE-SCE scenarios (i.e., A1B and A2) projected an average increase of 53% and 94% in the amount of developed cover within the boundaries of the warbler breeding habitat model by 2050 and 2070, respectively. Similarly, the most optimistic ICLUS scenarios (i.e., SSP2, RCP4.5 scenarios) projected an average increase of 15% and 25% in amount of developed cover within the boundaries of warbler breeding habitat model by 2050 and 2070, respectively, and the most pessimistic ICLUS scenarios (i.e., SSP5, RCP8.5 scenarios) projected an average increase of 45% and 76% in the amount of developed cover within the boundaries of the warbler breeding habitat model by 2050 and 2070, respectively. The projected increase in developed cover was most pronounced in the central portion of the warbler's breeding range.

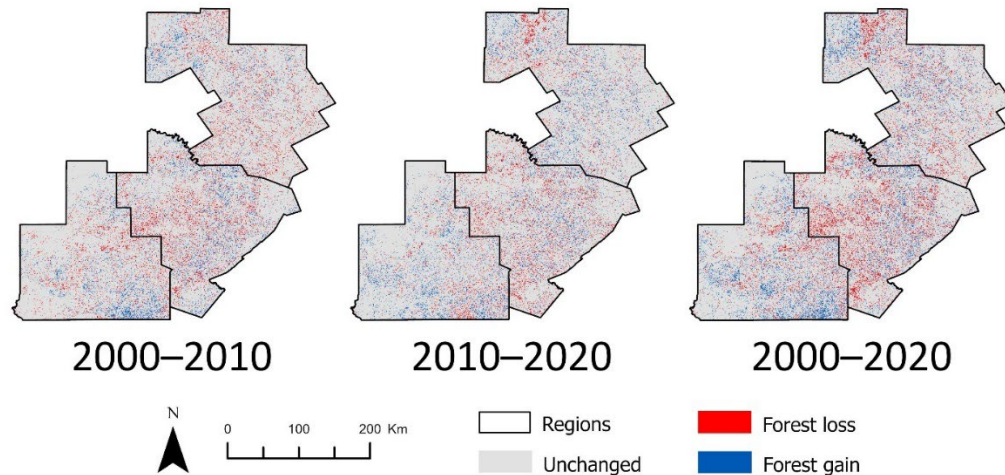


Figure 11. Land cover change in the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range. The forest class included only the land cover types that best aligned with warbler breeding habitat (i.e., evergreen and mixed forest); we grouped all other land cover types into their own class (other).

IMPLICATIONS FOR FUTURE RESEARCH AND BENEFITS: The U.S. Department of Defense (DoD) manages >10 million ha of ecologically diverse land on approximately 520 military installations and is a steward of nearly 490 species listed as Threatened or Endangered (T&E) under the Endangered Species Act (ESA) (Stein 2021, DoD 2022). Because many listed and at-risk species occur across large geographic extents, effective conservation of listed and at-risk species that occur on military installations requires knowledge of their spatial and temporal distributions both on and off-post. This information is challenging to acquire for highly mobile species, like migratory birds, that can travel long distances across environmental barriers (Åkesson and Hendström 2007), land use/land tenure types (Tack et al. 2019), and jurisdictional boundaries during their annual cycles (Kark et al. 2015); but is necessary to prioritize conservation actions when and where they are needed most.

Our SERDP-funded project provides the most thorough examination of golden-cheeked warbler movements during the non-breeding season to date and provides tools that can help identify focus areas for multi-agency conservation efforts on the warbler’s breeding, migration, and wintering grounds. We are particularly excited about how our work has and could be used to narrow sampling periods and locations for field-based surveys of non-breeding habitat. Knowing where and when individuals are located throughout the year is critical for warbler conservation because events during the non-breeding season could impact warbler population dynamics (e.g., mortality during migration, carry-over effects) and, thus, delay recovery, despite best efforts to manage threats on the warbler’s breeding grounds.

Our web application (Fig. 12) utilizes Google Earth Engine's extensive data catalog and cloud computing capabilities to visualize warbler breeding and wintering habitat, examine projected land cover, identify patches of breeding habitat that meet a minimum size, and more in an easy-to-use web application. Further, the flexible nature of Google Earth Engine application development provides us with opportunities to expand the current iteration of our web application to include additional features. Our app demonstrates an approach that could be adopted for other species and regions. However, as with any mapping application, it is important to consider the error and uncertainty that is inherent in all models. Information derived from our

app and others should be used as a guide; practitioners should evaluate potential plans based on app outputs prior to implementation, then conduct monitoring and adaptive management during implementation to ensure the activities are meeting their desired goals (Acyrigg et al. 2016).

The DoD has a long history of participation in landscape-scale partnerships (e.g., Sentinel Landscape Partnership, Legacy Resource Management Plan [LRMP], Readiness and Environmental Protection Integration Program [REPI]) and proactive stewardship activities that maintain and improve habitat for sensitive species beyond their fences, and there are a considerable number of programs and partnerships on the warbler's breeding and wintering grounds that provide financial assistance and foster cooperation for conservation of migratory birds. However, continued and increased support is critical to ensure warbler population persistence and will simultaneously protect co-occurring species that could impact military training if their populations are listed under the ESA.

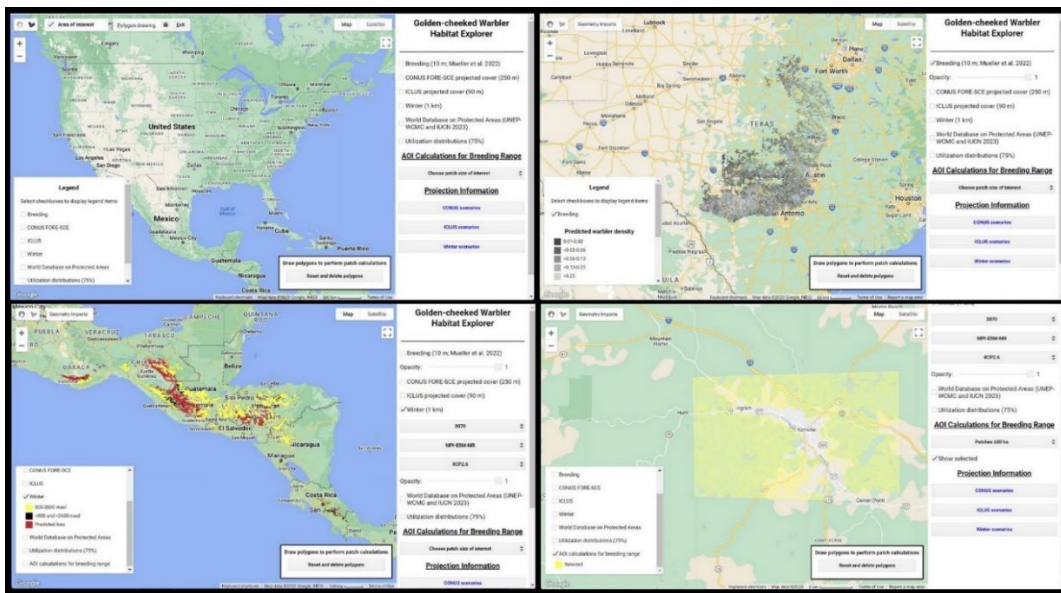


Figure 12. Demonstration of our Google Earth Engine web application for visualizing golden-cheeked warbler (*Setophaga chrysoparia*) breeding and wintering habitat. The top-left shows the landing page for our app; the top-right shows the breeding habitat model from Mueller et al. (2022); the bottom-left shows the winter species distribution models from our project; and the bottom-right demonstrates the function to select breeding habitat patches. All images show the root panel (right) and the legend (bottom left).

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3. Objectives

Identifying focus areas for multi-agency conservation efforts on landscapes that include Department of Defense (DoD) facilities is essential to protect military readiness and maintain populations of threatened and endangered (T&E) species. Achieving this goal requires that we know where species occur, when they move, and how their habitats might change over time. We lack this information for most migratory songbirds, many of which have experienced significant population declines over the past century and are often too small to track with devices that record their movements across broad spatial and temporal scales.

We responded to a Statement of Need from the Strategic Environmental Research and Development Program that requested advanced approaches for management of species and ecosystems in a non-stationary world. Our goal was to demonstrate how remotely sensed data and miniaturized light-level geolocator technology (hereafter geolocator) could be used to help inform off-post landscape-scale conservation planning for small migratory songbirds that occur on DoD lands. Our specific objectives were to (1) use geolocators to examine the migratory behavior of a small (~10 g) endangered songbird, the golden-cheeked warbler (*Setophaga chrysoparia*, hereafter warbler); (2) use remotely sensed data to develop an updated winter habitat model for the warbler and to identify areas of highest risk of habitat conversion on the warblers breeding and wintering grounds, and (3) create tools that could help inform conservation planning during all stages of the species' annual cycle.

4. Background

The U.S. Department of Defense (DoD) manages >10 million ha of ecologically diverse land on approximately 520 military installations and is a steward of nearly 490 species listed as Threatened or Endangered (T&E) under the Endangered Species Act (ESA) (Stein 2021, DoD 2022). Thousands more species that occur on DoD lands are currently petitioned or under review for federal listing by the U.S. Fish and Wildlife Service (USFWS), are considered at-risk based on NatureServe and International Union for Conservation of Nature (IUCN) assessments, or have been designated as Species of Greatest Conservation Need (SCGN) in State and Tribal Wildlife Action Plans (Sperry et al. 2016, Stein 2021, USGS 2023). Given the significant number of listed and at-risk species on military lands, the DoD plays a vital role in the protection and conservation of their populations (Boice 2006, Stein et al. 2008, Stein 2021). Notably, military installations are often safeguarded from development and other forms of disturbance, which can reduce the potential impacts of habitat fragmentation and isolation on both flora and fauna (Boice 2006, Stein 2021). In addition, disturbances caused by military training activities and management practices used to facilitate operations or maintain healthy ecosystems on military installations can create and restore habitat conditions necessary to support listed and at-risk species and to prevent future listings (e.g., Warren et al. 2007, Zografou et al. 2017, White and Tuberville 2017). The DoDs efforts to sustain biodiversity on installations simultaneously provide high-quality and realistic training opportunities for troops, protect human health and safety, afford recreational opportunities to the public, and ensure legal compliance with federal statutes (e.g., Sikes Act, ESA, Migratory Bird Treaty Act) (Stein 2021).

Because many listed and at-risk species occur across large geographic extents, effective conservation of listed and at-risk species that occur on military installations requires knowledge of their spatial and temporal distributions both on and off-post. Such data can be difficult to

collect for species that are cryptic and elusive, inhabit remote or inaccessible locations, or are highly mobile. There are additional challenges when filling these data gaps for migratory birds, which often travel long distances across environmental barriers (Åkesson and Hendström 2007), multiple land use/land tenure types (Tack et al. 2019), and jurisdictional boundaries during their annual cycles (Kark et al. 2015). Migratory birds also exhibit complex behaviors with respect to timing of their movements, which vary by species and are influenced by genetics, hormones, sex, age, body condition, environmental factors (e.g., day length, weather conditions), experience, and resource availability, among others (Åkesson and Hendström 2007, Newton 2008, Justen and Delmore 2022). In addition, migratory birds are incredibly diverse with respect to size and shape, which requires a wide range of research techniques and expertise to study their movements. From a natural resource perspective, overcoming these challenges for listed and at-risk migratory birds that occur on DoD installations is critical to maintain military readiness, as threats that impact any one part of a migratory bird's annual cycle can affect the entire population and military compliance with environmental laws intended to protect T&E species can restrict soldiers' ability to train at full capacity. More broadly, science and technology from research on migratory birds that occur on DoD installations can contribute to conservation of species that have experienced significant population declines over the past several decades.

Tracking technologies for small birds

For hundreds of years, observations of unmarked birds and recaptures or resights of marked birds (e.g., string, paint, bands) were the only methods available to explore migration ecology. We now have many tools to examine broad-scale avian movements, including stable isotope analysis (Hobson 1999) and genetic techniques (Justen and Delmore 2022). Each approach is valuable but may not provide data that spans a bird's annual cycle or exist at a geographic scope and resolution that can be used to make conservation decisions. In more recent years, advancements in tracking technologies have improved our knowledge of avian movements, though each device has strengths and limitations. For example, Global Positioning Systems (GPS) trackers (Bouten et al. 2013) and satellite transmitters (Fuller et al. 1995) allow researchers to accurately locate birds anywhere in the world (A and B in Fig. 1). However, individuals must weigh several hundred grams to accommodate the weight of the device's battery and the devices can be cost prohibitive (>\$1,500 per unit). Nanotags (e.g., Bulluck et al. 2019) and very high frequency (VHF) tags (e.g., González et al. 2020) used in conjunction with automated radio tracking systems (e.g., Paxton et al. 2022) are small enough for songbirds that weigh <200 g (C in Fig. 1), but location data are often restricted to short time intervals given the battery life of the tags or to small areas where receivers are located.

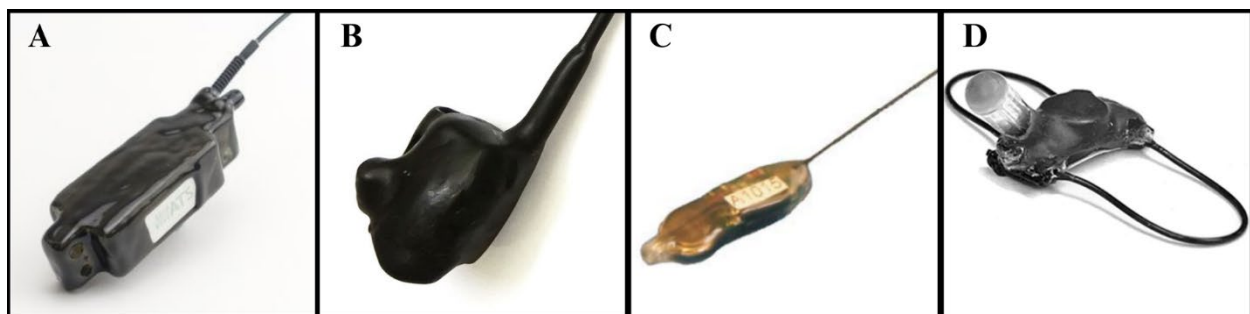


Figure 1. Examples of tracking technologies for available for birds, including (A) 65 g W510 Wildlink GPS logger manufactured by Advanced Telemetry Systems, (B) 65g TW-AAx2 VHF

tag manufactured by Lotek Wireless Inc, (C) 0.55–1.3 g Series A1005 VHF transmitter manufactured by Advanced Telemetry Systems, and (D) 0.49 g Intigeo series geolocator manufactured by Migrate Technology Ltd.

When we began our study in 2017, light-level geolocators (hereafter geolocators) represented the only low-cost, lightweight option for tracking long-distance movements of small (<50 g) migratory species (Bridge et al. 2013, McKinnon et al. 2013) (D in Fig. 1). Initially used for research on marine vertebrates (Wilson et al. 1992, Welch and Eveson 1999, Phillips et al. 2004, Croxall et al. 2005), geolocators record light levels at regular intervals and once retrieved, data recorded by the device's light sensor (i.e., sunrise, sunset, and solar noon) can be used to estimate the latitude and longitude of an individual's location (Bridge et al. 2013, McKinnon et al. 2013). In 2007, Stutchbury et al. (2009) were the first to deploy miniaturized versions of the archival data loggers on small terrestrial birds. Their study included 20 purple martins (*Progne subis*; 43–54 g) and 14 wood thrushes (*Hylocichla mustelina*; 47–55 g) equipped with 1.5-g devices mounted on the lower back of each bird using a leg-loop harness. They recovered seven of the tags they deployed, identified each individual's migration routes and wintering locations, and ushered in a new era for migration studies with small-bodied species. Geolocators do not have the same precision as GPS and satellite transmitters (the accuracy of geolocators typically depends on location, bird behavior, weather, and habitat, and can change throughout the tracking period; Lisovski et al. 2019), and they are not suitable for all species because individuals must be captured twice (once to deploy the units and again to retrieve the units), but miniaturization of these devices has provided unprecedented access to an individual's movements, including the timing and duration of migration, non-breeding locations, and connectivity networks (McKinnon and Love 2018).

For example, Wolfe and Johnson (2015) showed that a male prothonotary warbler (*Protonotaria citrea*) traveled over 7,950 km through seven countries during migration and spent almost equal time in fall migration (30%), on the wintering grounds (30%), and on the breeding grounds (34%). Prothonotary warblers have experienced steep population declines over the past 50 years, and acquiring such data is a critical step toward conservation of the species' core habitat during non-breeding periods. In addition, repeated tracking of 10 wood thrushes revealed flexibility in individual migration routes, but consistency in the timing of migration, which may limit the ability of wood thrushes to adjust their migration schedules in response to climate change (Stanley et al. 2012). Geolocator data from three aquatic warblers (*Acrocephalus paludicola*) revealed a previously unknown migration route for the globally threatened species (Salewski et al. 2013) and Streby et al. (2015) used geolocator data to document movements of five golden-winged warblers (*Vermivora chrysoptera*) in advance of an approaching storm system.

As summarized by McKinnon and Love (2018), there are now more than 100 published studies using geolocators to describe migration routes, overwintering locations, sex- and age-based differences in migration strategies, and more for birds weighing <100 g. Data collected to quantify migratory connectivity, or the degree to which breeding and non-breeding populations of a migratory species are linked (Webster et al. 2002, Marra et al. 2006) (Fig. 2), has been particularly insightful and are critical for conservation planning that considers potential threats across a species' annual cycle. Strong migratory connectivity suggests that individuals caught at a breeding site migrate to the same location on their wintering grounds, whereas weak migratory connectivity suggests that individuals from the same breeding site disperse to several locations on their wintering grounds (Webster et al. 2002, Ambrosini et al. 2009). For species with strong

migratory connectivity, localized threats on the wintering grounds could have more profound effects on the species' demographics than they would experience with weak migratory connectivity (Webster et al. 2002, Cohen et al. 2018). Hallworth et al. (2015) used data from 28 geolocators to evaluate migratory connectivity for the ovenbird (*Seiurus aurocapilla*) and found complete separation of eastern and western ovenbird populations throughout their annual cycle. The strong migratory connectivity they observed suggested that changes in ecological conditions or habitat could impact ovenbirds differently in eastern or western parts of their distributions, and the origin maps Hallworth et al. (2015) developed could be used to focus conservation efforts or predict the influence of disturbances on specific populations. Conversely, Burgess et al. (2020) analyzed geolocator data from 20 whinchats (*Saxicola rubetra*) breeding at three locations in Britain and found weak migratory connectivity, suggesting that whinchat populations may be somewhat buffered against changes in local conditions.

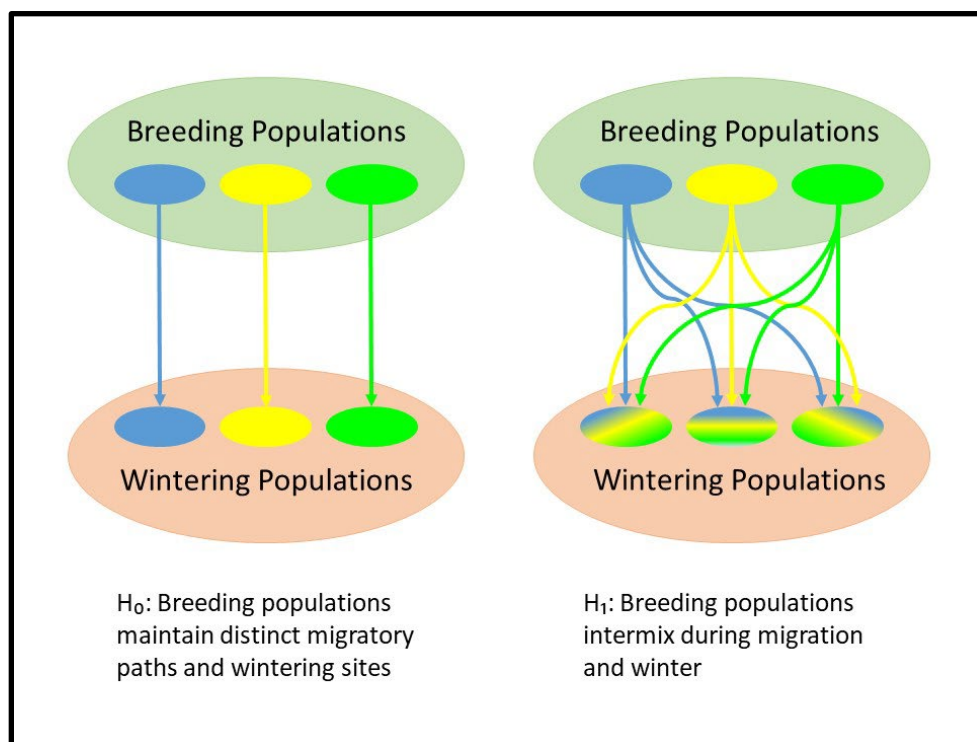


Figure 2. Schematic diagram illustrating strong and weak migratory connectivity. Figure produced by James Mueller.

Geolocator technology has been enthusiastically adopted by avian ecologists and we learn more about the migratory behavior of birds with each study, but we still lack data to describe winter habitat associations and migratory behavior for most species, especially very small songbirds (<12 g). Until recently, the smallest geolocators weighed >0.50 g and scientific programs that grant permits to bird banders (e.g., USGS Bird Banding Laboratory) typically restrict the total weight of all attachments (geolocator, harness, bands) to <5% of an individual's body weight to help minimize stress and risk of injury or death of birds involved in research. In addition, it is difficult to obtain adequate sample sizes from multiple geographically distinct study sites due to low return rates, low retrieval rates, battery failures, and cost (McKinnon and Love 2018). These challenges are evident in the peer-reviewed literature. Notably, Sharp et al.

(2023) used geolocator data from 112 painted buntings (*Passerina ciris*) captured at 11 breeding sites in the U.S. to describe migratory connectivity of disjunct eastern and interior populations of painted buntings, and Kramer et al. (2018) used geolocator data from 41 golden-winged warblers and 25 blue-winged warblers (*Vermivora cyanoptera*) marked at several sites across their breeding grounds to assess migratory connectivity of these two closely related species with inverse population trends. However, most geolocator studies quantify migratory connectivity using data recovered from <30 individuals and the study sites represent a small portion of the species' breeding ranges. Further, because there have been few geolocator studies on very small songbirds, we lack data to quantify the potential impacts of these devices on the survival and behavior of birds that are tracked in this manner, which is necessary to identify appropriate questions, species, study sites, and methods needed to obtain migration data.

Since 2013, the Motus Wildlife Tracking System (hereafter, Motus), a global automated radio telemetry network (<https://motus.org/>), has also emerged as a promising tool for researchers to track small songbirds (Taylor et al. 2017, Griffin et al. 2020, Bani Assadi et al. 2022) and study movement patterns that would otherwise go undetected (DeLuca et al. 2015, Cooper and Marra 2020). Under this coordinated network, radio transmitters and receivers are programmed to operate at the same frequencies. Detection ranges for the receivers can vary based on many factors (e.g., tower height, terrain, antenna type and orientation), but Motus stations generally detect transmitters moving within 15 km of the receiver. When an animal is detected, location data are transmitted automatically to a centralized data hub or can be downloaded directly from the station. Once the data are uploaded, locations and tracks can be viewed in real-time through Motus' on-line platform. There are currently >1,600 Motus receiver stations in 34 countries around the world (Fig. 3) and >38,000 animals of >300 species have been tagged as part of this collaborative tracking effort.

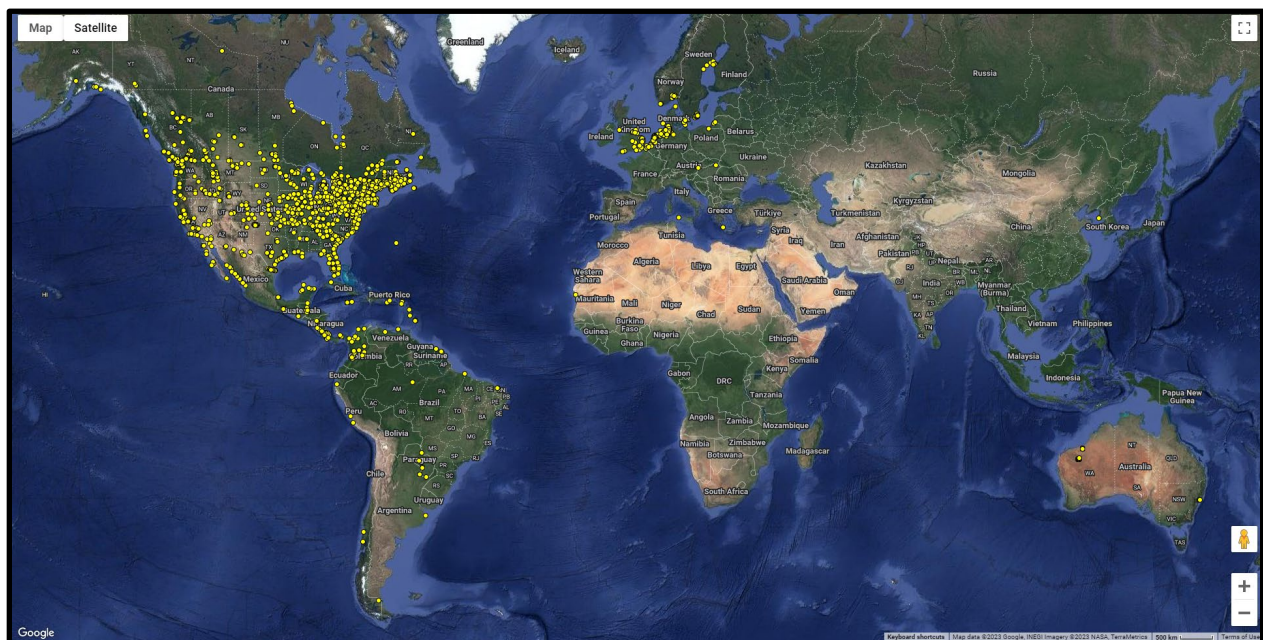


Figure 3. Map of active receiving stations in the Motus network as of 23 May 2023. Available at <https://motus.org/>.

The Motus network currently supports NanoTags (Lotek Wireless Inc) and three different radio transmitters manufactured by Cellular Tracking Technologies (CTT) called PowerTags, HybridTags, and LifeTags. These radio transmitters are relatively inexpensive (<\$300), weigh as little as 0.15 g (NanoTags), and can be programmed at intervals that optimize the life of the tag (NanoTags, PowerTags) or integrate solar technology that allows for data collection over an animal's lifespan (HybridTags, LifeTags). Within the last five years, these devices have rapidly expanded our ability to collect broad-scale movement data on small-bodied species (e.g., tracking monarch migration, identifying seasonal and nightly activity patterns of bats). And as an extension of this technology, researchers can now install mini-base stations (called “nodes”) on their study sites that receive signals from the tags, transmit those data to a Motus station, and can be localized for high resolution tracking (Fig. 4). However, the tags, transmitters, and nodes remain untested for many species and environments.

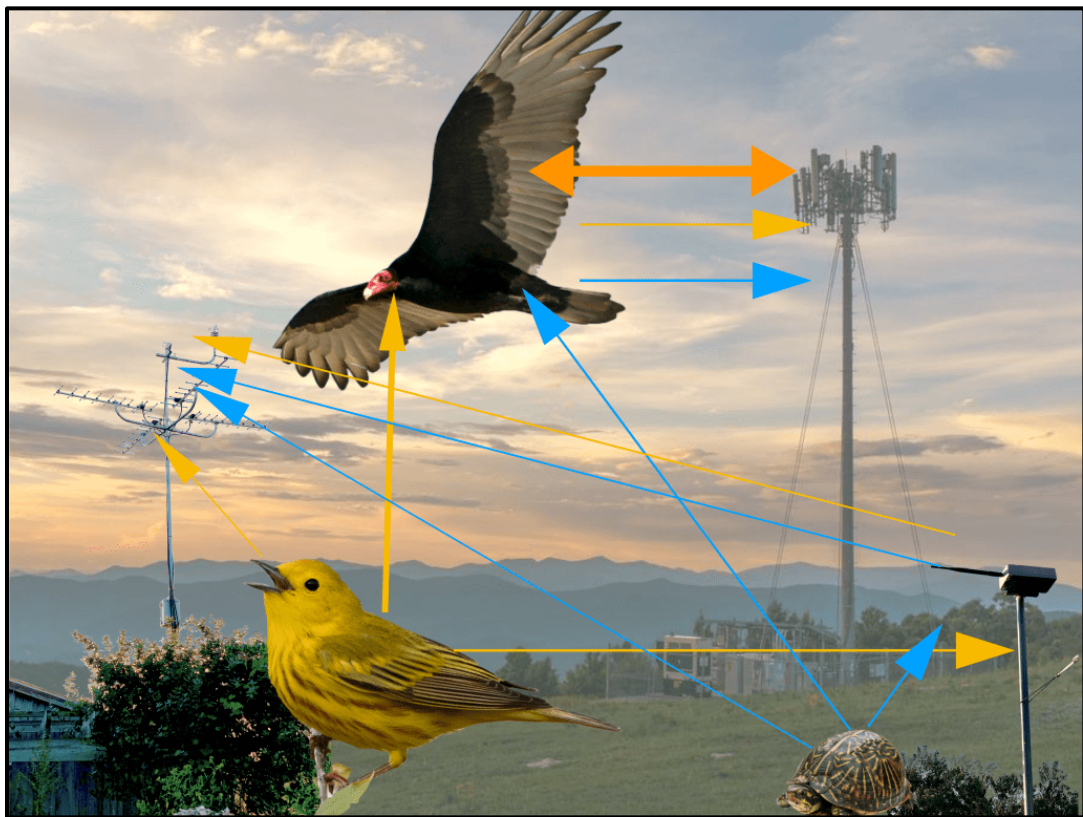


Figure 4. Schematic diagram of automated radio telemetry system. Broad-scale movements of tagged animals are detected by Motus towers (left) and fine-scale movements of tagged animals are recorded by nodes (bottom right). Certain tags can also transmit data to cellular towers (top right). Diagram previously available at <https://celltracktech.com/>.

Study species

The golden-cheeked warbler (*Setophaga chrysoparia*; hereafter warbler) is a federally endangered songbird that breeds exclusively in mature oak-juniper (*Quercus-Juniperus*) woodlands of central Texas and winters in montane pine-oak forests of southern Mexico, Guatemala, El Salvador, Honduras, and Nicaragua (Lass and Gass 2020) (Fig. 5). The warbler's breeding habitat is well-defined (e.g., Collier et al. 2012, Mueller et al. 2022) and includes the

U.S. Army's Fort Cavazos Military Installation (formerly named Fort Hood Military Installation), the U.S. Air Force's Joint Base San Antonio-Camp Bullis (hereafter Camp Bullis), and the U.S. Army's Camp Stanley (hereafter Camp Stanley) (Fig. 6). At present, there are three published models of warbler habitat for the wintering grounds (Rappole et al. 2000, ACMPOF 2007, Navarro and Peterson 2007). Each is valuable, but all cover a relatively small spatial extent (e.g., single country), were developed using data collected over an extended period of time, and represent conditions that were present more than 15 years ago.

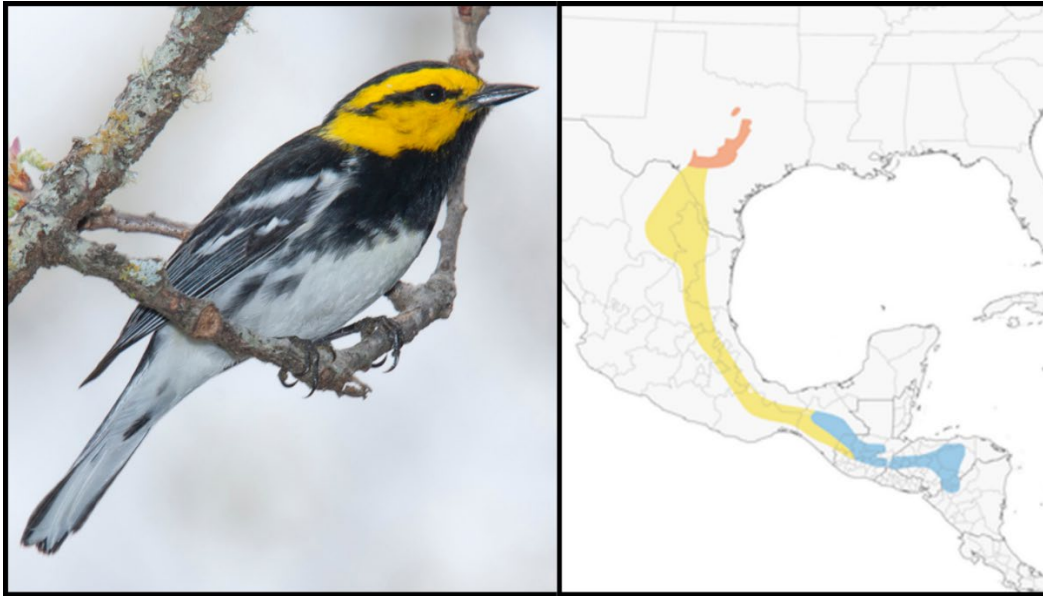


Figure 5. Left: photo of a male golden-cheeked warbler (*Setophaga chrysoparia*) taken by Jill Wussow. Right: map of the golden-cheeked warbler's breeding range (orange), migration route (yellow), and winter range (blue) as identified by Ladd and Gass (2020).

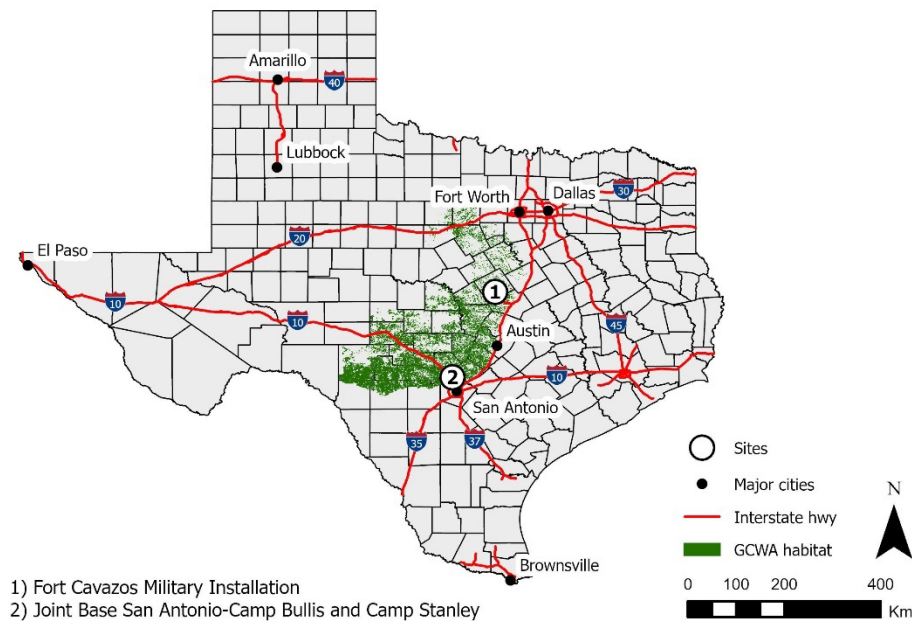


Figure 6. Spatial distribution of golden-cheeked warbler (*Setophaga chrysoparia*) breeding habitat in central Texas (Mueller et al. 2022) and military installations where the golden-cheeked warbler occurs.

As with all migratory species, warbler recovery, and thus minimization of potential impacts to the military mission (e.g., training restrictions, changes to existing infrastructure, increased financial investment, disproportionate responsibility of DoD to conserve T&E species habitat), depends on our ability to identify and manage potential risks during all stages of the species' annual cycle. The USFWS cites habitat loss and fragmentation as the biggest threats to warbler population persistence (USFWS 2014). On the breeding grounds, warbler habitat loss most often occurs via urbanization along the Interstate 35 corridor where Fort Cavazos, Camp Bullis, and Camp Stanley are located (Fig. 6). Similar to the breeding grounds, the greatest threats to warblers on their proposed migration route and on their wintering range are habitat loss and fragmentation (Fig. 5; Perez et al. 2008, USFWS 2014). However, models of warbler wintering habitat are limited and we lack predictive models to forecast habitat conversion risk on the warbler's breeding and non-breeding grounds, which could aid development of a more effective conservation prioritization strategy for this species (Guisan et al. 2013).

In addition, though researchers have banded thousands of warblers on the breeding grounds (example in Fig. 7), no banded birds have been detected on the wintering grounds. As such, we cannot examine winter site fidelity and migratory connectivity for this species. Understanding migratory connectivity for warblers is of particular importance because spatial segregation of breeding populations or age classes during the non-breeding period could have major implications for warbler population dynamics (Sherry et al. 2018). For example, if a large number of warblers from a single breeding location use a single wintering location, conversion of that particular wintering location to another land type could result in concurrent loss of warblers at the breeding location. Warblers represented a good candidate species for the current research because male warblers have high annual return rates (24–67%; Groce et al. 2010, Macey and Collins 2022), strong site fidelity (Jette et al. 1998, Maas-Burleigh 1998), and high

recapture rates (>75%; J. Macey, unpublished data). In addition, there are monitoring data available from long-term study sites to assess potential impacts of tracking technologies on aspects of warbler survival and breeding ecology.



Figure 7. Photo of a male golden-cheeked warbler (*Setophaga chrysoparia*) with bands. Photo by Stephanie Augustine.

5. Methods

Study area

We deployed geolocators and radio transmitters from March to August of 2017–2023 at five study sites separated by 51–110 km across the warbler’s breeding range in Texas. Starting at the north of the warbler’s breeding range, these study sites included Dinosaur Valley State Park (DVSP), Fort Cavazos Military Installation (FCMI), Balcones Canyonlands National Wildlife Refuge (BCNWR), Joint Base San Antonio-Camp Bullis (CB), and Kerr Wildlife Management Area (KWMA) (Fig. 8). The boundaries of these study sites ranged from 617 to 86,994 ha and the total area of warbler habitat at each study site ranged from 437 to 19,977 ha (Table 1). The elevation of these study sites ranges from 152 to 661 masl; minimum and maximum monthly temperatures ranged from -1.67°C to 36.11°C; and annual precipitation ranged from 81.28 to 88.90 cm (NOAA 2021; Table 1).

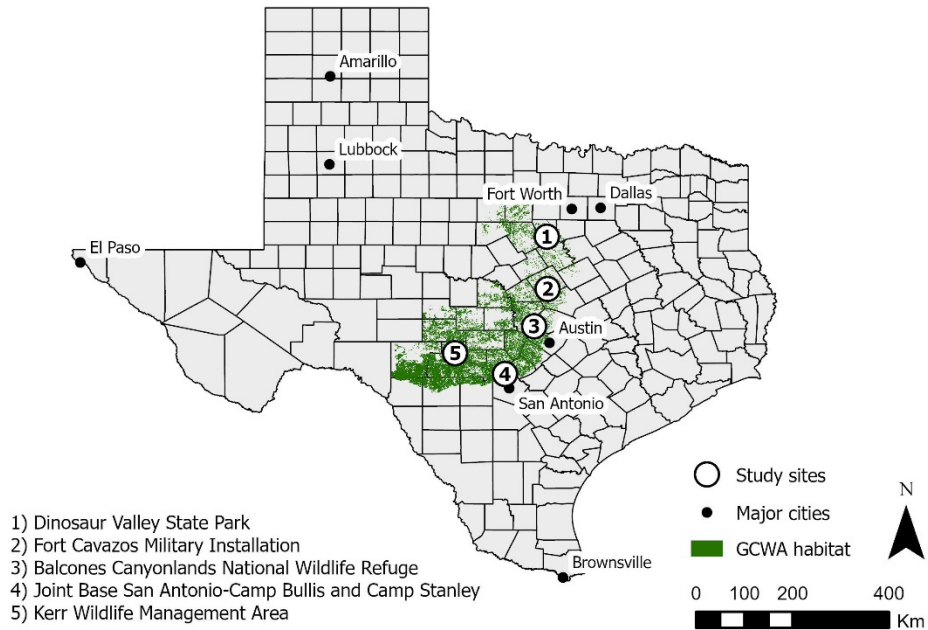


Figure 8. Map of study sites we used from 2017–2023 to examine movements of golden-cheeked warblers (*Setophaga chrysoparia*) and the distribution of golden-cheeked warbler breeding habitat in Texas (Mueller et al. 2022).

Table 1. Characteristics of the five study in Texas we used to examine movements of golden-cheeked warblers (*Setophaga chrysoparia*) from 2017–2021.

Study Site ^a	Area Total (ha)	Warbler Habitat (ha)	County	Latitude, Longitude	Elevation ^g (masl)	Low (c) ^f	High (c) ^f	Annual Precipitation (cm) ^f
DVSP	617 ^b	437 ^b	Somervell	32°15'11.7"N, 97°49'07"W	207–259	-1.67	36.11	88.90
FCMI	86,994 ^c	19,977 ^c	Bell, Coryell	31°19'50"N, 97°74'13"W	152–349	1.11	35.56	86.36
BCNWR	11,128 ^d	4,653 ^d	Burnet, Travis	30°37'21"N, 98°04'06"W	212–455	1.67	34.44	83.82
CB	11,285 ^e	3,431 ^e	Bexar	29°62'51"N, 98°57'00"W	314–455	5.00	35.56	83.82
KWMA	2,628 ^b	1,027 ^b	Kerr	30°06'33"N, 99°50'66"W	594–661	1.11	34.44	81.28

^aStudy site acronyms: DVSP = Dinosaur Valley State Park; FCMI = Fort Cavazos Military Installation, BCNWR = Balcones Canyonlands National Wildlife Refuge; CB = Joint Base San Antonio-Camp Bullis; KWMA = Kerr Wildlife Management Area.

^bwww.tpwd.state.tx.us

^cMacey and Collins 2022

^dS. Rowan, U.S. Fish and Wildlife Service, personal communication

^eFinn et al. 2019

^fNOAA 2021

^gNGS 2013

From 2017–2021, we mapped and monitored the territories of male warblers with and without geolocators on three, 75–100-ha plots at FCMI and three, 674–890-ha plots at CB to examine the potential impacts of geolocators on aspects of warbler breeding ecology and behavior. We chose FCMI and CB for this portion of our research given the availability of long-term warbler data and staff necessary to conduct intensive mapping and monitoring for the duration of each warbler breeding season. One plot at FCMI has been continuously monitored since 2003, one plot at FCMI has been continuously monitored since 2016, and one plot at FCMI was continuously monitored from 2000–2013 and has been monitored continuously since 2016. Warblers at all three CB plots have been continuously monitored since 2015.

By 2021, CTT developed sufficiently small radio transmitters that we could deploy on warblers that worked in conjunction with the automated telemetry technologies described above. Thus, in 2022 and 2023, we deployed radio transmitters (PowerTags and LifeTags) on male and female warblers and installed automated telemetry stations at KWMA. We chose KWMA for this aspect of our research because noise, shadowing (i.e., objects blocking a signal), and reflection (i.e., signal bouncing off an object) can affect the accuracy of localizations based on radio waves; KWMA is relatively undisturbed, and has lower percent canopy cover and less understory vegetation compared to other portions of the warbler’s breeding range, including DSVP, FCMI, BCNWR, and CB (Long et al. 2021). We chose a study site at KWMA with the highest density of warblers (Long et al. 2017, Long et al. 2021), and we installed our solar-powered automated telemetry equipment (Motus tower equipped with SensorStation and grid of 40 [2022] then 54 [2023] nodes spaced ~100 m apart; Fig. 9) in a location that would maximize the elevation of the Motus tower, minimize distances from the nodes to the tower, and minimize potential interference due to topographic obstructions. We also monitored birds without radio transmitters at this study site for our impact assessment. In 2023, we additionally attached a small number of Lotek’s NanoTags to male warblers at KWMA and FCMI. NanoTags do not work in conjunction with the nodes, but they could be detected by Motus towers located along the warbler’s migration route or on their wintering grounds.

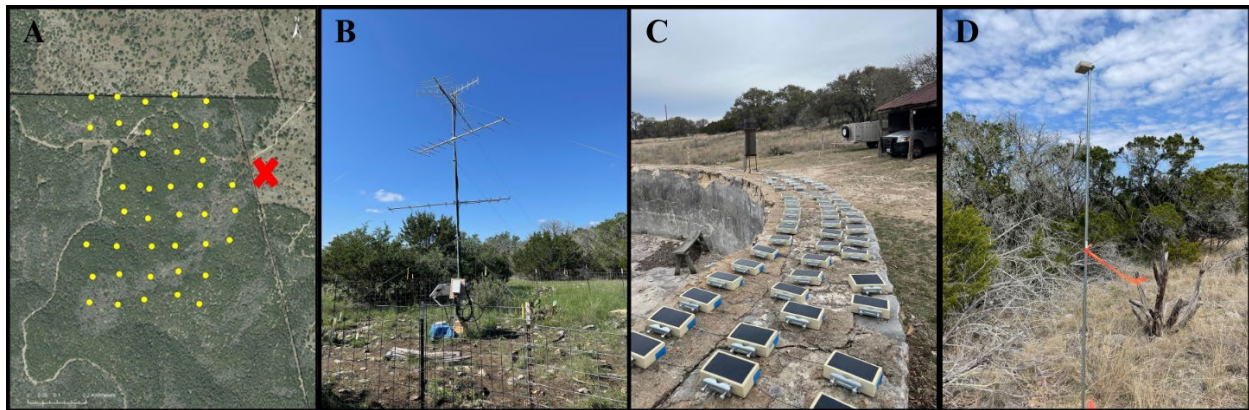


Figure 9. A: Map of Motus station (red X) and grid of automated telemetry nodes (yellow dots) at Kerr Wildlife Management Area in Texas. B: Motus tower. C: Nodes charging prior to installation. D: Node at a grid point. Photos by Michael Gamble.

Field methods

Beginning in early March of each field season, we searched each study site from sunrise to ~1300 daily for warblers that returned to the breeding grounds. When we detected a warbler

by sight or sound, we used a GPS unit to record the bird's latitudinal and longitudinal coordinates and we noted the warbler's sex and the color combination of any bands present on the bird's legs. We did not use these data for analyses purposes, but rather to relocate individuals during subsequent capture and monitoring attempts. After behavioral observations indicated that warblers had established their territories, and thus, were unlikely to move long distances from our study sites, we used standard mist-netting techniques with playback of conspecific songs to capture warblers (NABC 2001). We banded warblers with a U.S Geological Survey (USGS) aluminum leg band and two to three plastic color legbands. We recorded the USGS band number, color combination, date, time, body mass to the nearest 0.01 g, and age, and we used GPS units to identify the Universal Transverse Mercator (UTM) coordinates of all banding locations. We aged individuals as hatch year (HY), second year (SY), or after second year (ASY), and sexed each bird according to Pyle (1997) and Peak and Lusk (2009, 2011).

From 2017–2020, we attached geolocators developed by Migrate Technology (Migrate Technology Intigeo P30Z11-7 Dip with a 5-mm light stalk) to male warblers at all study sites using a modified version of the leg loop harness (Rappole and Tipton 1991, Streby et al. 2015) (Left and Center in Fig. 10). Individuals with geolocators weighed ≥ 9.2 g so that the weight of all attachments (USGS band, color bands, and geocator) did not exceed 5.5% of the bird's body weight. In 2022 and 2023, we used the same modified leg loop harnesses (Rappole and Tipton 1991, Streby et al. 2015) to attach radio transmitters (CTT PowerTags, CTT LifeTags, and Lotek Nanotags) to male and female warblers at KWMA (Fig. 11). Individuals with radio transmitters weighed ≥ 9.0 so that the weight of all attachments (USGS band, color bands, and radio transmitter) did not exceed 6.2% of the bird's body weight. We received experimental authorization for our attachments to exceed standard weight restrictions, which required annual reports to document any potential impacts the devices had on warblers prior to continuation of our study. Also, as stipulated by our permits, we did not re-deploy geolocators or radio transmitters on individuals that were tagged in a previous year.

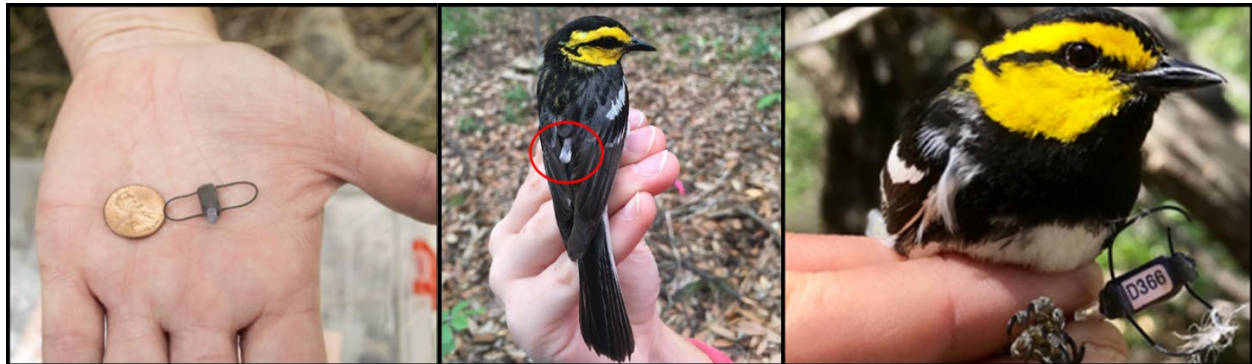


Figure 10. Left: Geocator with a 5-mm light stalk and leg-loop harness (0.41 g). Center: Geocator attached to male golden-cheeked warbler (*Setophaga chrysoparia*). Right: Geocator retrieved from a male golden-cheeked warbler the year after it was attached.

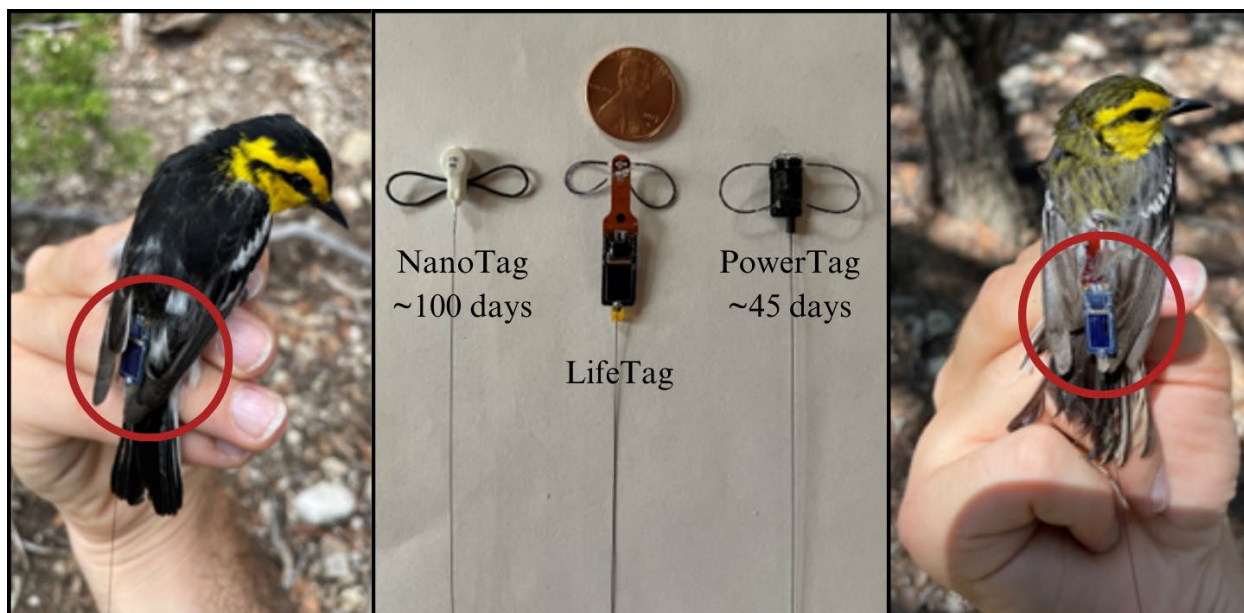


Figure 11. Center: Radio transmitters deployed on golden-cheeked warblers (*Setophaga chrysoparia*) in 2022 and 2023. NanoTags are manufactured by Lotek Wireless Inc. PowerTags and LifeTags are manufactured by Cellular Tracking Technologies. Left: Male golden-cheeked warbler with a radio transmitter. Right: golden-cheeked warbler female with a radio transmitter. Photos by Michael Gamble.

From 2018–2021, we returned to each study site to recapture warblers with geolocators (Right in Fig. 10), which is necessary to retrieve data stored on the devices. We used the same mist-netting and data collection techniques described above, but additionally recorded observations of body condition upon recapture. From 2017–2022, we also mapped and monitored the territories of male warblers with and without geolocators at FCMI and CB for our study examining the potential impacts of geolocators on aspects of warbler survival and breeding ecology. We visited each territory three times per week, and during each territory monitoring visit, we recorded the date, time, color band combination, presence, or absence of a female, and presence or absence of fledglings <2 weeks old with a banded adult. During each territory visit, we searched for up to two hours to relocate the banded birds. Once we relocated a male warbler, we used handheld GPS units to record the male's location every three min for two hours, or until the bird was no longer visible. We also recorded points to identify the female's location whenever possible during this sampling period. We used the location information to define the boundaries of each male's territory (i.e., male relocated in the same area for >2 weeks with >20 location points) and to assist with relocation efforts during the current and following breeding seasons.

While mapping each territory, we recorded behavioral observations of each banded male to determine their reproductive status. We defined pairing success as the presence of a female within the focal male's territory for >2 weeks. We defined fledging success as the presence of ≥ 1 fledged young <2 weeks of age interacting with the male or female within a paired male's territory (Fig. 12). We determined that a male had returned if we found the individual on the plot in a subsequent season. For this aspect of our project, we included a 200-m buffer around each plot to help us relocate any birds that established territories outside our plots when they returned. We also used behavioral cues to search for warbler nests during our territory monitoring efforts

(e.g., female gathering nest building material or a food carry) (Fig. 12). If we located a nest, we monitored the nest every 1–2 days to document the number of eggs, nestlings, and fledglings. In 2022 and 2023, we used the same methods described above to map and monitor warblers with and without radio transmitters at KWMA, but also used a handheld antenna to assist with locating nests of tagged birds. We conducted all field activities in accordance with the following permits: USFWS #TE023643-11, TE32917C-1, and #TE082496-0; USGS #21999 and #24126; TPWD #SPR-0409-079 and # SPR-0417-097.



Figure 12. Left: Male golden-cheeked warbler (*Setophaga chrysoparia*) feeding a fledgling. Photo by Dianne Robinson. Right: Female golden-cheeked warbler sitting on a nest. Photo by Stephanie Augustine.

Analysis

Geolocator data

We used the R package BASTag (Wotherspoon et al. 2016) to import raw light data from each geolocator, convert the .lux file to “TAGS” format (<https://www.nceas.ucsb.edu>), and to detect/validate twilights (Fig. 13). Consistent with other studies on other forest-dwelling songbirds, we used a light threshold limit of 1.5 to define separation of day and night (Lisovski et al. 2019). We visually inspected each twilight event and removed false twilights that occurred due to shading of the light’s sensor (i.e., quick transitions from light to dark and vice versa) (Lisovski et al. 2019) (Fig. 14). We then used the R package FLIGHTR (Rakhimberdiev et al. 2017) to estimate latitudinal and longitudinal coordinates from the processed light data (Fig. 15). FLIGHTR has a hidden Markov chain model that combines an animal movement model with an observational model of light measurements and estimates locations based on position information from both current and adjacent twilights (Rakhimberdiev et al. 2017). Prior to running each model, we used deployment coordinates and the maximum time we could confirm that each warbler was in a specific location on their breeding grounds to calibrate our analyses (i.e., establish the relationship between observed and expected light levels for each device). We defined the spatial extent for our analyses as 500 km beyond the known range of the warbler, set the maximum distance a warbler could travel per day to 750 km, and programmed the animal movement model so that individuals could not be stationary over water. However, we did not prohibit over-water crossings altogether; while we expected warblers to migrate over land, we could not rule out the possibility of trans-Gulf migrations. Model outputs included location

means and medians with their associated credible intervals, arrival and departure dates, and stopover durations (Fig. 16) (Rakhimberdiev et al. 2015, 2017). We used two methods to calculate accuracy of our geolocator data. We first calculated differences in latitudinal and longitudinal distances between each individual's capture point and the individual's mean geolocated coordinates during the breeding period. We then calculated overall mean and SD of the distances for latitude and longitude. Second, we calculated the mean and SD distances for the upper and lower credible intervals for latitude and longitude per period (breeding, fall migration, winter, and spring migration).

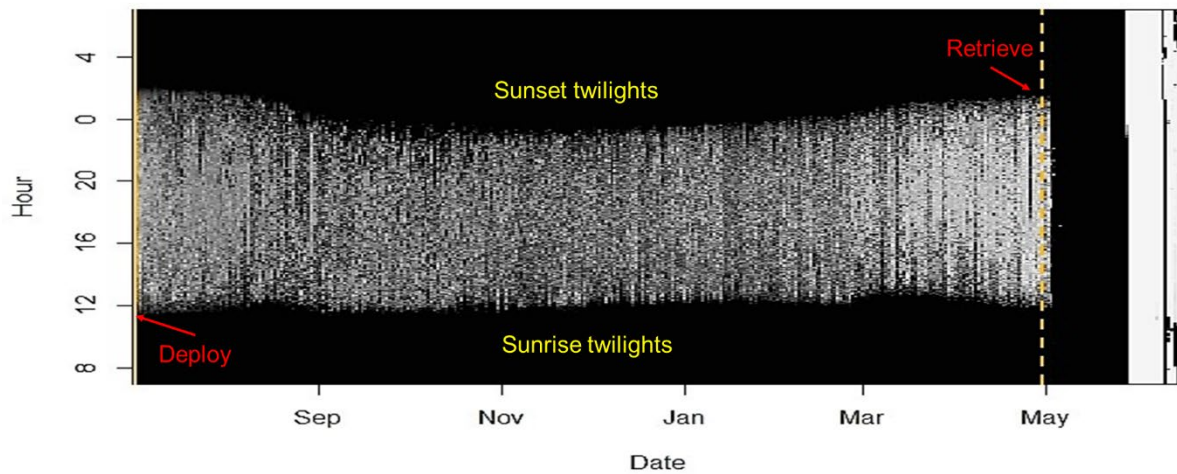


Figure 13. Example of raw light data (.lux format) recorded by a geolocator for each 24-hour period from the day the geolocator was attached to a golden-cheeked warbler (*Setophaga chrysoparia*) until the day the geolocator was retrieved.

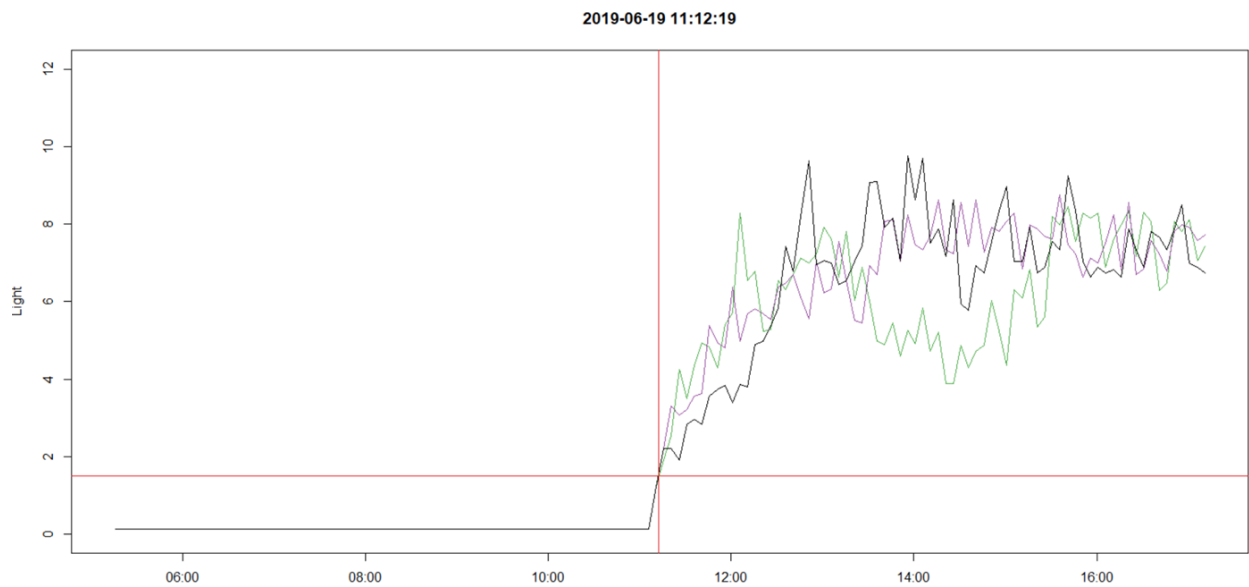


Figure 14. Example of process used to edit twilights. The black line represents twilight on the day of interest and the green/purple lines represent twilights on the day before and the day after.

All three twilights are smooth before the red crosshair, indicating the twilight on the day of interest can be used for analyses.

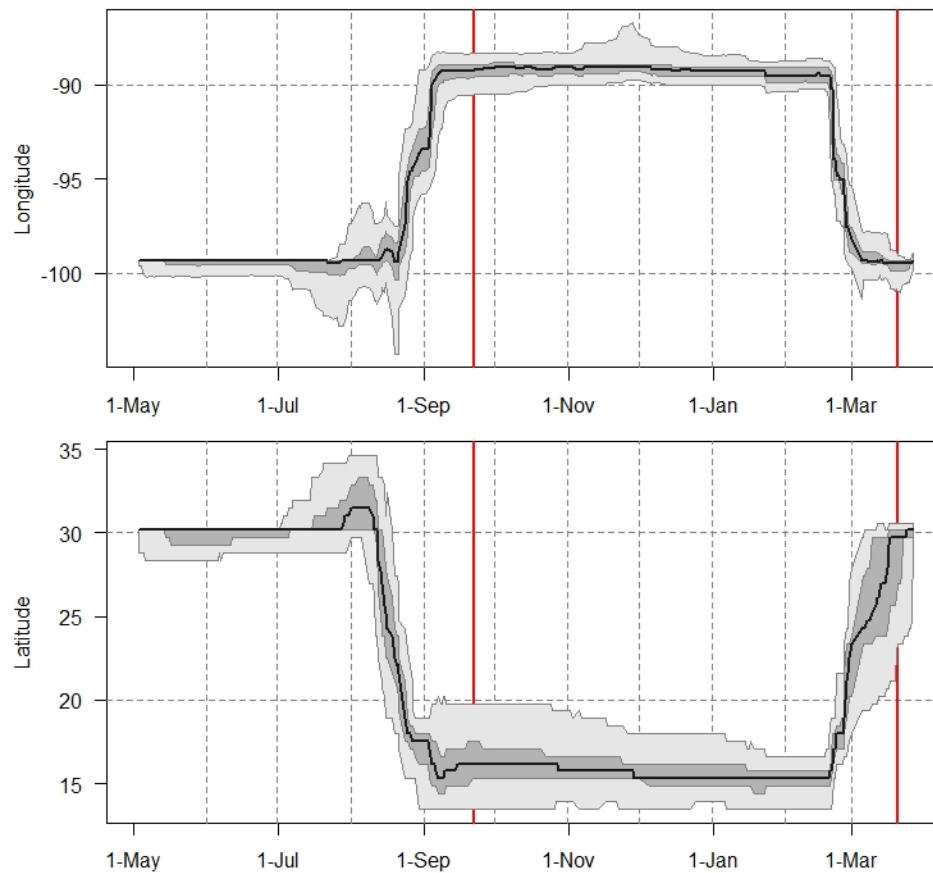


Figure 15. Example of estimated coordinates and credible intervals from the processed light data as output by FLIGHTR. See Fig. A.1 for more examples.

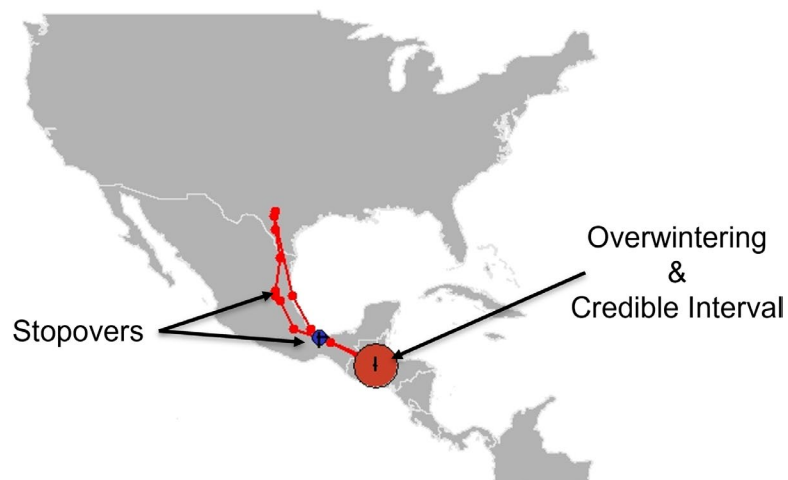


Figure 16. Example output from FLightR illustrating migratory stopovers (small red dots), longer stopover period (blue dot), and overwintering location (large red dot) along with the associated credible intervals.

We used spring and fall departure dates as well as evidence of short- and long-distance flights to help us define the breeding, post-breeding, migration, stopover, and winter periods. We considered long-distance movements as sustained flights >100 km and stationary periods (e.g., stopovers) as locations sustained for ≥ 3 days. We used the mean latitude and longitude and the associated credible intervals to identify an individual's location during each period. We used the output from FLightR to calculate distances traveled between points identified as breeding and wintering locations, measure durations, and to convert arrivals and departures to Julian date for each individual. We calculated means for each of these variables and used analysis of variance (ANOVA; Fisher 1925) or *t*-tests (Student 1908) to compare the means across years, locations, and age classes. When $P \leq 0.05$ for ANOVAs, we used Tukey honestly significant difference (HSD) tests to determine which means were significantly different from each other. We used the R packages UD-sp (Pebesma and Bivand 2005) and adehabithR (Calenge 2006) to calculate 25%, 50%, and 75% utilization distributions (UD) for each period (i.e., visual representation of space use based on the relative frequency of occurrence). We calculated UD's separately for individuals, individuals per location, individuals per age class, and for all birds combined within each period. We visualized our results in ArcGIS 10.8.3 (ESRI, Redlands, CA, USA).

Migratory connectivity

We formatted the spatial data necessary to estimate migratory connectivity using the R package sf (V. 1.0-10; Pebesma 2018). We defined our origin points as each bird's capture location on the breeding grounds and our target points as the centroids of each bird's 50% UD on their wintering grounds. There was one bird with insufficient data to estimate a 50% UD. In this case, we used the centroid of the bird's 75% UD on the wintering grounds as the target point. Fifty-five birds moved locations during winter, resulting in >1 50% UD for these individuals; in these cases, we identified the target points as centroids from UD's where the individuals spent the longest time.

We then used the R package geosphere (V. 1.5.18; Hijmans 2022) to calculate the mean distance between all target points on the wintering grounds as a measure of spread (Burgess et al. 2020). We also calculated the standard error, range (minimum–maximum), and 95% confidence interval for the mean distance, then repeated these calculations for individual years. We used ANOVA to determine if the mean distances were different across years, and determined which pairs of years were significantly different using a Tukey HSD test ($\alpha = 0.05$; Tukey 1949).

We estimated migratory connectivity based on Mantel's correlation coefficient (*r*M). Specifically, *r*M quantifies the correlation between distances of individuals during the breeding and wintering periods to examine whether individuals remain similarly close or distant from one another during the wintering period when compared to the breeding period (Ambrosini et al. 2009). We chose this metric to estimate migratory connectivity rather than the extension of *r*M that estimates transition probabilities between populations and incorporates error for sampling efforts that are not proportional to abundance (Migratory Connectivity, or MC) because we could not delineate the warbler breeding or winter range into distinct populations (Cohen et al. 2018) and previous studies did not find genetic differentiation across the warbler's breeding range (Lindsey et al. 2008).

The rM calculations require an estimate of location error for studies that use geolocators because these devices do not record the exact locations of individuals, so we used methods described by Cohen et al. (2018) to estimate this metric. We first calculated differences in latitudinal and longitudinal distances between each individual's capture point and their geolocated coordinates during the breeding period. We then calculated the means of these values, which resulted in a dataset with one latitude error and one longitude error for each bird. Next, we created intercept-only linear models using the latitude and longitude error as dependent variables, which allowed us to estimate bias (i.e., the intercept coefficient) for latitude and longitude, as well as the variance-covariance matrix between latitude and longitude error. Last, we used the bias and variance-covariance matrix as an estimate of location error for the wintering grounds. We acknowledge that breeding period location error may not be representative of wintering period location error, but we could not estimate wintering period location error without capturing birds on the wintering grounds (see Cohen et al. 2018).

We used the origin points, target points, and location bias and variance-covariance matrix to calculate rM based on 1,000 bootstraps with the `estMantel` function in `MigConnectivity` package available through Program R (V. 0.4.1; Hostetler et al. 2021) (Ambrosini et al. 2009). We also calculated location error and rM with our geocator data subset by year. We examined rM estimates and their 95% confidence intervals, and following Finch et al. (2015), we defined strong migratory connectivity as $rM > 0.5$ and weak migratory connectivity as $rM \leq 0.5$. We created figures visualizing the results from our migratory connectivity analyses using the R package `ggplot2` (V. 3.3.5; Wickham et al. 2016).

Geocator impact assessment

Based on previous geocator studies and our prior research on warblers, we predicted that warblers with and without geolocators would resume normal activities (e.g., foraging, singing, preening) following handling and remain on site for the rest of the breeding season. We did not expect the geolocators to negatively impact warbler pairing or fledgling success (Peterson et al. 2015, Raybuck et al. 2017, Brlík et al. 2020) but predicted that geolocators could have a weak negative effect on warbler return rates (Barron et al. 2010, Arlt et al. 2013, Brlík et al. 2020). For the current study we described our observations of warbler behavior following attachment of the geolocators and summarized the number of banded birds with and without geolocators that we resighted within breeding seasons. We then analyzed data for each study site (FCMI and CB) separately and included study site, year, and age class in our analyses because previous research found geographic and temporal variation in warbler responses (e.g., density, reproductive success; Groce et al. 2010, Long et al. 2021) that we thought could influence our results. We developed *a priori* models including single variables and two-way interactions between combinations of variables that we hypothesized would cause variation in male warbler pairing success, fledgling success, and return rates, including geocator (Y/N), year, age (SY, ASY), and plot. We used generalized linear models (GLM) to examine warbler responses, Akaike Information Criteria corrected for small sample sizes (AIC_c) to rank the models, and ΔAIC_c along with model weight (w_i ; Burnham and Anderson 2002) to determine relative support for each model; we considered models with a $\Delta AIC_c \leq 2.0$ equally plausible. We calculated the 95% confidence intervals (CIs) for each response variable in our best fit models to examine the extent of variation around the predicted values (Burnham and Anderson 2002). We graphed the results to determine the potential statistical or biological significance of each relationship by examining the extent of overlap among CIs. We also described our observations of body

condition upon retrieval of the geolocators and used paired t -tests ($\alpha = 0.05$) to identify potential differences in mean body mass when we deployed and retrieved the devices.

Radio telemetry data

As described above, automated telemetry can be used to collect both broad- and fine-scale movement data. By installing a Motus tower at KWMA and using the existing Motus network, we hope to record new locations for both male and female warblers during migration and on their wintering grounds that will complement our geocator data. This network includes approximately 20 Motus towers along the warbler's migration route and on their wintering grounds with additional towers planned for installation across these areas in the near future. Following installation of our Motus tower in spring 2022, we regularly accessed Motus' online database to log detections of warblers and other tagged species recorded by our station and to log warblers detected at other stations in the network. The Motus tower at KWMA will remain active after our project is complete and we will continue to monitor the Motus database after our project ends, as some radio transmitters we attached to the warblers should remain active for several months following the 2023 breeding season and other radio transmitters that we attached to the warblers should remain active for the life of the bird.

We used the grid of nodes that we installed in spring 2022 to examine fine-scale movements of male and female warblers during the 2022 and 2023 breeding seasons. Each node is solar powered and equipped with an omnidirectional antenna that detects signals from the radio transmitters and transmits those data to the Motus tower's SensorStation. We used the Received Signal Strength (RSS) based trilateration method to estimate individual locations within the grid of nodes (Krull et al. 2018, Wallace et al. 2021). This method is based on the relationship between RSS values (i.e., signal strength received by each node when a tag is detected) and the distance from each node to the signal (i.e., tag location). To calibrate the RSS-distance relationship, we attached a radio transmitter with a 75-sec pulse interval on a 3 m nonconductive pole and recorded signal strength at set distances from nodes (1, 10, 20, 30, 40, 50, 75, 100, and 125 m) within the grid. We calculated these relationships for 50% of the nodes in our grid (i.e., 27 nodes), which ensured that our tests covered the range of vegetative and topographic conditions within the grid and that transmitter and antenna positions during our tests mimicked radio transmitter positions on birds. At each test location, we held the pole stationary for 10 min and we recorded the start and end time of each test as well as the coordinates of each location. We conducted a total of 217 tests, then downloaded the calibration data from the SensorStation and used a non-linear least square approach in Program R to run an exponential decay model that represented the relationship between RSS values and distance of the nodes from each test location.

As described by Paxton et al. (2022), we applied RSS and distance filters to our calibration dataset to assess localization error. We filtered our data with RSS cutoff values of -90, -95, -100, and -105 (dB) to examine location accuracy and data loss. We also tested distance filters that were multiples of the average grid spacing (i.e., 1.25x, 2x, 3x, and 4x). The average spacing in our grid was 100 m, which created distance filters of 125, 200, 300, and 400 m. In this analysis, we took the node with the strongest signal and then selected all other nodes that were within these distances of the node receiving the strongest signal to use in trilateration. This allowed for only nodes with the strongest signal to be used in trilateration. More stringent RSS

filters are expected to result in less location error but could lead to increases in data loss (Paxton et al. 2022). The 2023 field season was in progress during preparation of this report, so we summarized our 2022 and 2023 data below. Future analyses will quantify sex-specific home range sizes (95% minimum convex polygons and 50% autocorrelated kernel densities), distances that warblers traveled outside their home ranges (i.e., extraterritorial forays), and the amount of spatial overlap between male and female warblers. We will also identify departure dates for tagged warblers and compare return rates, pairing success, and nest success for warblers with and without radio transmitters.

Winter habitat models

Species distribution modeling (or environmental niche modeling) is an effective statistical approach used to identify potential geographic distributions of species given biophysical conditions at known species locations and across large landscapes (Guisan and Thuiller 2005, Elith et al. 2006, Hu et al. 2010). Species distribution models (SDMs) are often used to prioritize areas in which to search for rare species (e.g., Williams et al. 2009, Oleas et al. 2014, Colón et al. 2015) or implement conservation actions (e.g., Trisurat et al. 2012, Morato et al. 2014), among other ecological applications. Increasingly, SDMs are utilized to predict the potential effects of climate change on species of conservation concern (e.g., Peterson et al. 2002, Hamann and Wang 2006, Jarvie and Svenning 2018, Zhang et al. 2019). The resulting forecasts may be overly simplistic as most SDMs ignore biotic interactions (Araújo and 2007, Van der Putten et al. 2010, Bateman et al. 2012). However, evidence suggests they can provide realistic predictions of distributional shifts, at least for birds (Araújo et al. 2005, Watling et al. 2013), allowing for more informed conservation planning (Araújo, & Rahbek, 2006).

We used SDMs to predict the wintering distribution of warblers under current and projected climate conditions and identified locations that may be key for population persistence. We focused on climate change as a driver of warbler winter habitat conversion because montane forests where warblers occur are particularly vulnerable to the impacts of climate change and there is growing evidence that some bird species that rely on montane forests in winter may be unable to adapt to changing conditions. In addition, there are many potential sources of natural and anthropogenic habitat loss and degradation on the warbler's wintering grounds (e.g., agricultural expansion, logging, forest fires) that vary considerably across countries, but from 2000–2020, ~90% of forest cover within the warbler's core elevation range (800–2600 masl, see below) was stable and ~10% of change that occurred was attributed to stand-replacement disturbances or degradation (e.g., wildfires) (Global Land Cover and Land Use Change dataset; Potapov et al. 2022). Most forest loss in countries where warblers overwinter occurred below the species core elevation range where agricultural and urban development are most intense.

Study area

Most accounts describe the warbler's wintering range as extending from central Chiapas through parts of Guatemala, El Salvador, Honduras, and Nicaragua (Pulich 1976, Vidal, Macías-Caballero and Duncan 1994, Ladd and Gass 2020, Rappole et al. 2000; Fig. 5). However, warblers have also been detected in Oaxaca, Mexico (Molina, Pronatura Sur A. C., pers. comm.), Belize (Jones and Komar 2009, eBird 2020), and Costa Rica (Jones 2005, May 2005; Jones and Komar 2006, 2008; Sandoval et al. 2010; eBird, 2020) during winter months, and the IUCN Red List of Threatened Species lists the warbler as extant in Belize and Costa Rica, albeit potentially vagrant and with uncertain origin (IUCN 2020). As such, we allowed models to consider the full

spatial extents of Oaxaca, Chiapas, and all Central American countries from Guatemala to Costa Rica. Though we found two reported cases of warblers in Panama (Jones 2005, eBird, 2020), both were near the Costa Rican border, and we did not include Panama in our analyses. Literature describing wintering habitat for golden-cheeked warblers suggests the species prefers pine-oak forest habitat within a core elevation zone from 800 to 2,600 meters above sea level (Vidal et al. 1994; Rappole et al. 1999, 2000; King et al. 2008; Komar 2011). We did not restrict our study area by ecoregion or elevation as doing so could have introduced error into estimates of the species' true distribution (Peterson et al. 2018), but we did identify the core elevation zone in some maps below.

Environmental variables

We considered 24 environmental variables as potential predictors of the warbler's wintering distribution in our models, including 19 climatic variables, two topographic variables, and three variables we considered proxies for vegetation condition. We obtained the bioclimatic variables at 30-arc second resolution (~1 km) from the Climatologies at High Resolution for the Earth's Land Surface Areas website (CHELSA; <http://chelsa-climate.org/bioclim>). These data represent annual trends, seasonality, and extremes in temperature and rainfall over a 30-year period (1979–2013; Karger et al. 2017a, 2017b) and may have greater predictive power for species distribution models in high altitude regions compared to other commonly used climate datasets (Bobrowski and Schickhoff 2017).

We used Google Earth Engine (GEE; Gorelick et al. 2017) to extract all other environmental predictors, including slope and elevation from the 30-m resolution Shuttle Radar Topography Mission digital elevation model (Farr et al. 2007) and canopy height from the 1-km resolution Global Forest Canopy Height dataset (Simmard and Baccini 2011). We also used GEE to create multi-year average measures of vegetation phenology and thermal seasonality, which others have used to improve the performance of species distribution models (e.g., Cord and Rödder 2011, Naimi et al. 2014). Specifically, we calculated average annual mean enhanced vegetation index (hereafter mean EVI) and average annual mean land surface temperature (hereafter mean LST) from 2000 to 2019 using 1-km resolution Moderate Resolution Imaging Spectroradiometer (MODIS) land cover products (MOD11A2 v. 6, MOD13A2 v. 6). We cropped all datasets to the extent of the study area and resampled the resulting outputs to match the resolution of the canopy height dataset. We tested for collinearity among predictor variables by calculating their variance inflation factors (VIFs), which measure how much each variable is explained by the others (Marquardt 1970), and we excluded variables with the highest VIFs in a stepwise manner until we removed all collinear variables (i.e., $VIF > 5$; Naimi and Araújo 2016; Naimi and Araújo 2019).

Occurrence data

We collated warbler occurrence records from field surveys reported in peer-reviewed (Rappole et al. 2000, King et al. 2008, Morales et al. 2008) and gray literature (Altamirano et al. 2004, Potosome and Muñoz 2007, González Callejas 2008, Komar 2011). To increase our sample size (Wisn et al. 2008), we also extracted records with geographic coordinates from two crowd-sourced databases, eBird and iNaturalist (eBird 2020, iNaturalist 2020). Despite concerns regarding spatial bias, possible species misidentification, and positional uncertainty (Guisan et al. 2017, Zhang and Zhu 2018), crowd-sourced data are widely used to inform species distribution models (e.g., Jackson et al. 2015, Lin et al. 2015, Coxen et al. 2017) that often yield comparable

outputs to those derived from field survey data alone (e.g., Jackson et al. 2014, Steen et al. 2019). Crowd-sourced data are especially useful in identifying the distributions of species that occur over large geographic extents where comprehensive field survey efforts would be cost prohibitive (Devictor et al. 2010).

To maximize the likelihood of correspondence between occurrence locations and current environmental conditions, we only used records from the year 2000 or later to inform our models. We similarly limited records to those occurring between October and February to minimize inclusion of migratory locations in our models (Rappole et al. 2003). We simultaneously removed duplicate locations and reduced sampling bias (Beck et al. 2014, Boria et al. 2014, Zhang 2019) by mapping points atop a 10-km² grid of our study area and excluding points so that no grid cell contained more than one point. We prioritized field survey points over crowd-sourced data and retained the most recent record where multiple records of the same collection type occurred within the same grid cell. We randomly selected one record per grid cell where multiple prioritized records occurred on the same date. Our final dataset contained 175 points (49 field survey and 126 crowd-sourced), with an average distance of 16 km $\pm$ 18 SD (R 1–115 km) between each point and its nearest neighbor (Fig. 17).

In winter, golden-cheeked warblers forage in mixed-species flocks that often include similarly plumaged congeners (i.e., black-throated green warbler [*S. virens*], Townsend’s warbler [*S. townsendi*], hermit warbler [*S. occidentalis*]; Vidal et al. 1994, Thompson 1995, Rappole et al. 1999, Morales et al. 2008). Thus, we could not rule out possible misidentifications in the crowd-sourced data. However, all retained eBird records ($n = 126$) were approved by the Cornell Lab of Ornithology, with unusual species records flagged and reviewed by regional experts (Sullivan et al. 2009), and all retained iNaturalist records ($n = 3$) were listed as research grade and included high-quality photographs. We similarly could not address location accuracy in the crowd-sourced data, however, previous research suggests positional errors in species location data have little effect on model predictions (Graham et al. 2008)—especially when spatial autocorrelation exists within environmental predictors (Osborne and Leitão 2009, Naimi et al. 2011, Naimi et al. 2014).

We summarized environmental characteristics at all occurrence locations (i.e., mean, standard deviation [SD], minimum, and maximum), then examined potential environmental differences in our occurrence data according to the record type. We used the ‘vegan’ package (Oksanen et al. 2019) in program R v. 3.6.3 (R Core Team 2019) to perform a multivariate analysis of similarity (ANOSIM; Bray-Curtis distance; 999 permutations; Clarke 1993) comparing characteristics at field survey and crowd-sourced locations, followed by post hoc Welch’s *t*-tests to quantify potential univariate differences. We calculated Cohen’s *d* and its 95% confidence intervals as measures of effect size for each univariate test, and we used a Bonferroni correction when assessing significance to account for multiple comparisons.

We examined spatial autocorrelation in the retained environmental predictors using omnidirectional, nonparametric correlograms generated with the open-source spatial analysis program GeoDa v. 1.14 (Anselin et al. 2006). We considered lag distances up to 10 km (at 1-km bins), which we assumed to be a reasonable level of possible positional error in occurrence data, and up to 100 km (at 10-km bins) to demonstrate changes in spatial autocorrelation across the broader landscape. Values of 1 and -1 indicate strong positive and negative autocorrelation, respectively, at specified lag distances, with 0 indicating no autocorrelation.

Modeling methods and evaluation

We built warbler distribution models using three regression-based algorithms (generalized additive models [GAM; Hastie and Tibshirani 1990], generalized linear models [GLM; McCullagh and Nelder 1989], and multivariate adaptive regression splines [MARS; Friedman 1991]) and five machine learning algorithms (boosted regression tree [BRT; Friedman 2001], classification and regression trees [CART; Breiman et al. 1984], maximum entropy [MaxEnt; Phillips et al. 2006], random forest [RF; Breiman 2001], and support vector machine [SVM; Vapnik 1999]). These algorithms are common in species distribution modelling (reviewed in Heikkinen et al. 2006) but vary in their spatial predictions, with no one method consistently outperforming all others (e.g., Bucklin et al. 2015). As such, we created an ensemble of the predictions from each algorithm. This technique combines the strengths of the different algorithms, while minimizing their weaknesses to yield more robust species distribution predictions (Thuiller 2004, Araújo and New 2007, Marmion et al. 2009, Grenouillet et al. 2011). We created all models using the ‘sdm’ package (v. 1.0-89; Naimi and Araújo 2019) in program R v. 3.6.3 (R Core Team 2019).

We used a bootstrap evaluation procedure with 25 model replicates per algorithm (i.e., 200 models). Bootstrapping is a repeated resampling method with replacement that uses unselected samples as test data in the evaluation of each run (Vertbyla and Litvaitis 1989, Efron and Tibshirani 1997); it is especially useful when working with small datasets (Efron 1983, Efron and Gong 1983). We evaluated variable importance across runs for each algorithm and overall using correlation statistics (Naimi and Araújo 2019) and examined the response curves of the most important variables (Elith et al. 2005). We assessed the predictive performance of each algorithm using the mean values for two metrics across runs: the area under the receiver operating curve (AUC; Fielding and Bell 1997) and the true skill statistic (TSS; Allouche et al. 2006). The former evaluates the discriminatory power of species distribution models (Phillips et al. 2006) and ranges from 0 for no agreement to 1 for complete agreement (but see Lobo et al. 2007, Jiménez-Valverde 2011, Golicher et al. 2012, Shabani et al. 2018). The latter compares the proportions of correctly classified presences (i.e., sensitivity) and absences (i.e., specificity) and ranges from -1 to 1, with 1 indicating complete agreement and values ≤ 0 suggesting performance similar to random (Allouche et al. 2006). When creating our ensemble model, we weighted the contributions of each algorithm according to average TSS scores and a threshold that maximized specificity and sensitivity (Araújo and New 2007, Marmion et al. 2009).

Several of the algorithms included in our ensemble model require information on species presence and absence. To address this, we randomly generated a set of 200 pseudo-absence (or background) points across the full extent of the study area then filtered the set so that no more than one point occupied a 10-km² grid cell and none shared a grid cell with an occurrence point. We then randomly removed points until our background and occurrence datasets were equal in size, as many of the algorithms we employed perform better under this scenario (Barbet-Massin et al. 2012, Liu et al. 2019). The average minimum distance between pseudo-absence and occurrence points was 103 km $\pm$ 104 SD (R = 9–447 km). Preliminary analyses indicated restricting pseudo-absence points to smaller extents (e.g., within 100, 200, and 300-m buffers of occurrence points), as suggested by VanDerWal et al. (2009), did not improve model performance.

To examine the effects of climate change on the wintering distribution of warblers, we replaced our contemporary bioclimatic predictors with optimistic and pessimistic projections for the years 2050 and 2070 derived from five general circulation models (GCMs; MPI-ESM-MR, MIROC5, CESM1-CAM5, IPSL-CM5A-MR, and MRI-CGC3) generated during the fifth phase

of the Coupled Model Intercomparison Project (CMIP5; Taylor et al. 2012). We selected these circulation models because they exhibited limited interdependency and represented a range of uncertainty (Knutti et al. 2013, Sanderson et al. 2015). We considered the Intergovernmental Panel on Climate Change (IPCC) representative concentration pathway (RCP) 2.6 our optimistic scenario and RCP8.5 our pessimistic scenario (IPCC 2014). The former is based on aggressive mitigation of greenhouse gas emissions and an increase in global temperatures between 0.3 and 1.7 °C (van Vuuren et al. 2011). The latter represents a substantial increase in greenhouse gas concentrations with an increase in global temperatures ranging from 1.4 to 4.8 °C (Riahi et al. 2011). We held other predictors constant as these are either unlikely to change significantly over time (i.e., slope) or are dependent on too many factors to adequately project to future dates without adding considerable uncertainty (e.g., Thuiller et al. 2006).

Post-modeling processing and analyses

We transformed our contemporary and future outputs to binary presence-absence maps using the threshold that maximized specificity and sensitivity (Liu et al. 2005, Jiménez-Valverde and Lobo 2007, Coetzee et al. 2009). To compare forecasts among GCMs, we calculated the percent pixel agreement among the five presence-absence maps for each scenario and year and ranked GCM severity as a function of predicted area.

We then used GEE to mask areas from all maps that were unlikely to provide suitable wintering habitat for warblers (e.g., agricultural, urban, and barren areas) given International Geosphere-Biosphere Programme land cover classifications identified in the 2018 MODIS Land Cover dataset (MCD12Q1.006; 500-m resolution). We considered the 2018 dataset representative of current conditions and an optimistic estimate of future land cover. This process generated a masked prediction of the warbler's current wintering distribution as well as 20 masked forecasts of potential future distributions (2 RCPs x 2 years x 5 models). We used ArcGIS v. 10.6 to overlay forecasted maps to create consensus maps for each RCP and year combination, wherein we retained all pixels present in at least three of five maps. We generalized all contemporary and future consensus maps by smoothing boundary edges and removing small fragments (<10 pixels), because binary range boundaries can include outliers and present problems for analyses, especially when sample sizes are small and abundance data are not available (Peters et al. 2014).

We identified the percentage of occupancy points that were coincident with the predicted areas in each of our final maps, calculated rangewide and regional predicted areas, and estimated forecasted losses in potential habitat under each RCP for 2050 and 2070 compared to the present. We also calculated the mean, standard deviation, and range of elevations occurring rangewide and regionally in each map as well as the percent area predicted to occur within the core elevation zone. We used the World Database on Protected Areas (UNEP-WCMC 2015) to estimate the extent and distribution of designated and inscribed protected areas within the distributions predicted under current and projected climate conditions. Last, we used the Hansen Global Forest Change v1.7 dataset (30-m resolution; Hansen et al. 2013) in GEE to examine the distribution and rate of small-scale forest cover loss within our predicted contemporary range and the protected areas contained within over the past 20 years (2000–2019).

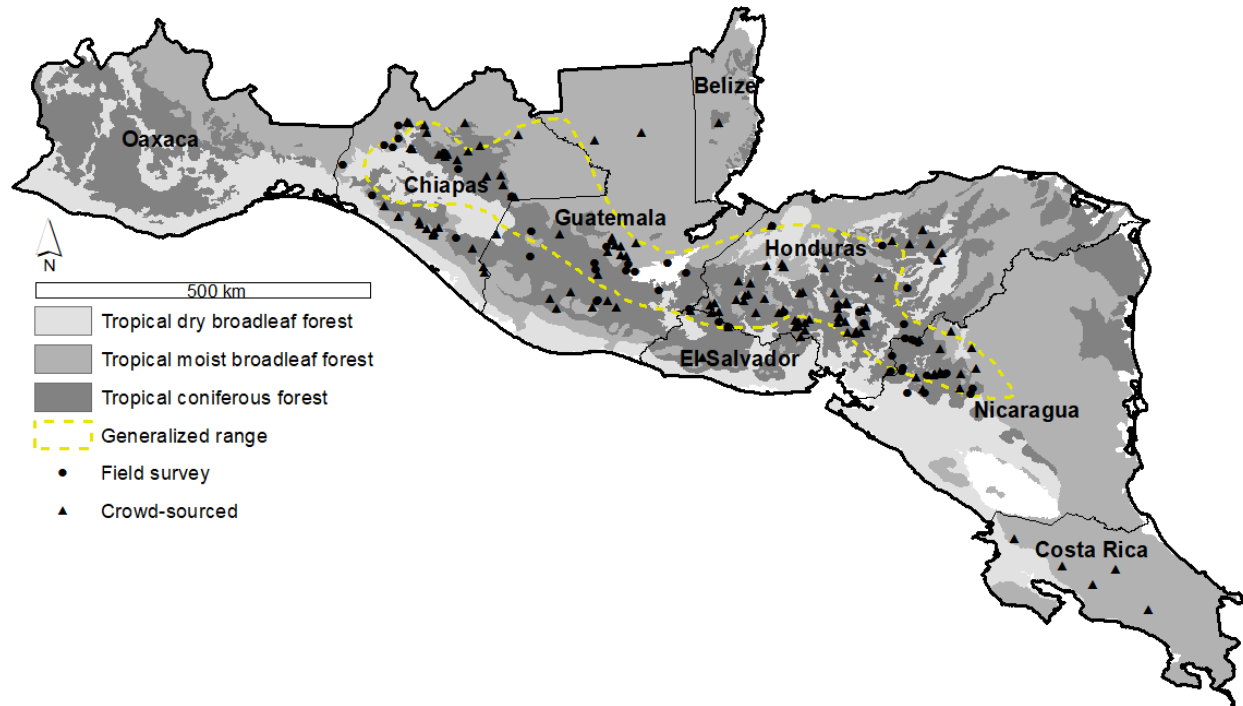


Figure 17. Distribution of field survey ($n = 46$) and crowd-sourced ($n = 129$) occurrence points used to generate current and future distribution models for the golden-cheeked warbler (*Setophaga chrysoparia*) on its wintering grounds with common biomes (Olson et al. 2001) and generalized winter range (BirdLife International 2020) identified.

Breeding habitat

Breeding range data acquisition and pre-processing

We classified Landsat 5 Thematic Mapper, Landsat 7 Enhanced Thematic Mapper Plus, and Landsat 8 Operational Land Imager Tier 1 Surface Reflectance imagery for the years 2000, 2010, and 2020 to examine land cover change for classes that best aligned with warbler breeding habitat. Landsat satellites collect imagery at 30-m resolutions for the visible (i.e., blue, green, red), near-infrared, and short-wave infrared bands, with Landsat 5 available from 1984–2012, Landsat 7 available from 1999 to present, and Landsat 8 available from 2013 to present (U.S. Geological Survey 2019). Landsat satellites orbit the earth every 16 days (U.S. Geological Survey 2019), allowing researchers to filter out images with noise (e.g., cloud cover) and examine variation in land cover over time.

We performed all data acquisition, pre-processing, and analyses in GEE (see Gorelick et al. 2017). We acquired Landsat collections for years of interest (i.e., 2000, 2010, and 2020) and filtered the resulting collections to separate summer (i.e., April–July) and winter (i.e., December–January) seasons to capture seasonal differences in the reflectance of land cover classes in our study area (Duarte et al. 2013, Heger and Hayes 2013). We removed pixels within 500 m of scene edges, which often have missing or inaccurate information (Fig. A.2; Zhang et al. 2016, Robinson et al. 2017), then used the pixel quality assessment band included with Landsat Tier 1 Surface Reflectance imagery to filter and mask pixels that were identified as clouds, cloud shadows, snow, and fill (Dwyer et al. 2018). We also masked pixels identified as hazy (i.e.,

atmospheric opacity score ≥ 300) from Landsat 5 and 7 imagery and similarly masked pixels identified as having high aerosol content from Landsat 8 imagery (Dwyer et al. 2018). We renamed and transformed Landsat 8 band values to align with Landsat 5 and 7 values (Roy et al. 2016), then stacked collections from Landsat satellites in operation for each year of interest (Table A.1). Last, we created a composite image for each year and season using the median values from these stacked collections, resulting in two multiband images per year (i.e., one for summer and one for winter; Roy et al. 2009, Xiong et al. 2016).

To fill masked pixels in the composite imagery, we first created climatology datasets using Landsat imagery collected in the four years prior to each year of interest (Robinson et al. 2017; Table A.2), which we again separated by season, filtered, masked, and stacked using the methods described above. We then filled masked pixels in the composite imagery for each year and season using their associated median climatology. We found that some pixels were still masked after this step, so we calculated the focal means of band values from the climatology composites within an eight-pixel radius of each missing pixel, then used these focal means to fill the masked pixels.

From each filled composite image, we selected the blue, green, red, and near-infrared bands, as well as the two short-wave infrared bands. As in previous classification studies (e.g., Duarte et al. 2013, Heger and Hayes 2013), we then stacked these bands for each season to create one multiband image per year of interest. In addition to Landsat data, we added elevation and slope from the USGS Digital Elevation Model to our stacked multiband images to increase the accuracy of our classifications (Lu and Weng 2007). We also calculated the Normalized Difference Vegetation Index for each year of interest using the summer red and near-infrared bands, which measures vegetation greenness and can help describe vegetative composition and biomass, and added this layer as well (Reed et al. 1994, Pettorelli et al. 2005, Özyavuz et al. 2015). Finally, because permanent water features can have similar reflectance values to shadows in remotely sensed imagery (Sawaya et al. 2003, Feyisa et al. 2014) and classifying water cover was not a goal of our study, we masked water features from our imagery. To do this, we stacked all land cover classified by the National Land Cover Database (NLCD; Dewitz and U.S. Geological Survey 2021) as open water from years 2001, 2004, 2006, 2008, 2011, 2013, 2016, and 2019, then used this stack as a mask for each year of interest.

Breeding range image classification and change detection

We divided our imagery into regions (i.e., north, central, and south; Hatfield et al. 2012) to account for differences in land cover compositions and elevations across our study area, then used a supervised approach to classify the stacked images per region using the random forest classifier (Breiman 2001). The random forest classifier requires a training dataset of locations with known land cover and their associated reflectance values, which it uses to predict the land cover of pixels in the imagery (Breiman 2001). The classifier also requires a user-specified number of decision trees, which are a series of decisions made by an algorithm using subsets of training points drawn without replacement (Breiman 2001). The random forest algorithm leverages the power of multiple trees to provide more robust classifications than those derived from a single decision tree (Kulkarni and Lowe 2016). After parameter tuning, we determined that 100 decision trees were suitable for all regions and years (Figure A.3).

Because we collected our data from a large study area and from several time periods, we were unable to gather ground-truthed land cover data for our study. Instead, we used NLCD to determine land cover that did not change over our 20-year study period and used these data as a reference dataset. We first re-classified NLCD land cover data from the years 2001, 2004, 2006, 2008, 2011, 2013, 2016, and 2019 into classes that best aligned with warbler breeding habitat for each region. We considered NLCD classes evergreen and mixed forest as most closely resembling warbler breeding habitat (Duarte et al. 2013, Dreiss et al. 2022). For the southern region, we reclassified NLCD into the classes “evergreen forest”, “mixed forest”, and “other”, which included all other land cover classes. We reclassified NLCD in the central and northern regions into the classes “forest” (i.e., evergreen and mixed forest classes) and “other”, because we found that the random forest classifier had more difficulty distinguishing mixed and evergreen forests in these regions and combining them increased our classification accuracy. We then used a stratified random sampling approach to collect 500 points from each class located in areas that did not change for the duration of our study period. We randomly selected 70% of the resulting dataset to train the random forest classifier and 30% for validation, which provided enough training points to classify our data and assess classification accuracy (Van Neil et al. 2005, Congalton and Green 2009). We assessed accuracy using several metrics, including overall accuracy, Cohen’s kappa statistic, and user’s and producer’s accuracies (Congalton 1991, Foody 2002), with a goal of reaching overall accuracies of $\geq 85\%$ and user’s and producer’s accuracies $\geq 70\%$ (see Thomlinson et al. 1999). We additionally aimed to reach kappa values $> 60\%$, which would suggest moderate agreement between our reference and classified datasets (McHugh 2012). After assessing the accuracies of our classifications, we combined the evergreen and mixed forest classes into a single “forest” class for the southern region. We then calculated the total area attributed to each class for each year of interest and region, as well as the area and proportion of forest (i.e., potential warbler breeding habitat) within each region that changed from forest to other (i.e., forest loss) and other to forest (i.e., forest gain) during each time step (i.e., 2000–2010, 2010–2020, 2000–2020).

Projected breeding habitat distribution

We calculated the total area of predicted warbler breeding habitat (Mueller et al. 2022) per region and rangewide. We also calculated the total area of predicted warbler habitat within protected areas per region and rangewide based on polygons included in the World Database on Protected Areas (UNEP-WCMC and IUCN 2023). Next, we clipped projections from the U.S. Geological Survey’s CONUS FORE-SCE model (CONterminous United States FOREcasting SCEnarios of future land cover; Sohl et al. 2018) and the Environmental Protection Agency’s Integrated Climate and Land Use Scenarios (ICLUS) project (EPA 2020) to the spatial extent of the warbler breeding habitat model. The CONUS FORE-SCE model produced land use and land cover (LULC) projections at 1-year increments from 2006–2100 with a spatial resolution of 250 m (Sohl et al. 2018) under four anthropogenic land use scenarios described in the Intergovernmental Panel on Climate Change’s (IPCC’s) Special Report on Emissions Scenarios (Table 2; IPCC 2000). The ICLUS model produced LULC projections at 10-year increments from 2020–2100 with a spatial resolution of 90 m (EPA 2020) under four future scenarios of population, housing density, and impervious surface that are based on Representative Concentration Pathways (van Vuuren et al. 2011), Shared Socioeconomic Pathways (O’Neill et

al. 2014), and two climate models—the Hadley Global Environment Model 2 Atmosphere-Ocean (HadGEM2-AO) and the First Institute of Oceanography-Earth System Model (FIO-ESM) (Tables 3, 4).

Each model includes a wide variety of LULC classes (Tables 5 and 6). We focused on the developed land cover class from the CONUS FORE-SCE projections (Table 5) and combined the developed land cover classes from the ICLUS projections (Table 6) for this portion of our project, but acknowledge that warblers breed in some vegetation classified as developed by the models, and that land uses other than developed (e.g., agriculture) can result in habitat loss. Because the ICLUS model categorizes the entire spatial extent of military installations as “institutional”, but military installations in central Texas have warbler habitat, we excluded this land cover class from our analyses (Table 6). We then calculated the area of projected development per region and rangewide in 2020, 2050, and 2070. We included projections from both models because they were created using different techniques, spatial resolutions, timesteps, LULC classes, and have different definitions for developed cover (e.g., CONUS FORE-SCE characterizes its developed class as impervious cover whereas ICLUS characterizes developed classes based on factors such as housing density and land use; Tables 5 and 6; Sohl et al. 2018, EPA 2020). Both models represent a wide range of plausible scenarios and can provide information on overall trends of major LULC classes.

Table 2. Summary of Special Report on Emissions Scenarios developed by the Intergovernmental Panel on Climate Change (IPCC 2000) and included in the U.S. Geological Survey’s CONUS FORE-SCE model (CONterminous United States FORecasting SCEnarios of future land cover; Sohl et al. 2018).

Scenario	Description
A1B	Rapid economic growth, reduction in regional differences in income. Global population peaks ~2050 and declines thereafter, growth in more efficient technologies that are a balance of fossil intensive and non-fossil energy sources.
A2	Local self-reliance. Continuously increasing global population. Economic development is regionally oriented, economic growth and technological change slower than other scenarios.
B1	Global population peaks ~2050 and declines thereafter. Rapid changes in economic structures toward a service and information economy. Emphasis on introduction of clean and resource-efficient technologies, focuses on solutions to economic, social, and environmental sustainability globally.
B2	Local solutions to economic, social, and environmental sustainability; focuses on local and regional levels. Continuously increasing global population, though rate is lower than A2. Intermediate levels of economic development, less technology changes than A1 and B1.

Table 3. Summary of model inputs for the Environmental Protection Agency’s Integrated Climate and Land Use Scenarios models (EPA 2020).

Input	Definition
Shared Socioeconomic Pathway (SSP)	Qualitative descriptions of future demographics, development, economy, lifestyle, policies and institutions, technologies, and the environment; SSP1: low population growth, SSP5: high population growth
Representative Concentration Pathways (RCP)	A set of four trajectories for greenhouse gas concentrations based on underlying socioeconomic assumptions; RCP4.5: low emissions, RCP8.5: high emissions
HadGEM2-AO	Hadley Global Environment Model 2 Atmosphere-Ocean Climate model highly sensitive to global emissions
FIO-ESM	First Institute of Oceanography-Earth System Model Climate model less sensitive to global emissions

Table 4. Summary of scenarios included in the Environmental Protection Agency’s Integrated Climate and Land Use Scenarios models (EPA 2020).

Scenario ¹	Description
HadGEM2-AO SSP1-RCP4.5	Lower population growth and lower emissions scenarios with climate model highly sensitive to global carbon emissions
HadGEM2-AO SSP5-RCP8.5	Higher population growth and higher emissions scenarios with climate model highly sensitive to global carbon emissions
FIO-ESM SSP1-RCP4.5	Lower population growth and lower emissions scenarios with climate model less sensitive to global carbon emissions
FIO-ESM SSP5-RCP8.5	Higher population growth and higher emissions scenarios with climate model less sensitive to global carbon emissions

¹SSP: Shared Socioeconomic Pathways; RCP: Representative Concentration Pathways

Table 5. Land use classes included in the U.S. Geological Survey’s CONUS FORE-SCE model (CONterminous United States FORecasting SCEnarios of future land cover; Sohl et al. 2018). We created a web application (see below), called the Golden-cheeked Warbler Habitat Explorer, that only included the developed land class from the CONUS FORE-SCE model (see “App class”).

Class Name	App class
Water	-
Developed	Developed
Mechanically disturbed National Forests	-
Mechanically disturbed other public lands	-
Mechanically disturbed private	-
Mining	-
Barren	-
Deciduous forest	-
Evergreen forest	-
Mixed forest	-
Grassland	-
Shrubland	-
Cropland	-
Hay/pasture land	-
Herbaceous wetland	-
Woody wetland	-
Perennial ice/snow	-

Table 6. Land use classes included in the Environmental Protection Agency’s Integrated Climate and Land Use Scenarios project (EPA 2020). We created a web application (see below), called the Golden-cheeked Warbler Habitat Explorer, that only included developed land classes from the ICLUS model (see “App class”).

Class Name	Additional info	App class
Natural water		-
Reservoirs, canals		-
Wetlands		-
Recreation, conservation		-
Timber		-
Grazing		-
Pasture		-
Cropland		-
Mining, barren land		-
Parks, golf courses		Developed
Exurban, low density	0.02–0.1 DUA ¹	Developed
Exurban, high density	0.1–0.4 DUA ¹	Developed
Suburban	0.4 – 1.6 DUA ¹	Developed
Urban, low density	1.6–10 DUA ¹	Developed
Urban, high density	>10 DUA ¹	Developed
Commercial		Developed
Industrial		Developed
Institutional		-
Transportation		Developed

¹DUA = dwelling units/acre

Golden-cheeked Warbler Habitat Explorer

In addition to the paper maps and spatial data we generated for our project, we created an interactive web-based tool that can be used to support strategic conservation planning for the warbler and demonstrate a mapping application that can enhance decision-making for other listed or at-risk species that occur on DoD lands. There are several software programs and platforms available for creating interactive web-based maps, but we chose Google Earth Engine (GEE) for the current project because GEE apps can utilize the extensive collection of geospatial data sets hosted on the GEE platform; can process and analyze large-scale geospatial datasets; can be easily updated to include new information as it becomes available; have free and user-friendly interfaces that do not require knowledge of remote sensing or GIS; and can be accessed by specific users without a GEE account from an application-specific URL, restricted for use by members of a private Google Group or made available to the public. GEE apps are built with the same functions used in GEE's code editor and have been used by researchers to develop tools that analyze volcanic thermal anomalies at a global scale (Genzano et al. 2020), map rangewide habitat suitability for the endangered Yuma Ridgeway's rail (*Rallus obsoletus yumanensis*; Harrity et al. 2020), and monitor algae blooms in South American reservoirs and lakes (Lobo et al. 2021), among others.

Within the app, which we called the Golden-cheeked Warbler Habitat Explorer, users can display warbler distribution models for the breeding and winter ranges, projected land cover, utilization distributions that we created for the warbler's migration route and wintering grounds, and locations of formally protected areas across the species' breeding and non-breeding ranges (Table 7). Users can also identify an area of interest (AOI) and use a function to highlight breeding habitat within the AOI that meets user-specified minimum patch size requirements to examine appropriate areas for management. We restricted the minimum threshold to 20 ha, which aligns with minimum patch size for warbler reproductive success according to Butcher et al. (2010).

The app includes a model of warbler density estimated across the species' breeding range by Mueller et al. (2022) (Table 7). It also includes our models of potential warbler winter habitat and the 75% utilization distributions for the warbler's migration route and wintering grounds that we created using our geolocator data (Table 7). In addition, we incorporated the land use and land cover (LULC) projections from USGS CONUS FORE-SCE model (CONterminous United States FORecasting SCENarios of future land cover; Sohl et al. 2018) and the Environmental Protection Agency's Integrated Climate and Land Use Scenarios (ICLUS) project (EPA 2020) described above (Tables 5 and 6). The World Database on Protected Areas that we included in the app provides the boundaries of wilderness areas, reserves, refuges, and others (Table 7; UNEP-WCMC and IUCN 2023) within and adjacent to the warbler's breeding range, migration route, and wintering range. See results and Appendix 10.B for more information.

Table 7. Layers included in the Golden-cheeked Warbler Habitat Explorer web application.

Dataset	Years	Type	Resolution
Golden-cheeked warbler density model ¹	2022	Raster	10 m
Conterminous United States Land Cover Projections	2010–2100	Raster	250 m
Integrated Climate and Land Use Scenarios	2000–2100	Raster	90 m
Golden-cheeked warbler wintering habitat model ²	2019, 2050, 2070	Raster	1 km
Copernicus Global Digital Elevation Model GLO-30 ³	2010–2015	Raster	30 m
World Database on Protected Areas	2023	Vector	NA
Mean migratory stationary period 75% utilization distributions ²	2017–2020	Vector	NA
Mean overwintering period 75% utilization distributions ²	2017–2020	Vector	NA

¹Data from Mueller et al. 2022

²Data created in our project

³Data used to visualize the wintering habitat model in our web application; GLO-30 data © DLR e.V. 2010-2014 and © Airbus Defence and Space GmbH 2014–2018 provided under COPERNICUS by the European Union and ESA; all rights reserved.

6. Results

Geolocator data

Summary

We attached 309 geolocators to male warblers across our study sites and recovered 80 (26%) of the devices (Table 8). Three males returned to the breeding grounds without their geolocators, and we were unable to use the light spectrums recorded by 19 (24%) of the geolocators that we recovered due to poor or corrupt data. Thus, our final analyses included 61 data sets (28 SY, 33 ASY). Fifty-five of the 61 geolocators (90%) recorded data from the date of attachment through the date we recovered the geolocator ($\bar{x}$ = 346 d, SD = 49.68 d) and 6 geolocators (10%) recorded light data from the date of attachment through at least 01 Dec ($\bar{x}$ = 251 d, SD = 74.85 d). The average distance from the warbler capture locations to the mean breeding season locations estimated from the geolocator data was 26.0 km (SD = 33.9 km) for latitude and 23.6 km (SD = 31.4) for longitude. See Table A.3 in the Appendix for error estimates by study site. We present the means and SD distances for the upper and lower credible intervals (latitudes and longitudes) per period (breeding, fall migration, winter, and spring migration) in Table 9.

Table 8. Summary of the mean and standard deviation distances (km) for the upper and lower credible intervals (latitudes and longitudes) per period (breeding, fall migration, winter, and spring migration) based on data from 61 light-level geolocators attached to golden-cheeked warblers (*Setophaga chrysoparia*) (2017–2021).

Location	2017 2018	2018 2019	2019 2020	2020 2021	All
DVSP	15 5 ^a	0 0	13 4	11 2	39 11
FCMI	25 12	19 6	28 7	18 6	90 31
BCNWR	20 7 ^a	0 1	20 3 ^a	20 7	60 18
CB	20 1	20 2	20 0	0 0	60 3
KWMA	20 2	0 0	20 5	20 10	60 17

^aNumber does not include one warbler captured without the geocator we attached to the individual during the previous breeding season.

Table 9. Summary of light-level geolocators attached to golden-cheeked warblers (*Setophaga chrysoparia*) per study site and year. Columns represent year the geocator was deployed | year the geocator was retrieved.

	Breeding	Fall Migration	Winter	Spring Migration
UCL Latitude	$\bar{x}$ = 76.66 SD = 97.77	$\bar{x}$ = 389.96 SD = 322.19	$\bar{x}$ = 214.42 SD = 213.31	$\bar{x}$ = 509.95 SD = 238.86
LCL Latitude	$\bar{x}$ = 139.99 SD = 175.54	$\bar{x}$ = 313.30 SD = 244.42	$\bar{x}$ = 171.09 SD = 116.66	$\bar{x}$ = 527.73 SD = 255.53
UCL Longitude	$\bar{x}$ = 46.66 SD = 63.33	$\bar{x}$ = 198.87 SD = 152.21	$\bar{x}$ = 114.43 SD = 86.66	$\bar{x}$ = 216.64 SD = 129.99
LCL Longitude	$\bar{x}$ = 67.77 SD = 78.88	$\bar{x}$ = 213.31 SD = 162.21	$\bar{x}$ = 107.77 SD = 95.55	$\bar{x}$ = 188.87 SD = 123.32

Post-breeding movements

On average, warblers spent 24 d (SD = 24 d, R = 0–83 d) traveling and moved 205 km (SD = 155 km, R = 0–599 km) from their breeding site to their furthest stationary location prior to fall migration (i.e., post-breeding movements) (Fig. 18). In total, 59% of individuals (n = 36) made post-breeding movements outside of the warbler’s breeding range in Texas; virtually all traveled in a west to north direction from the study site where they were captured during the breeding season, which included stopovers in New Mexico, Oklahoma, the Texas Panhandle, and west Texas (Fig. 18). Thirty-nine percent of warblers (n = 24) stayed within the warbler’s breeding range during the post-breeding period (Fig. 18). One warbler did not exhibit any post-breeding movements; this individual initiated migration immediately upon its departure from the study site where it was captured during the breeding season. We found no difference ($t_{59} = -0.09$, $P = 0.93$) between age classes with regards to furthest distance traveled during the post-breeding period (SY: $\bar{x}$ = 204 km, SD = 141 km, R = 19–504 km; ASY: $\bar{x}$ = 207 km, SD = 170 km, R = 0–599 km). However, we did find an age-based difference in departure dates ($t_{59} = 3.27$, $P < 0.01$) whereby SY males initiated fall migration several days before ASY males (SY: $\bar{x}$ = 01 Aug, SD = 13 d, R = 1 Jul–3 Sep; ASY: $\bar{x}$ = 11 Aug, SD = 11 d, R = 21 Jul–01 Sep).

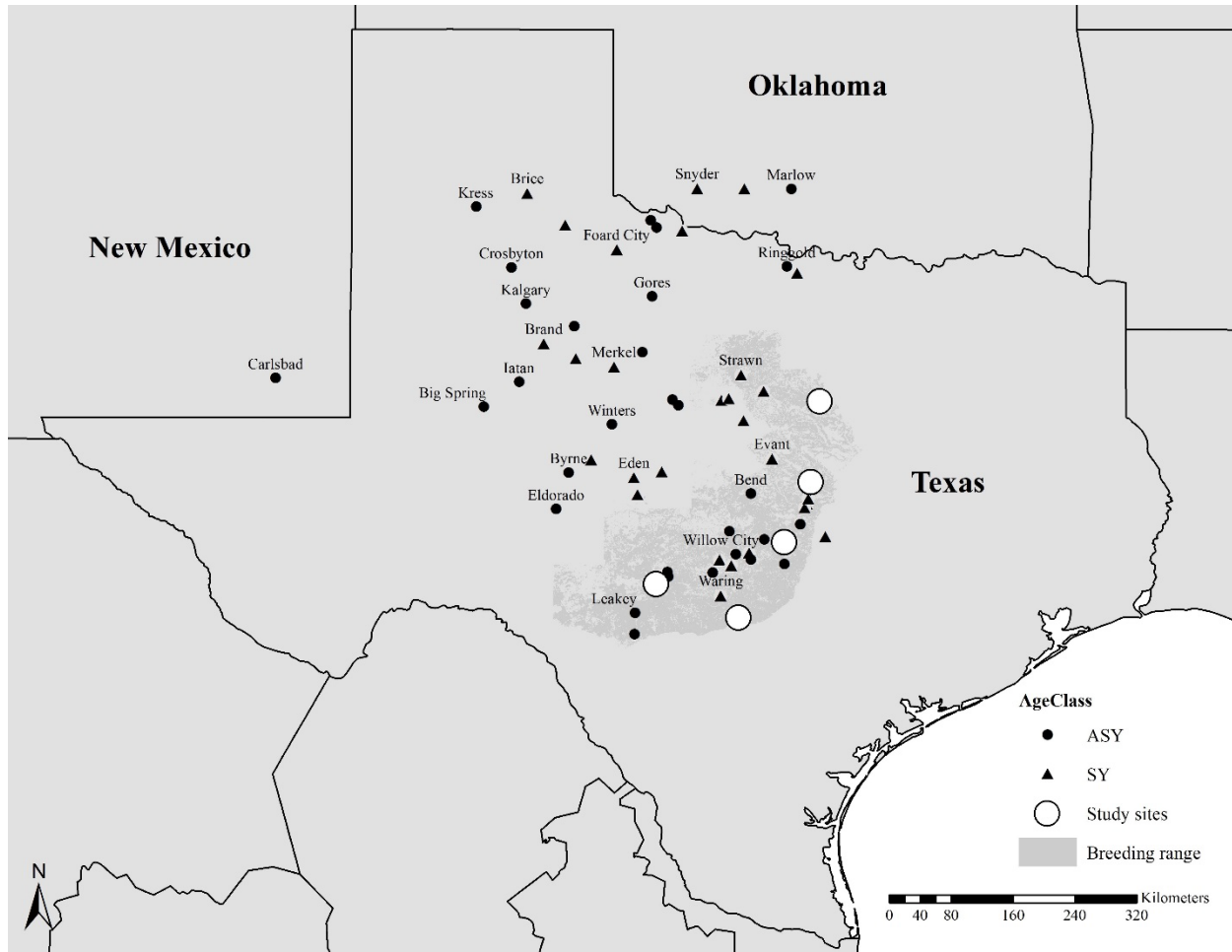


Figure 18. Furthest post-breeding stationary period of male golden-cheeked warblers (*Setophaga chrysoparia*; $n = 61$) prior to fall migration based on data from 61 light-level geolocators (2017–2021).

Fall and spring migration

Warblers initiated fall migration over a two-month period from early July to early September (Fig. 19, 20; Table 10). On average, warblers arrived on their wintering grounds 36 d after they left the breeding grounds, spent 165 d on their wintering grounds, initiated spring migration over a two-month period from mid-January to mid-March, and arrived on the breeding grounds 27 d after they left the wintering grounds (Fig. 19, 20; Table 10). The average distance from their last overwintering location to their capture location on the breeding grounds was 1,863 km (SD = 321 km, $R = 1,283$ –2,576 km). Eighty percent of warblers ($n = 49$) migrated along the Sierra Madres in fall, but 20% migrated over the Gulf of Mexico during fall ($n = 11$) or spring ($n = 1$) (Fig. 19, 21, 22; Table 10). Trans-Gulf migrants represented 21% of SY warblers ($n = 6$ of 28) and 18% of ASY warblers ($n = 6$ of 33) (Fig. 22).

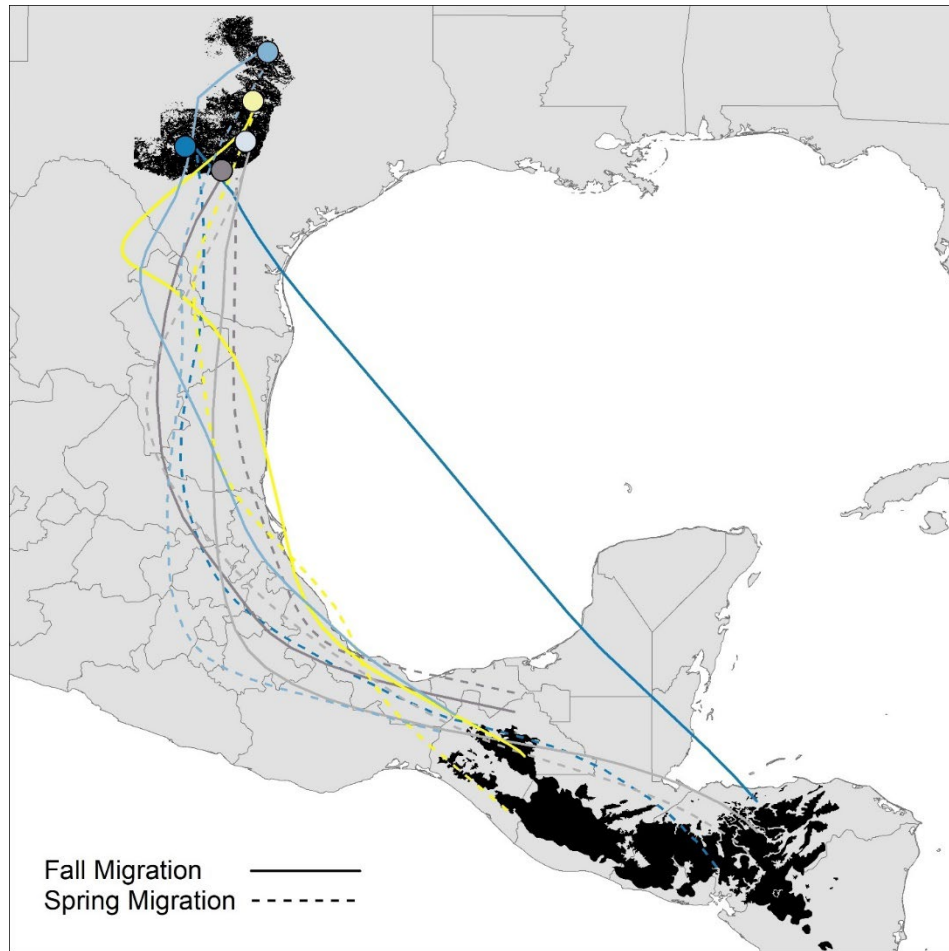


Figure 19. Example migration paths for one golden-cheeked warbler (*Setophaga chrysoparia*) per study site based on data from light-level geolocators.

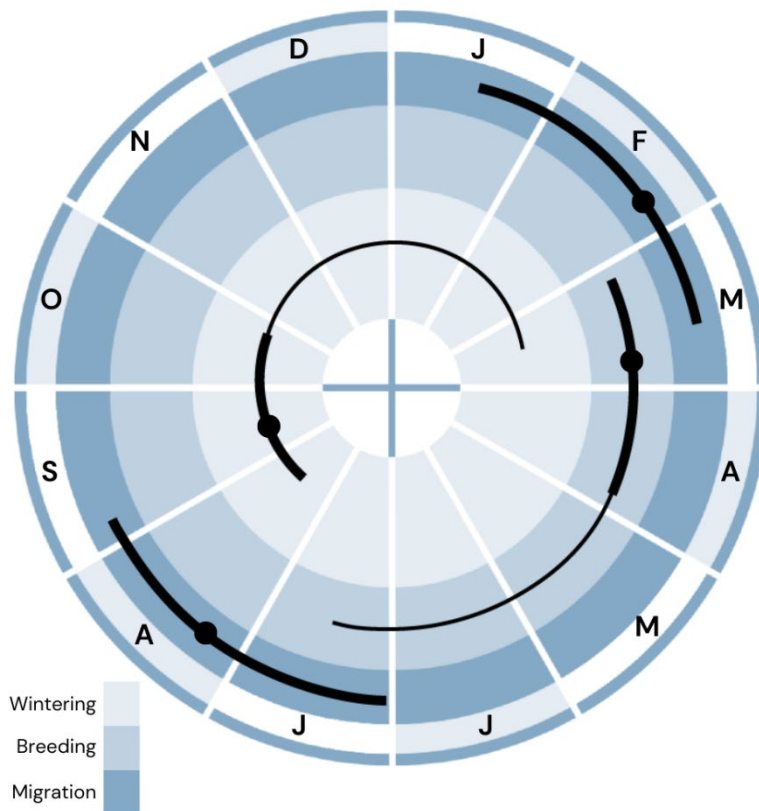


Figure 20. Golden-cheeked warbler (*Setophaga chrysoparia*) phenology based on data obtained from 61 light-level geolocators (2017–2021). Figure adapted from Birds of the World species accounts (<https://birdsoftheworld.org/bow/home>).

Table 10. Summary of departure/arrival dates and migration durations for male golden-cheeked warblers (*Setophaga chrysoparia*) based on data we obtained from 61 light-level geolocators (2017–2021).

Overall	Fall migration (n = 61) ^a	Spring migration (n = 55) ^a
Departure date	$\bar{x}$ = 06 Aug, SD = 12.93 d R = 01 Jul–03 Sep	$\bar{x}$ = 25 Feb, SD = 11.05 d R = 18 Jan–19 Mar
Duration	$\bar{x}$ = 36.44 d, SD = 18.63 d R = 5–106 d	$\bar{x}$ = 26.89 d, SD = 14.11 d R = 5–66 days
Arrival date	$\bar{x}$ = 11 Sep, SD = 19.04 d R = 13 Aug–27 Oct	$\bar{x}$ = 24 Mar, SD = 11.45 d R = 04 Mar–24 Apr
Land	Fall migration (n = 49)	Spring migration (n = 46)
Departure date	$\bar{x}$ = 05 Aug, SD = 10.65 d R = 19 Jul–01 Sep	$\bar{x}$ = 27 Feb, SD = 9.69 d R = 26 Jan–19 Mar
Duration	$\bar{x}$ = 34.27 d, SD = 14.33 d R = 5–78 days	$\bar{x}$ = 26.22 d, SD = 13.58 d R = 5–63 d
Arrival date	$\bar{x}$ = 08 Sep, SD = 17.31 d R = 13 Aug–27 Oct	$\bar{x}$ = 24 Mar, SD = 11.70 d R = 04 Mar–24 Apr
Gulf	Fall migration (n = 12)	Spring migration (n = 9)
Departure date	$\bar{x}$ = 12 Aug, SD = 19.27 d R = 01 Jul–03 Sep	$\bar{x}$ = 21 Feb, SD = 16.49 d R = 19 Jan–10 Mar
Duration	$\bar{x}$ = 45.33 d, SD = 30.04 d R = 8–106 d	$\bar{x}$ = 30.33 d, SD = 16.65 d R = 5–66 d
Arrival date	$\bar{x}$ = 26 Sep, SD = 18.63 d R = 24 Aug–06 Oct	$\bar{x}$ = 23 Mar, SD = 9.56 d R = 13 Mar–13 Apr

^aAbbreviations: $\bar{x}$ = mean, SD = standard deviation, d = days, R = range

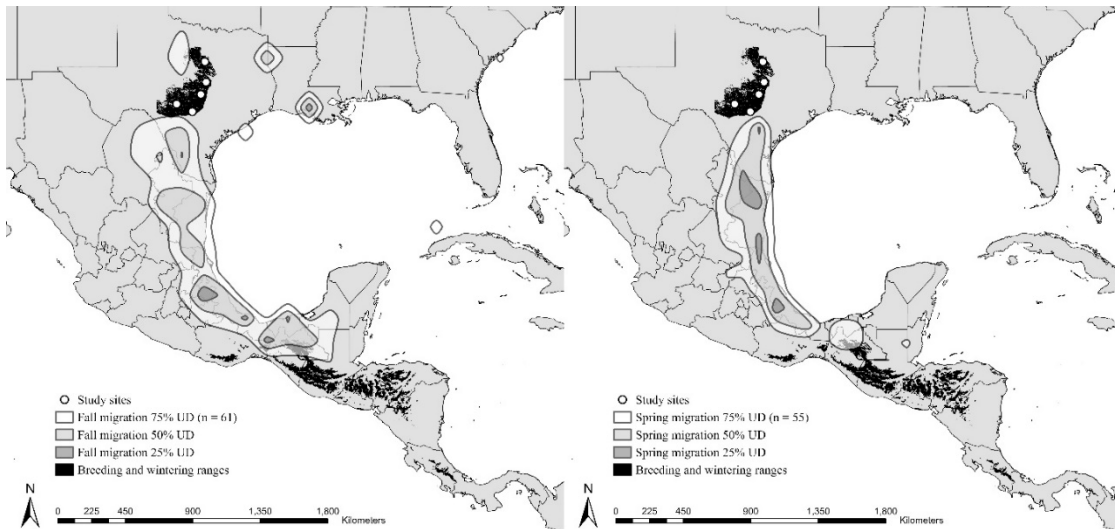


Figure 21. Utilization distributions for fall (left) and spring (right) migration of male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021).

Of the fall trans-Gulf migrants, two departed from Texas, three departed from Louisiana, one departed from Alabama, and five departed from Florida (Fig. 22). The one spring trans-Gulf migrant we identified departed from the Yucatán peninsula and arrived in Louisiana before traveling west to the warbler's breeding grounds (Fig. 22). Most trans-Gulf migrants were located at three study sites during the breeding season (29% from DVSP, 22% from FCMI, and 22% from KWMA); 7% were located at BCNWR during the breeding season and we did not identify any trans-Gulf migrants that spent the breeding season at CB. We had insufficient and uneven sample sizes to make statistical comparisons between warblers that migrated over land and warblers that completed trans-Gulf migrations. However, departure dates for fall and spring migration, the durations of fall and spring migrations, and the fall migration distances were similar between the two groups (Table 10).

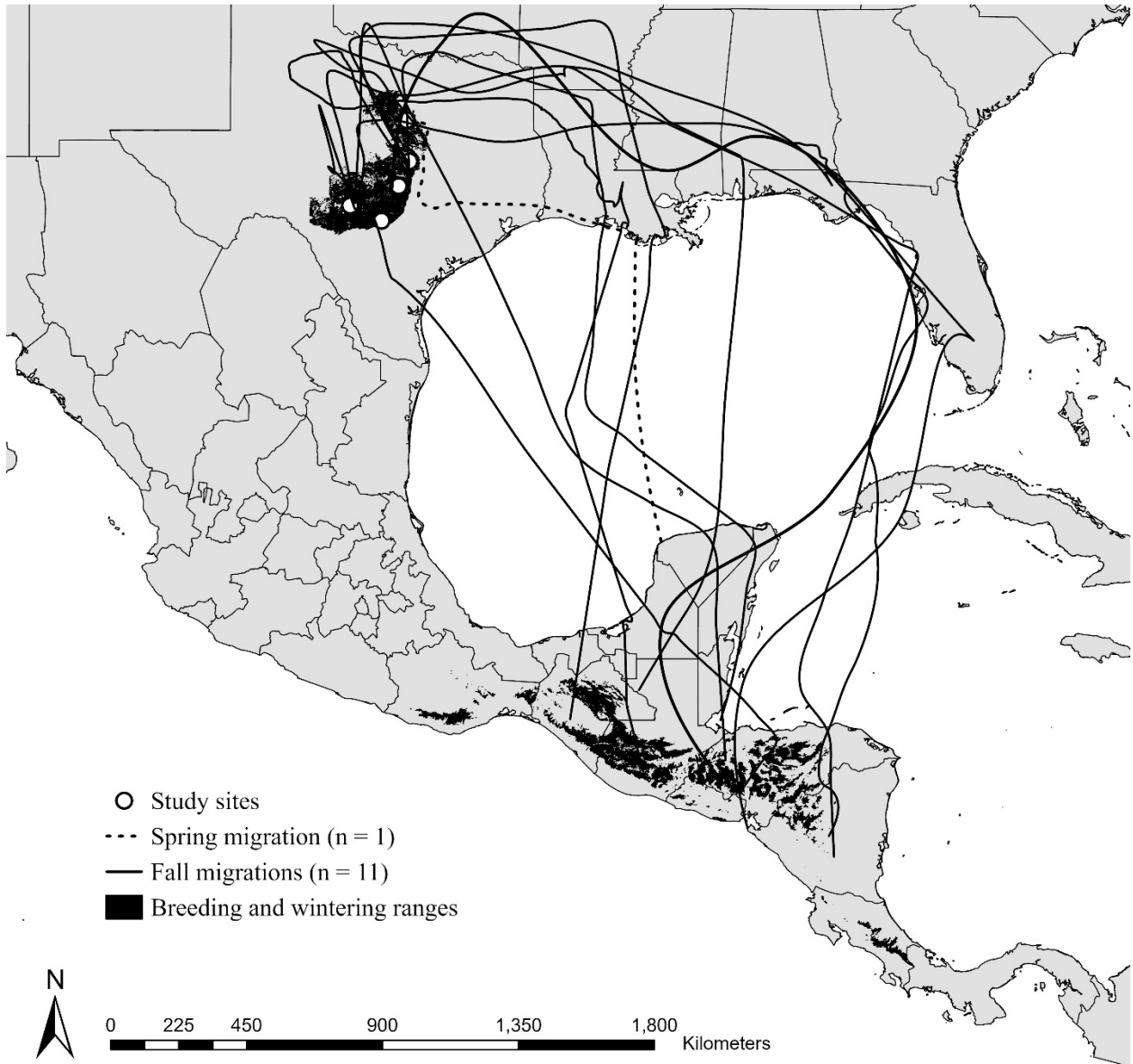


Figure 22. Trans-gulf migration routes of male golden-cheeked warblers (*Setophaga chrysoparia*; $n = 12$) based on data from 61 light-level geolocators (2017–2021).

We had datasets representing both spring and fall migration for 55 warblers. Fall migration was longer ($\bar{x} = 37$ d, $SD = 19$ d, $R = 5\text{--}106$ d) than spring migration ($\bar{x} = 27$ d, $SD = 14$ d, $R = 5\text{--}66$ d) ($t_{54} = 3.34$, $P < 0.01$). We found no correlations between fall and spring departure dates ($r = -0.02$, $P = 0.86$), fall and spring arrival dates ($r = 0.17$, $P = 0.23$), or spring departure and arrival dates ($r = 0.21$, $P = 0.13$). However, we did find a moderate and positive correlation between fall departure and arrival dates ($r = 0.34$, $P = 0.01$). We found no statistically significant differences between initiation dates for fall or spring migration, the durations of fall or spring migrations, or the distances of fall or spring migrations across study sites (Fig. 23, Table 11) or years (Fig. 24, Table 12). When we compared these metrics for SY and ASY warblers, we found no statistically significant differences between initiation dates for spring

migration, the durations for fall or spring migration, or the distances of fall or spring migration (Fig. 25, Table 13). However, SY warblers initiated their fall migrations earlier than ASY warblers (Fig 25, Table 13).

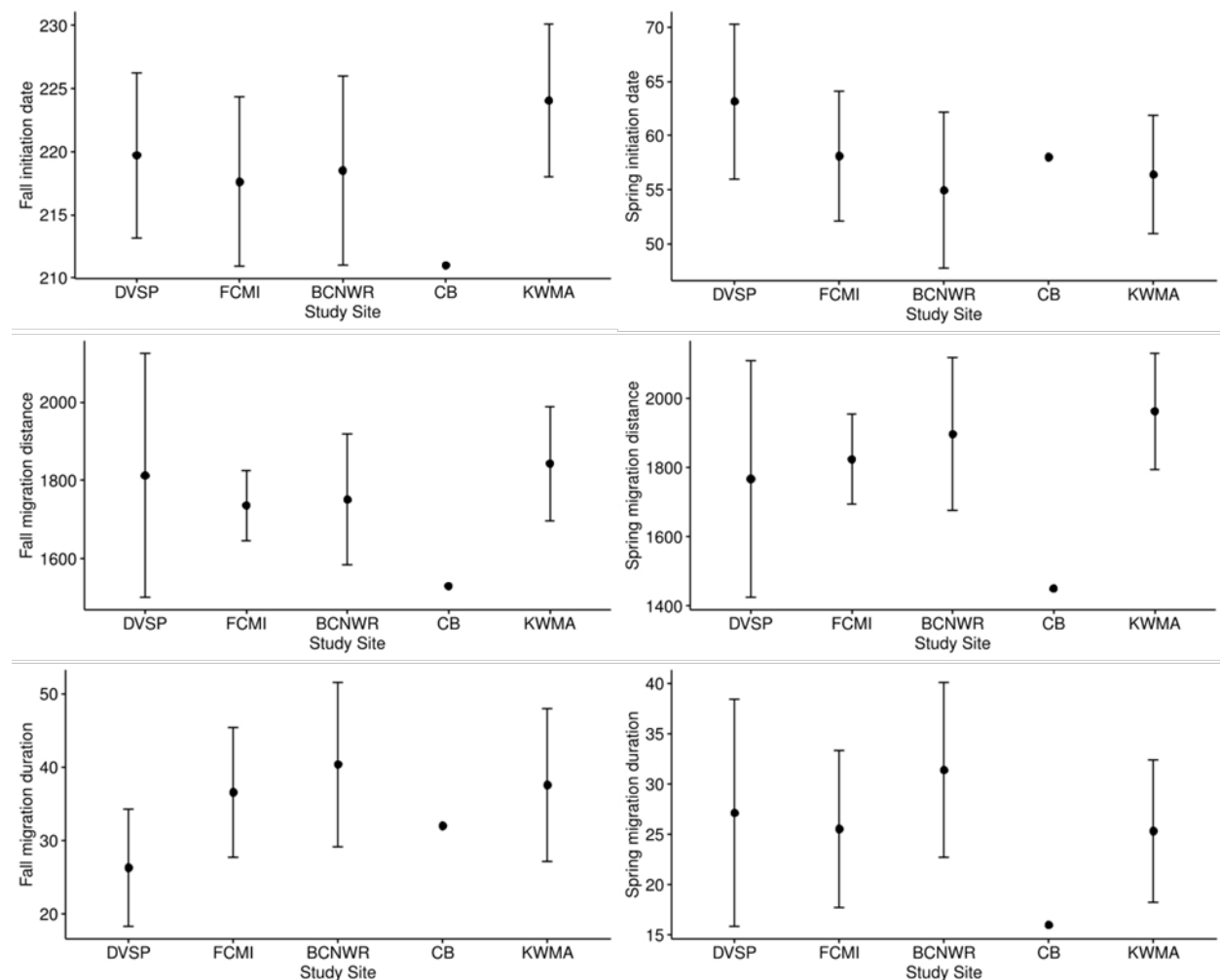


Figure 23. Comparisons of fall and spring migration initiation dates (Julian date), fall and spring migration durations (days), and fall and spring migration distances (km) across study sites for male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021). Our study sites included Dinosaur Valley State Park (DVSP), Fort Cavazos Military Installation (FCMI), Balcones Canyonlands National Wildlife Refuge (BCNWR), Joint Base San Antonio-Camp Bullis (CB), and Kerr Wildlife Management Area (KWMA) in Texas. Figure includes points for CB, but CB data were excluded from analyses due to low sample sizes. See Table 11 for more details.

Table 11. Summary of means ($\bar{x}$), standard deviations (SD), ranges (R), and results from our analysis of variance tests comparing fall and spring migration initiation dates (Julian date), fall and spring migration durations (days [d]), and fall and spring migration distances (km) across study sites for male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021). Our study sites included Dinosaur Valley State Park (DVSP), Fort Cavazos Military Installation (FCMI), Balcones Canyonlands National Wildlife Refuge (BCNWR), Joint Base San Antonio-Camp Bullis (CB), and Kerr Wildlife Management Area (KWMA) in Texas. See Fig. 23 for more details.

	DVSP (n = 7)	FCMI (n = 23)	BCNWR (n = 14)	CB (n = 1)	KWMA (n = 16)	Results
Fall initiation	$\bar{x}$ = 07 Aug SD = 7.06 d R = 29 Jul–17 Aug	$\bar{x}$ = 05 Aug SD = 15.50 d R = 01 Jul–03 Sep	$\bar{x}$ = 05 Aug SD = 13.00 d R = 18 Jul–31 Aug	29 Jul . .	$\bar{x}$ = 11 Aug SD = 11.30 d R = 29 Jul–01 Sep	$F_{4,56} = 0.72$ P = 0.58
Fall duration	$\bar{x}$ = 26.3 d SD = 8.67 d R = 14–39 d	$\bar{x}$ = 36.6 d SD = 20.40 d R = 15–106 d	$\bar{x}$ = 40.4 d SD = 19.30 d R = 16–91	32 d . .	$\bar{x}$ = 37.6 d SD = 19.05 d R = 5–73 d	$F_{4,56} = 0.67$ P = 0.61
Fall distance	$\bar{x}$ = 1,812 km SD = 337 km R = 1,546–2,546 km	$\bar{x}$ = 1,736 km SD = 208 km R = 1,110–2,151 km	$\bar{x}$ = 1,751 km SD = 289 km R = 1,439–2,291 km	1,530 km . .	$\bar{x}$ = 1,843 km SD = 276 km R = 1,460–2,184 km	$F_{4,56} = 0.67$ P = 0.61
Spring initiation	$\bar{x}$ = 03 Mar SD = 7.71 d R = 18 Feb–10 Mar	$\bar{x}$ = 27 Feb SD = 12.70 d R = 19 Jan–17 Mar	$\bar{x}$ = 23 Feb SD = 11.09 d R = 26 Jan–11 Mar	27 Feb . .	$\bar{x}$ = 25 Feb SD = 9.83 d R = 05 Feb–19 Mar	$F_{4,51} = 0.66$ P = 0.63
Spring duration	$\bar{x}$ = 27.1 d SD = 12.20 d R = 13–43 d	$\bar{x}$ = 25.5 d SD = 16.20 d R = 5–66 d	$\bar{x}$ = 31.4 d SD = 14.40 d R = 10–60 d	16 d . .	$\bar{x}$ = 25.3 d SD = 12.80 d R = 9–63 d	$F_{4,50} = 0.55$ P = 0.70
Spring distance	$\bar{x}$ = 1,767 km SD = 370 km R = 1,420–2,565 km	$\bar{x}$ = 1,823 km SD = 286 km R = 1,283–2,527 km	$\bar{x}$ = 1,897 km SD = 365 km R = 1,471–2,565 km	1,451 km . .	$\bar{x}$ = 1,962 km SD = 302 km R = 1,456–2,538 km	$F_{4,52} = 1.05$ P = 0.39

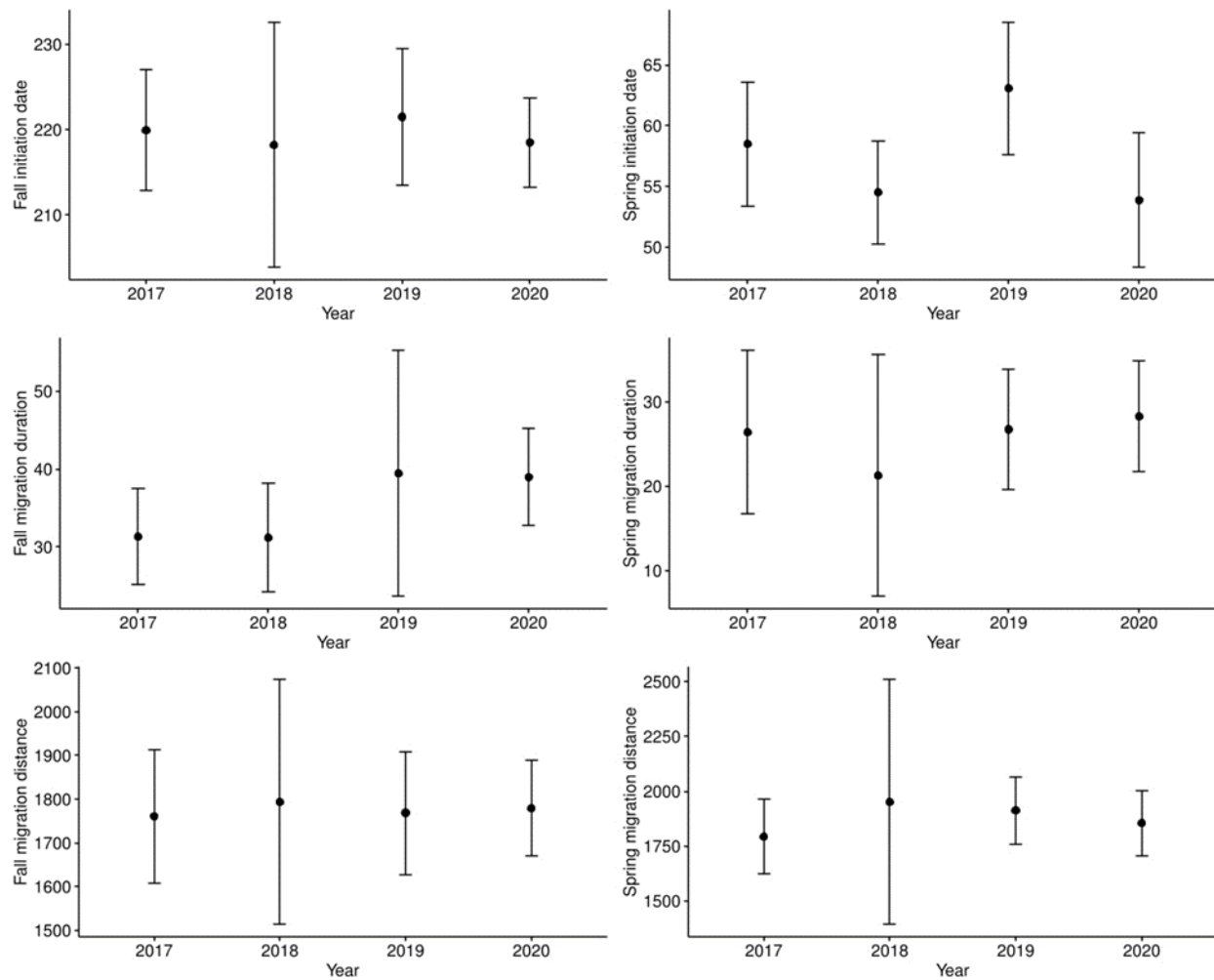


Figure 24. Comparisons of fall and spring migration initiation dates (Julian date), fall and spring migration durations (days), and fall and spring migration distances (km) across years for male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021). Our study sites included Dinosaur Valley State Park (DVSP), Fort Cavazos Military Installation (FCMI), Balcones Canyonlands National Wildlife Refuge (BCNWR), Joint Base San Antonio-Camp Bullis (CB), and Kerr Wildlife Management Area (KWMA) in Texas. Figure includes points for CB, but CB data were excluded from analyses due to low sample sizes. See Table 12 for more details.

Table 12. Summary of means ($\bar{x}$), standard deviations (SD), ranges (R), and results from our analysis of variance tests comparing fall and spring migration initiation dates (Julian date), fall and spring migration durations (days [d]), and fall and spring migration distances (km) across years for male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021). Our study sites included Dinosaur Valley State Park, Fort Cavazos Military Installation, Balcones Canyonlands National Wildlife Refuge, Joint Base San Antonio-Camp Bullis, and Kerr Wildlife Management Area in Texas. See Fig. 24 for more details.

Year	2017 (n = 16)	2018 (n = 5)	2019 (n = 16)	2020 (n = 24)	Results
Fall initiation	$\bar{x}$ = 07 Aug SD = 13.20 d R = 21 Jul–03 Aug	$\bar{x}$ = 05 Aug SD = 11.60 d R = 26 Jul–21 Aug	$\bar{x}$ = 09 Aug SD = 15.00 d R = 01 Jul–31 Aug	$\bar{x}$ = 05 Aug SD = 12.50 d R = 19 Jul–31 Aug	$F_{3,57} = 0.19$ P = 0.91
Fall duration	$\bar{x}$ = 21.3 d SD = 11.60 d R = 16–62 d	$\bar{x}$ = 31.2 d SD = 5.63 d R = 23–38 d	$\bar{x}$ = 39.4 d SD = 29.60 d R = 5–106	$\bar{x}$ = 39.0 d SD = 14.70 d R = 8–78 d	$F_{3,57} = 0.80$ P = 0.50
Fall distance	$\bar{x}$ = 1,761 km SD = 287 km R = 1,110–2,291 km	$\bar{x}$ = 1,794 km SD = 226 km R = 1,530–2,151 km	$\bar{x}$ = 1,769 km SD = 264 km R = 1,514–2,546 km	$\bar{x}$ = 1,779 km SD = 259 km R = 1,439–2,180 km	$F_{3,57} = 0.03$ P = 1.00
Spring initiation	$\bar{x}$ = 27 Feb SD = 8.86 d R = 16 Feb–14 Mar	$\bar{x}$ = 23 Feb SD = 2.65 d R = 21 Feb–27 Feb	$\bar{x}$ = 03 Mar SD = 9.80 d R = 18 Feb–19 Mar	$\bar{x}$ = 22 Mar SD = 12.80 d R = 19 Feb–10 Mar	$F_{3,52} = 2.36$ P = 0.08
Spring duration	$\bar{x}$ = 26.4 d SD = 16.00 d R = 9–63 d	$\bar{x}$ = 21.2 d SD = 9.00 d R = 14–34 d	$\bar{x}$ = 26.7 d SD = 12.90 d R = 5–51 d	$\bar{x}$ = 28.3 d SD = 15.10 d R = 6–66 d	$F_{3,51} = 0.28$ P = 0.84
Spring distance	$\bar{x}$ = 1,761 km SD = 293 km R = 1,283–2,382 km	$\bar{x}$ = 1,951 km SD = 450 km R = 1,451–2,527 km	$\bar{x}$ = 1,914 km SD = 277 km R = 1,420–2,576 km	$\bar{x}$ = 1,854 km SD = 345 km R = 1,456–2,565 km	$F_{3,53} = 0.47$ P = 0.71

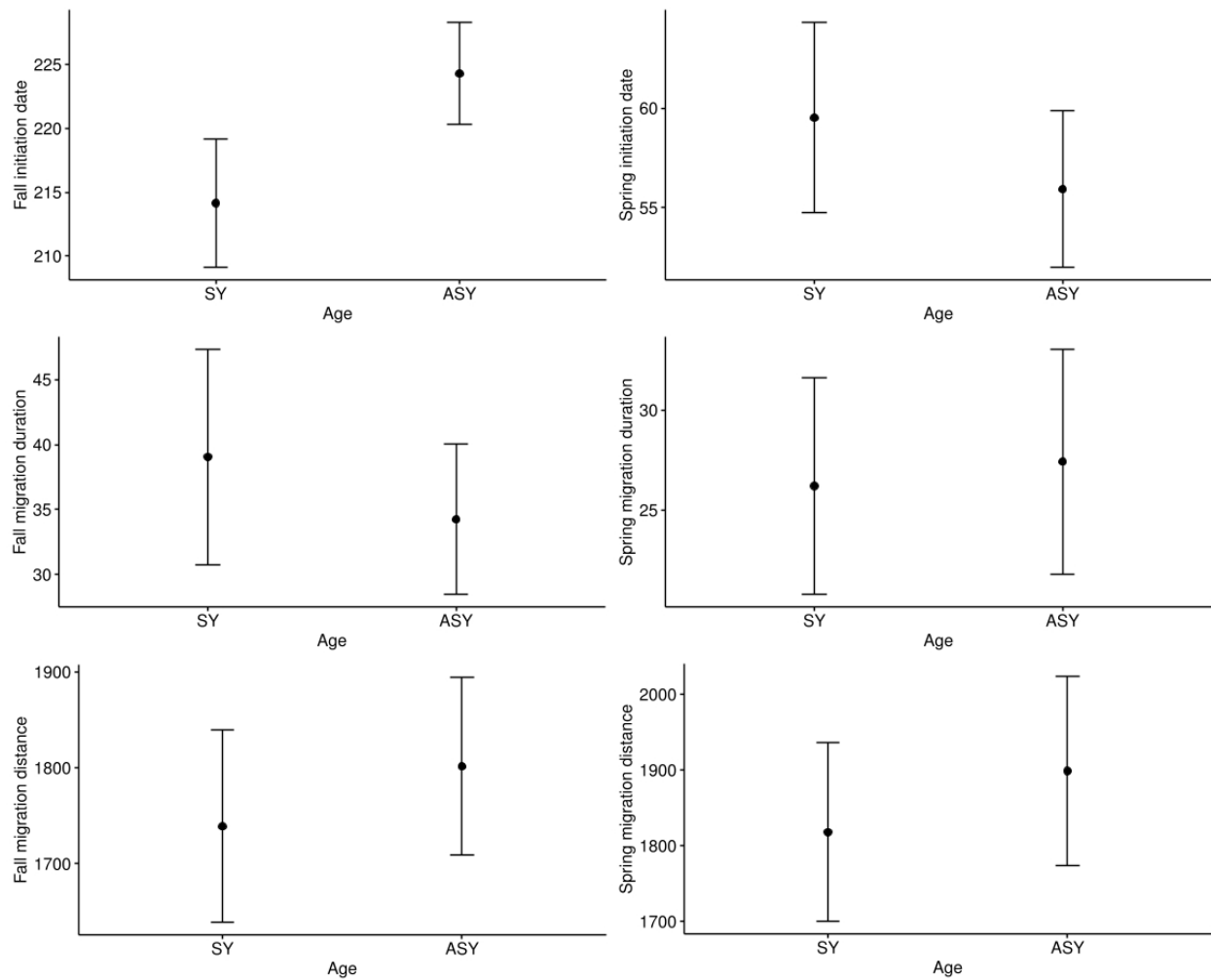


Figure 25. Comparisons of fall and spring migration initiation dates (Julian date), fall and spring migration durations (days), and fall and spring migration distances (km) between second year (SY) and after second year (ASY) male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021). Our study sites included Dinosaur Valley State Park, Fort Cavazos Military Installation, Balcones Canyonlands National Wildlife Refuge, Joint Base San Antonio-Camp Bullis, and Kerr Wildlife Management Area in Texas. See Table 13 for more details.

Table 13. Summary of means ($\bar{x}$), standard deviations (SD), ranges (R), and results from our *t*-tests comparing migration durations (days) and fall and spring migration distances (km) between second year (SY) and after second year (ASY) male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021). Our study included Dinosaur Valley State Park, Fort Cavazos Military Installation, Balcones Canyonlands National Wildlife Refuge, Joint Base San Antonio-Camp Bullis, and Kerr Wildlife Management Area in Texas. See Fig. 25 for more details.

	SY ^a (n = 28)	ASY ^a (n = 33)	Results
Fall initiation	$\bar{x}$ = 01 Aug SD = 13.00 d R = 01 Jul–03 Sep	$\bar{x}$ = 11 Aug SD = 11.30 d R = 21 Jul–01 Sep	$t_{59} = 3.27$ P = 0.00
Fall duration	$\bar{x}$ = 39.0 d SD = 21.3 d R = 8–106 d	$\bar{x}$ = 34.2 d SD = 16.30 d R = 5–73 d	$t_{59} = 0.99$ P = 0.33
Fall distance	$\bar{x}$ = 1,739 km SD = 258 km R = 1,439–2,546 km	$\bar{x}$ = 1,802 km SD = 261 km R = 1,110–2,291 km	$t_{59} = 0.94$ P = 0.35
Spring initiation	$\bar{x}$ = 28 Feb SD = 11.60 d R = 26 Jan–17 Mar	$\bar{x}$ = 24 Feb SD = 10.70 d R = 19 Jan–19 Mar	$t_{54} = 1.20$ P = 0.24
Spring duration	$\bar{x}$ = 26.2 d SD = 12.90 d R = 5–60 d	$\bar{x}$ = 27.4 d SD = 15.30 d R = 9–66 d	$t_{53} = 0.31$ P = 0.76
Spring distance	$\bar{x}$ = 1,818 km SD = 286 km R = 1,456–2,576 km	$\bar{x}$ = 1,899 km SD = 346 km R = 1,283–2,565 km	$t_{55} = 0.94$ P = 0.35

^aAbbreviations: $\bar{x}$ = mean, SD = standard deviation, d = days, R = range

Stopover locations

Warblers made 0–5 stopovers ($\bar{x} = 1.72$ stopovers, $SD = 1.04$ stopovers) and were stationary for 0–54 d per stopover ($\bar{x} = 10.30$ d, $SD = 9.49$ d) during fall migration. Warblers also made 0–5 stopovers ($\bar{x} = 1.64$ stopovers, $SD = 1.15$ stopovers) during spring migration and were stationary for 0–65 d per stopover ($\bar{x} = 10.30$ d, $SD = 12.67$ d) (Fig. 26). We found no differences in the number of stopovers ($t_{52} = 0.81$, $P = 0.42$) or the durations per stopover ($t_{91} = 0.00$, $p = 1.00$) between fall and spring migration. However, the duration of stopovers varied along the warbler’s migration route with the longest duration (>40 d) stopovers occurring in southern Texas; along the coast of Tamaulipas in Mexico; and at the junction of Veracruz, Puebla, and Oaxaca, Mexico (Fig. 26). We used all stopover data to construct UD_s for the warbler’s migration route (Fig. 27). Based on the 50% UD_s, the two largest stopover locations used by warblers during fall and spring migration were both located in Mexico; the northernmost 50% UD included portions of Nuevo Leon, Tamaulipas, Coahuila, and Veracruz and the southernmost 50% UD included portions of Veracruz, Hidalgo, Tlaxcala, Puebla, and Oaxaca (Fig. 27).

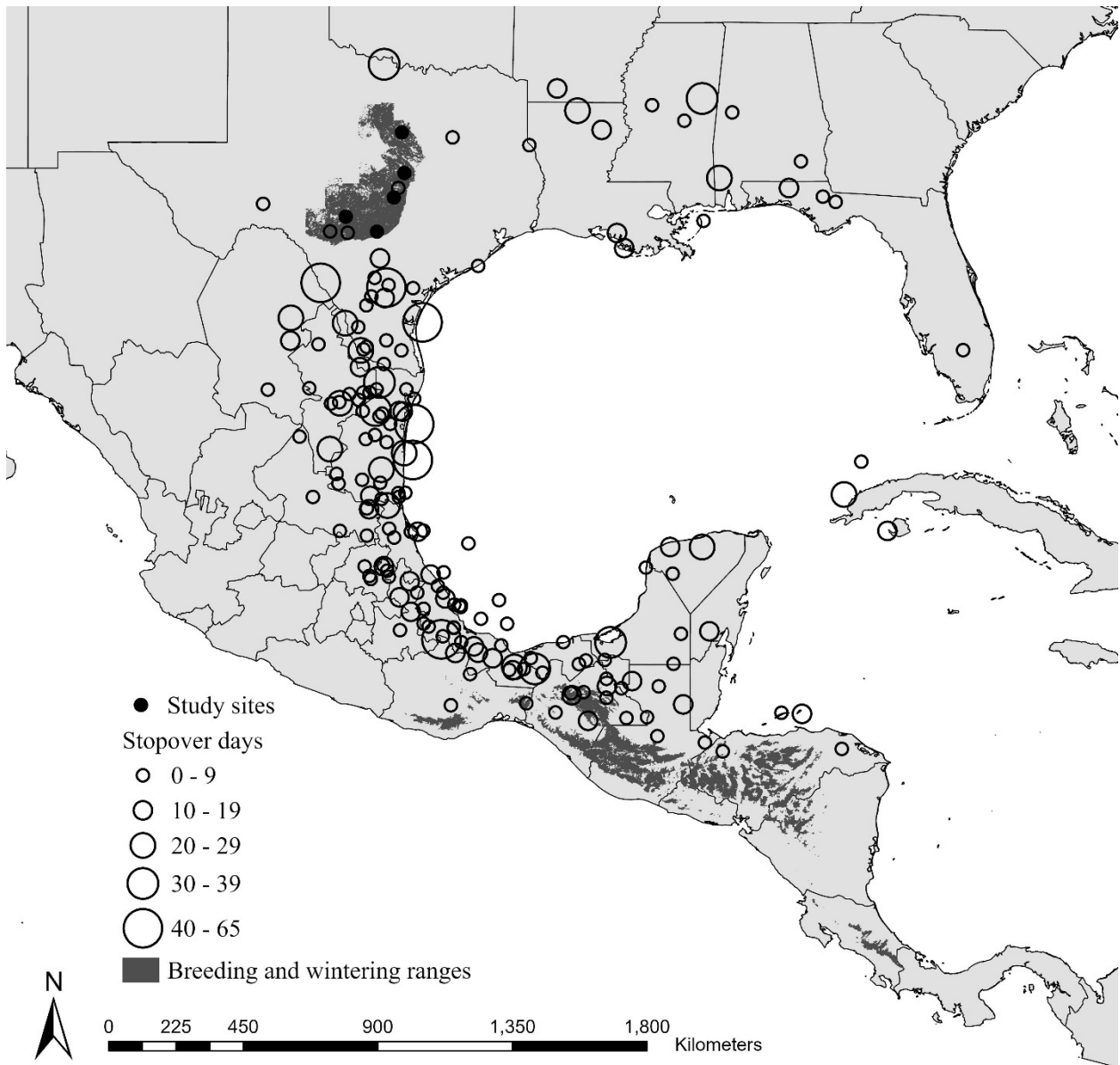


Figure 26. Migration stopover locations and durations for male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021).

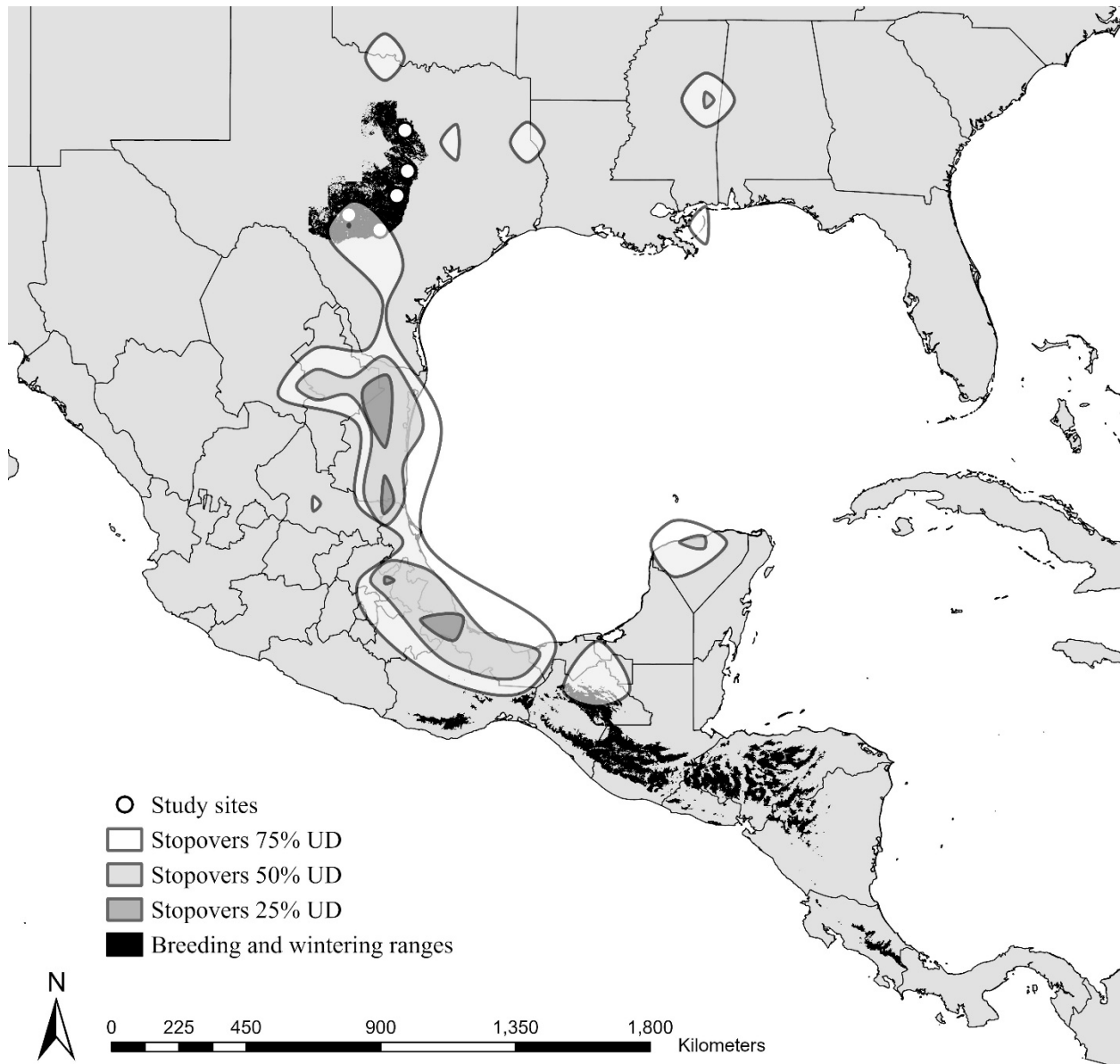


Figure 27. Utilization distributions for male golden-cheeked warblers (*Setophaga chrysoparia*) stopover locations during migration based on data we obtained from 61 light-level geolocators (2017–2021).

Winter

All warblers arrived on their wintering grounds between mid-August and mid-October and, on average, spent 165 d in this region (SD = 23 d, R = 105–204 d). The mean number of overwintering locations per individual was 1.6 (SD = 0.85, R 1–6 locations). Based on the 75% UD we created with points from individual warblers, most birds overwintered within or in close proximity to the warbler’s winter range in southern Mexico and Central America (Fig. 28); the highest percentages of individual warbler points were located in Chiapas, Mexico (30%); Guatemala (18%); and Honduras (15%) (Fig. 28). The 75% UD created with points from

individual warblers notably included several locations outside the warbler's winter range in the Mexican states of Veracruz, Oaxaca, Tabasco, Campeche, Quintana Roo, and Yucatán, and the countries of Belize, Costa Rica, Panama, and Columbia (Fig. 28). However, utilization distributions (25%, 50%, and 75%) created using points from all birds combined showed more pronounced use of habitat within the warbler's known wintering range (Fig. 29), with the 75% UDs including Chiapas, Mexico; Guatemala, El Salvador, Honduras, and small portions of Veracruz and Oaxaca, Mexico; Belize; and Nicaragua (Fig. 29).

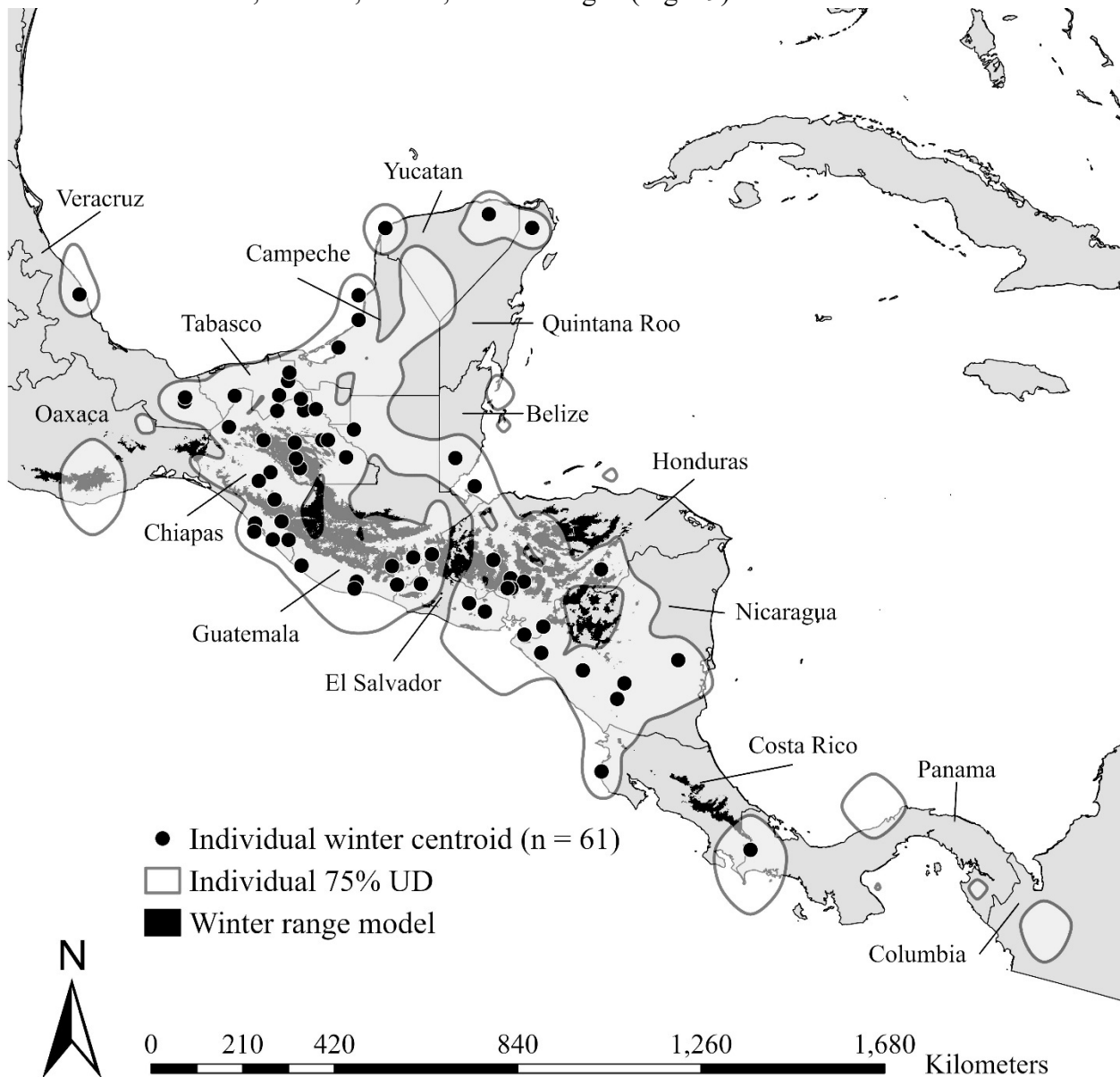


Figure 28. Centroid for overwintering locations and 75% utilization distributions for individual male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021).

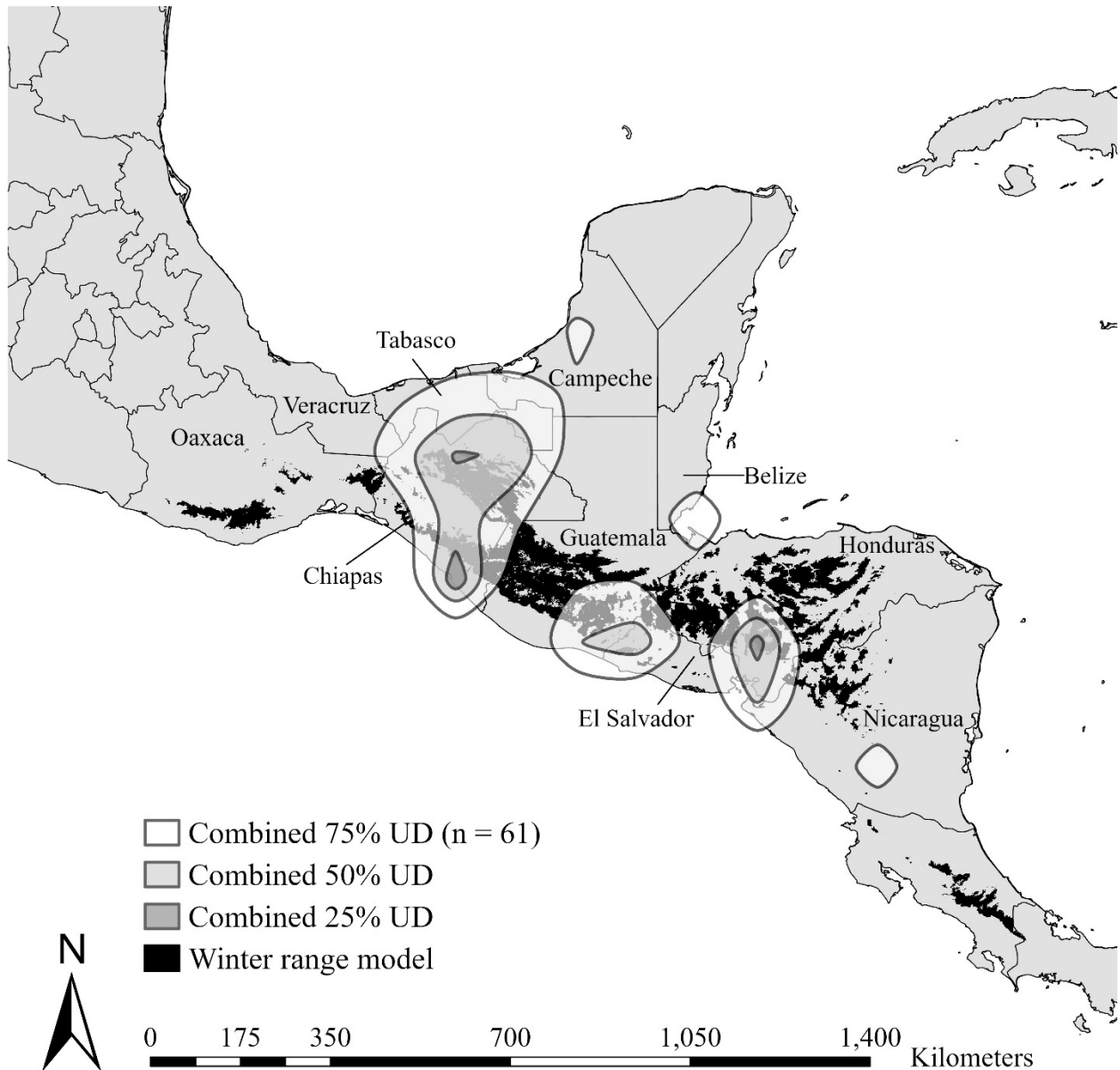


Figure 29. Utilization distributions for combined overwintering locations of male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021).

We also constructed UD based on the locations of warblers from individual study sites (Fig. 30) and locations of birds in each age class (Fig. 31). We found overlap between 75% UD constructed for warblers from each study site (Fig. 30) but quantify migratory connectivity below. The 75% UD we constructed with points from SY ($n = 26$ warblers) and ASY ($n = 29$ warblers) birds overlapped by 41–59% (Fig. 31). We found no significant difference in the number of overwintering locations for SY ($\bar{x} = 1.62$, $SD = 0.68$, $R = 1\text{--}3$ locations) and ASY ($\bar{x} = 1.59$, $SD = 0.97$, $R = 1\text{--}5$ locations) warblers ($t_{28} = 0.13$, $P = 0.90$).

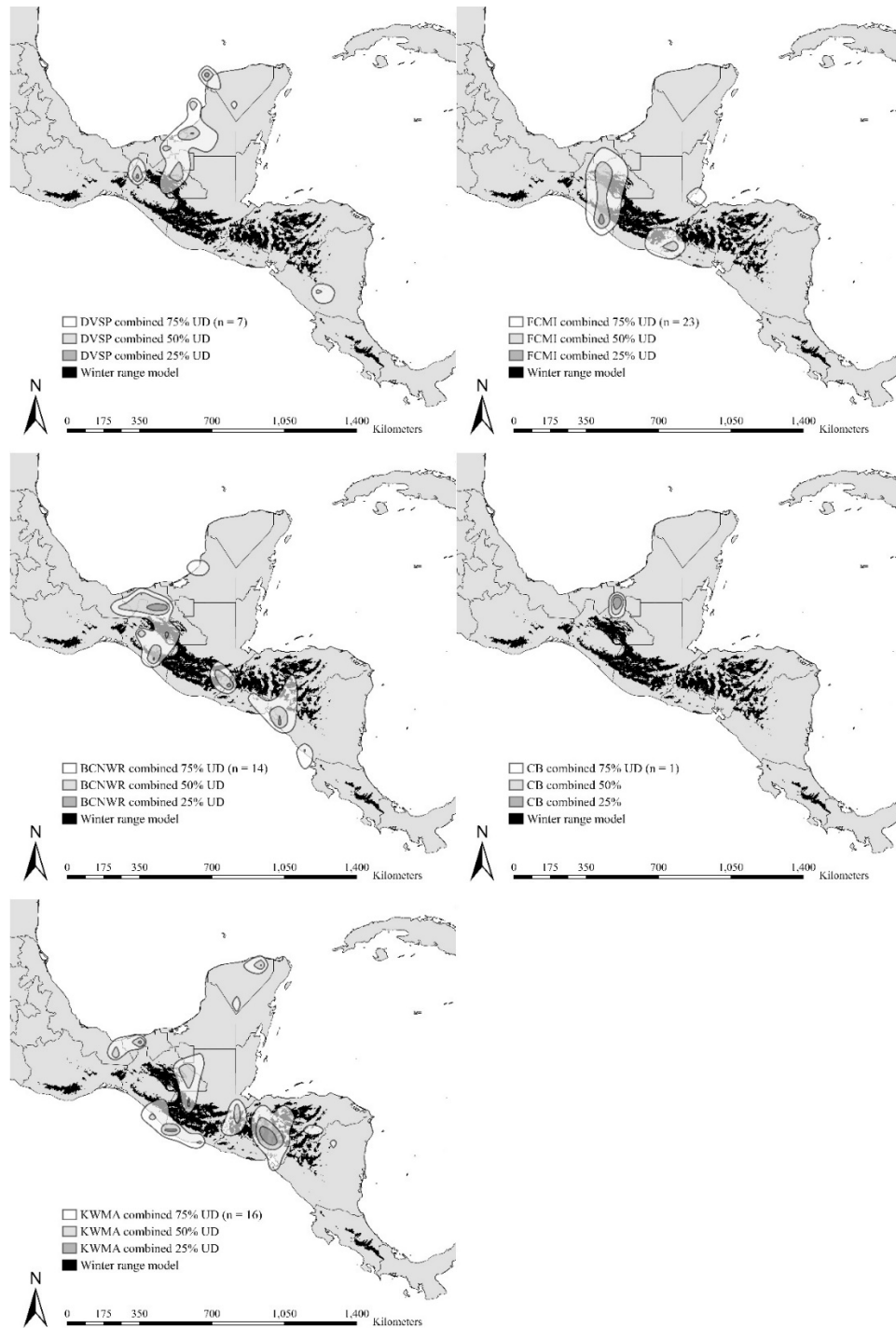


Figure 30. Utilization distributions for combined overwintering locations of male golden-cheeked warblers (*Setophaga chrysoparia*) per study site based on data from 61 light-level geolocators (2017–2021). Our study sites included Dinosaur Valley State Park (DVSP), Fort Cavazos Military Installation (FCMI), Balcones Canyonlands National Wildlife Refuge

(BCNWR), Joint Base San Antonio-Camp Bullis (CB), and Kerr Wildlife Management Area (KWMA) in Texas.

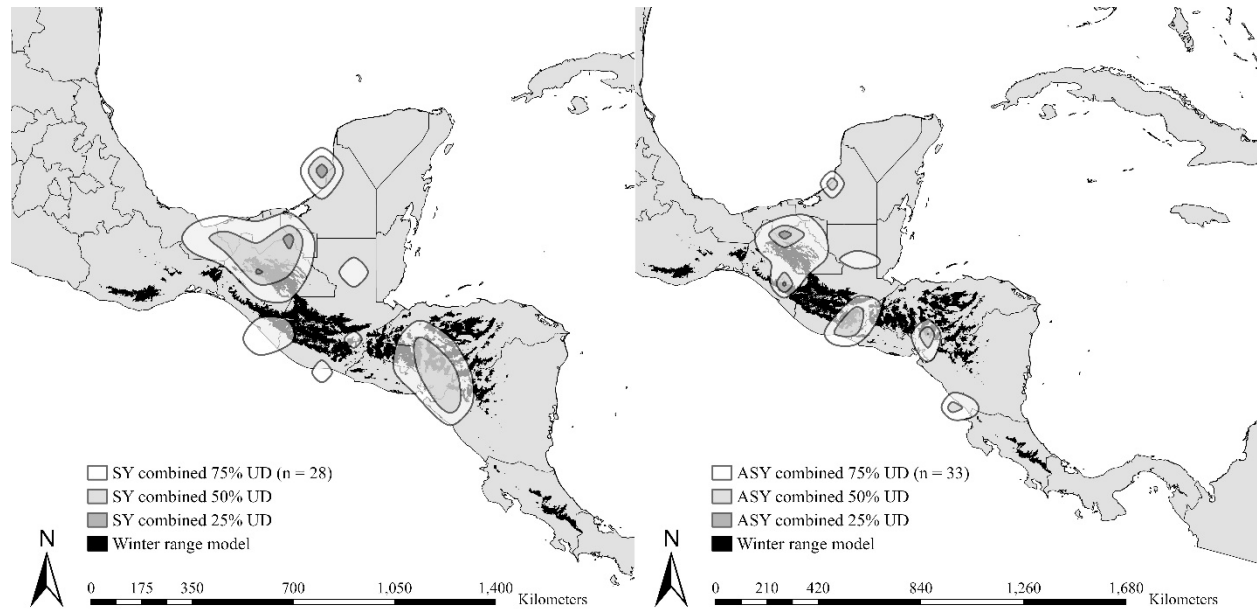


Figure 31. Utilization distributions for combined overwintering locations for second year (SY; left) and B) after second year (ASY; right) male golden-cheeked warblers (*Setophaga chrysoparia*) based on data from 61 light-level geolocators (2017–2021).

Migratory connectivity

The mean distance between wintering centroids for all years combined was 495 km (Table 14). We found that mean distance was significantly different among years ($P < 0.05$), with the mean distance of centroids in 2018 being 1.6 times greater than in 2019 (Table 14, Fig. 32). However, the low sample size for birds in 2018 ($n = 5$) likely influenced mean distance, and the 95% confidence interval was broad for this year (Fig. 32). Together, our results suggest that the mean distance between wintering centroids was likely similar (~500 km; Table 14) during all years of our study.

The rM estimate that included all years of data, as well as the estimates for the years 2017, 2018, and 2020, were ≤ 0.5 and had 95% confidence intervals that included zero (Table 15, Figs. 33–34). The 95% confidence interval did not include zero for the 2019 analysis (Table 15); however, the rM estimate suggested weak migratory connectivity (i.e., ≤ 0.5 ; Table 15, Fig. 34). Together, our results suggest that warblers from the same breeding sites were not located a similar distance from one another in the wintering grounds.

Table 14. Mean distance (km) $\pm$ standard error (SE) between utilization distribution centroids in the wintering grounds for all golden-cheeked warblers (*Setophaga chrysoparia*) caught during the duration of the study (“all years”) and for each year individually. Column “n” denotes the number of geolocated birds during each period.

Year	n	Mean $\pm$ SE
All years	61	495 $\pm$ 40
2017	16	512 $\pm$ 81
2018	5	713 $\pm$ 216
2019	16	436 $\pm$ 56
2020	24	514 $\pm$ 62

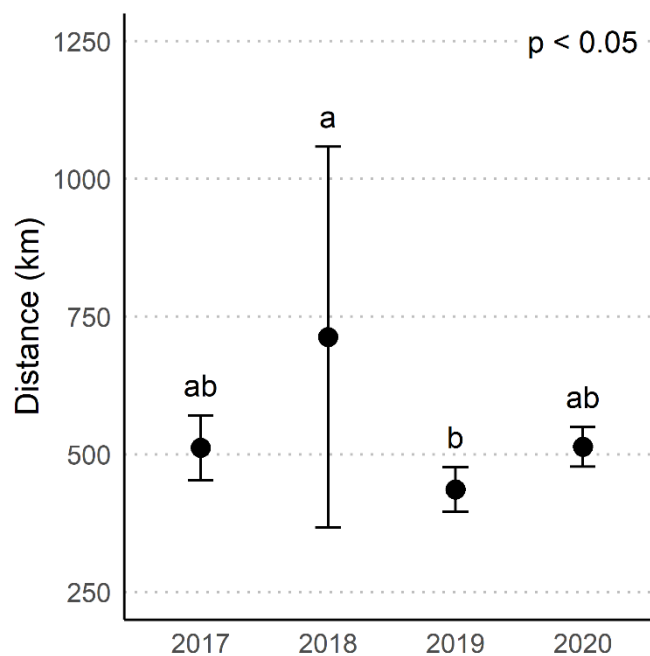


Figure 32. Graph showing the difference in the mean distance between golden-cheeked warbler (*Setophaga chrysoparia*) utilization distribution centroids in the wintering grounds among years with 95% confidence intervals.

Table 15. Mantel correlation coefficient estimates (r_M) $\pm$ standard error and 95% confidence intervals (CI) for all golden-cheeked warblers golden-cheeked warbler (*Setophaga chrysoparia*) caught during the duration of the study (“all years”) and for each year individually.

Year	n	r_M	95% CI
All years	61	0.04 $\pm$ 0.06	-0.05, 0.17
2017	16	0.02 $\pm$ 0.14	-0.20, 0.35
2018	5	0.35 $\pm$ 0.46	-0.29, 1.00
2019	16	0.23 $\pm$ 0.11	0.03, 0.49
2020	24	0.09 $\pm$ 0.11	-0.07, 0.35

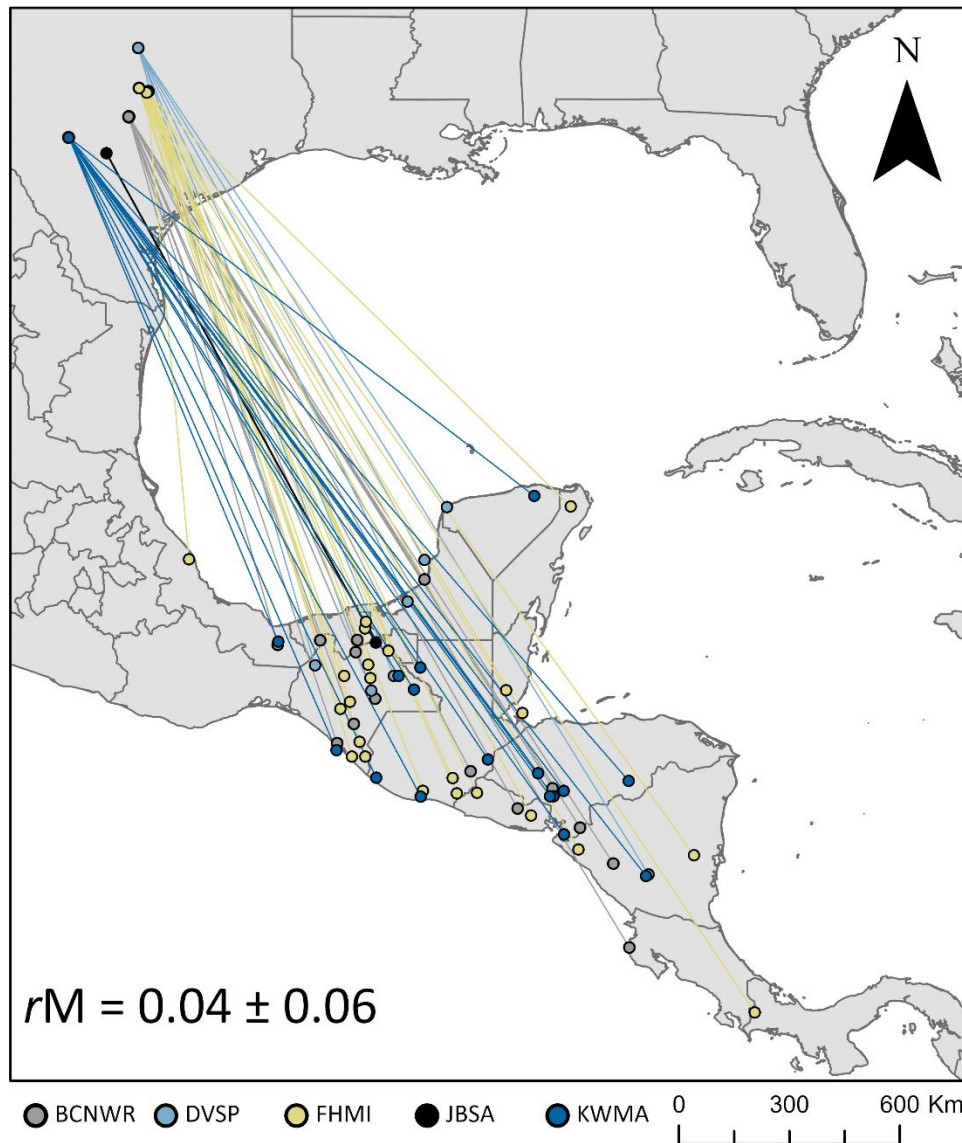


Figure 33. Map of deployment locations in the breeding range and utilization distribution centroids in the wintering range for all golden-cheeked warblers (*Setophaga chrysoparia*) geolocated during our study. Migratory connectivity is described by the Mantel correlation value (rM) $\pm$ standard error. Lines connect individual birds to their breeding and wintering location and do not describe their migratory path.

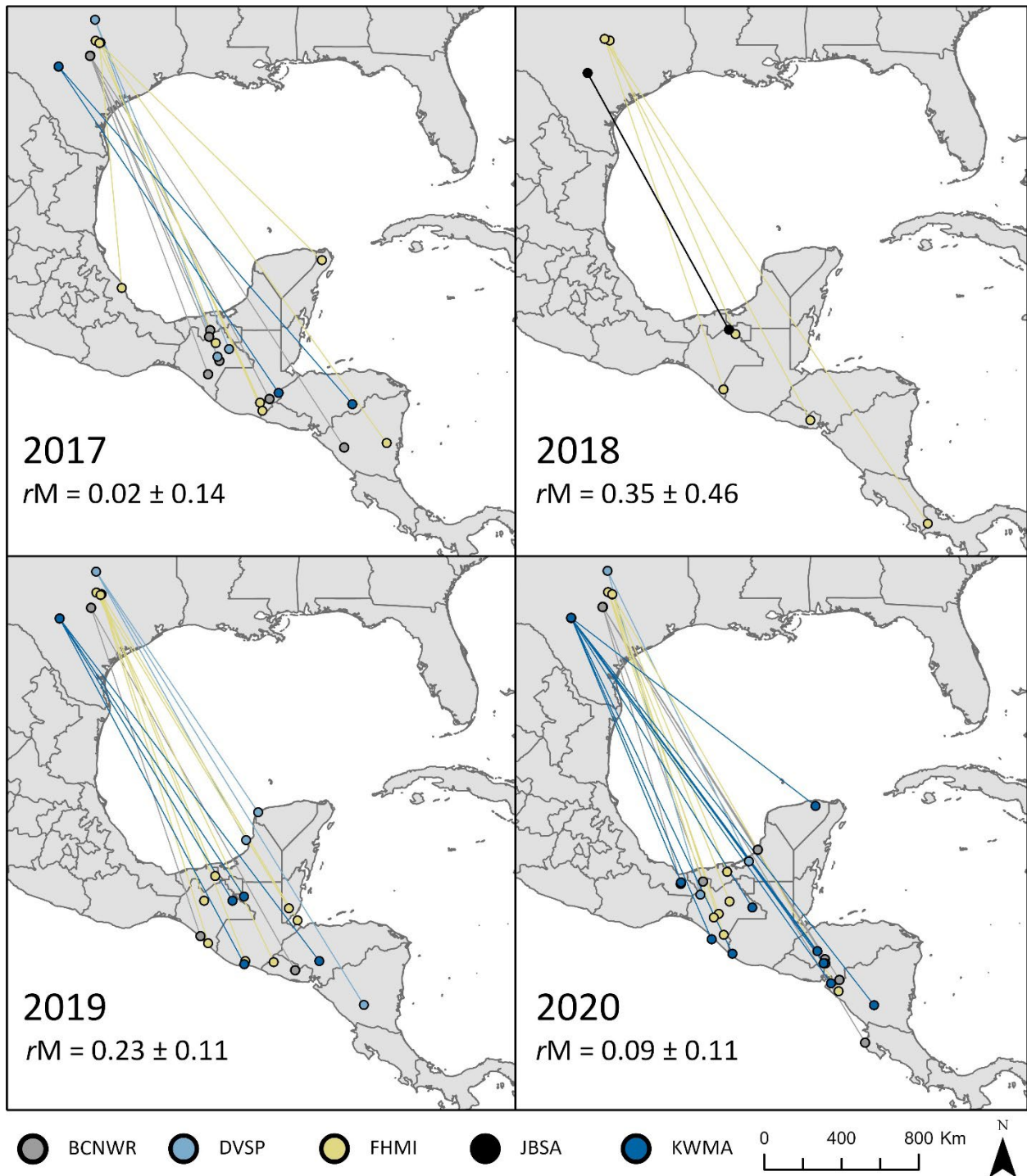


Figure 34. Map of deployment locations in the breeding range and utilization distribution centroids in the wintering range for golden-cheeked warblers (*Setophaga chrysoparia*) geolocated during our study, separated by year. Migratory connectivity is described by the Mantel correlation value (rM) $\pm$ standard error. Lines connect individual birds to their breeding and wintering location and do not describe their migratory path.

Geolocator impact assessment

We monitored 88 warblers (49 SY, 39 ASY) with geolocators and 47 warblers (21 SY, 26 ASY) without geolocators at FCMI (Table 16). We monitored 34 warblers (13 SY, 21 ASY) with geolocators and 66 (18 SY, 48 ASY) warblers without geolocators at CB (Table 16). The mean weight of warblers at FCMI prior to banding and attaching a geolocator was 9.68 g (SE = 0.04, R = 9.20–11.20) and the mean weight of warblers at CB was 9.70 g (SE = 0.04, R = 9.20–10.68). We resighted 96% of warblers with geolocators and 100% of warblers without geolocators at FCMI, and 100% of warblers with and without geolocators at CB at least 3 times and for at least 2 weeks after handling and prior to fall migration. Almost all warblers quickly resumed normal activities (e.g., singing, foraging, territory defense, mate guarding) within 30 min after handling. We noted that 13 (11%) of the warblers with geolocators were slow to fly off, had balance issues, or acted as if they were still captured upon initial release. However, these warblers also resumed normal behavior within 30 min. We were unable to recapture 8 (19%) warblers with geolocators that returned to our study sites in subsequent years despite >5 recapture attempts each on separate days throughout the breeding season. However, we did visually confirm that the geolocators were still attached to these birds.

Table 16. Summary of sample sizes (n), percentages (%), standard errors (SE), and 95% confidence intervals (CI) per year for pairing success, fledging success, and annual return rates of male golden-cheeked warblers (*Setophaga chrysoparia*) with and without geolocators (Geo = 1 or 0) at Fort Cavazos Military Installation (FCMI) and Joint Base San Antonio-Camp Bullis (CB), Texas, USA.

Location	Year	Geo	Total		Paired				Fledged				Returned			
			n	%	n	%	SE	CI	n	%	SE	CI	n	%	SE	CI
FCMI																
	2017	1	24	69	21	88	0.62	0.68–0.96	7	29	0.45	0.15–0.50	13	54	0.41	0.35–0.73
		0	10	29	9	90	1.05	0.53–0.98	5	50	0.63	0.22–0.78	1	10	1.05	0.01–0.47
	2018	1	19	68	17	90	0.75	0.66–0.97	10	53	0.46	0.31–0.73	6	32	0.49	0.15–0.55
		0	9	32	9	100	1318.7	0.00–100.00	7	78	0.8	0.42–0.94	2	22	0.8	0.06–0.58
	2019	1	28	72	21	75	0.44	0.56–0.88	10	36	0.39	0.20–0.55	8	29	0.42	0.15–0.48
		0	11	28	9	82	0.78	0.49–0.95	7	64	0.63	0.34–0.86	3	27	0.68	0.09–0.59
	2020	1	17	49	14	82	0.64	0.57–0.94	8	47	0.49	0.26–0.70	6	35	0.51	0.17–0.60
		0	17	49	14	82	0.64	0.57–0.94	11	65	0.51	0.40–0.83	5	29	0.53	0.13–0.54
	All	1	88	65	73	83	0.28	0.74–0.90	35	40	0.22	0.30–0.50	33	38	0.22	0.28–0.48
		0	47	35	41	87	0.44	0.74–0.94	30	64	0.3	0.49–0.76	11	23	0.34	0.14–0.38
CB																
	2017	1	17	27	13	76	0.57	0.51–0.91	8	47	0.49	0.26–0.70	5	29	0.53	0.13–0.54
		0	47	73	41	87	0.44	0.74–0.94	33	70	0.32	0.56–0.82	24	51	0.29	0.37–0.65
	2018	1	17	47	13	76	0.57	0.52–0.91	11	65	0.51	0.40–0.83	4	24	0.57	0.09–0.49
		0	19	53	18	95	1.03	0.71–0.99	14	74	0.52	0.50–0.89	14	74	0.52	0.50–0.89
	All	1	34	34	26	76	0.4	0.59–0.88	19	56	0.35	0.39–0.71	9	27	0.39	0.14–0.44
		0	66	66	59	89	0.4	0.79–0.95	47	72	0.27	0.59–0.81	38	58	0.25	0.45–0.69

Overall, 83% of warblers with geolocators and 87% without geolocators at FCMI paired and 76% of warblers with geolocators and 89% without geolocators at CB paired (Table 16). The best fit model for pairing success at FCMI included age as a main effect (Table 17), but we found no differences in the predicted probability of pairing success between warblers with ($n = 88$) and without geolocators ($n = 47$) at FCMI (Fig. 35). The best fit model for pairing success at CB was the null model (Table 17), suggesting that pairing success at CB was unrelated to our covariates. Overall, 40% of warblers with geolocators and 64% without geolocators at FCMI fledged young and 56% of warblers with geolocators and 72% without geolocators at CB fledged young (Table 16). The best fit model for fledgling success at FCMI included the interaction between geolocator and age (Table 18), but we found no differences in the predicted probability of fledgling success for warblers with ($n = 88$) and without geolocators ($n = 47$) at FCMI (Fig. 36). The best fit model for fledgling success at CB was the null (Table 18), suggesting that fledgling success at CB was unrelated to our covariates.

Table 17. Modeling results for pairing success of golden-cheeked warblers (*Setophaga chrysoparia*) with and without geolocators that were monitored at Fort Cavazos Military Installation (FCMI) and Joint Base San Antonio-Camp Bullis (CB), Texas, USA (2017–2021). Best fit models are identified in bold.

Location	Model	DF ^a	Log likelihood	AIC _c ^b	ΔAIC _c ^c	w _i ^d
FCMI	Geocator * Age	4	-52.294	112.9	0.00	0.626
	Age	2	-55.255	114.6	1.71	0.267
	Null	1	-58.351	118.7	5.84	0.034
	Site * Age	6	-53.178	119.0	6.12	0.029
	Geocator	2	-58.131	120.4	7.46	0.015
	Site	3	-57.308	120.8	7.90	0.012
	Year	4	-56.432	121.2	8.28	0.010
	Geocator * Site	6	-54.756	122.2	9.27	0.006
	Year * Age	8	-54.144	125.4	12.54	0.001
	Geocator * Year	8	-55.592	128.1	15.23	0.000
	Site * Year	12	-53.102	132.8	19.87	0.000
CB	Geocator	2	-40.871	85.9	0.00	0.347
	Null	1	-42.271	86.6	0.72	0.243
	Age	2	-41.949	88.0	2.15	0.118
	Year	2	-42.243	88.6	2.74	0.088
	Geocator * Year	4	-40.418	89.3	3.39	0.064
	Geocator * Age	4	-40.427	89.3	3.41	0.063
	Site	3	-42.045	90.3	4.47	0.037
	Year * Age	4	-41.838	92.1	6.23	0.015
	Geocator * Site	6	-39.998	92.9	7.03	0.010
	Site * Year	6	-40.085	93.1	7.21	0.009
	Site * Age	6	-40.651	94.2	8.34	0.005

^aDegrees of freedom

^bAkaike's Information Criteria corrected for small sample sizes.

^cΔAIC_c relative to the best-fit model.

^dModel weight

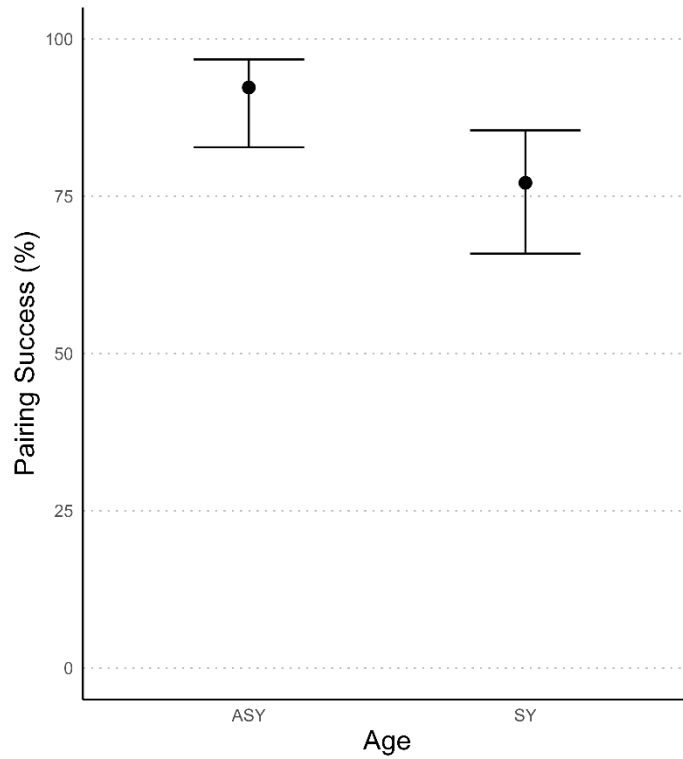


Figure 35. Predicted probability of golden-cheeked warbler (*Setophaga chrysoparia*) pairing success and associated 95% confidence interval in relation to age (ASY = after second year, SY = second year) using data collected from 2017–2021 at Fort Cavazos Military Installation in Texas.

Table 18. Modeling results for fledgling success of golden-cheeked warblers (*Setophaga chrysoparia*) with and without geolocators that were monitored at Fort Cavazos Military Installation (FCMI) and Joint Base San Antonio-Camp Bullis (CB), Texas, USA (2017–2021). Best fit models are identified in bold.

Location	Model	DF ^a	Log likelihood	AIC _c ^b	ΔAIC _c ^c	w _i ^d
FCMI	Geocator * Site	6	-83.601	179.9	0.00	0.518
	Geocator * Age	4	-86.551	181.4	1.55	0.239
	Site	3	-88.844	183.9	4.01	0.070
	Geocator	2	-89.899	183.9	4.03	0.069
	Age	2	-89.926	183.9	4.08	0.067
	Site * Age	6	-86.643	185.9	6.08	0.025
	Null	1	-93.482	189.0	9.14	0.005
	Year	4	-90.877	190.1	10.20	0.003
	Year * Age	8	-86.707	190.6	10.70	0.002
	Geocator * Year	8	-87.580	192.3	12.44	0.001
	Site * Year	12	-83.310	193.2	13.32	0.001
CB	Geocator	2	-62.947	130.0	0.00	0.270
	Null	1	-64.104	130.2	0.23	0.241
	Site * Year	6	-59.467	131.8	1.82	0.109
	Age	2	-63.884	131.9	1.87	0.106
	Year	2	-63.954	132.0	2.01	0.099
	Geocator * Year	4	-62.367	133.2	3.14	0.056
	Site	3	-63.720	133.7	3.67	0.043
	Geocator * Age	4	-62.807	134.0	4.02	0.036
	Year * Age	4	-63.196	134.8	4.79	0.025
	Geocator * Site	6	-61.662	136.2	6.21	0.012
	Site * Age	6	-63.246	139.4	9.38	0.002

^aDegrees of freedom

^bAkaike's Information Criteria corrected for small sample sizes.

^cΔAIC_c relative to the best-fit model.

^dModel weight

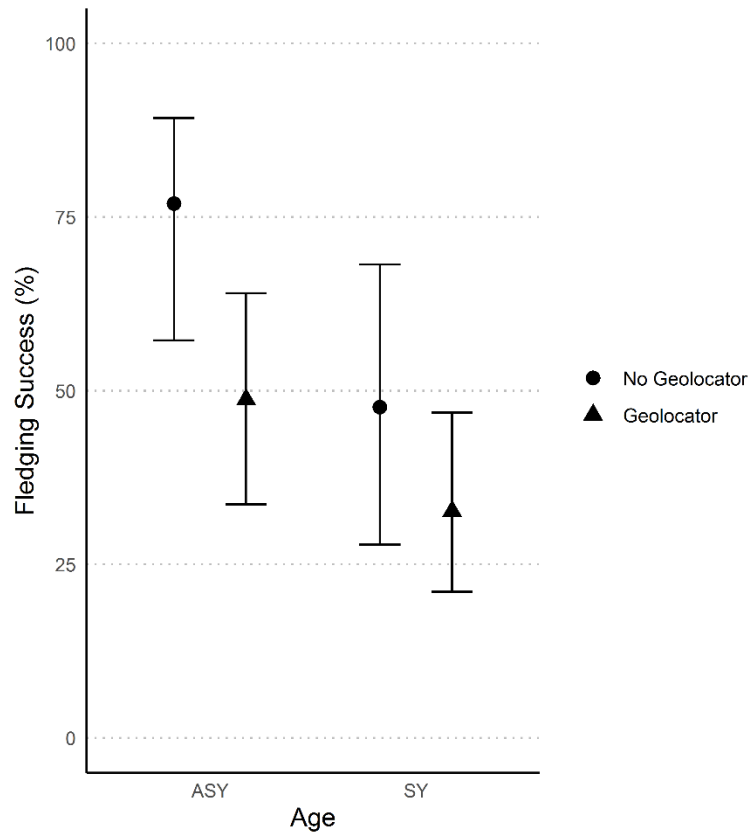


Figure 36. Predicted probability of golden-cheeked warbler (*Setophaga chrysoparia*) fledgling success and associated 95% confidence interval in relation to age (ASY = after second year, SY = second year) using data collected from 2017–2021 at Fort Cavazos Military Installation in Texas.

Overall, 38% of warblers with geolocators and 23% without geolocators at FCMI returned and 24% of warblers with geolocators and 74% without geolocators at CB returned (Table 16). The best fit model for return rate at FCMI was the null model (Table 19), suggesting that annual return rates at FCMI were unrelated to our covariates. The best fit model for return rate at CB included the interaction between geolocator and age (Table 19). We found no differences in the predicted probability of returns for ASY warblers with geolocators and ASY warblers without geolocators (Fig. 37). In addition, we found no differences in the predicted probability of returns for ASY warblers with geolocators, ASY warblers without geolocators, and SY warblers with or without geolocators. However, the mean return rate for SY warblers with geolocators was 64% higher than the mean return rate for SY warblers without geolocators; our results likely reflect unusually high return rates for SY warblers without geolocators and low sample sizes for SY birds with geolocators at this location rather than a negative impact of the geolocators on SY birds.

Table 19. Modeling results for return rates of golden-cheeked warblers (*Setophaga chrysoparia*) with and without geolocators that were monitored at Fort Hood Cavazos Installation (FCMI) and Joint Base San Antonio-Camp Bullis (CB), Texas, USA (2017–2021). Best fit models are identified in bold.

Location	Model	DF ^a	Log likelihood	AIC _c ^b	ΔAIC _c ^c	w _i ^d
FCMI	Site	3	-82.657	171.5	0.00	0.241
	Geocator	2	-83.791	171.7	0.18	0.221
	Null	1	-85.220	172.50	0.97	0.148
	Age	2	-84.684	173.50	1.96	0.090
	Geocator * Age	4	-82.693	173.7	2.20	0.080
	Site * Age	6	-80.547	173.7	2.25	0.078
	Site * Year	12	-73.863	174.3	2.79	0.060
	Geocator * Site	6	-80.851	174.4	2.86	0.058
	Year	4	-84.390	177.1	5.59	0.015
	Geocator * Year	8	-80.953	179.0	7.55	0.006
	Year * Age	8	-81.468	180.1	8.58	0.003
CB	Geocator * Age	4	-61.345	131.1	0.00	0.648
	Geocator	2	-64.637	133.4	2.29	0.207
	Geocator * Year	4	-63.091	134.6	3.49	0.113
	Geocator * Site	6	-62.745	138.4	7.28	0.017
	Null	1	-69.135	140.3	9.20	0.007
	Site	3	-67.755	141.8	10.65	0.003
	Year	2	-69.033	142.2	11.08	0.003
	Age	2	-69.104	142.3	11.22	0.002
	Site * Year	6	-66.415	145.7	14.62	0.000
	Year * Age	4	-68.955	146.3	15.22	0.000
	Site * Age	6	-67.120	147.1	16.03	0.00

^a Degrees of freedom

^b Akaike's Information Criteria corrected for small sample sizes.

^c ΔAIC_c relative to the best-fit model.

^d Model weight

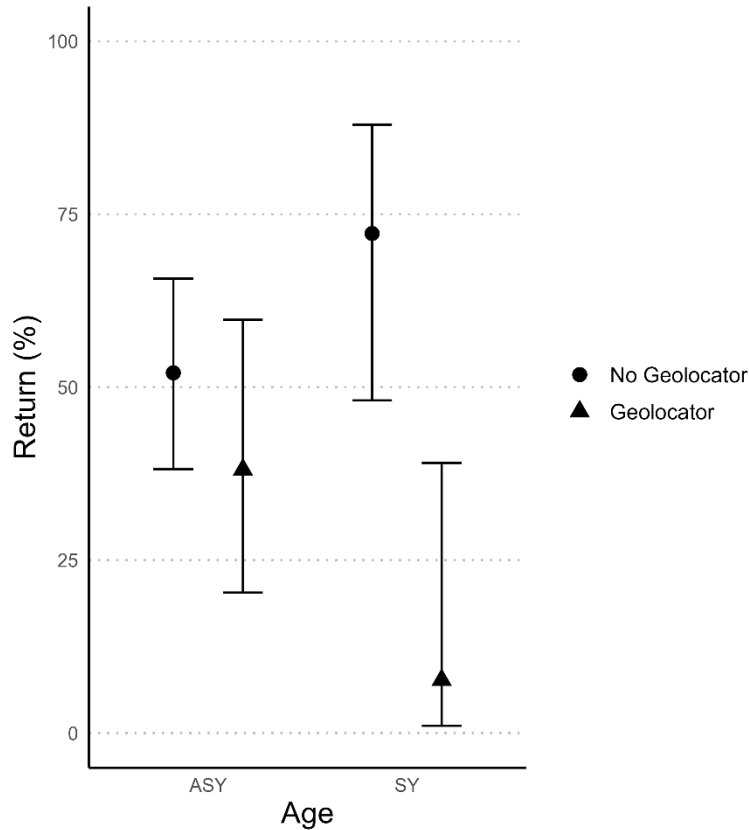


Figure 37. Predicted probability of golden-cheeked warbler (*Setophaga chrysoparia*) return rate and associated 95% confidence interval in relation to age (ASY = after second year, SY = second year) using data collected from 2017–2021 at Joint Base San Antonio–Camp Bullis in Texas.

Upon recapturing warblers with geolocators, we documented minor feather abrasions under the geolocators and slight skin irritation under the legs from the harnesses in 7 (17%) individuals. We found no statistically significant difference between the mean mass of warblers when we deployed ($\bar{x}$ = 9.72 g, SD = 0.35 g, R = 9.20–10.60 g) and retrieved ($\bar{x}$ = 9.77 g, SD = 0.46 g, R = 8.70–10.49 g) geolocators at FCMI (t_{29} = -0.54, P = 0.59). We were unable to make statistical comparisons for mean mass of warblers at Camp Bullis due to low samples sizes for recaptures (n = 2), but the mean mass of warblers when we deployed the geolocators was 9.56 g (SD = 0.18 g, R = 9.43–9.68 g) and the mean mass of warblers when we retrieved the geolocators was 9.43 g (SD = 0.22 g, R = 9.27–9.58 g).

Radio telemetry

In 2022, we attached radio transmitters to 26 warblers within our grid of 40 automated telemetry nodes that we set up across our study site at KWMA prior to the breeding season: 15 males and 11 females (Fig. 9, 11; Table 20). All birds resumed normal activities after we attached the tags, and we recorded signals through the nodes or with a handheld antenna from all 26 transmitters ≥ 1 d after we attached the units (Table 20). We monitored 19 individuals with tags (73%) for the duration of the breeding season (Table 20). Pairing success was 91% and fledging success was 30% for male warblers with tags (Table 20), which is similar to other

studies on warblers, but lower than pairing success (100%) and fledging success (79%) we observed for 14 males without tags that we monitored at KWMA during the 2022 breeding season.

Table 20. Summary of 2022 tagging results for golden-cheeked warblers (*Setophaga chrysoparia*) at Kerr Wildlife Management Area in Texas.

	Deployed	Detected ¹	Resighted ²	Monitored ³	Paired ⁴	Fledged ⁴
Male	15	15	13	11	10	3
Female	11	11	8	8	NA	NA

¹Detected by nodes or handheld telemetry ≥ 1 day after the tag was deployed

²Resighted during the breeding season; bands confirmed

³Consistently monitored for duration of breeding season

⁴Number of monitored males that paired with a female or fledged ≥ 1 young

Of the tagged birds we did not monitor for the duration of the breeding season ($n = 7$), three did not establish territories within the boundaries of our study site based on resights and our efforts to relocate the birds using a handheld antenna (Table 20). However, we know these three individuals periodically returned to our study site during the breeding season based on location data recorded by the nodes. Two of the seven individuals were females that we captured late in the breeding season; we did not detect these two birds at our study site prior to capture and we suspect these birds were moving through the site after breeding elsewhere based on their body condition ($BP = 4$) and location data recorded by the nodes after we deployed the tags. We were unable to confirm the fate of two individuals that were tagged within the grid based on node data or field observations.

In 2022, the node grid collected 160,211 total location points we could use for analyses, which included 124,304 male and 35,907 female location points. The duration of data collection ranged from 2–51 d and the number of location points recorded per bird ranged from 36–33,507. We determined departure dates for 3 males: 18 July 2022, 03 Aug 2022, and 08 Aug 2022. Applying RSS and distance filters reduced our localization error compared to using no filters. Without filters, our median localization error was approximately 50 m. The most stringent filters provided location estimates with a median localization error ranging from approximately 31 to 38 m (Table 21). Figure 38 shows examples of localizations for the tagged birds we monitored in 2022.

Table 21. Summary of localization error (difference in meters between the true and estimated location) of trilateration location estimates for a field-based node network on Kerr WMA with uniform spacing among nodes (100 m).

Filter	Location Loss (%)	Mean Nodes (n)	Mean error	Lower 95% CI	Upper 95% CI	Median Error	Min Error	Max Error
No Filter	0	7.36	57.53	52.87	62.20	50.18	4.00	266.00
Distance 1.25x (125 m)	17	3.95	47.14	42.13	52.15	38.63	2.38	189.28
Distance 2x (200 m)	2	5.38	48.43	43.66	53.19	40.14	0.67	266.00
Distance 3x (300 m)	1	7.00	52.24	47.78	56.69	45.63	0.67	266.00
Distance 4x (400 m)	0	7.33	55.85	51.28	60.43	48.81	4.00	266.00
RSS -90 dB	95	3.09	32.93	25.55	40.31	31.28	18.09	60.61
RSS -95 dB	66	3.51	39.16	33.48	44.84	34.68	3.12	113.41
RSS -100 dB	25	4.50	44.95	40.61	49.28	39.97	2.72	161.60
RSS -105 dB	2	6.67	53.42	49.12	57.72	45.53	6.63	140.36

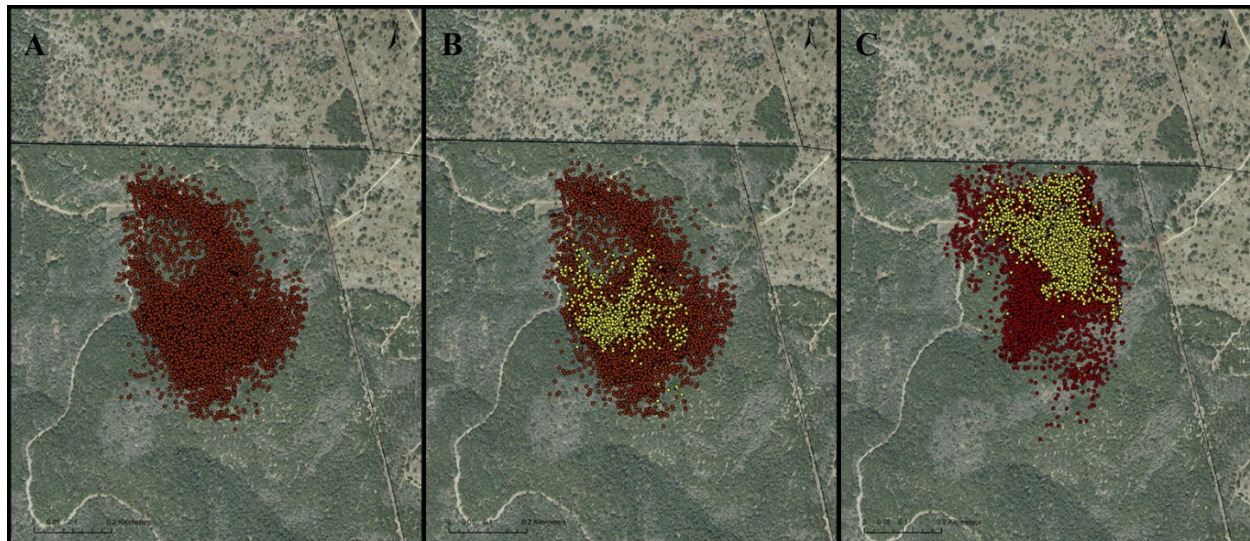


Figure 38. A: Localizations from a male golden-cheeked warbler (*Setophaga chrysoparia*) recorded from 08 Apr–27 May 2022 (50 days, 25,644 red points). B) Localizations from the male golden-cheeked warbler presented in A and from a female golden-cheeked warbler recorded from 08 Apr–12 Apr 2022 (5 days, 1,934 yellow points). Individuals were paired during the breeding season. C) Localizations from an adjacent pair of golden-cheeked warblers; male recorded from 08 Apr–05 May 2022 (45 days, 24,592 red points) and female recorded from 08 Apr–17 Apr 2022 (10 days, 4,263 yellow points).

In 2023, we expanded our grid of nodes from 40 to 54 and data collection is ongoing. However, to date we have attached radio transmitters to 37 warblers within our grid: 23 males and 14 females. We are also monitoring the territories of 20 males without radio transmitters that are located outside the grid. The warblers we tagged in 2022 were not detected by any other Motus towers along the warbler's route or on their wintering grounds. However, the Motus tower we installed at KWMA detected an American kestrel (*Falco sparverius*) on 05 Apr 2022 that was tagged in Minnesota on 09 Jun 2021; a Sprague's pipit (*Anthus spragueii*) on 30 Oct 2022 that was tagged in Montana on 23 Jun 2022; a sage thrasher (*Oreoscoptes montanus*) on 05 Nov 2022 that was tagged in Wyoming on 03 Jul 2022; a grasshopper sparrow (*Ammodramus savannarum*) on 14 Apr 2023 that was tagged in Nuevo Leon, Mexico on 12 Feb 2023; and a Swainson's thrush (*Catharus ustulatus*) on 21 May 2023 that was tagged in British Columbia, Canada on 04 Sep 2022.

Winter habitat models

Data points and environmental predictors

Based on our multicollinearity analysis, we retained 11 predictors for use in developing winter distribution models for warblers: slope, canopy height, mean EVI, mean LST, and seven bioclimatic variables (i.e., mean diurnal range, isothermality, mean temperature of the wettest quarter, precipitation of the wettest month, precipitation seasonality, precipitation of the warmest quarter, and precipitation of the coldest quarter; Table 22). Correlograms suggested spatial autocorrelation was high within 10 km and declined with increasing distance for all environmental predictors, except mean LST (Fig. 39). ANOSIM indicated multivariate similarity in the predictors at occurrence locations recorded during field surveys and as part of crowd-sourced projects (ANOSIM $R^2 = -0.02$, $P = 0.68$). However, there were a few univariate differences in environmental characteristics at field survey locations compared to crowd-sourced locations—specifically, higher mean LST and lower precipitation during the wettest month and warmest quarter (Table 22).

Table 22. Mean $\pm$ standard deviation (range) values of environmental predictors for all field survey and crowd-sourced occurrence points used to model the winter distribution of the golden-cheeked warbler (*Setophaga chrysoparia*), with Welch's *t*-test statistics comparing data by collection type and Cohen's *d* as a measure of effect size.

Variable	Overall (<i>n</i> = 175)	Field survey (<i>n</i> = 49)	Crowd-sourced (<i>n</i> = 126)	Statistics
Slope (°)	8 $\pm$ 4 (1–22)	9 $\pm$ 4 (1–17)	8 $\pm$ 4 (1–22)	$t_{99.63} = 1.10, d = 0.19 (-0.15, 0.52)$
Canopy height (m)	24 $\pm$ 8 (0–36)	21 $\pm$ 8 (0–33)	24 $\pm$ 8 (0–36)	$t_{81.20} = 2.35, d = 0.40 (0.06, 0.73)$
Mean EVI ^a	0.4 $\pm$ 0.1 (0.3–0.6)	0.4 $\pm$ 0.1 (0.3–0.5)	0.4 $\pm$ 0.1 (0.3–0.5)	$t_{87.06} = 2.10, d = 0.35 (0.02, 0.69)$
Mean LST (°C) ^a	24 $\pm$ 3 (16–32)	25 $\pm$ 3 (19–32)	24 $\pm$ 3 (16–32)	$t_{93.74} = -3.13, d = -0.53 (-0.86, -0.19)^*$
<i>Temperature</i>				
Mean diurnal range (°C) ^b	7 $\pm$ 1 (3–8)	7 $\pm$ 0 (6–8)	7 $\pm$ 1 (3–8)	$t_{163.03} = 1.51, d = 0.25 (-0.08, 0.59)$
Isothermality (%) ^c	59 $\pm$ 3 (49–64)	58 $\pm$ 2 (53–63)	59 $\pm$ 3 (49–64)	$t_{114.00} = 2.19, d = 0.37 (0.03, 0.70)$
Wettest quarter mean (°C)	19 $\pm$ 2 (11–26)	20 $\pm$ 2 (13–26)	19 $\pm$ 2 (11–26)	$t_{88.94} = -1.69, d = -0.28 (-0.62, 0.05)$
<i>Precipitation</i>				
Wettest month (mm)	325 $\pm$ 99 (157–675)	286 $\pm$ 73 (160–499)	340 $\pm$ 104 (157–675)	$t_{124.51} = 3.83, d = 0.64 (0.31, 0.98)^*$
Seasonality (%) ^d	76 $\pm$ 14 (39–102)	78 $\pm$ 13 (45–102)	75 $\pm$ 15 (39–102)	$t_{102.63} = -1.27, d = -0.21 (-0.55, 0.12)$
Warmest quarter (mm)	402 $\pm$ 158 (69–1055)	348 $\pm$ 121 (73–793)	423 $\pm$ 165 (69–1055)	$t_{119.42} = 3.32, d = 0.56 (0.22, 0.90)^*$
Coldest quarter (mm)	149 $\pm$ 197 (11–1619)	106 $\pm$ 101 (12–482)	166 $\pm$ 221 (11–1619)	$t_{168.7} = 2.47, d = 0.42 (0.08, 0.75)$

^a Average annual mean enhanced vegetation index and average annual mean land surface temperature from 2000 to 2019 derived from MODIS Terra products.

^b Annual mean of monthly maximum temperature minus monthly minimum temperature.

^c Measure of day-to-night temperature oscillation relative to summer-to-winter oscillation.

^d Measure of variation in monthly precipitation over the course of a year.

* Indicates statistical significance after accounting for multiple comparisons (i.e., $\alpha \leq 0.004$).

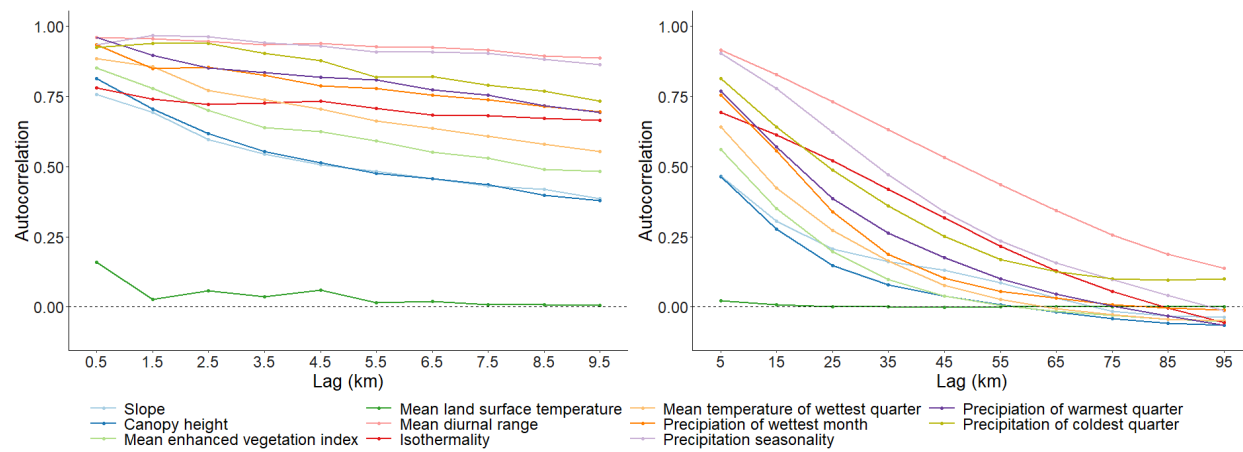


Figure 39. Correlograms showing spatial autocorrelation in environmental predictors at 1-km lag distances to 10 km and 10-km lag distances to 100 km within a study area including Oaxaca and Chiapas, Mexico and Central American countries from Guatemala to Costa Rica.

Predicted winter distribution

The average fit of the SDMs given current climate conditions was high ($\bar{x}_{AUC} = 0.94$, $\bar{x}_{TSS} = 0.81$; Table 23). Mean temperature of the wettest quarter, mean LST, mean diurnal range, and precipitation of the coldest quarter contributed to our models more consistently than other predictors (Fig. 40) and were the most important contributors in 67%, 18%, 11%, and 4% of models, respectively. Across models, species response curves indicated a decline in the probability of warbler occurrence with increasing temperature during the wettest quarter, particularly at temperatures greater than 21 °C. The probability of occurrence also declined with mean LST above 23 °C, mean diurnal range above 7.5 °C, and precipitation during the coldest quarter, with the lowest probability in areas with greater than 640 mm (Fig. 40).

Our ensemble model predicted 103,891 km² of potentially suitable wintering habitat for the warbler across the study area, more than half of which occurred in Honduras (35%) and Guatemala (29%; Fig. 41, Table 24). Chiapas contained 18% of the predicted distribution, with Nicaragua and El Salvador accounting for 6% and 1%. Oaxaca and Costa Rica—locations not typically included in distribution maps for this species—contained 6% and 5% of the predicted distribution, respectively (Fig. 41, Table 24); excluding these two regions resulted in a total predicted area of 92,569 km². Ninety-two percent of occurrence points used to build our model were coincident with the predicted distribution. However, our model did not identify potential habitat in Belize or the Petén region of Guatemala, despite the inclusion of occurrence points in these regions (Fig. 41).

Ninety-one percent of the predicted wintering distribution occurred within the core elevation zone (800–2600 masl; Table 24), with predicted areas at higher elevations more common in Guatemala, Costa Rica, and Oaxaca and predicted areas at lower elevations more common in Honduras and Nicaragua (Fig. 41). Protected areas comprised ~21% of the warbler's predicted wintering range (Fig. 42), with little area in Oaxaca (2%) protected compared to Costa Rica (77%) and other regions (14–46%; Fig. 42). Seven percent of the predicted distribution experienced forest cover loss from 2000 to 2019, with a rangewide rate of 382 km (± 293 SD) lost per year. Total forest cover loss and mean annual rate of loss were greatest in Honduras (Table 25). Forest cover loss was slightly lower (5%) within the protected areas of the predicted range during the same period, with an average annual loss of 58 km (± 52 SD) per year. Chiapas and Guatemala lost forest cover in protected areas at lower rates than their regional levels, whereas elsewhere percent loss in protected areas was similar (within 1%) to regional losses (Table 25).

Table 23. Mean area under the receiver operating curve (AUC) and true skill statistics (TSS) for models predicting the golden-cheeked warbler's (*Setophaga chrysoparia*) wintering distribution under contemporary (average 1979–2013) climate conditions using eight modeling algorithms (25 replicates each) and the AUC and TSS values for weighted ensemble model.

Algorithm	AUC	TSS
Generalized additive model (GAM)	0.95	0.82
Generalized linear model (GLM)	0.93	0.79
Multivariate adaptive regression splines (MARS)	0.90	0.79
Boosted regression tree (BRT)	0.91	0.74
Classification and regression trees (CART)	0.95	0.79
Maximum entropy (MaxEnt)	0.93	0.79
Random forest (RF)	0.97	0.88
Support vector machine (SVM)	0.96	0.84
Ensemble	0.98	0.87

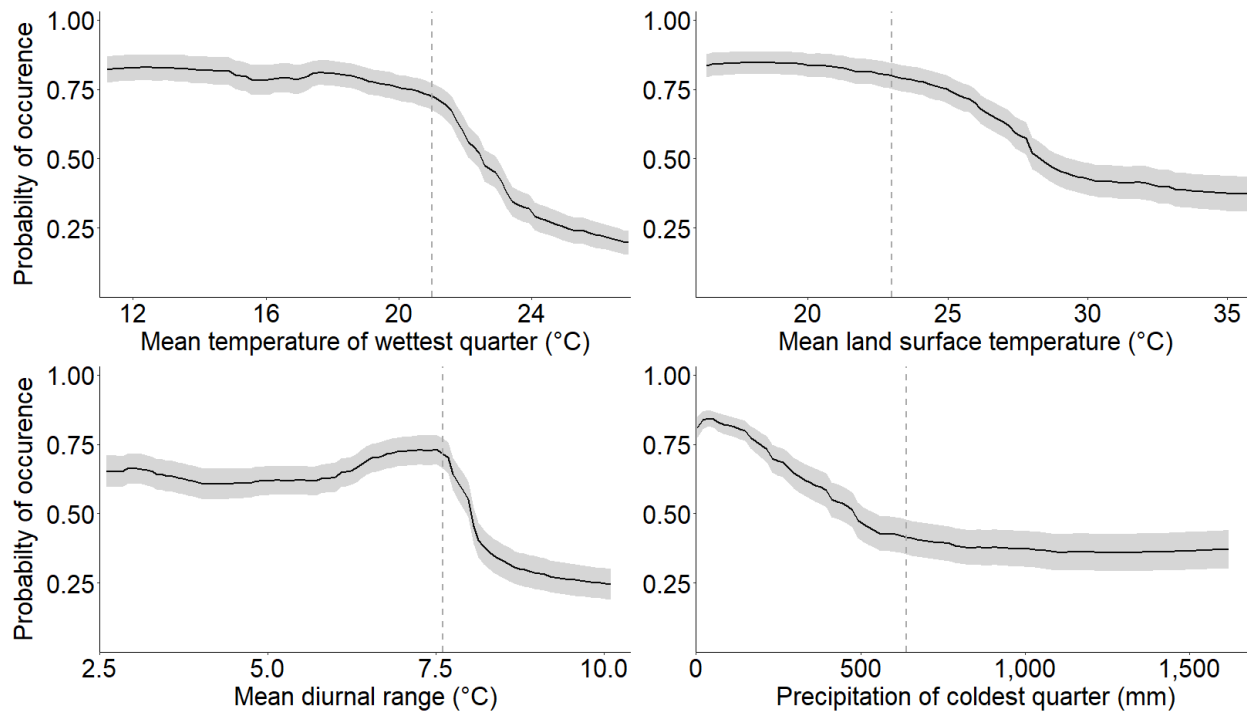


Figure 40. Response curves for environmental variables contributing the most to models of the golden-cheeked warbler's (*Setophaga chrysoparia*) wintering distribution. Black lines indicate mean values across 200 model runs (8 algorithms x 25 replicates), and gray bands indicate the confidence intervals. Dashed lines show breaks where curve trends change to or from relatively flat lines.

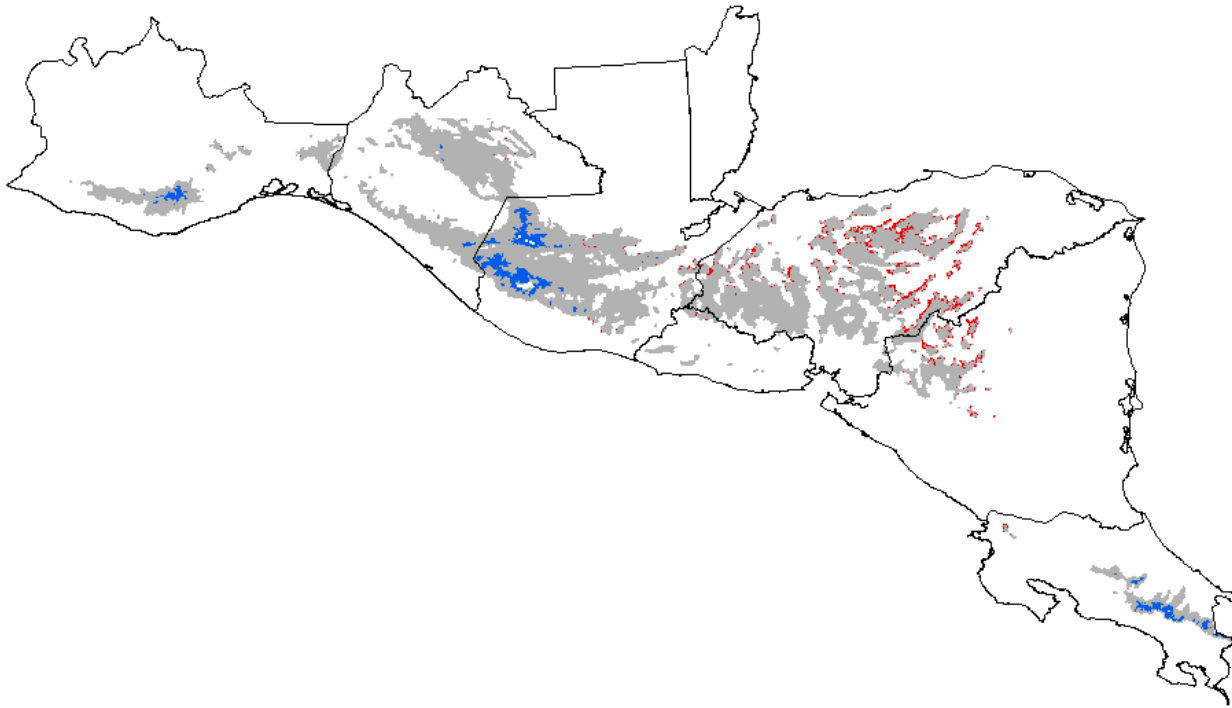


Figure 41. Predicted golden-cheeked warbler (*Setophaga chrysoparia*) wintering distribution under current climate conditions, with core elevation zone of 800 to 2,600 meters above sea level in gray and areas above and below that range in blue and red, respectively.

Table 24. Total area (km²) and percent area within core elevation zone of 800 to 2,600 meters above sea level (in parentheses), followed by mean elevation $\pm$ standard deviation and range.

Region	Present ^a	2050 2.6	2050 8.5	2070 2.6	2070 8.5
Oaxaca (Mexico)	6,532 (93%) $\bar{x} = 1,673 \pm 546$ 697–3,527	3,132 (91%) $\bar{x} = 1,721 \pm 563$ 797–3,527	2,486 (87%) $\bar{x} = 1,848 \pm 550$ 930–3,527	2,942 (91%) $\bar{x} = 1,746 \pm 554$ 797–3,527	1,370 (87%) $\bar{x} = 2,067 \pm 459$ 1,179–3,527
Chiapas (Mexico)	18,386 (99%) $\bar{x} = 1,552 \pm 429$ 672–3,705	5,203 (98%) $\bar{x} = 1,553 \pm 423$ 690–3,705	2,883 (97%) $\bar{x} = 1,727 \pm 412$ 858–3,705	3,986 (97%) $\bar{x} = 1,608 \pm 434$ 779–3,705	1,582 (95%) $\bar{x} = 1,896 \pm 375$ 983–3,705
Guatemala	30,085 (88%) $\bar{x} = 1,828 \pm 573$ 553–3,826	12,299 (89%) $\bar{x} = 1,766 \pm 546$ 651–3,526	8,923 (89%) $\bar{x} = 1,830 \pm 511$ 737–3,826	10,997 (90%) $\bar{x} = 1,750 \pm 541$ 616–3,826	5,327 (91%) $\bar{x} = 1,918 \pm 461$ 885–3,826
Honduras	36,121 (91%) $\bar{x} = 1,167 \pm 322$ 355–2,712	20,362 (94%) $\bar{x} = 1,187 \pm 326$ 474–2,712	12,879 (99%) $\bar{x} = 1,288 \pm 320$ 626–2,712	18,666 (94%) $\bar{x} = 1,176 \pm 316$ 474–2,712	7,779 (100%) $\bar{x} = 1,446 \pm 322$ 760–2,712
El Salvador	1,521 (98%) $\bar{x} = 1,233 \pm 318$ 674–2,487	831 (100%) $\bar{x} = 1,410 \pm 314$ 850–2,487	534 (100%) $\bar{x} = 1,553 \pm 298$ 967–2,487	780 (100%) $\bar{x} = 1,427 \pm 315$ 850–2,487	372 (100%) $\bar{x} = 1,656 \pm 279$ 1,101–2,487
Nicaragua	6,456 (87%) $\bar{x} = 1,008 \pm 186$ 502–1,851	4,782 (92%) $\bar{x} = 1,040 \pm 185$ 557–1,851	2,702 (99%) $\bar{x} = 1,117 \pm 173$ 704–1,851	4,453 (93%) $\bar{x} = 1,047 \pm 185$ 601–1,851	1,220 (100%) $\bar{x} = 1,211 \pm 164$ 824–1,851
Costa Rica	4,790 (81%) $\bar{x} = 2,112 \pm 515$ 571–3,650	3,061 (71%) $\bar{x} = 2,354 \pm 440$ 765–3,650	3,032 (71%) $\bar{x} = 2,360 \pm 428$ 928–3,650	3,229 (73%) $\bar{x} = 2,336 \pm 440$ 754–3,650	2,311 (63%) $\bar{x} = 2,483 \pm 387$ 1,106–3,650
Rangewide	103,891 (91%) $\bar{x} = 1,493 \pm 551$ 355–3,826	49,670 (91%) $\bar{x} = 1,464 \pm 546$ 474–3,826	33,439 (93%) $\bar{x} = 1,600 \pm 544$ 626–3,826	45,053 (91%) $\bar{x} = 1,467 \pm 549$ 474–3,826	19,961 (92%) $\bar{x} = 1,760 \pm 525$ 760–3,826

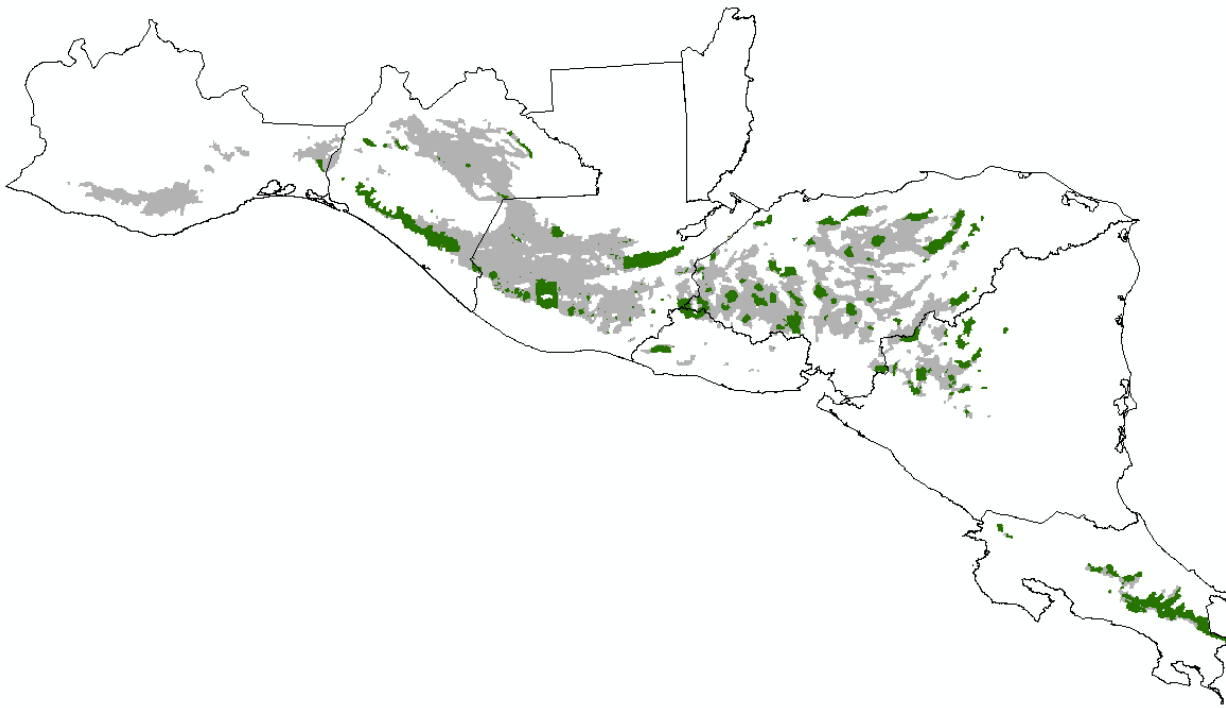


Figure 42. Protected areas within the predicted wintering distribution of the golden-cheeked warbler (*Setophaga chrysoparia*) under current climate conditions.

Table 25. Regional and rangewide area of forest loss (km²) from 2000 to 2019 and mean area lost per year $\pm$ standard deviation within the predicted wintering distribution of the golden-cheeked warbler (*Setophaga chrysoparia*). Areas derived from Hansen Global Forest Change dataset v. 1.7 (Hansen et al. 2013), with percent of predicted area in parentheses.

Region	<u>Whole region</u>		<u>Protected areas</u>	
	Forest loss	Mean loss per year	Forest loss	Mean loss per year
Oaxaca	236 (4%)	12 $\pm$ 12	5 (4%)	0 $\pm$ 0
Chiapas	1,464 (8%)	77 $\pm$ 41	105 (3%)	6 $\pm$ 3
Guatemala	1,568 (5%)	83 $\pm$ 36	146 (3%)	8 $\pm$ 5
Honduras	3,510 (10%)	185 $\pm$ 205	658 (9%)	34 $\pm$ 38
El Salvador	57 (4%)	3 $\pm$ 4	23 (3%)	1 $\pm$ 2
Nicaragua	398 (6%)	21 $\pm$ 14	157 (7%)	8 $\pm$ 6
Costa Rica	35 (1%)	2 $\pm$ 1	13 (<1%)	1 $\pm$ 1
Rangewide	7,268 (7%)	382 $\pm$ 293	1,107 (5%)	58 $\pm$ 52

Potential effects of climate change

The effect of climate change on the predicted distribution of wintering habitat for golden-cheeked warblers was considerable under both emissions scenarios with an increase in effect strength evident over time (Fig. 43). There was agreement between 95% (RCP2.6) and 94% (RCP8.5) of pixels in the 2050 forecasts generated by the five GCMs and 93% and 95% agreement among pixels in the 2070 forecasts. The severity of predicted climate change effects according to GCMs ranked from MPI < MRI < CESM < MIROC < IPSL for both scenarios in 2050 but varied by scenario in 2070 with MPI < MIROC < CESM < IPSL < MRI under the optimistic scenario and MRI < MIROC < CESM < MPI < IPSL under the pessimistic scenario. Based on our consensus maps, the forecasted range loss was 52% and 57% for 2050 and 2070 under the optimistic scenario (RCP2.6) and 68% and 81% under the pessimistic scenario (RCP8.5). The most discernible losses occurred in the central highlands of Chiapas and the western highlands of Guatemala (Fig. 43). Forty-seven and 39% of our occurrence points were coincident with the 2050 forecasts under optimistic and pessimistic scenarios, with only 45% and 29% of points coincident with the 2070 forecasts. Ninety-two percent of the range forecasts for 2050 and 2070 occurred within the core elevation zone; though ~2% more low-elevation area occurred under RCP2.6 than RCP8.5, regardless of year (Fig. 43). Currently protected lands cover 31% and 36% of the range forecasted under the optimistic climate change scenario and 33% and 45% of the range forecasted under the pessimistic scenario, for 2050 and 2070, respectively (Fig. 44).

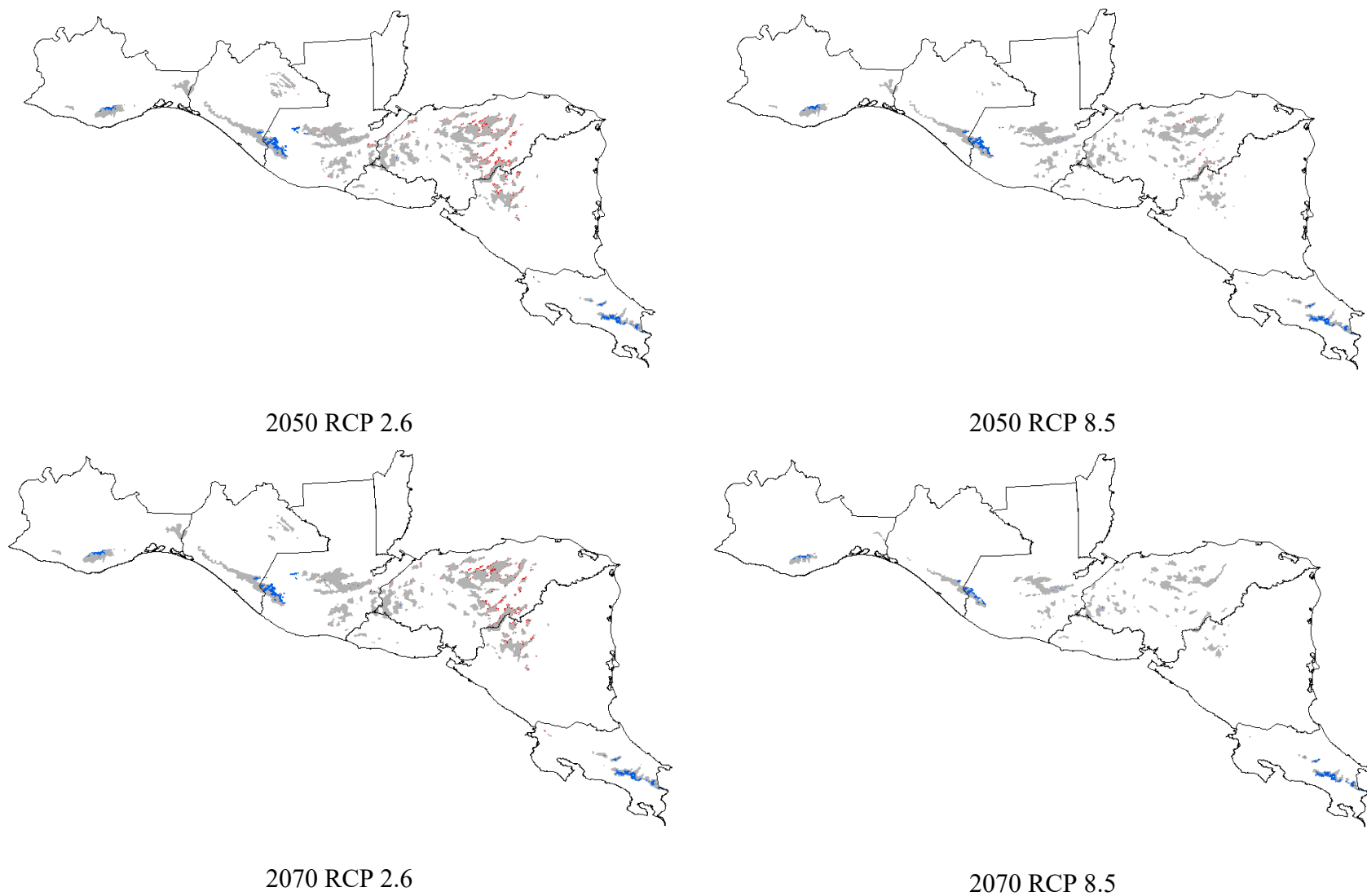


Figure 43. Forecasts of golden-cheeked warbler (*Setophaga chrysoparia*) wintering habitat distribution for 2050 and 2070 under optimistic and pessimistic Representative Concentration Pathway (RCP) scenarios (RCP 2.6 and RCP 8.5).

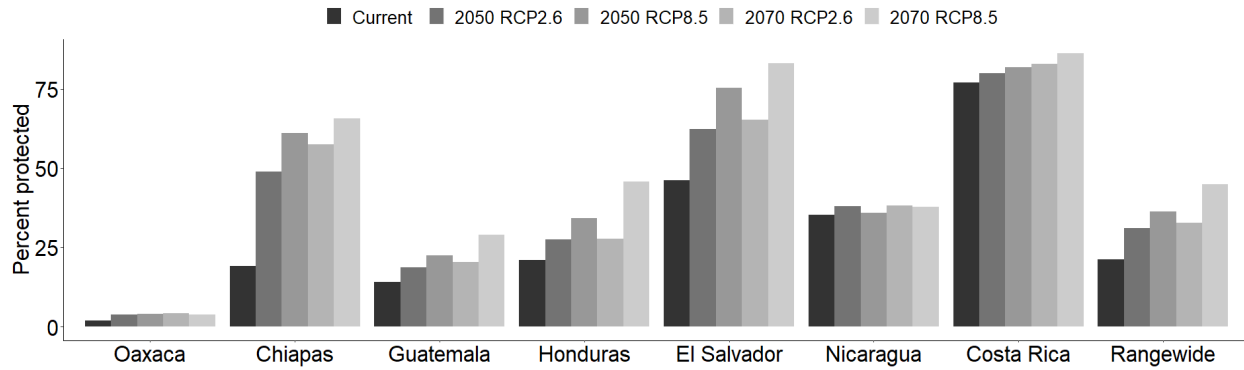


Figure 44. Percent of currently protected lands within the predicted wintering range of the golden-cheeked warbler (*Setophaga chrysoparia*) under current and under pessimistic (RCP2.6) and optimistic (RCP8.5) climate projections for 2050 and 2070.

Breeding habitat

Breeding range classification and change detection results

Overall accuracy ranged from 81–89% across all regions and years, and all but two classifications had an overall accuracy of $\geq 85\%$ (Table 26). In addition, kappa values ranged 63–83% across all regions and years (Table 26). The classifications with the lowest overall accuracies and kappa values were from the year 2020 in the north and central regions (Table 26). User’s and producer’s accuracies ranged 78–92% across all regions, years, and land cover classes, which aligned with our goal of $\geq 70\%$ (Table 27; see confusion matrices in Table A.4). Again, classifications in the north and central regions for the year 2020 generally had lower user’s and producer’s accuracies when compared to other years (Table 27).

Total forest cover across the warbler’s breeding range was similar in 2000 and 2020, reflecting a total loss over the 20-year period of $\sim 1\%$ (Fig. 45, Table 28). However, total forest cover, as well as the amount of forest lost and gained between time steps, varied between years by region (Figs. 45–46, Tables 28–29). In the north, forest loss was greater than forest gain from 2000–2010, whereas forest gain was greater from 2010–2020 (Table 29, Fig. 46). In contrast, we found greater forest loss than forest gain across all time steps in the central region (Table 29, Fig. 46). Last, forest gain was greater than forest loss across all time steps in the south region (Table 29, Fig. 46). Importantly, warblers require strips of mature (>20 years) Ashe juniper bark to build their nests (Ladd and Gass 2020) and it can take several decades for oak-juniper woodland to become viable breeding habitat for warblers. If we exclude forest gains from consideration, we estimated a 28% rangewide loss in forest cover between 2000 and 2020, with the highest percent loss of forest cover occurring in the central portion of the warbler’s breeding range (Table 29).

Table 26. Overall accuracies and kappa values for our supervised classification results across the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range separated by region.

Region	Year	Overall	Kappa
North	2000	89%	78%
	2010	87%	74%
	2020	84%	69%
Central	2000	88%	76%
	2010	86%	72%
	2020	81%	63%
South	2000	88%	83%
	2010	88%	82%
	2020	89%	83%

Table 27. User's and producer's accuracies for our supervised classification results across the golden-cheeked warbler (*Setophaga chrysoparia*) range separated by region. We classified the north and central regions to two classes, including forest (evergreen and mixed forest) and other (all other land cover classes), whereas we classified the south region to three classes, including evergreen forest, mixed forest, and other.

Region	Year	Type	Other	Forest	Evergreen	Mixed
North	2000	User's	87%	91%	-	-
		Producer's	90%	88%	-	-
	2010	User's	86%	89%	-	-
		Producer's	90%	85%	-	-
	2020	User's	83%	86%	-	-
		Producer's	85%	84%	-	-
Central	2000	User's	89%	88%	-	-
		Producer's	87%	89%	-	-
	2010	User's	88%	84%	-	-
		Producer's	86%	87%	-	-
	2020	User's	78%	85%	-	-
		Producer's	86%	78%	-	-
South	2000	User's	89%	-	87%	89%
		Producer's	92%	-	86%	87%
	2010	User's	89%	-	87%	88%
		Producer's	87%	-	87%	90%
	2020	User's	86%	-	88%	92%
		Producer's	87%	-	89%	91%

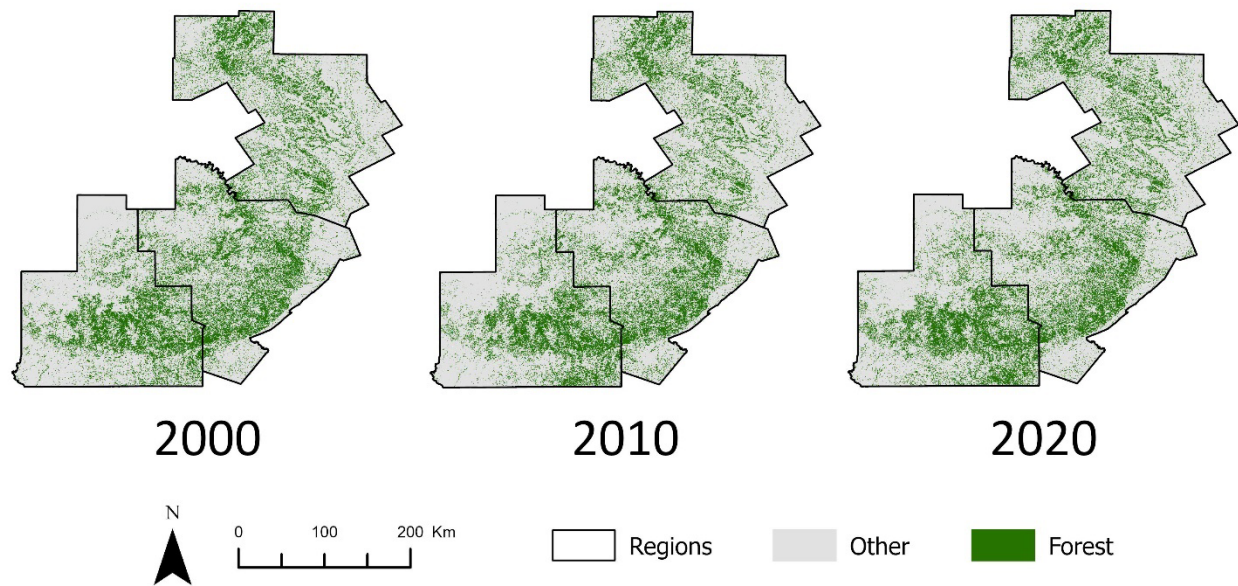


Figure 45. Classification of land cover in the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range for the years 2000, 2010, and 2020. The forest class included only the land cover types that best aligned with warbler breeding habitat (i.e., evergreen and mixed forest); we grouped all other land cover types into their own class (other).

Table 28. Area (ha) attributed to each class by region and year for our classifications of the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range. We combined evergreen and mixed forest classes for the southern region.

Region	Year	Other	Forest
North	2000	2,331,631	725,562
	2010	2,382,598	674,596
	2020	2,333,397	723,797
Central	2000	1,958,962	893,895
	2010	2,000,994	851,864
	2020	2,077,109	775,748
South	2000	2,151,797	725,334
	2010	2,142,638	734,494
	2020	2,049,891	827,240
Entire range	2000	6,442,390	2,344,791
	2010	6,526,230	2,260,954
	2020	6,460,397	2,326,785

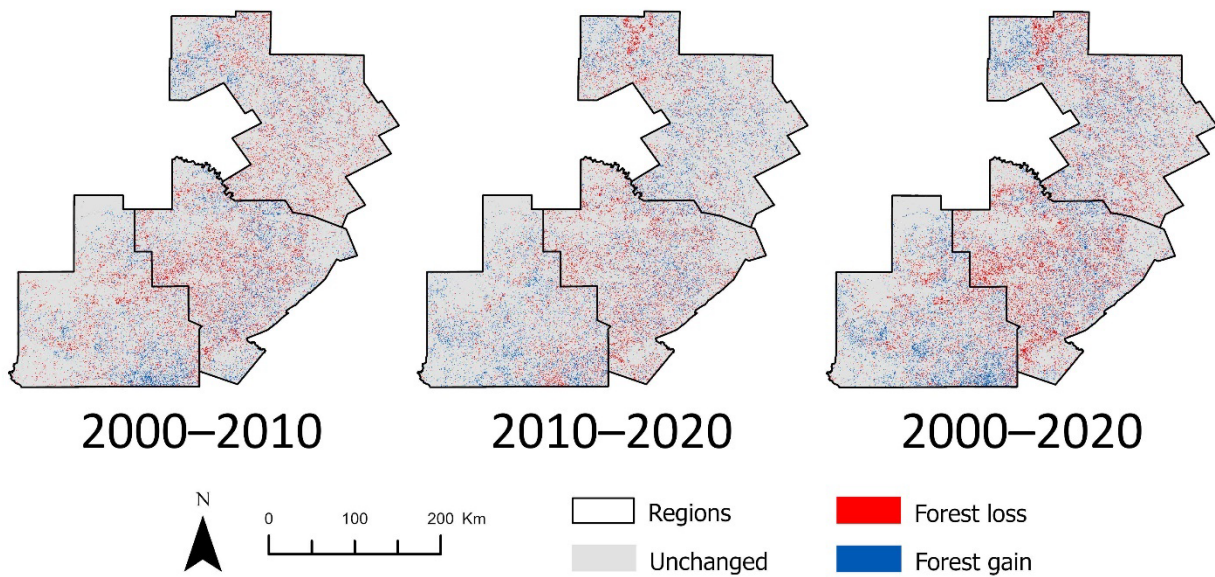


Figure 46. Land cover change in the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range. The forest class included only the land cover types that best aligned with warbler breeding habitat (i.e., evergreen and mixed forest); we grouped all other land cover types into their own class (other).

Table 29. Area (ha) and percent change in forest by region and time step for our classification of golden-cheeked warbler (*Setophaga chrysoparia*) habitat. We combined evergreen and mixed forest classes for the southern region.

Region	Years	Original forest	Forest loss	Forest gain
North	2000–2010	725,562	183,228	132,261
	2010–2020	674,596	130,320	179,521
	2000–2020	725,562	203,128	201,363
Central	2000–2010	893,895	216,138	174,106
	2010–2020	851,864	216,365	140,249
	2000–2020	893,895	296,404	178,256
South	2000–2010	725,334	136,489	145,649
	2010–2020	734,494	102,098	194,845
	2000–2020	725,334	140,452	242,358
Entire range	2000–2010	2,344,791	535,855	452,016
	2010–2020	2,260,954	448,783	514,615
	2000–2020	2,326,785	639,984	621,977

Projected warbler habitat distribution

Protected areas cover 2% of the 25,889 km² of warbler breeding habitat that is estimated to occur rangewide (Mueller et al. 2022). The northern portion of the warbler's breeding range has the least amount of protected land (<1% of warbler breeding habitat in the north region) and the central portion of the warbler's breeding range has the most (4% of warbler breeding habitat in the central region) (Table 30). On average, the most optimistic CONUS FORE-SCE scenarios (i.e., B1 and B2) projected a 25% and 37% increase in the amount of developed cover within the boundaries of the warbler breeding habitat model by 2050 and 2070, respectively, and the most pessimistic CONUS FORE-SCE scenarios (i.e., A1B and A2) projected an average increase of 53% and 94% in the amount of developed cover within the boundaries of the warbler breeding habitat model by 2050 and 2070, respectively (Table 30). The projected increase in developed cover was most pronounced in the central portion of the warbler's breeding range (18–82% increase in developed cover from 2020–2070, depending on the scenario) (Table 30); the projected increase in developed cover ranged from 27–179% in the northern portion of the warbler's breeding range and 15–164% in the southern portion of the warbler's breeding range from 2020–2070, depending on the scenario (Table 30). Similarly, the most optimistic ICLUS scenarios (i.e., SSP2, RCP4.5 scenarios) projected an average increase of 15% and 25% in amount of developed cover within the boundaries of warbler breeding habitat model by 2050 and 2070, respectively, and the most pessimistic ICLUS scenarios (i.e., SSP5, RCP8.5 scenarios) projected an average increase of 45% and 76% in the amount of developed cover within the boundaries of the warbler breeding habitat model by 2050 and 2070, respectively (Table 30). Again, the projected increase in developed cover was most pronounced in the central portion of the warbler's breeding range (8–66% increase in developed cover from 2020–2070, depending on the scenario) (Table 30); the projected increase in developed cover ranged from 29–128% in the northern portion of the warbler's breeding range and 16–107% in the southern portion of the warbler's breeding range from 2020–2070, depending on the scenario (Table 30).

Table 30. Total area (km²) by region of golden-cheeked warbler (*Setophaga chrysoparia*) breeding habitat (Habitat), golden-cheeked warbler breeding habitat contained within protected areas (Protected), and golden-cheeked warbler breeding habitat projected to contain developed cover by CONUS FORE-SCE and ICLUS models in the years 2020, 2050, and 2070.

Region	Habitat ¹	Protected ²	CONUS FORE-SCE											
			A1B			A2			B1			B2		
			2020	2050	2070	2020	2050	2070	2020	2050	2070	2020	2050	2070
North	4,489	2	80	146	189	71	129	198	69	105	127	62	75	79
Central	9,906	348	417	604	688	395	566	718	371	486	545	363	411	427
South	11,494	190	61	109	142	59	100	156	57	79	90	55	62	63
All	25,889	540	556	859	1,020	525	795	1,071	496	670	762	480	548	569
Region	Habitat ¹	Protected ²	ICLUS ³											
			SSP2, RCP4.5 HadGEM2-AO			SSP5, RCP8.5 HadGEM2-AO			SSP2, RCP4.5 FIO-ESM			SSP5, RCP8.5 FIO-ESM		
			2020	2050	2070	2020	2050	2070	2020	2050	2070	2020	2050	2070
North	4,489	2	679	897	1,040	801	1,478	1,823	654	761	843	773	1,323	1,667
Central	9,906	348	2,993	3,450	3,774	3,174	4,452	5,281	2,938	3,079	3,167	3,085	3,963	4,712
South	11,494	190	679	945	1,185	743	1,170	1,538	653	718	758	711	1,045	1,335
All	25,889	540	4,350	5,292	5,999	4,718	7,101	8,642	4,245	4,558	4,768	4,569	6,330	7,714

¹Mueller et al. 2022

² UNEP-WCMC and IUCN 2023

³Combined ICLUS classes that represented developed cover (EPA 2020)

Golden-cheeked Warbler Habitat Explorer

The landing page for the Golden-cheeked Warbler Habitat Explorer (hereafter app) includes a root panel on the right side of the screen and a legend in the bottom left corner (Fig. 47). The root panel contains check boxes that allow users to toggle layers on and off in the app. In brief, the layers include distribution models for the warbler's breeding (Mueller et al. 2022) and winter ranges (Fig. 47), projected land cover (EPA 2020, Sohl et al. 2018), utilization distributions that we created for the warbler's migration route and wintering grounds, and locations of formally protected areas across the warbler's breeding and non-breeding ranges (UNEP-WCMC and IUCN 2023) (Table 7). Colors depicted on the map represent different values within each dataset. For example, the app shows potential winter habitat within the core elevation range (800–2,600 masl) in yellow and potential winter habitat outside the core elevation range in black. Users can click on the legend to identify the information represented by each color, allowing them to view and consider multiple datasets simultaneously. Users can also use sliders to change the opacities of the habitat models. To explore projections that overlap with warbler breeding habitat, users must select a model (CONUS FORE-SCE or ICLUS) and a land use scenario (Tables 2, 4) from the app-generated drop-down menu, then use a slider to select the year of interest. To explore projections that overlap with warbler winter habitat, users must select a year of interest (2050 or 2070), then choose a model and climate scenario. By clicking buttons under the "Projection Information" heading in the root panel, users can view pop-up windows on the map that describe the scenarios included in each model. Clicking the "close" button at the top of the pop-up window will allow users to remove the descriptions from the screen.

Users can assess the risk of conversion of specific patches of breeding habitat using the "AOI Calculations for the Breeding Range" function in the root panel (Fig. 47). To utilize this function, users must first create one or more polygons that defines their AOI. The polygon drawing tool is located at the top left corner of the screen. After clicking the polygon tool, users must move to the location where they want their first point, click on the map to create a point, and repeat this step until their polygon is the desired shape and size. Users must then click on the first point to close the polygon. Users can use the hand button in the top left corner of the screen to select or delete individual polygons. After creating polygons, users can choose a minimum patch size from the drop-down menu under "Breeding habitat patch size". Twenty hectares is the smallest patch size from which users can choose, as this size aligns with minimum patch size thresholds for warbler reproductive success according to Butcher et al. (2010). Users can then add projected land cover layers to view the risk of conversion for each patch within their AOI. See user manual in Appendix 10.B for more information.

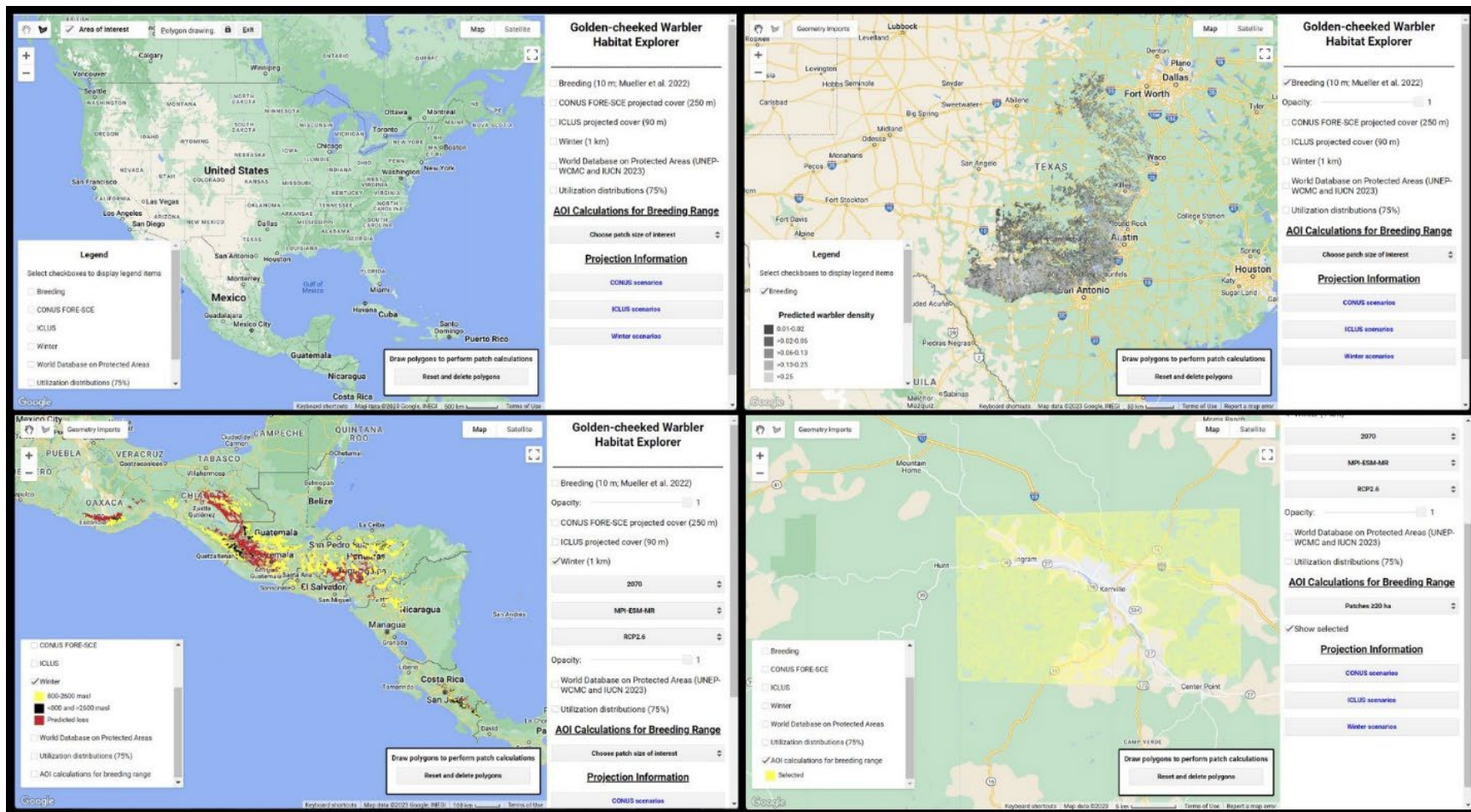


Figure 47. Demonstration of our Google Earth Engine web application for visualizing golden-cheeked warbler (*Setophaga chrysoparia*) breeding and wintering habitat. The top-left shows the landing page for our app; the top-right shows the breeding habitat model from Mueller et al. (2022); the bottom-left shows the winter species distribution models from our project; and the bottom-right demonstrates the function to select breeding habitat patches. All images show the root panel (right) and the legend (bottom left).

7. Discussion and Opportunities for Further Study

Sixty percent of neotropical migratory songbirds have experienced population declines over the last century (Finch 1991, North American Bird Conservation Initiative 2009, Sauer and Link 2011), which includes an estimated loss of three billion North American songbirds since 1970 (Rosenberg et al. 2019). The drivers of these population declines are species-specific but there is growing evidence that events during non-breeding periods may play a considerable role (Finch 1991, Keller and Yahner 2006, Taylor and Stutchbury 2016). Unfortunately, we still lack data to describe winter habitat associations and migratory behavior for most species, including the timing, location, and duration of migration, and the extent to which individuals from a specific breeding location spend the non-breeding period in distinct areas (i.e., migratory connectivity) (Marra et al. 2006, Cohen et al. 2018, Hill and Renfrew 2019). Such information is necessary to develop and implement more effective conservation strategies that address concerns across a bird's annual cycle, especially at-risk species.

The miniaturization of tracking technologies has revolutionized our ability to obtain broad-scale movement data on small migratory songbirds, which could help us identify habitat that is in most need of protection (e.g., Salewski et al. 2013) and implement actions that support conservation agreements, initiatives, or memoranda of understanding for species that cross jurisdictional boundaries (e.g., Partners in Flight, Working Lands for Wildlife, Americas Flyways Initiative, Migratory Birds Joint Venture, Convention on the Conservation of Migratory Species of Wild Animals). However, there are still logistical constraints associated with tracking studies on small migratory songbirds (e.g., size of available devices, battery life, cost) (McKinnon and Love 2018, Brlik et al. 2019). As such, most geolocator studies have low sample sizes and measure movements of individuals that originate from a small portion of the species' breeding range. In addition, we still lack data necessary to identify appropriate questions, species, study sites, and methods needed to obtain migration data for songbirds weighing <12 g (e.g., Adams et al. 2022). From a DoD perspective, overcoming these challenges for listed and at-risk migratory birds that occur on military installations is critical to maintaining mission readiness, as we lack data to describe the non-breeding movements of many species that are in decline. However, threats that impact any part of a migratory bird's annual cycle can affect the entire population and military compliance with environmental laws that protect T&E species can restrict soldiers' ability to train at full capacity. Beyond compliance with federal laws and regulations (e.g., Sike's Act, Migratory Bird Treaty Act, Endangered Species Act), the DoD's work toward conservation of migratory birds helps maintain overall biodiversity and ecological integrity; demonstrates the DoD's commitment to environmental sustainability; provides opportunities for scientific research and public outreach; and can serve to strengthen the strong and diverse partnerships that DoD has developed with public, private, and industrial stakeholders to conserve habitat for birds.

From 2017–2021, we attached 309 miniaturized light level geolocators to male golden-cheeked warblers at five locations across their breeding range to examine the migratory behavior of this ~10 g endangered species. We recovered 80 geolocators and were able to analyze warbler movements with data from 61 devices. Our results provided novel insights into the species' migratory and winter behavior. For example, we found that most warblers made extensive movements both within and outside their breeding range prior to fall migration (i.e., post-breeding movements). We also found that 80% of warblers migrated along the Sierra Madres to their wintering grounds in southern Mexico and Central America as expected but that 20% migrated over the Gulf of Mexico or traveled further east before arriving on their wintering

grounds. We identified several areas along the warbler's migration route and on their wintering grounds that were used by most birds we tracked. We also found locations outside the known winter range where warblers may occur; one of these locations has already been confirmed by field-based surveys in Oaxaca, Mexico. Our results suggested that warblers exhibit weak migratory connectivity, but given their relatively small winter range ($\sim 104,000 \text{ km}^2$) and habitat losses forecasted to occur under optimistic climate change scenarios ($\sim 43,000 \text{ km}^2$), continued and increased conservation along the warbler's migration route and on their wintering grounds are necessary to ensure population persistence and would simultaneously help protect co-occurring species.

Post-breeding movements

Post-breeding movements have been described for several passerines (e.g., Hobson and Kardynal 2015, Brown 2016). Distance traveled and locations used during the post-breeding period may differ for juveniles and adults (e.g., Teitelbaum and Mueller 2019), but often reflect movements from the breeding grounds to areas with higher food availability so that individuals can meet the energy requirements necessary for molt (Rivera et al. 1999) and/or to quickly acquire fat reserves necessary for migration (e.g., Vitz and Rodewald 2007, Knight et al. 2019); reduce competition with conspecifics or heterospecifics (e.g., Smith et al. 2011); limit their interactions with potential predators (e.g., Rivera et al. 1999), avoid unfavorable climatic conditions or weather events (e.g., Sauter et al. 2010); or allow individuals to benefit from a combination of these factors. Our results demonstrated that warblers exhibit relatively long post-breeding movements and many individuals traveled outside the breeding range during this period. We found considerable variation in the shortest and longest post-breeding movements and, by extension, the vegetation conditions at their farthest stationary points prior to fall migration. The precision and accuracy of geolocators depends on many factors, including location, bird behavior, weather, and habitat, and can change throughout the tracking period. Thus, exact positions are unknown and we must use caution when interpreting these data (Lisovski et al. 2019), but the locations we identified during the post-breeding period are consistent with field-based observations of warblers in Eunice, NM (23 Aug 2009; NMBRC 2023); Midland, TX (1–11 Aug 2011; eBird 2023); Wichita Mountains Wildlife Refuge in Comanche County, OK (06 May 2013; Long et al. 2014); St. Louis County, MO (Apr 2013; ebird 2023); San Angelo Nature Trail in Tom Green County, TX (11 Aug 2022; eBird 2023), Big Bend National Park in south Texas (eBird 2023), and others.

We can only speculate why warblers made these long-distance post-breeding movements from the locations where they spent the breeding season. The highest annual temperatures and the lowest monthly rainfall totals that warbler's experience on their breeding grounds occurs during the post-breeding period (NOAA 2021). Warblers generally moved in a north to west direction from their breeding grounds, and though they often moved to locations during the post-breeding period that are comparably hot and dry. It is possible that warblers are moving to locations or using substrates with seasonally available food resources (Smith-Hicks et al. 2016, Colón et al. 2019, Trumbo et al. 2021). It is also possible that warblers are moving to locations where their potential predators are less active, and thus, their chances of survival are higher at the post-breeding locations than they would be at their breeding locations during this critical period (Anders et al. 1998, Vitz and Rodewald 2007). By spreading out during the post-breeding period, warblers may also limit competition among individuals for resources or increase opportunities for prospecting (Greenwood and Harvey 1982, Jackson 1994). Further, the speed and direction of

prevailing winds could have contributed to the post-breeding movements we observed (Sauter et al. 2010). It is likely that a combination of these factors influenced warbler movements during the post-breeding period; many of these factors would be extremely challenging to study given low detection probabilities during the post-breeding season and the variability and scale at which these post-breeding movements occur. However, we can explore how prevailing winds or extreme weather events might influence post-breeding movements of warblers using the current data set, and plan to address this topic in the future.

Migration route

Prior to the current research, warblers were thought to migrate over land between the Sierra Madre Oriental Mountain Range and the Gulf of Mexico, with a possibility of a trans-Gulf migration based on a least accumulated-cost analysis (Winters 2015). Predictions from the least accumulated-cost analyses indicated that trans-Gulf migrations would be most advantageous for warblers during spring given stronger prevailing winds during this time of year. Our research showed that 80% of warblers migrated south over land, but that 20% migrated over the Gulf, with most trans-Gulf migrations (92%) occurring in fall. Similar to our results for post-breeding movements, the migration locations that we identified outside the direct southern land route to the wintering grounds using geolocator data are consistent with field based observations in St. Croix, Virgin Islands (23 Nov 1939 to 8 Jan 1940; Beatty 1943) Pinellas County, FL (24 Aug 1964; Woolfenden 1967), Galveston Island, TX (Aug 1977; Lasley 1990), South Padre Island, TX (09 Mar 2012, 06 Jul 2014, 17 Jul 2020; eBird 2023) and Aransas NWR, TX (Jul 1999; Lockwood 2001). These observations have been described as rare, but songbirds are difficult to detect during the non-breeding period and our data suggests that some warblers do indeed traverse water from these regions during migration.

Migratory songbirds that breed within the central flyway typically migrate over land while species that occur along the eastern flyway typically migrate along the Gulf coastline or across water in the Gulf of Mexico (La Sorte et al. 2014). However, there is greater variation in the migration strategies of birds that breed in the central flyway compared to the eastern flyway, and at least some warblers moved along migration paths more typical of birds that breed in the eastern flyway. It remains unclear why we found variation in migration paths of warblers. We did not find evidence that the differences we observed were related to age, departure date, or location on the breeding grounds. Similar to post-breeding movements, other factors such as prevailing winds (Gauthreaux et al. 2005), extreme weather events (Briedis et al. 2017), resource availability along the migration route (Alterstam 2011), body condition (Deutschlander and Muheim 2009), or risk of predation (Alerstam 2011) could influence warbler migration routes, but elucidating the mechanisms that drive differences in the migratory paths of warblers was beyond the scope of our current research and would require additional study. We will also continue to monitor Motus' online database after our project ends, as there are multiple towers along the warbler's migration route with more planned for installation in the near future and some radio transmitters we attached to the warblers should remain active for several months following the 2023 breeding season while others should remain active for the life of the birds. Migration data recorded by the Motus towers could supplement the migration route, timing, and location data we obtained from the geolocators.

Migration timing

Similar to other studies that used geolocators to explore the migratory behavior of songbirds (e.g., Stutchbury et al. 2009, Bächler et al. 2010, Tøttrup et al. 2012), our results indicated that the length of spring migration was shorter than fall migration for warblers. However, the departure dates for fall and spring migration both spanned approximately two months and we found limited evidence that fall and spring departure dates were related. The timing of migration is heavily influenced by photoperiod (Dawson et al. 2001), but many factors can influence migration initiation dates and durations. For example, molt is energetically expensive (Cyr et al. 2008). Warblers molt between June and August, and resource availability on the warbler's breeding grounds prior to fall migration may influence when molt occurs. Molt timing could vary across locations and years, thus influencing departure dates and the durations of fall migration (Studds and Marra 2007, 2011; Fox and Walsh 2012). In addition, weather patterns may be less predictable in fall than spring, meaning warblers may need to adjust their migration routes or timing to avoid large storms, and research suggests that migratory songbirds could take advantage of tailwinds in spring that are not available in fall (Kemp et al. 2010, Winters 2015).

There are also fewer time constraints during fall migration compared to spring migration. In spring, birds must reach the breeding grounds quickly so that they have sufficient time to establish their territories, pair, and fledge young; early arrival on the breeding grounds may reflect strong selection pressures (Kokko 1999, Morbey and Ydenberg 2001) and may result in higher pairing and fledging success for warblers as some have found that warbler daily nest survival decreases as the breeding season progresses (e.g., Peak and Thompson 2014, Reidy et al. 2017). Warbler arriving earlier on the breeding grounds may also have more time to initiate another nest following nest failure or have time to double-brood. In addition, resource availability along their migration routes may be greater in spring than fall, reducing the need for extended stopovers during spring. Food abundance on the wintering grounds can also advance or delay migration (Bridge et al. 2010) and there is evidence of seasonal differences in hypothalamic gene expression that cause songbirds to gain more fat and body mass during spring compared to fall (Sharma et al. 2018). While we cannot comment on these specific factors, we did find that age may influence initiation dates for fall migration, as SY males started fall migration ~10 d earlier than ASY males, and SY males tend to arrive on the breeding grounds 1–2 weeks later than ASY males. Age-based differences in the timing of migration are relatively common for songbirds and could reflect experience, body condition, or social dominance behaviors (Cooper et al. 2009, Woodworth et al. 2015, Patchett et al. 2022).

Stopovers

Stopover sites are critical for migratory songbirds as these locations represent places where individuals pause to rest or refuel en route to their breeding or wintering grounds, and the condition of stopover sites can ultimately impact survival or breeding success (Hutto 1998, Faaborg et al. 2010). Geolocators have revealed unexpectedly long stopovers (>7 days) for some species in the fall (e.g., Stutchbury et al. 2011, McKinnon et al. 2013), spring (e.g., Callo et al. 2013, McKinnon et al. 2013), or during both migrations (e.g., Kristensen et al. 2013, McKinnon et al. 2013). Many of these long duration stopovers exceed the amount of time needed for refueling based on energetic models alone (Alerstam 1991). However, the relationship between stopover duration and energetic needs is complicated and can be influenced by fuel deposition rates, distances between stopovers, predation risk, and wind conditions, among others (Alerstam

2011). We found that warblers spent much of their migratory periods at stopover sites; 48% of the stopovers lasted ≥ 8 days and 18% of stopovers lasted for ≥ 20 days at a single location. Due to the accuracy of geolocators, the exact locations of warbler stopover locations are unknown, but based on the 50% UD, the two largest stopover locations used by warblers during fall and spring migration were both located in Mexico; the northernmost 50% UD included portions of Nuevo Leon, Tamaulipas, Coahuila, and Veracruz and the southernmost 50% UD included portions of Veracruz, Hidalgo, Tlaxcala, Puebla, and Oaxaca. We can only assume that warblers are using these areas to obtain food resources, to rest, or to reduce their risk of mortality due to predation, but using geolocators to identify these locations, then following geocator studies up with field-based surveys to pinpoint where warblers occur, is an important step toward understanding the function and relative importance of a given stopover site so that we can protect areas that are critical to the survival of warblers during the non-breeding season (Mehlman et al. 2005).

Wintering

Few warblers in our study were stationary during winter, which has been documented in other songbirds (Fraser et al. 2012, Stach et al. 2012, Jahn et al. 2013) and may be associated with changes in the weather (Sauter 2010), resources (Levey and Stiles 1992, Telleria et al. 2014, Knight et al. 2019), age (Fudickar et al. 2013, Teitelbaum and Mueller 2019), or interactions with co-occurring species (Smith et al. 2011) on a bird's wintering grounds. However, based on the 75% UD created from our geocator data, most warblers overwintered within or in close proximity to where our model predicted the warbler's current winter range to occur in southern Mexico and Central America. We identified three areas of particular importance to warblers during the winter, including one in Chiapas, Mexico; one across the borders of Guatemala, El Salvador, Honduras, and one across small portions of Veracruz and Oaxaca, Mexico; Belize; and Nicaragua (Fig. 41). Because most overwintering locations occurred within a relatively small spatial extent, warblers that occur in these areas may be at higher risk from catastrophic weather events, wildfire, or land use change. We did not find evidence that warbler's segregated on their wintering range by age class. Though sex-based segregation occurs on the wintering grounds for some species (Catry et al. 2004, Woodworth et al. 2016), we did not have data to explore this phenomenon for warblers.

Our ensemble model predicted $\sim 104,000 \text{ km}^2$ of potentially suitable wintering habitat for the warblers across the study area. More than 80% of the predicted habitat occurred in Honduras, Guatemala, and Chiapas (i.e., core areas), and our geocator data supported relatively high use of these areas compared to other portions of the predicted range. From 2000–2019, forest cover loss and the mean annual rate of forest loss within the predicted winter range of warblers was highest in Honduras compared to other regions and forecasted winter habitat loss was 44% under the most optimistic climate scenario. Forecasted losses were even higher in Guatemala and Chiapas (59% and 72% loss of winter habitat under the most optimistic climate scenario, respectively), and these losses will likely be exacerbated by continued land use pressures in the regions. Existing protected areas cover $\sim 20\%$ of the current winter habitat in both Honduras and Chiapas, and $\sim 14\%$ of the current winter habitat in Guatemala, but protected areas are not impenetrable to change. In Honduras and Guatemala, the level of forest loss within protected areas Guatemala was similar (within 1–2%) to rates of loss we observed across predicted habitat in each country, whereas loss of forested habitat in protected areas in Chiapas was slightly better at 5% lower than that seen across the state. Given the high use of these core areas by warblers

and the continued loss of habitat that is expected to occur within the next several decades, increased conservation in and outside of currently protected areas may be critical to maintaining warbler populations.

Though Oaxaca, Mexico is not typically included in the description of warbler winter habitat, our models, geolocator results, and observations during field-based surveys by scientists on the wintering grounds support their use of this region. With the considerable forecasted loss of suitable habitat in core areas, warblers may rely more heavily on forests at the edges of their wintering range in the future. Protected areas comprised only 2% of the warbler's predicted range in Oaxaca, and though forest loss was 4% from 2000–2019, the forecasted losses in Oaxaca ranged from 55–79%, depending on the scenario and year. Predicted habitat in Costa Rica could offer refuge to warblers in a changing climate as this area experienced little habitat lost from 2000–2019 and was forecasted to experience less habitat loss due to climate change than core areas. However, warbler reports in Costa Rica are relatively uncommon as is, and evidence suggests the southern limits of many Neotropical migrant's breeding ranges have been shifting northward since the mid-1980's (Rushing et al. 2020). If the same pattern occurs on the warbler's wintering grounds, the presence of potentially suitable forests in Costa Rica will likely provide little conservation value for this species. Finally, our geolocator results identified several areas used outside the predicted winter range (e.g., Yucatán, Mexico; Belize, Panama). It is not clear how much sampling has occurred for warblers in these areas, especially at higher elevations, and field-based surveys would be necessary to inform future modeling efforts.

Migratory connectivity

Our study represents the first effort to explore migratory connectivity for warblers and one of the most extensive geolocator studies for a small migratory songbird. Our results suggested that warblers exhibit weak migratory connectivity and disperse widely on the wintering grounds. To date, the results from similar research has been mixed, with some songbirds exhibiting strong migratory connectivity (e.g., Hahn et al. 2013, Hallworth et al. 2015, Kramer et al. 2018, Brunner et al. 2022) and others exhibiting weak migratory connectivity (e.g., Fraser et al. 2017, Finch et al. 2017, Kramer et al. 2018). While populations with strong connectivity and individuals with high winter site fidelity may be better adapted to local conditions (Webster et al. 2002), events on the wintering grounds can influence the migration phenology (Marra et al. 1998), survival (Silllett and Holmes 2002, Faaborg et al. 2010), and reproductive success (Norris et al. 2004) of migratory songbirds. Thus, populations that diffuse across their winter range may be more resilient to local variation in resource availability. Similarly, the effects of habitat loss or natural disturbances on the populations breeding or wintering grounds may be less pronounced for species that exhibit weak migratory connectivity compared to species that exhibit strong migratory connectivity (Cresswell 2014, Ambrosini et al. 2016). In addition, populations with weak migratory connectivity may exhibit genetic variation in their migratory behavior (e.g., direction and timing) that allows them to adapt more quickly to changes on their breeding or wintering grounds (Webster et al. 2002).

Understanding linkages between the breeding grounds and wintering grounds is essential for conservation of migratory species. Given the weak migratory connectivity we observed, warblers may be more resilient to habitat loss or environmental change than a species that relies on a small number of non-breeding sites or exhibits a high degree of temporal synchrony in the timing of migration. However, given their relatively small winter range (~104,000 km²), habitat losses forecasted to occur under the most optimistic climate change scenario (~43,000 km²), and

uncertainties in how songbirds will adapt to rapid change if current climate trajectories are maintained (e.g., physiologically, morphologically, behaviorally), continued and increased conservation along the warbler's migration route and on their wintering grounds are necessary to ensure population persistence. Such efforts would simultaneously help protect co-occurring species for which the DoD may have a legal responsibility. Future research that integrates data from geolocators or other tracking devices with complementary techniques (e.g., isotopes, genetics) or that allows for more robust analyses (e.g., analyses that account for abundance among sampling regions [Hallworth et al. 2015], survivorship bias [Rushing et al. 2021]) could further advance our understanding of the migratory ecology of warblers and other species. In addition, we were not able to address any questions related to sexual segregation on the wintering grounds or migratory connectivity of female warblers, which is an obvious bias and limitation for most migration studies. Habitat loss or variation in environmental conditions could have under- or over-proportional effects on a species' population dynamics if the sexes exhibit differential habitat use during migration or on the wintering grounds (Harrison et al. 2011, Briedis and Bauer 2018). Thus, understanding migration patterns and winter habitat use by both male and female warblers, as well as the relative contribution of both sexes to population growth, could help us target conservation efforts where and when they would most benefit the species.

Impact assessment

Our multi-year study that included 235 individuals monitored across six plots at two geographically separated study sites demonstrated that 0.41 g geolocators attached with a leg-loop harness had minimal impacts on warbler pairing success, fledging success, return rates, and body condition. Our results are consistent with other research on birds weighing <100 g (Costantini and Møller 2013, Bodey et al. 2018, Brlík et al. 2020) and with the small number of studies on birds <16 g that showed weak or no negative impacts on apparent survival and other aspects of behavior (Salewski et al. 2012, Peterson et al. 2015, Bell et al. 2017). Return rates were considerably lower for SY birds with geolocators ($\bar{x}$ = 8%) compared to SY birds without geolocators ($\bar{x}$ = 72%) at CB. However, our sample size for SY birds with geolocators at CB was low (n = 1 retrieved of 13 deployed). In addition, the return rates we observed for SY birds without geolocators at CB was unusually high compared to SY birds without geolocators at FCMI during this study (35%), 11% higher than any values recorded at FCMI prior to the current study, and 8% higher than any values we could find reported the peer-reviewed or gray literature (R = 0–66%; e.g., Groce et al. 2010, Tavis County 2000, Macey and Collins 2022). Thus, we do not have evidence that the low return rate we observed for SY warblers at CB was due solely to our attachment of the geolocators. Overall, our results support further use of geolocators to obtain critical broad-scale movement data on songbirds, including species weighing <12 g. However, we urge continued research on the potential impacts of geolocators on very small songbirds to help scientists identify the most ethical methods for their questions and to help governing bodies (e.g., USGS BBL, USWFS) make permitting decisions.

The need for such research is evident based on the mixed results from other studies on small songbirds. Brlík et al. (2020) found a weak negative impact of geolocators on apparent survival on small (<100 g) birds, while Bridge et al. (2013) found decreased return rates in 9 out of 24 (38%) species for birds weighing 12–80 g and smaller species were more likely to be affected. In addition, research indicated that geolocators may negatively impact return rates of cerulean warblers (Raybuck et al. 2017), common yellowthroats (*Geothlypis trichas*; Taff et al. 2018), and prairie warblers (*S. discolor*; Campbell et al. 2022). Reduced apparent survival has

been linked to high loads from geolocators (high ratio of geolocator mass to body mass) (Brlík et al. 2020, Campbell et al. 2022). However, smaller body mass does not always equate to reduced return rates when carrying a geolocator. Salewski et al. (2013) and Peterson et al. (2015) found no evidence that geolocators had a negative impact on return rates of golden-winged warblers and aquatic warblers, respectively.

Other avian responses that researchers could consider include nest success and adult behavior during the nesting period. For example, Arlt et al. (2013) found that northern wheatears (*Oenanthe oenanthe libanotica*) with geolocators had later egg laying dates and lower nest success than northern wheatears without geolocators. Conversely, Raybuck et al. (2017) found no evidence that geolocators had a negative effect on nest survival and provisioning rates of cerulean warblers. Bell et al. (2017) similarly found that geolocators did not have a negative impact on provisioning effort, nestling growth, or nest success of pied flycatchers (*Ficedula hypoleuca*). We did not examine nest survival rates, provisioning rates, or nest timing for the current study, and our results for pairing success and fledging success are consistent with a geolocator meta-analysis on small (<100 g) birds (Brlík et al. 2020), which found no evidence that geolocators negatively affect breeding performance, but we acknowledge that inclusion of different metrics may have yielded different results.

We did examine body mass of males prior to attachment of the geolocators and upon removal of the geolocators in subsequent seasons. Similar to others (Peterson et al. 2015, and Raybuck et al. 2017), we did not find any differences in mass at FCMI (CB excluded from statistical analyses due to low sample sizes). We also found limited evidence of skin abrasions or feather wear due to the geolocator harness. While these results are encouraging with respect to migration research, it is important to note that we received experimental authorization to exceed standard weight restrictions, such that all birds with geolocators weighed >9.2 g. Warbler weights range between 8 and 12 g. As such, we may have attached geolocators to individuals in better overall body condition when they arrived to the breeding grounds. In addition, warblers with geolocators that returned to our study sites in subsequent seasons may have been in better body condition than warblers with geolocators that did not return. We will also add here that of the 13 warblers with geolocators that were slow to fly off, had balance issues, or acted as if they were still captured upon initial release following our attachment of the geolocators, only 2 returned the following season. Though decisions should be made on a case-by-case basis and further documentation is needed to confirm if these results are consistent across studies, researchers may want to consider recapturing an individual that exhibits these behaviors and removing the geolocator for use on another bird.

Warblers were a good candidate for the current research because they have high annual return rates (Groce et al. 2010, Macey and Collins 2022), strong site fidelity, (Jette et al. 1998, Maas-Burleigh 1998), and high recapture rates. In addition, the warblers at our study sites are monitored consistently across the breeding season. Thus, we were able to obtain large sample sizes across multiple study sites and years for our project. We acknowledge that not all species exhibit these behaviors and survey effort depends on many factors (e.g., funding, access to sites where the study species occurs). However, there are many outstanding questions regarding the migration ecology of songbirds that warrant further study and could be addressed with geolocators. One of particular importance relates to female warbler movements. We were not authorized to attach geolocators to females for the current study and our focus on males allowed us to obtain a robust sample size. However, the migratory behavior of female warblers, and females of most species, is still virtually unknown. We were also unable to attach geolocators to

male warblers in consecutive breeding seasons, but continuous monitoring of warblers and other species would provide important insight into migration route and winter site fidelity.

In addition, differences in migration strategies across species could contribute to variation in return rates or apparent survival (DeLuca et al. 2015). For example, songbirds with geolocators that migrate over land and can forage or rest en route may have higher return rates than songbirds with geolocators that make long-distance flights over the water (DeLuca et al. 2015). Comparing return rates of individuals with and without geolocators that have mixed migration strategies could be informative. Last, the weight of geolocators and other tracking devices will likely decrease further in the future, but until such time, our research contributes to the growing number of studies that suggest smaller-bodied species may be capable of carrying devices that exceed current weight restrictions. Migration data on very small songbirds is critical to reversing their population declines. Thus, governing bodies that oversee the permitting process should continue to be cautious and require annual reports before permits are reauthorized, but also consider species- or group-specific weight restrictions once sufficient data are available.

Breeding habitat

We estimated a 28% loss in warbler breeding habitat between 2000 and 2020, with the greatest losses occurring in the central portion of the warbler's breeding range. This estimate does not account for forest gains during the same period; oak-juniper forests can take several decades to mature before warblers use them for nesting (Groce et al. 2010, Ladd and Gass 2020), so we cannot assume that estimated gains between 2000 and 2020 represent equivalent gains in warbler habitat. In addition, our 2020 classification accuracies were generally lower than other years, which could be related to a series of severe droughts that occurred during the decade (NOAA 2023) because forests with widespread or localized tree mortality reflect light differently than living evergreen and mixed forests (Yuhas and Scuderi 2009, Garrity et al. 2013). Further, Heger and Hayes (2013) found that drought affected their classifications of golden-cheeked warbler habitat because forests with tree mortality were often classified as shrubland.

Forest losses were predominately located near urban areas (e.g. Austin, San Antonio), but considerable losses also occurred to the south of Fort Cavazos Military Installation. The forest losses we observed track with locations that have experienced considerable human population growth and accompanied development over the past two decades (USCB 2011, USCB 2021), and despite differences in classification methods, our results generally align with estimates by others who have quantified rangewide change in warbler habitat over time (Duarte et al. 2013, Dreiss et al. 2022). The warbler population is estimated to be >200,000 males (Mathewson et al. 2012, Mueller et al. 2022), and warblers can nest in urban areas, but research has found lower occupancy in patches in urban areas (e.g., Reidy et al. 2007), and smaller patch sizes and habitat fragmentation can negatively impact warbler productivity and nest success in both urban and rural settings (Robinson et al. 2018, Reidy et al. 2017).

Demographers anticipate an even more aggressive human population growth trajectory for the megaregion that includes Austin and San Antonio over the next several decades (Texas Demographic Center 2022). The projected locations and magnitudes of forest loss we estimated using the CONUS FORE-SCE and ICLUS models reflect these expected trends. Pham et al. (2022) predicted an expansion of golden-cheeked warbler breeding habitat due to climate change over the next several decades. Alternatively, neotropical migrants like warblers may experience southern range contraction and northward shift from their current ranges (Rushing et al. 2020).

The largest contiguous patches of warbler habitat occur in the southern portion of their breeding range. Thus, a northward shift of the warbler's breeding range accompanied by forest loss in the central and northern portions of the warbler's breeding could be problematic for warblers. Increased conservation of warbler habitat in the central and northern portions that maximum patch size and maintain or increase connectivity could help protect their population.

8. Conclusions

The DoD must first, and above all, deter war and protect national security. Key to that mission is providing troops with realistic military training and testing opportunities, which requires the DoD to protect and manage a wide range of natural resources that support combat readiness. While doing so, the DoD must also comply with all federal environmental legislation and policies, including those that are critically important to the conservation of plants and animals that occur on military lands. Moreover, the DoD has a disproportionate responsibility for biodiversity conservation relative to other federal land management agencies considering they own only 3% of federal lands, but those lands have some of the greatest numbers and highest densities of threatened, endangered, or otherwise imperiled species found in the U.S. (Flather et al. 1994, Groves et al. 2000, Stein et al. 2008). Aware of the importance of military lands for conservation, the DoD manages on-post natural resources and ecosystems to perpetuate and recover at-risk species (Boice 2006). The DoD also has a long history of participation in landscape-scale partnerships (e.g., Sentinel Landscape Partnership, Legacy Resource Management Plan [LRMP], Readiness and Environmental Protection Integration Program [REPI]) and proactive stewardship activities that maintain and improve habitat for sensitive species beyond their fences. Off-post conservation, including habitat enhancement, can promote recovery of T&E species, prevent future listings, and ease encroachment problems, thereby minimizing potential restrictions on military activities. However, the DoD and its partners must know where species occur, when they move, and anticipate how their habitats and behaviors might change over time for conservation efforts to be successful. This information is challenging to acquire for highly mobile species, like migratory birds, that can travel long distances across environmental barriers (Åkesson and Hendström 2007), land use/land tenure types (Tack et al. 2019), and jurisdictional boundaries during their annual cycles (Kark et al. 2015); but is necessary to prioritize conservation actions when and where they are needed most.

Our SERDP-funded project provides the most thorough examination of golden-cheeked warbler movements during the non-breeding season to date and provides tools that can help identify focus areas for multi-agency conservation efforts on the warbler's breeding, migration, and wintering grounds. We are particularly excited about how our work has and could be used to narrow sampling periods and locations for field-based surveys of non-breeding habitat. Knowing where and when individuals are located throughout the year is critical for warbler conservation because events during the non-breeding season could impact warbler population dynamics (e.g., mortality during migration, carry-over effects) and, thus, delay recovery, despite best efforts to manage threats on the warbler's breeding grounds.

Our project also provided data in support of actions recommended by USFWS in their last 5-year golden-cheeked warbler status review (e.g., protect and manage warbler habitat on the breeding, migration, and wintering ranges; determine the effects of climate change on warbler

habitat; identify priority stopover sites within the warbler's migration corridor) (USFWS 2014). More recently (2021), the USFWS initiated a species status assessment (SSA) for the golden-cheeked warbler, which is expected to be completed in 2023. During the SSA process, a core team of USFWS biologists (1) identify species' needs; (2) describe current habitat conditions, recent demographics, and probable explanations for past and ongoing changes in abundance and distribution with species' ecological settings; and (3) forecast species' responses to scenarios of plausible future environmental conditions and conservation efforts (USFWS 2016). The SSA is meant to serve as a living document and provide the foundation for ESA protections, critical habitat designations, recovery planning, and more (USFWS 2016). As noted in Long et al. (2019), a major challenge for development of SSAs includes inconsistent or incomplete monitoring throughout a species' range, which can result from complex life histories, geopolitical boundaries, detectability of rare and elusive species, and inadequate time and funding to obtain such data prior to policy decisions (Culver et al. 2009, Murphy and Weiland 2016, Earl et al. 2017). We have provided updates to the golden-cheeked warbler SSA team throughout the duration of our project, and we will continue to share data and peer-reviewed publications resulting from our work to the SSA team moving forward.

In the Discussion section above, we detailed the results of our geolocator impact assessment and described how our results could help inform geolocator studies for other songbirds, but our project will also provide data to examine warbler ecology using automated tracking technologies. By installing a Motus tower at KWMA and using the existing Motus network, we hope to record new locations for both male and female warblers during migration and on their wintering grounds that will complement our geolocator data. In addition, data recorded across our grid of automated telemetry receivers during the 2022 and 2023 warbler breeding seasons will allow us to quantify sex-specific home range sizes, distances that warblers travel outside their home ranges (i.e., extraterritorial forays), and the amount of spatial overlap between male and female warblers. We will also identify migration departure dates for tagged warblers and compare return rates, pairing success, and nest success for warblers with and without radio transmitters.

Beyond warblers, the Motus tower we installed at KWMA has and will continue to detect movements of wildlife tagged by other researchers, and the knowledge we gain from installing a grid of receivers (i.e., nodes) for high-resolution tracking of warblers will contribute to overall testing of automated tracking technologies for wildlife. Increased adoption of automated tracking technologies on DoD lands could help protect existing populations, prevent future listings, and ensure installation resilience, but requires validation under operational conditions at DoD facilities and human capital, specifically natural resource staff with the knowledge, skills, and experience necessary to 1) choose or evaluate appropriate tracking methods and devices for their objectives; 2) plan, install, and maintain equipment; and 3) retrieve, analyze, and interpret data. Research conducted using automated wildlife tracking on military lands could be used to inform Integrated Natural Resources Management Plans, Bird/Wildlife Aircraft Strike Hazard Plans, Biological Assessments, Biological Opinions, Species Status Assessments, Habitat Conservation Plans, National Environmental Policy Act documents (e.g., Categorical Exclusions, Environmental Assessments, Environmental Impact Statements), critical habitat designations, recovery plans, and more. This type of research also aligns with DoD participation in conservation initiatives/partnerships that maintain healthy landscapes and training lands (e.g.,

DoD Partners in Flight [PIF], DoD Partners in Amphibian and Reptile Conservation [PARC], Sentinel Landscapes, Pollinator Partnership, LRMP, REPI).

To be effective, protected areas must be located where at-risk species and ecosystems occur and can provide the most benefits for conservation, but historically, we have established protected lands in locations with limited commercial value or where the primary benefits are bestowed to humans (e.g., recreation, scenic views) (Pressey 1994, Dietz et al. 2015). For example, in the U.S., Jenkins et al. (2015) found that though most protected areas are located in the west, but the most vulnerable endemic species are concentrated in the southeast. Similarly, protected areas are often disconnected, leaving ecosystems vulnerable to fragmentation and less able to support dispersal and other biological processes needed for population persistence (Hansen et al. 2014, Belote et al. 2016, 2017). Strategic prioritization of how to spend limited conservation funds is essential to maintaining populations of at-risk species. When considering land acquisition or other protection measures (e.g., easements, incentives, restoration), conservation planners must account for the biological benefits of particular areas (e.g., minimum area to support survival and reproduction, proximity and connectivity with other areas) as well the potential for land-use conversion and climate change factors that could render lands unsuitable in the future (Newburn et al. 2005; Hodgson et al. 2009, 2011). Failure to consider these factors could result in protecting habitat that has little conservation value and missed opportunities to protect vulnerable populations. Unfortunately, decision makers may not always have the necessary expertise or resources to make informed decisions.

Mapping applications, such as the Golden-cheeked Warbler Habitat Explorer app that we created, are powerful spatial prioritization tools for conservation that can help connect decision-making with science (e.g., identify areas at risk of habitat conversion) and be an effective means of communication among stakeholders. The tool we created could be used to help identify and prioritize locations for off-site habitat protection or mitigation that meet or exceed minimum patch size requirements for the warbler (i.e., ≥ 20 ha; Butcher et al. 2010), enhance connectivity, complement the distribution of existing protected areas, and account for projected changes in land use and land cover. Our app demonstrates an approach that could be adopted for other species and regions. However, as with any mapping application, it is important to consider the error and uncertainty that is inherent in all models. For example, the models we included in our analyses and app were created with different methods and at different spatial scales, and users must consider multiple lines of evidence prior to making any conservation planning decisions. Information derived from our app should be used as a guide; practitioners should evaluate potential plans based on app outputs prior to implementation, then conduct monitoring and adaptive management during implementation to ensure they are meeting their desired goals (Acyrigg et al. 2016).

The primary benefits of using GEE to create mapping tools is that the platform is easy to access, does not require users to have a background in remote sensing or GIS, and the maps and models generated can be updated and refined with new developments and available data. GEE's public catalog of imagery and diverse datasets (e.g., climate and weather, topography, land cover, fire, land and sea surface temperature, protected areas, human population trends) spans more than 30 years and is updated daily, with more than one petabyte of information added each month. Conservation practitioners and decision makers can easily integrate new data from the GEE catalog or from their own collections into GEE-based apps to ensure outputs used to

develop conservation actions remain relevant, informed, and accurate. For instance, app builders might want to incorporate spatial information regarding land characteristics (e.g., value and ownership) to help users identify stakeholders and set conservation priorities (Newburn et al. 2005). Further, our app could include new habitat or projection models as they become available, locations of protected lands that are not represented by the World Database on Protected Areas, real-time data that could alert users to potential impacts on warbler habitat (e.g., forest fires), and identification of habitat patches that maximize connectivity. GEE also allows users to download inputs and outputs generated in apps for sharing or use in other software programs (e.g., Program R, ArcGIS, QGIS). Example functions that could prove informative for users of our app include summaries of current and project land cover in AOIs or estimates of the warbler population based on various LUCL scenarios at rangewide, recovery region, or user-specified scales.

For the current research and mapping application, we focused on development and climate change as the primary drivers of habitat conversion, but there are certainly more threats that impact warbler habitat with and without formal protections. On the warbler's breeding grounds, examples include wildfires (Baccus et al. 2007, Long et al. 2021), oak defoliation caused by the fungus *Bretziella fagacearum* (Appel and Camilli 2010, Stewart et al. 2014), and lack of oak regeneration (Reidy et al. 2021). On the wintering grounds, potential threats to forests used by warblers and co-occurring species include unsustainable forest management practices, illegal timber harvest, and wildfires (ACMPOF 2012). There are an extensive number of agencies and organizations who conduct research, protect and manage habitat, and conduct public outreach on the warbler's breeding grounds (e.g., DoD, USFWS, TPWD, City of Austin, American Bird Conservancy, various Audubon chapters, university-based researchers), voluntary conservation and incentive programs that encourage private landowners to adopt practices that benefit warblers, and an increasing number of conservation banks that can help offset warbler habitat loss. On the wintering grounds, the Alliance for the Conservation of Mesoamerican Pine-Oak Forests (Alianza para la Conservación de los Bosques de Pino-Encino de Mesoamérica—a partnership formed in 2003 with representation from Mexico (Instituto de Historia Natural y Ecología, and Pronatura Sur, Guatemala (Fundación Defensores de la Naturaleza), Honduras (Fundación EDUCA), El Salvador (SalvaNATURA), and Nicaragua (Alianza para las Áreas Silvestres) along with organizations from the U.S. (TPWD, TNC)—has been critical for obtaining information about warblers on their wintering grounds and educating the public.

There are also a considerable number of programs and partnerships that originate in the U.S. and provide financial assistance and foster international cooperation toward the conservation of migratory birds. For example, the Neotropical Migratory Bird Conservation Act program has provided >\$75 million in grants to support >600 projects in 35 countries since 2002 (<https://www.fws.gov/program/neotropical-migratory-bird-conservation>). This includes >\$3 million toward efforts to benefit golden-cheeked warblers and co-occurring species. However, continued and increased support for local organizations (e.g., Pronatura Sur, Defensores de la Naturaleza) that conduct research, manage and restore habitat, and lead education and outreach programs on the warbler's wintering grounds, as well as partnerships that promote conservation of temperate forests across the warbler's non-breeding range (e.g., Alliance for the Conservation of Central American Pine-Oak Forest), are critical to ensure warbler population persistence and will simultaneously protect co-occurring species that could impact military training if their populations are listed as Threatened or Endangered under the ESA.

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10. Appendix

A. Supporting data

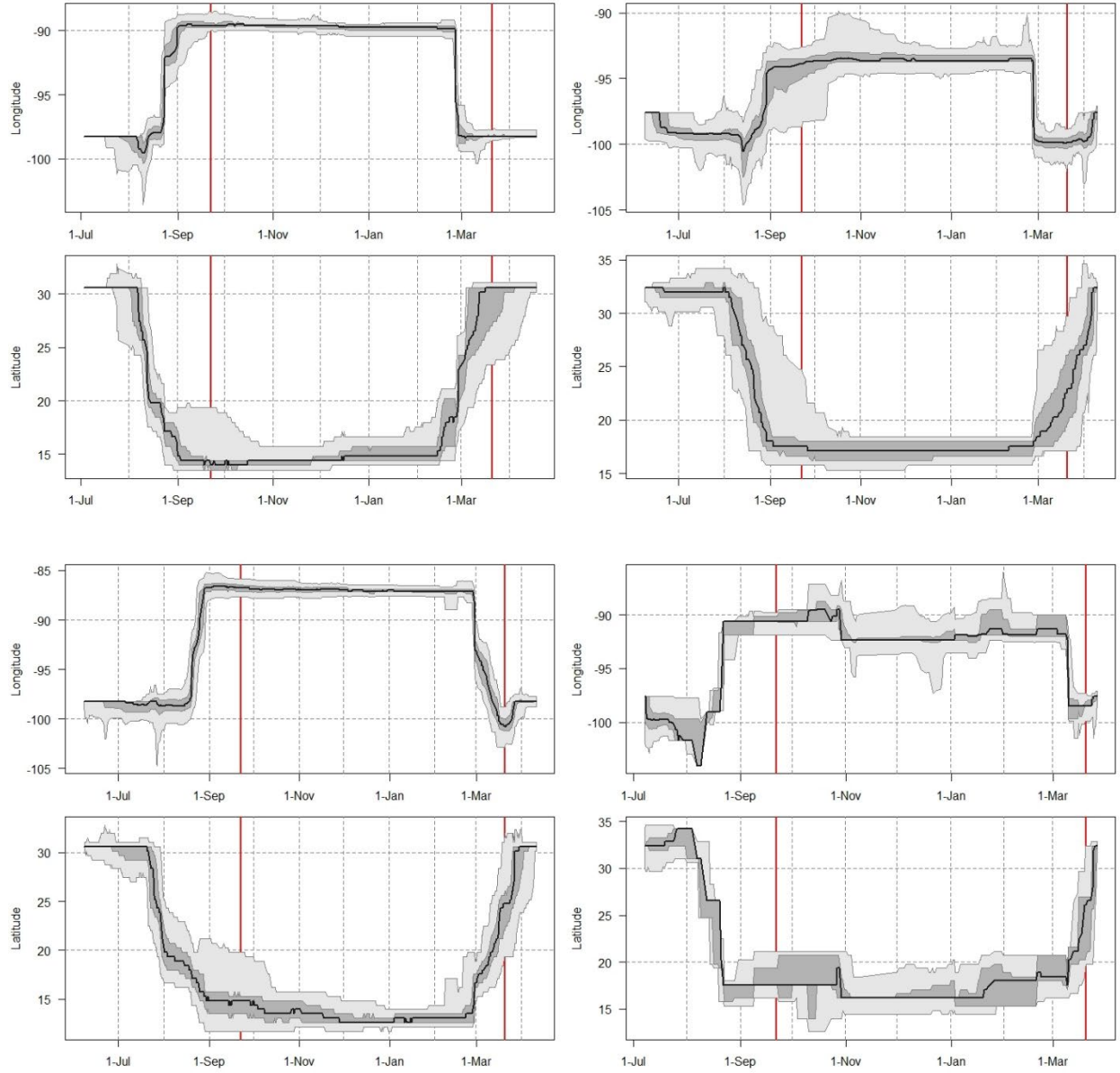


Figure A.1. The figures on the left illustrate longitude and latitude estimates (solid line) along with credible intervals (grey shaded area) for two data sets with very good accuracy results, and the two data sets on the right illustrate data sets with greater uncertainty and wider credible intervals. The two red lines indicate equinox time periods, which usually result in more uncertainty during the equinox period.

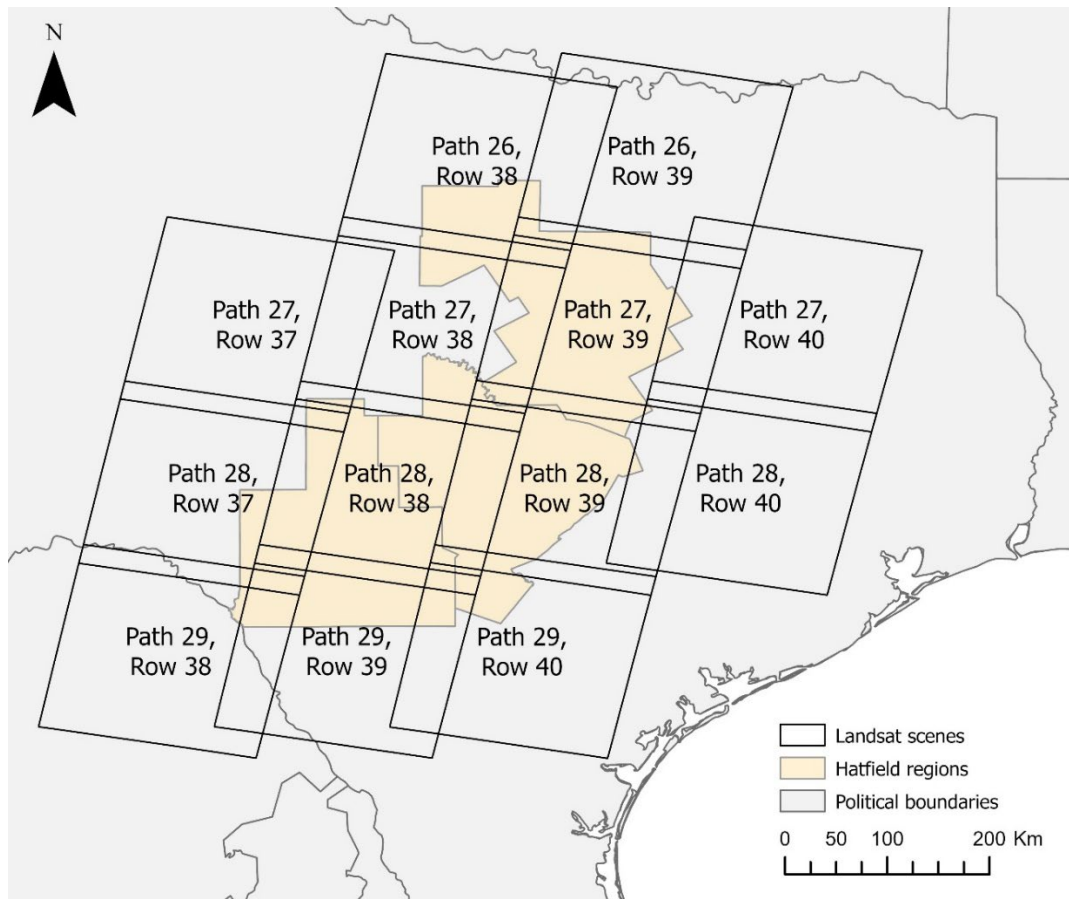


Figure A.2. Landsat scene path and row information for the golden-cheeked warbler's (*Setophaga chrysoparia*) breeding range in Texas.

Table A.1. Number of Landsat scenes used to create initial seasonal composites for our classifications of the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range.

Year of interest	Landsat 5		Landsat 7		Landsat 8	
	Summer	Winter	Summer	Winter	Summer	Winter
2000	83	23	91	31	-	-
2010	80	41	83	35	-	-
2020	-	-	66	33	91	42

Table A.2. Number of Landsat scenes used to create climatology seasonal composites used as fill for our classifications of the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range.

Year of interest	Data years	Landsat 5		Landsat 7		Landsat 8	
		Summer	Winter	Summer	Winter	Summer	Winter
2000	1996–1999	314	128	26	41	-	-
2010	2006–2009	295	97	301	144	-	-
2020	2016–2019	-	-	300	140	355	155

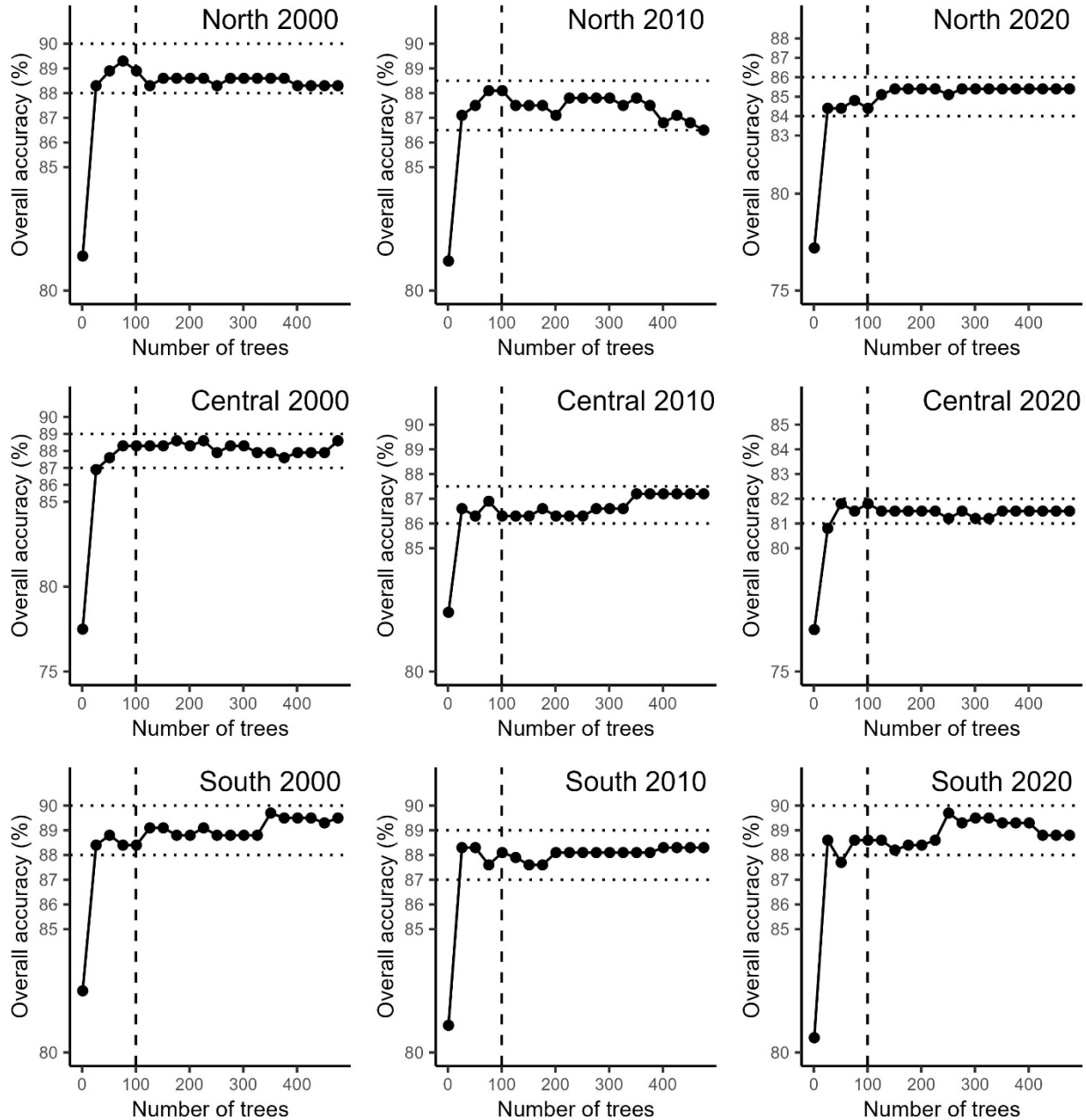


Figure A.3. Before creating our final classifications of the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range, we computed the overall accuracies for classifiers run with 1–500 decision trees, increasing by 25 trees at each step. We then determined the number of trees that maximized accuracy while minimizing processing time across all classifications. In the following graphs, dashed vertical lines indicate the number of trees that we ultimately chose for our classifications (i.e., 100), whereas horizontal dotted lines delineate the accuracy range we considered.

Table A.3. Distance (km) from the study sites where golden-cheeked warblers (*Setophaga chrysoparia*) were located during the breeding season to their locations estimated from the geolocator data.

Site	n	Unit	Mean	SD
All sites	61	Latitude	26.0	33.9
		Longitude	23.6	31.4
BCNWR	14	Latitude	26.4	6.1
		Longitude	11.6	17.7
DVSP	7	Latitude	46.3	61.0
		Longitude	30.3	33.0
FHMI	23	Latitude	30.4	42.1
		Longitude	40.2	40.2
JBSA	1	Latitude	11.9	-
		Longitude	1.3	-
KWMA	16	Latitude	11.4	3.9
		Longitude	8.6	4.4

Table A.4. Confusion matrices for each year of interest and region for our classifications of the golden-cheeked warbler (*Setophaga chrysoparia*) breeding range. Confusion matrices include the number of points accurately identified to each class in the classification when compared to a reference, as well as points inaccurately identified to another class. We used these confusion matrices to calculate our accuracy metrics (i.e., overall accuracy, Cohen’s kappa statistic, user’s accuracy, and producer’s accuracy; Congalton 1991).

North region

Confusion matrix for 2000 image classification.

	Reference data	
		Other Forest
Classification	Other	130 20
	Forest	14 143

Confusion matrix for 2010 image classification.

	Reference data	
		Other Forest
Classification	Other	138 23
	Forest	16 126

Confusion matrix for 2020 image classification.

	Reference data	
		Other Forest
Classification	Other	124 25
	Forest	22 131

Central region

Confusion matrix for 2000 image classification.

	Reference data	
		Other Forest
Classification	Other	128 16
	Forest	19 135

Confusion matrix for 2010 image classification.

	Reference data	
		Other Forest
Classification	Other	144 19
	Forest	24 126

Confusion matrix for 2020 image classification.

		Reference data	
		Other	Forest
Classification	Other	131	36
	Forest	22	124

South region

Confusion matrix for 2000 image classification.

		Reference data		
		Other	Evergreen	Mixed
Classification	Other	143	11	7
	Evergreen	8	127	11
	Mixed	4	10	118

Confusion matrix for 2010 image classification.

		Reference data		
		Other	Evergreen	Mixed
Classification	Other	132	14	3
	Evergreen	7	124	11
	Mixed	12	4	122

Confusion matrix for 2020 image classification.

		Reference data		
		Other	Evergreen	Mixed
Classification	Other	125	11	9
	Evergreen	10	117	6
	Mixed	9	4	148

B. Other supporting information

Golden-cheeked Warbler Habitat Explorer User Guide

Our Google Earth Engine web application is currently set for restricted access. Users can request access and a copy of the user manual by emailing the project director, Dr. Ashley Long, at amlong@lsu.edu; the final set up for permissions to access the app will be made in consultation with the SERDP program manager.

App layout



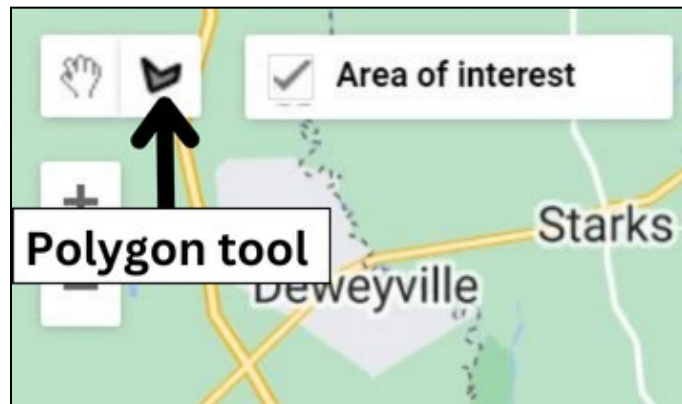
1. **Drawing tools:** Tools that you can use to create polygons on the map. You can turn on and off the polygon creation tool from this location.
2. **Layer panel:** Shows the user-drawn polygon map layer. Click the checkbox next to the label that says “Area of interest” in the top left corner of the map screen to turn off the polygon layer; this displays a faint outline of user-drawn polygons rather than the distinct polygon outlines.
3. **Background panel:** Options that you can use to change the background imagery of the map. By default, the background map (“Map”) shows features like interstates, highways, water bodies, city extents, etc., as well as their associated names. Alternatively, there is the option to view satellite imagery (“Satellite”) as the background map.
4. **Root panel:** Displays multiple tools that you can use to turn on and off map layers, identify patches of breeding habitat, and view information about layers.
5. **Map:** Displays the map layers. You can turn on and off map layers in the root panel.
6. **Legend:** Defines the colors that appear on the map for each layer.
7. **Loading label:** Displays loading labels here when functions are processing.

8. **Instructions and warning label:** Explains how the app works (draw polygons to perform patch calculations). When there is an issue running a function, a warning appears in this box in red. This is also the location of the reset and delete polygons button, which resets the app.

Drawing polygons

Draw polygons around areas of interest to examine patches of breeding habitat. By default, the polygon drawing tool is automatically turned on.

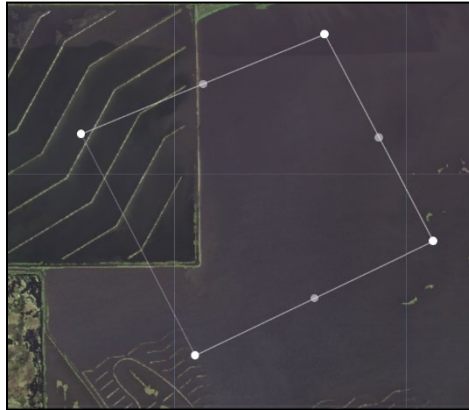
- 1) If the polygon drawing tool is not turned on, click the polygon button in the top left corner of the map screen.



- 2) Click on the map to create vertices for the polygon—the polygon can have as many vertices as necessary.



- 3) To finish drawing the polygon, click on the first vertex that you created.



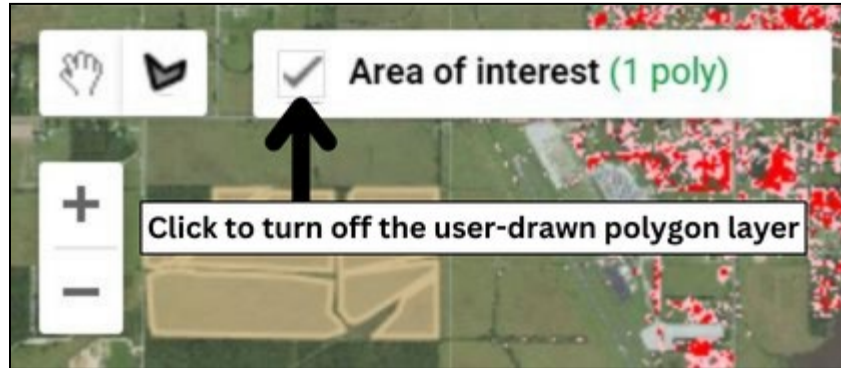
You can also turn off the polygon drawing tool for easier map navigation.

- 1) Click the hand button in the top left corner of the map screen to turn off the polygon drawing tool.



2) **Optional:** Click the checkbox next to the label that says “Area of interest” in the top left corner of the map screen to turn off the polygon layer; this action displays a faint outline of the polygon rather than the distinct polygon outline, which makes map layers easier to see under the polygon.

- Note that the polygon layer turns back on if you select the polygon tool.



**User-drawn polygon
layer turned on**



**User-drawn polygon
layer turned off**



You can delete a singular polygon to remove it from analyses.

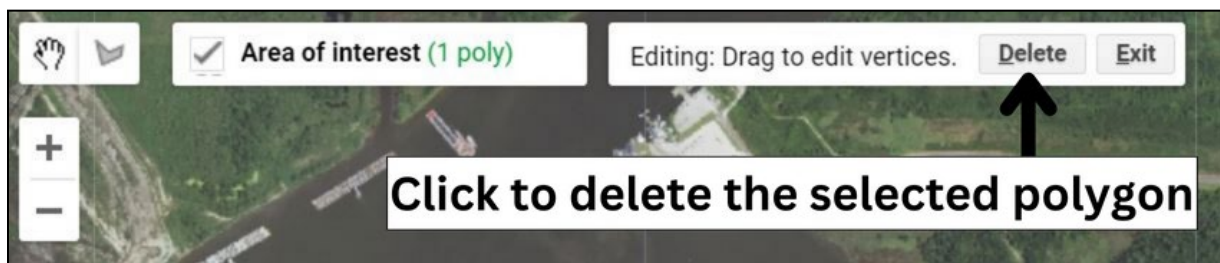
- 1) Click on the hand button in the top left corner of the map screen to turn off the polygon drawing tool.



- 2) Select the polygon on the map that you want to delete. This highlights the polygon (showing the vertices).



- 3) Select the “Delete” button on the top of the screen next to “Editing: Drag to edit vertices”.



Last, you can reset the app and delete all polygons by clicking the “Reset and delete polygons” button [at the bottom-right of the map](#).

Root panel

The root panel contains options to turn on and off map layers, adjust layer opacity, and perform patch calculations within your user-drawn polygons. This section details each option available in the root panel.

Breeding (10 m; Mueller et al. 2022)

1. This checkbox turns on and off the map layer that contains the predicted warbler density model for the breeding range, created by Mueller et al. (2022).
2. You can change the opacity of this layer using the opacity slider under the checkbox.

CONUS FORE-SCE projected cover (250 m)

1. This checkbox turns on and off the map layer that contains the CONUS FORE-SCE projected land use and land cover imagery for the breeding habitat, including only the developed class (see classes [here](#)).
2. After checking the box, you are prompted to choose the climate scenario of interest (you can find the meanings of each scenario [here](#)).
3. Last, a date slider appears that you can use to look at projected developed cover for the selected scenario from 2020–2100.

ICLUS projected cover (90 m)

1. This checkbox turns on and off the map layer that contains the ICLUS projected land use and land cover imagery for the breeding habitat, including only the developed classes (see classes [here](#)).
2. After checking the box, you are prompted to choose a climate scenario of interest (you can find the meanings of each scenario [here](#)).
3. Last, a date slider appears that you can use to look at the projected developed cover for the selected scenario from 2020–2100.

Winter (1 km)

1. This checkbox turns on and off the map layer that contains the warbler habitat models in the wintering grounds.
2. After checking the box, you are prompted to choose a year of interest (i.e., 2019, 2050, or 2070).
3. If you chose 2050 or 2070, you are now prompted to choose a climate model of interest.
4. Next, you are prompted to choose a climate scenario of interest (you can find the meanings of each scenario [here](#)).
5. You can change the opacity of this layer using the opacity slider under the climate scenario prompt.

World Database on Protected Areas (UNEP-WCMC and IUCN 2023)

This checkbox turns on and off the map layer that contains the World Database on Protected Areas for warbler breeding, migration, and wintering ranges.

Utilization distributions (75%)

1. This checkbox turns on and off the map layer that contains mean 75% utilization distributions for warblers geolocated in our study from 2017–2020.
2. After checking the box, you are prompted to choose a period of interest (i.e., migration or wintering).

AOI Calculations for Breeding Range

This prompt returns a map layer that identifies patches of breeding habitat within your polygons that meet a minimum patch size. We delineated breeding habitat as the bounds of the warbler density model (Mueller et al. 2022).

1. Draw one or more polygons (you can find instructions on creating polygons [here](#)).
2. Choose a minimum patch size for breeding habitat within your polygons.
3. The app now searches for patches that match your patch size requirements within your polygons.
4. When finished, the app displays the patches it found on the map in yellow. You now also have the option to turn on and off the patch layer via the “show breeding habitat patches” checkbox.

Projection Information

These buttons display pop-ups in the map with information about the CONUS FORE-SCE scenarios, ICLUS scenarios, and scenarios we used in our winter habitat models.

1. Click on the button for the scenarios you want to know more about.
2. A pop-up will appear on the right-side of the map, displaying information about each scenario.
3. Click the “Close” button at the top of the pop-up to remove the pop-up from the map.

Reading the legend

The legend defines the colors displayed for each layer.

- To view legend items, click the checkbox next to their labels in the legend panel; these expand to show each color's meaning.
- Some colors may be distorted by polygon colors. You can turn off polygon layers to better view the colors in the [root panel and layer panel](#).

Warning messages

Occasionally, warning messages may appear in the bottom panel of the screen. These messages are meant to alert you to instances when the app cannot complete operations. Potential warning messages and their causes are as follows:

No patches detected within polygon/s with these selection parameters: This warning message occurs when there are no patches that meet the selected patch size (e.g., you chose the option for patches ≥ 20 ha but patches within your polygon/s are < 20 ha in size).

No polygons drawn: This warning message occurs when you are trying to run the AOI calculations tool from the root panel but haven't created any polygons. User-drawn polygons are necessary for this tool to work.

Data sources

Breeding

Data source: Mueller, J. M., S. E. Sesnie, S. E. Lehnen, H. T. Davis, J. J. Giocomo, J. N. Macey, and A. M. Long. 2022. Multi-scale species density model for conserving an endangered songbird. *Journal of Wildlife Management* 86:e22236.

Resolution: 10 m

Winter

Data source: Long, A. M., J. N. Macey, M. R. Colón, and J. M. Kunberger. 2023. Using remotely sensed data and light-level geolocator technology to inform off-post landscape-scale conservation planning for an endangered species. Technical report to the Department of Defense Strategic Environmental Research and Development Program. In review.

Resolution: 1 km

Copernicus Global Digital Elevation Model GLO-30

Data source: © DLR e.V. 2010-2014 and © Airbus Defence and Space GmbH 2014-2018 provided under COPERNICUS by the European Union and ESA; all rights reserved.

Resolution: 30 m

Note: Used to display winter habitat models.

World Database on Protected Areas

Data source: UNEP-WCMC and IUCN. 2023. Protected planet: the World Database on Protected Areas (WDPA) [On-line], 2023. UNEP-WCMC and IUCN, Cambridge, UK. Available at www.protectedplanet.net (accessed 6 June 2023).

Utilization distributions (75%)

Data source: Long, A. M., J. N. Macey, M. R. Colón, and J. M. Kunberger. 2023. Using remotely sensed data and light-level geolocator technology to inform off-post landscape-scale conservation planning for an endangered species. Technical report to the Department of Defense Strategic Environmental Research and Development Program. In review.

Conterminous United States Land Cover Projections (Forecasting Scenarios of land use [FORE-SCE] model)

Data source: Sohl, T. L., K. L. Sayler, M. A. Bouchard, R. R. Reker, A. M. Freisz, S. L. Bennett, B. M. Sleeter, R. R. Sleeter, T. Wilson, C. Soulard, M. Knuppe, and T. Van Hofwegen. 2018. Conterminous United States land cover projections - 1992 to 2100. U.S. Geological Survey data release. DOI: 10.5066/P95AK9HP.

Resolution: 250 m

CONUS FORE-SCE Scenarios

Scenario	Description (from IPCC 2000 ¹)
SRES A1B	Rapid economic growth, reduction in regional differences in income. Global population peaks ~2050, then declines. Growth in more efficient technologies that are a balance of fossil intensive and non-fossil energy sources.
SRES A2	Local self-reliance. Continuously increasing global population. Economic development is regionally oriented, economic growth and technological change slower than other scenarios.
SRES B1	Global population peaks ~2050, then declines. Rapid changes in economic structures toward a service and information economy. Emphasis on introduction of clean and resource-efficient technologies, focuses on solutions to economic, social, and environmental sustainability globally.
SRES B2	Local solutions to economic, social, and environmental sustainability; focuses on local and regional levels. Continuously increasing global population, though rate is lower than A2. Intermediate levels of economic development, less technology changes than A1 and B1.

¹ Intergovernmental Panel on Climate Change (IPCC). 2000. IPCC special report emissions scenarios: summary for policymakers. Cambridge University Press, Cambridge, UK. <<https://www.ipcc.ch/site/assets/uploads/2018/03/sres-en.pdf>>. Accessed 7 June 2023.

CONUS FORE-SCE cover classes

Original land use/land cover class	App class
Water	-
Developed	Developed
Mechanically disturbed National Forests	-
Mechanically disturbed other public lands	-
Mechanically disturbed private	-
Mining	-
Barren	-
Deciduous forest	-
Evergreen forest	-
Mixed forest	-
Grassland	-
Shrubland	-
Cropland	-
Hay/pasture	-
Herbaceous wetland	-
Woody wetland	-
Perennial ice/snow	-

Integrated Climate and Land Use Scenarios (ICLUS)

Data source: US Environmental Protection Agency [EPA]. 2020. ICLUS Version 2.1.1. <<https://www.epa.gov/gcx/iclus-downloads>>. Accessed 7 June 2023.

Resolution: 90 m

ICLUS scenario term definitions

Scenario term	Definition (from EPA 2017 ²)
SSP	Shared Socioeconomic Pathways Qualitative descriptions of future demographics, development, economy, lifestyle, policies and institutions, technologies, and the environment SSP 2: low population growth; SSP 5: high population growth
RCP	Representative Concentration Pathways A set of four trajectories for greenhouse gas concentrations based on underlying socioeconomic assumptions. RCP 4.5: low emissions; RCP 8.5: high emissions
HadGEM2-AO	Climate model that is highly sensitive to global emissions
FIO-ESM	Climate model that is less sensitive to global emissions

ICLUS Scenarios

Scenario	Description (from EPA 2017 ²)
SSP 2, RCP 4.5, HadGEM2-AO	Lower population growth and lower emissions scenarios, with climate model highly sensitive to global carbon emissions
SSP 5, RCP 8.5, HadGEM2-AO	Higher population growth, higher emissions scenarios, with climate model highly sensitive to global carbon emissions
SSP 2, RCP 4.5, FIO-ESM	Lower population growth and lower emissions scenarios, with climate model less sensitive to global carbon emissions
SSP 5, RCP 8.5, FIO-ESM	Higher population growth, higher emissions scenarios, with climate model less sensitive to global carbon emissions

² U.S. Environmental Protection Agency [EPA]. 2017. Updates to the demographic and spatial allocation models to produce integrated climate and land use scenarios (ICLUS) Version 2. National Center for Environmental Assessment, Washington, DC.

ICLUS cover classes

Land use class	Additional information	App class
Natural water		-
Reservoirs, canals		-
Wetlands		-
Recreation, conservation		-
Timber		-
Grazing		-
Pasture		-
Cropland		-
Mining, barren land		-
Parks, golf courses		Developed
Exurban, low density	0.02–0.1 DUA ³	Developed
Exurban, high density	0.1–0.4 DUA ³	Developed
Suburban	0.4 – 1.6 DUA ³	Developed
Urban, low density	1.6–10 DUA ³	Developed
Urban, high density	>10 DUA ³	Developed
Commercial		Developed
Industrial		Developed
Institutional	Includes military installations	-
Transportation		Developed

³DUA = dwelling units/acre

Winter scenarios

Scenario	Description (from IPCC 2014) ⁴
RCP2.6	Mitigation of greenhouse gas emissions and an increase in global temperatures between 0.3–1.7 °C
RCP8.5	Substantial increase in greenhouse gas emissions and an increase in global temperatures between 1.4–4.8 °C

⁴Intergovernmental Panel on Climate Change (IPCC). 2014. Climate change 2014: synthesis report. Contribution of working groups I, II, and III to the fifth assessment report of the IPCC. Core Writing Team, R. K. Pachauri & L. A. Meyers, editors. IPCC, Geneva, Switzerland.