



NATURE NOTES

The first documentation of the Nearctic–Paleotropical migratory route of the Arctic Warbler

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Abstract

The Arctic Warbler (*Phylloscopus borealis*) is a cryptically plumed songbird with an uncommon Nearctic–Paleotropical migratory strategy. Using light-level geolocators, we provide the first documentation of the migratory routes and wintering locations of two territorial adult male Arctic Warblers from Denali National Park and Preserve, Alaska. After accounting for position estimation uncertainties and biases, we found that both individuals departed their breeding grounds in early September, stopped over in southeastern Russia and China during autumn migration, then wintered in the Philippines and the island of Palau. Our documentation of Arctic Warbler wintering on Palau suggests that additional study is needed to document their wintering range. Our study provides hitherto unknown information on stopover and wintering locations for Arctic Warblers and indicates that this species may migrate further overwater than previously thought.

KEYWORDS

Arctic Warbler, bird migration, light-level data logger, Nearctic–Paleotropic migration, non-breeding grounds

TAXONOMY CLASSIFICATION

Movement ecology; Phenology; Spatial ecology

1 | INTRODUCTION

Description of broadscale migratory movements in songbirds has begun using individual tracking (McKinnon & Love, 2018), but many species and migratory routes lack representation in the current state of the science. The Arctic Warbler (*Phylloscopus borealis*) is one of a handful of songbirds that make an annual journey from the Old World to the New World (Bairlein et al., 2012; Kessel, 1989) and is the only species in the genus *Phylloscopus* that breeds in North America (Bairlein et al., 2006). Despite recent research detecting

cryptic species in the clade (Alström et al., 2011), information on Arctic Warbler breeding and movement ecology in North America is scarce (Kessel, 1989; Lowther & Sharbough, 2020). Alaskan migratory strategies are bifurcated around the 150th meridian, with western Alaskan birds often taking western migratory routes (Sivakumar et al., 2021); Arctic Warblers fall into this group as they fly a southwestern route to wintering grounds in Southeast Asia. Little is known about their passage in either geography or timing (Alerstam et al., 2008; Kessel, 1989; Lowther & Sharbough, 2020), despite the route providing a mechanism for the transcontinental

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spread of avian influenza (Winker et al., 2007) and Arctic Warblers being a high-priority study species (Pearce & Ramey, 2006).

The Arctic Warbler's conservation status is currently unclear, although it is considered a species of continental stewardship in Alaska (Handel et al., 2021). Like nearly all migratory songbirds that nest in Alaska, the Arctic Warbler spends only a fraction of its annual cycle at the breeding grounds (approximately June through August). Moreover, movements and connectivity across the full annual cycle can be a critical driver of speciation and further complicate conservation activities (Webster & Marra, 2005). Thus, effective conservation efforts require knowledge of space and resource use during the breeding and non-breeding season and an understanding of migratory movement and connectivity (Runge et al., 2014). Using light-level geolocators to track individual movements (Cooper et al., 2017; Deluca et al., 2015; Jahn et al., 2013; McKinnon & Love, 2018; Tonra et al., 2019), we describe results from the first individual tracking study of Arctic Warblers, including migration behavior, migratory routes, and wintering locations of two individuals.

2 | METHODS

Arctic Warblers were captured on their breeding grounds where we affixed light-level geolocators to males. After tagged birds were recaptured the following year and the data were downloaded from the data logger, we used Bayesian movement models to determine the most likely daily positions of these animals and estimate migratory routes and timings.

2.1 | Geocator deployment and recovery

From 2016 to 2019, we captured adult male Arctic Warblers using mist nets with decoys and playback of conspecific songs and alarm calls. We banded each bird with a USGS aluminum leg band, sexed and aged them (Pyle, 1997), measured their mass with a digital scale (± 0.01 g), and took standard morphological measurements. We also collected incidentally shed feathers in 2017 and feather and blood samples from 10 birds for contaminant analysis in 2018 (Stenhouse et al., 2019). In 2016, we attached 0.4 g archival light-level geolocators (Lotek ML6040) to 27 after-second-year (adult) males. In 2018, we attached 0.3 g geolocators (Intigeo tags; Migrate Tech) to 15 adult males. We attached geolocators to birds in both years using a modified Rappole-Tipton harness (Rappole & Tipton, 1991; Streby et al., 2015) constructed of 0.5 mm black stretch jewelry cord. We assessed and adjusted the harness fit before release. Geocator mass was approximately 3%–4% of the body mass of each bird. All geolocators were deployed on presumed breeding territories in Denali National Park and Preserve, Alaska (63.49° N, 150.07° W), from early June to early July, with most (33 of 42) deployed within a 101-ha study area.

Initially, we attempted to recapture tagged birds using the same capture methods at the initial capture sites from early June to early

July in subsequent years (2017–2019). When tagged birds were not sighted or recaptured at these sites, we expanded our recapture efforts to suitable breeding habitats (i.e., tall shrubs in riparian zones) within 500 m of the initial capture sites. Upon recapturing tagged birds, we recorded their band number, removed the geocator, measured the bird, and released it. The data were then downloaded and readied for processing.

2.2 | Geocator data processing

After downloading the data from the recovered geolocators, twilight times were estimated using the BASTag package in R (R Core Team, 2022; Wotherspoon et al., 2016). A light threshold of 1.5 with a dark time minimum of 30 min was used to calculate initial estimates of twilight. A biologist audited this process's results and edited twilights when they were obviously incorrect based on the surrounding estimates. The intervention was rare (e.g., no more than three edits were made per track) to avoid process reproducibility issues. Latitude estimation is unreliable around the equinoxes and we only used values 2 weeks or more away from these days. These twilight times were used to estimate initial positions for each day. Outlier positions with more than 2 standard deviations from the running 7-day average of twilight times were removed (Lisovski et al., 2016).

2.3 | Movement analysis

We estimated the zenith angle of the filtered data over the wintering period using the Hill-Ekstrom method to calibrate each tag for differences in light detection (package probGLS; Lisovski et al., 2012). Similar processes for estimating zenith angle at the breeding grounds using known capture locations were challenging due to limited nighttime and transmitters being attached later in the breeding season. We assumed each individual was stationary from November 15 to April 10 to use the winter calibration method. Other calibration techniques were tested, although we found only slight variation in the predicted tracks based on the different calibrations. A threshold model estimated latitude and longitude after correcting for twilight bias during the calibration period. Data collection began too late in the summer for one Arctic Warbler (USGS band 1780-53921) to effectively calibrate the geocator, so we used calibration data from the other Arctic Warbler (1760-53520) as the best estimate of twilight detection bias for that individual.

The Markov Chain Monte Carlo (MCMC) modeling process used to estimate position was implemented using the SGAT package in R (Lisovski & Hahn, 2012; R Core Team, 2022; Sumner et al., 2009). These models combine a position estimation model with a movement model to determine the animal's path in a Bayesian framework. We used estimates of passerine migratory movements to parameterize the movement speed and bearing parameters of the movement model. The distribution of terrestrial habitat contributed to the posterior estimates of position. We created a raster that categorized

each cell as land or water and built a probability mask where overland travel was given a higher prior probability of use [$\log(2)$ vs. $\log(1)$, for example] (Hill & Renfrew, 2019). However, position estimation was unrestricted across the globe. Thus, while the probability mask increases the likelihood of terrestrial position estimates, it does not prevent overwater position estimates. Three MCMC chains were run with a 5000 iteration burn-in, then a 10,000-iteration posterior sample. Posterior estimates of locations were visually checked for chain convergence.

Final location estimates are the median of the three-chain posterior for each position, and the uncertainty in each is displayed using the point intensity of the location estimate MCMC posteriors across a grid system. We estimated arrival and departure dates from the breeding and wintering grounds using multiple changepoint analyses to detect shifts in modeled latitude with a segmented neighborhood method (Killick & Eckley, 2014). We used a cumulative probability test for non-normal data, with a penalty value of 0.9 to identify changes in mean longitude (for departing the breeding grounds) and latitude (for arriving at the wintering grounds). Estimated transition dates were visually assessed to determine accuracy, and data are publically available on Movebank.

3 | RESULTS AND DISCUSSION

We recaptured 6 of the 61 adult male Arctic Warblers (9.8%) banded from 2016 to 2018, including 4 of the 42 (9.5%) with attached geolocators. All recaptures occurred within the 101-ha study area and we had no evidence that geolocators fell off (Appendix S1). The distance between capture and recapture locations in subsequent years for the four tagged birds averaged 213 m (range = 120–365 m). Two of the four geolocators had useful data to track individuals from their breeding territories to their wintering grounds in Southeast Asia, one of which also extended into the early portion of spring migration (Figure 1). Unfortunately, the other two tags failed.

The warblers departed the breeding grounds in Denali by 8/29/18 and 9/3/16 (1780-53921 and 1760-53520, respectively) and flew northwest, leaving North America from the western edge of the Lisburne Peninsula (Figure 1). They arrived at the wintering grounds by 10/20 and 10/15, respectively (Figure 2). The autumn migration route included overwater flights from Alaska to Russia and China and Japan into the Philippines and the surrounding Pacific Islands (Figure 1a). Both individuals appeared to linger in southeastern Russia, then again in southeast China and Japan,

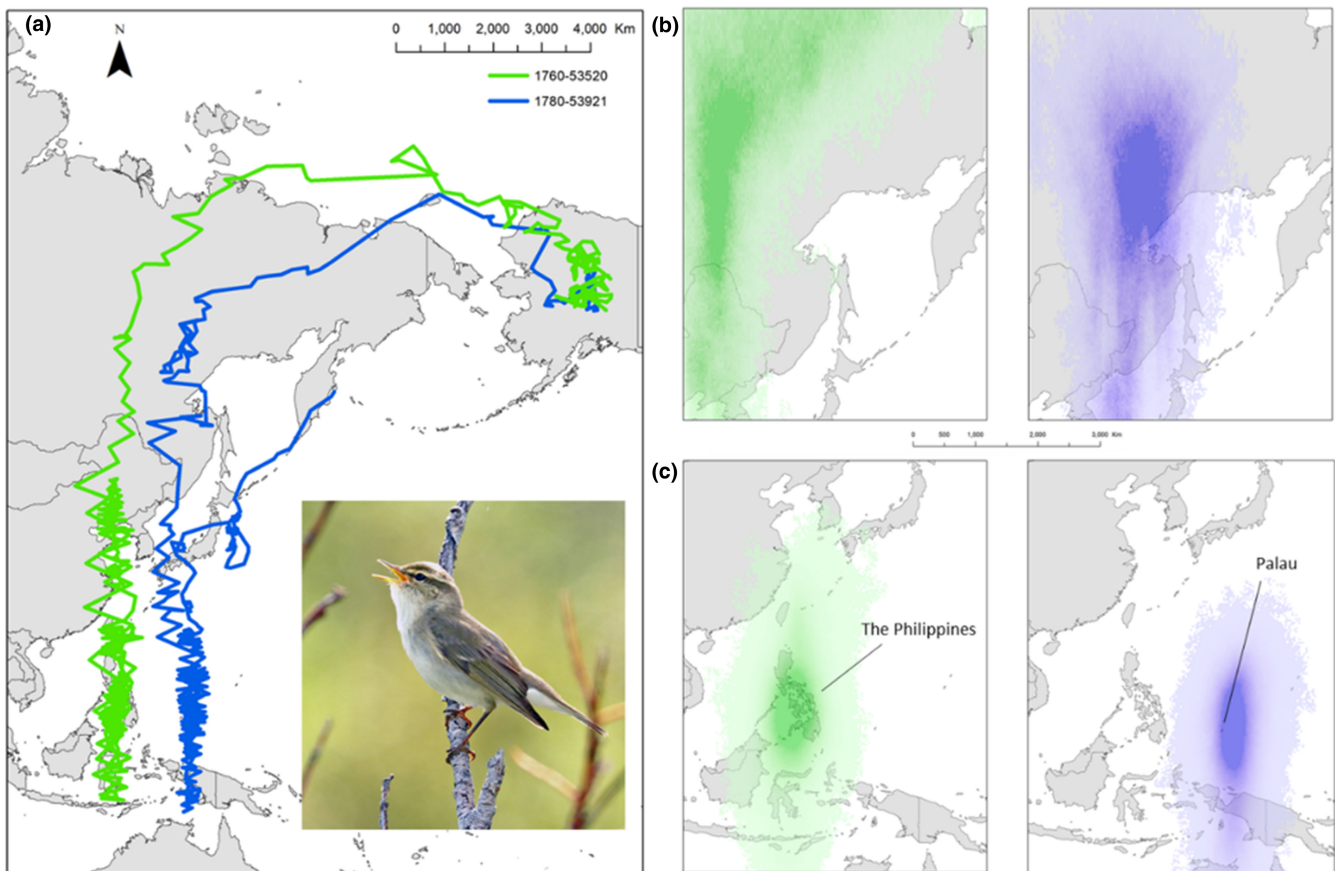


FIGURE 1 Median location estimates for two adult male Arctic Warblers from summer to spring (a). Space use maps describing the position estimation posterior distribution from the Bayesian state-space model during fall migration (top: b, c) and winter (bottom: b, c). The color of the line and the space use maps are the same among individuals (green = 1760-53520 tagged in 2016 and blue = 1780-52921 tagged in 2018). Step length and bearing were estimated for each individual, and a movement model was used to improve location estimates from these light-logging geolocators. Photo: Alan Schmierer (CC 1.0).

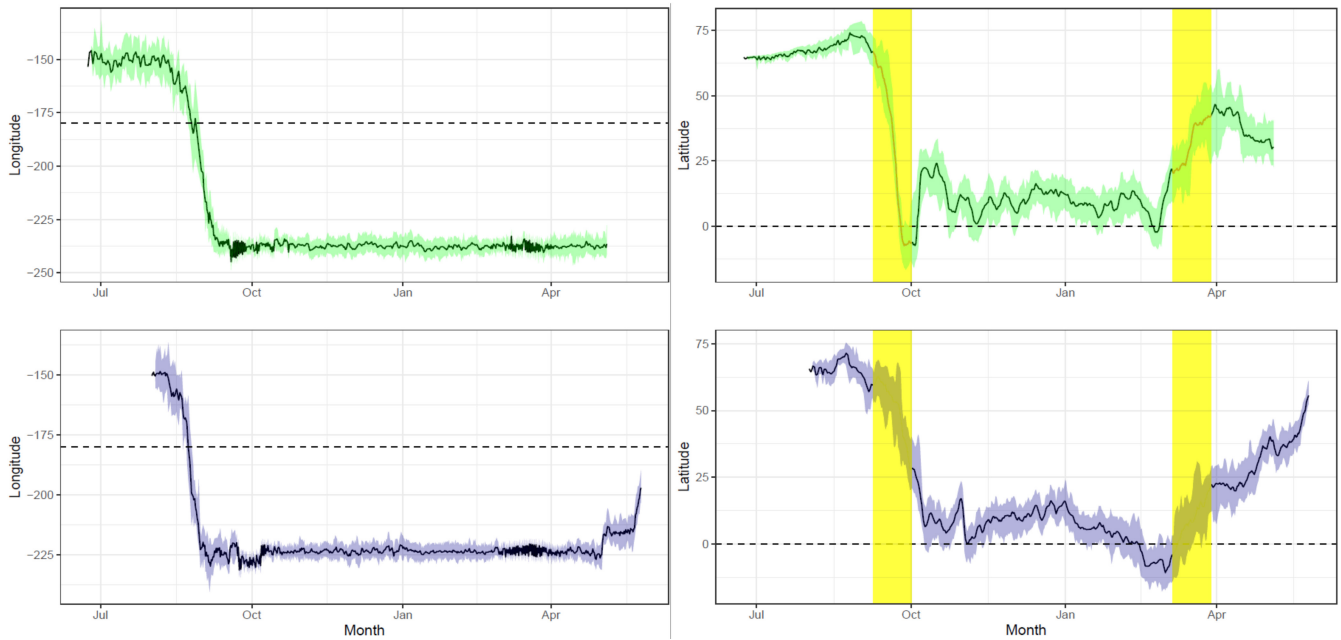


FIGURE 2 Median latitude and longitude estimates for each individual with 95% credible intervals (green = 1760-53520 tagged in 2016 and blue = 1780-52921 tagged in 2018). Yellow areas in the latitude figures indicate periods of time where latitude was not estimable using the raw data and position estimates are only based on model inputs. Dashed lines represent the international date line and the equator, note that longitude values west of the dateline do not reset to positive values.

during fall migration before arriving at their respective wintering grounds (Figure 1b). Their autumn migration orientation is apparently consistent with the great circle migratory pattern reported by Alerstam et al. (2008), although more information is needed to confirm this observation. The birds traveled approximately 8500 and 8700 km to the mean wintering locations and averaged 197 and 181 km/day, respectively. One individual's wintering location was centered on the island of Palawan in the Philippines, while the other individual's wintering location was centered on Palau (Figure 1c). There is no prior evidence of Arctic Warblers wintering on Palau, either in the eBird database or in the English scientific literature (Dendy et al., 2015; Olsen & Eberdong, 2009; VanderWerf et al., 2006). Both geolocators failed before the birds returned to Alaska, but a portion of spring migration along the western coast of Japan and the Kamchatka Peninsula was documented for one bird (1780-53921).

All previous evidence suggested that Arctic Warblers primarily wintered in the Philippines (Lowther & Sharbough, 2020), necessitating overwater migration to their breeding grounds. However, wintering on remote islands like Palau (about 890 km from the Philippines) requires more and/or longer overwater flights. Such flights are not uncommon for small birds; many songbirds and hummingbirds make a flight of similar length across the Gulf of Mexico annually (Deppe et al., 2015; Weidensaul et al., 2020). However, extending such flights increase mortality risk during migration due to encounters with extreme weather events (Newton, 2007). Given the potential for longer overwater flights, the importance of stopover habitat before those legs increases as greater fuel loads are required for successful flights (Vincze et al., 2019).

The geolocators we used in our study are low-precision position estimation tools that can be persistently shaded by feathers and vegetation. Bird behavior and environmental conditions can cause errors in the data collection that systematically bias the results (Fudickar et al., 2012). Thus, these position estimates could be confounded by systemic shading issues and the different tag models for each individual (Intigeo for 1780-53921 and Lotek for 1760-53520). Therefore, our confidence in the Palau wintering location is not high, given the lack of prior evidence of this species wintering there. While our data suggest that one bird wintered on Palau, this pattern could be influenced by a systematic bias in sunrise or sunset time estimation. These biases can be quantified in some situations, but both data loggers stopped recording before recapturing. Alternatively, if these data are correct, we have documented a previously unknown wintering location for the species, and the winter range for this species should be reevaluated. Given the lack of eBird data collected on the island, the non-descript plumage of *Phylloscopus* warblers, and the potential for recent range shifts, this overwinter location seems possible. While we found no evidence of our data being systematically biased, the result's novelty suggests that caution is needed until the Arctic Warbler's presence can be confirmed on Palau. More research and monitoring are needed for this species on the non-breeding grounds; a range-wide survey with expansion to potential locations that currently have poor survey effort is important to better understand its ecology.

This study has documented the migratory pathway and suggests new wintering locations for Arctic Warblers that breed in interior Alaska. Geolocators and similar methods that track movements across the full annual cycle in small songbirds continue to

be powerful tools in illuminating idiosyncratic movements for poorly studied species and advancing our understanding of factors affecting the conservation of migrants with complex life histories (Tonra et al., 2019). However, the costs of such studies to the tagged individuals also need to be considered as does the probability of recapturing the tagged bird. Our recovery rate of tagged birds was 9.5%, much lower than the 35% resighting rate of color-banded Arctic Warblers at a different study site, 210 km east of our study area (Lowther & Sharbough, 2020). Low recapture rates may have resulted from low breeding site fidelity and low survival rates (DeSante et al., 2015; Ralph et al., 1993), geolocators reducing survival (Brlík et al., 2020; Costantini & Møller, 2013), low detectability of tagged birds in the study area, low territoriality of males in the study area, or individual dispersal to new breeding habitat (Hedlund et al., 2017; Mizel et al., 2016). Furthermore, we noted intra-season movements that indicated large territories or inter-territory movements (average = 235 m, range = 85–630; $n = 6$ banded/tagged birds) that may have contributed to our low recapture rate. More information is needed on Arctic Warblers throughout their annual cycle, including their fidelity to breeding sites, to assess their conservation status (Runge et al., 2014) and maximize the return on studies such as this.

Arctic Warblers are currently altering their breeding range and habitat preference as a result of climate change at their Alaskan breeding grounds (Mizel et al., 2016; Thompson et al., 2016). Thus, this species' risk profile has increased, and we recommend expanding current efforts to understand Arctic Warbler population status and the ecological drivers of population trends across their annual cycle.

AUTHOR CONTRIBUTIONS

Evan M. Adams: Data curation (lead); formal analysis (lead); investigation (lead); methodology (lead); validation (lead); visualization (lead); writing – original draft (lead); writing – review and editing (lead). **Iain J. Stenhouse:** Conceptualization (equal); investigation (equal); methodology (equal); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Andrew T. Gilbert:** Methodology (supporting); validation (supporting); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Jill Boelsma:** Investigation (supporting); methodology (supporting). **George Gress:** Investigation (supporting); methodology (supporting). **C. Scott Weidensaul:** Conceptualization (supporting); investigation (equal); methodology (equal); writing – original draft (supporting); writing – review and editing (supporting). **Charles Grigsby:** Investigation (supporting); methodology (supporting). **Emily J. Williams:** Investigation (equal); methodology (equal); project administration (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Laura Phillips:** Investigation (equal); methodology (equal); project administration (supporting); supervision (supporting); writing – original draft (supporting); writing – review and editing (supporting). **Carol L. McIntyre:** Conceptualization (lead); data curation (supporting); funding acquisition (lead);

investigation (equal); methodology (equal); project administration (lead); supervision (lead); visualization (supporting); writing – original draft (supporting); writing – review and editing (supporting).

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CONFLICTS OF INTEREST

The authors declare no conflicts of interest.

OPEN RESEARCH BADGES



Is the author interested in applying for an Open Research Badge?: Yes. Our analysis code is accessible at: https://github.com/evanmadams/denali_songbird_tracking.

DATA AVAILABILITY STATEMENT

Geocator raw data are publically available on Movebank (www.movebank.org) at the Denali National Park Critical Connections project page https://www.movebank.org/cms/webapp?gwt_fragment=page%3Dstudies%2Cpath%3Dstudy2225554945.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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