Research Article

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Revealing migratory path, important stopovers and non-breeding areas of a boreal songbird in steep decline

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Abstract: The Olive-sided Flycatcher (Contopus cooperi) is a steeply declining aerial insectivore with one of the longest migrations of any North American passerine. We deployed light-level geolocators and archival GPS tags on breeders in boreal Alaska to determine migratory routes, important stopovers and non-breeding locations. Data from 16 individuals revealed a median 23,555 km annual journey (range: 19,387, 27,292 km) over 95 days (range: 83, 139 days) with wintering occurring in three regions of South America (NW Colombia/Ecuador, central Peru and W Brazil/S Peru). We developed a new method to identify “Important Stopovers” by quantifying intensity of use (a function of bird numbers and stop durations) along migratory routes. We identified 13 Important Stopovers that accounted for ~66% of the annual migratory period, suggestive of refueling activities. Some sites coincided with key areas previously identified for other Neotropical-Nearctic migrants. Percent land “protected” at Important Stopovers, as defined by IUCN, ranged from 3.8% to 49.3% (mean [95% CI]: 17.3% [9.6, 25.0]). Total migration speed did not differ by season (median: 255 km day⁻¹, range: 182, 295 km day⁻¹), despite greater spring travel distances. Birds with longer non-breeding periods, however, migrated north faster. Climate-driven mismatches in migratory timing may be less of a concern for western than for eastern flycatcher populations, given recent congeneric analyses (C. sordidulus, C. virens). However, accelerated high-latitude changes, may nonetheless impact boreal breeders.

Keywords: Bird migration; Contopus cooperi; aerial insectivore; stopover; migratory connectivity

1 Introduction

The decline of migratory songbirds by the billions underscores an urgent need to identify threats and drivers of avian mortality [1]. Assessing places that declining species use most throughout their annual life cycle is a critical first step toward understanding factors that limit populations [e.g., 2, 3], while also revealing potentially important locations for future conservation and management actions [e.g., 4-8]. It is essential not only to know where birds breed, but also where they spend stationary
non-breeding months [e.g., 2, 9, 10]. In addition, identifying key stopover sites, where birds rest and refuel during migration [3, 8, 11], as well as conditions experienced aloft between stopovers [10, 12], can be particularly crucial, given that individual mortality is often greatest during migration [e.g., 13-16].

Marked losses in aerial insectivore abundance in North America (e.g., swallows, swifts, nightjars, and flycatchers) are of particular concern and highlight the need for full annual cycle information [17-20]. Though mechanisms of aerial insectivore loss are poorly understood and may involve multiple or species-specific drivers [e.g., 18, 19], steep declines in several species of swallows (Hirundinidae) appear linked with deficits in adult survival [e.g., 21, 22] and/or adult condition that “carry over” from the non-breeding period to negatively impact reproduction [23]. Losses are also relatively more acute among aerial insectivores that migrate long distances, compared to those that migrate short distances [17]. Collectively, these patterns suggest that a decline in adult survival and condition may be linked to, and potentially exacerbated by, stressors occurring during periods of long-distance migration, or when birds are stationary on the non-breeding grounds in Latin America [e.g., 17, 18, 21, 22]. Finally, long-distance migrants that nest in high-latitude environments are also thought to be at relatively greater risk of impacts due to climate change compared to those nesting at temperate latitudes [e.g., 24-27].

The Olive-sided Flycatcher (Contopus cooperi) is an aerial insectivore that embarks on one of the longest migrations of any Nearctic breeding passerine [28]. This species has experienced a 78% reduction in global population size since 1970 [29], resulting in a “Near Threatened” status [30], and a “sensitive” or a “species of concern” designation by state and federal agencies in the U.S. and in Canada [e.g., 31-33]). Greatest relative losses have occurred in the western core of the breeding distribution [28], including declines in western forests (~3.5%/year [34]) and northwestern interior forests in Alaska (~2.8%/year [35]), where Olive-sided Flycatchers are considered a “Species of Greatest Conservation Need” [32]. Habitat loss due to deforestation on the non-breeding grounds is suggested to be a particularly high threat [28, 29]. Further, the genus Contopus also exhibits one of the lowest reproductive rates among passerines in North America [28], which may exacerbate decline, but highlights the need to conserve quality, non-breeding habitat to maintain a high probability of adult survival [28]. We notably lack information, however, on the annual life cycle of individuals, important migratory stopover sites, stationary non-breeding areas, degree of spatial overlap between breeding and non-breeding populations (i.e., migratory connectivity [9]), and the problems that climate change may pose over trans-hemispheric migration.

We studied full annual cycle movements by fitting adults in the northernmost portion of the species’ range in boreal Alaska with either a light-level geolocator or an archival GPS tag, as part of a multi-year field effort focused on both breeding and non-breeding behavior [36]. The primary goals of the study were to: (1) quantify full annual cycle movements, including stationary non-breeding areas, migratory connectivity and seasonal variation in the distance, duration and timing of migration, (2) provide a method to identify locations and conservation status of important migratory stopovers of Alaskan breeding populations, and (3) offer insight into climate-driven threats, by comparing flycatcher migratory patterns to recent analyses of habitat change [e.g., 37, 38] and altered seasonal timing [e.g., 39, 40].

2 Methods

2.1 Study area

Our 5-year migration study (deployments: 2013–2017) occurred in three areas of boreal Alaska within Bird Conservation Region (BCR) 4 (Fig. 1, [41]). Two areas were located in central Alaska (Fairbanks vicinity and Tetlin National Wildlife Refuge) and a third was in south-central Alaska (Anchorage vicinity). Deployment of tracking devices near Fairbanks were made over a larger area than Anchorage or Tetlin and therefore included multiple deployment sites (Table 1). Detailed information on each location, number of each tag-type used, and recovery outcomes are summarized in Table 1.

Olive-sided Flycatchers in the boreal forest typically establish breeding territories along the open edges of wet coniferous woodlands with emergent snags used as feeding perches [28, 42, 43]. Primary habitat types include “scattered woodland/dwarf forest and coniferous forest” described in [44] (as habitat types VI.d. and VI.b., respectively), which is comparable to open needleleaf forest of [45] (habitat types I.A.2, especially I.A.2.e, f, g). Birds also nest in mixed deciduous-coniferous forest and in drier, upland deciduous forest (VI.a.c [44]; I.B.2.a,b and I.C.2.a [45]). Openings and forest-edge within territories represent both undisturbed and “disturbed” habitats (e.g., associated with wildland fire or logging [46, 47]).
2.2  Bird capture and deployments

Breeding individuals are typically site-faithful and build nests near the previous years’ locations (~100 m [28, 42]). We searched areas in central and south-central Alaska with recent summer sightings (from eBird and Breeding Bird Survey data) and suitable habitat (e.g., 5-15 years post-burn, wetland-forest interfaces; [28]) to discover breeding pairs. We provide recommended methods for target-netting and recovering tags from this species in supplementary materials (see: 6.1: Target netting methods and Fig. S1).

In total, we fitted 95 birds with one of two possible tag types: archival light-level geolocators (n = 66 birds) and archival GPS tags (n = 29 birds; Table 1). Archival light-level geolocators (hereafter geolocators) infer daily locations of individuals over the annual cycle at a relatively "coarse" spatial scale (e.g., ±150 km [48, 49]). The geolocators we deployed (Integeo model P65C27, Migrate Technology) had a 7-mm light pipe, which minimizes plumage interference and increases precision and accuracy by 1.8–4.3 degrees of latitude and longitude [50]. Each had a battery life of up to 2-years. Units weighed 0.75 g and were attached to individuals via a modified leg-loop harness [51] made of 1 mm diameter Stretch Magic™ (Pepperell Braiding Company, Pepperell, MA) for a total weight of ~1.0g (~3% of 32 g average adult body mass). For further information on harness construction and deployment, see supplementary materials (6.2 Harnessing method).

Archival GPS tags (hereafter GPS tags), in contrast to geolocators, offer more precise location estimates from satellite fixes (e.g., ±10 m [52]). However, battery weight limits the number of points logged per year. Data-logging technology of the GPS model we used (Lotek PP10;
Lotek Wireless, Newmarket, Ontario, Canada) changed notably over the study period, resulting in tags capable of taking either 10 points or 80 points annually (Table 1). The primary goal of 10-point GPS tags was to identify locations of the stationary non-breeding grounds in Latin America, where birds remain over a multi-month period, coincident with winter in the Northern Hemisphere (e.g., November-March [28]). By contrast, 80-point GPS tags focused on stopovers made during the spring and fall migratory movement periods that occur on either side of breeding. Each unit weighed 1.0 g, resulting in a total weight with harness of ~1.25 g (~4% of adult body mass). Data from our initial 10 geolocator recoveries informed a pre-programmed annual schedule (loaded onto GPS tags) that determined when to attempt satellite fixes, such as during weeks when birds were most likely at prolonged migratory stopovers or on the stationary non-breeding grounds. Details are provided in supplementary materials (6.3 Pre-programmed schedules of archival GPS tags). All tag deployments were conducted under Federal Bird Banding Permits #33295 to JCH and #23598 to SMM. Both permits were associated with ADF&G IACUC Protocol #0033.

Only one individual per breeding pair typically received a geolocator or GPS tag. Our large sample of males (Table 1) reflected a greater response to decoys and playback. All captured birds received a USGS size 1B aluminum leg band and up to 3 colored plastic (Darvic) leg bands for individual identification. Darvic bands were cut in half to accommodate the birds’ short tarsus and ends sealed via a battery-powered soldering iron. Sex was determined by the presence of a brood patch [53] and verified from sex-specific behaviors observed over multiple site visits to nesting areas [28, 46]. Standard morphometric data, blood and feather samples were also collected at capture.

Table 1: Deployment (n = 95) and recovery (n = 22) of archival light-level geolocators and GPS tags on adult Olive-sided Flycatchers (*Contopus cooperi*) breeding in boreal Alaska (2013–2018). Tallies indicate the total tags deployed (number of females) and recovered of 3 tag types used (light-level geolocators, 10-point GPS, 80-point GPS) at seven general study areas. The final two columns denote failure of all recovered tag types (e.g., battery malfunction, bird eluding capture). Multiple sites were located within ~250 km of Fairbanks, Alaska, except for Anchorage and Tetlin National Wildlife Refuge.

<table>
<thead>
<tr>
<th>Site Description</th>
<th>Latitude</th>
<th>Longitude</th>
<th>Geo*†</th>
<th>GPS (10pt)‡</th>
<th>GPS (80pt)§</th>
<th>Tag failed to collect data¶</th>
<th>Bird returned but tag not recovered</th>
<th>Total Tag Deployed (females)</th>
<th>Total Tag Recovered (females)</th>
<th>Failures</th>
</tr>
</thead>
<tbody>
<tr>
<td>Anchorage</td>
<td>61.28°</td>
<td>-149.75°</td>
<td>7(1)</td>
<td>5(3)</td>
<td>3(1)</td>
<td>2</td>
<td>2</td>
<td>66(20)</td>
<td>19(8)</td>
<td>10(3)</td>
</tr>
<tr>
<td>Elliott Highway</td>
<td>65.40°</td>
<td>-148.91°</td>
<td>11(3)</td>
<td>4(3)</td>
<td>1</td>
<td>4(1)</td>
<td>2(1)</td>
<td>4(1)</td>
<td>2(1)</td>
<td>4(1)</td>
</tr>
<tr>
<td>Fairbanks</td>
<td>64.94°</td>
<td>-147.76°</td>
<td>10(5)</td>
<td>2</td>
<td>4(2)</td>
<td>1</td>
<td>0</td>
<td>3(1)</td>
<td>1(1)</td>
<td>3(1)</td>
</tr>
<tr>
<td>Steese Highway</td>
<td>65.36°</td>
<td>-146.12°</td>
<td>4(2)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>2(1)</td>
<td>1(1)</td>
<td>1(1)</td>
</tr>
<tr>
<td>Tetlin National Wildlife Refuge</td>
<td>65.14°</td>
<td>-142.27°</td>
<td>12(1)</td>
<td>5(2)</td>
<td>0</td>
<td>3</td>
<td>1</td>
<td>3(1)</td>
<td>1(1)</td>
<td>1(1)</td>
</tr>
<tr>
<td>White Mountains National</td>
<td>65.34°</td>
<td>-146.94°</td>
<td>11(4)</td>
<td>2</td>
<td>0</td>
<td>3</td>
<td>0</td>
<td>3(1)</td>
<td>1(1)</td>
<td>1(1)</td>
</tr>
<tr>
<td>Recreation Area</td>
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<td>-147.01°</td>
<td>11(4)</td>
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<td>2</td>
<td>3(1)</td>
<td>0</td>
<td>3(1)</td>
<td>1(1)</td>
<td>1(1)</td>
</tr>
<tr>
<td>Sub-totals</td>
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<td>19(8)</td>
<td>10(3)</td>
<td>17(2)</td>
<td>4(1)</td>
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<td>Total</td>
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<td>22(3)</td>
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<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>8(1)</td>
</tr>
</tbody>
</table>
2.3 Tag recoveries

We conducted annual searches at deployment sites over 3 consecutive years and estimated that our search protocol provided a minimum 90% detection probability, based on detection distances and singing rates quantified in [42] and described in supplementary materials (6.4 Re-sight protocol for tagged birds). We recovered 17 geolocators (Table 1) and re-sighted 3 others (2 males, 1 female), for a return rate of 30% (20 of 66 deployed, 95% CI = 19, 41%). Excluding 1 battery failure, we successfully retrieved geolocator data from 14 adults (12 males, 2 females), including 9 birds from Fairbanks, 3 from Anchorage, and 2 from Tetlin. Data represented 17 round-trip migrations, with 3 birds providing 2 consecutive annual cycles of data (1 each from Anchorage, Fairbanks and Tetlin; 2 males, 1 female). One 2-year bird acquired an injury (1-cm skin lesion) during its second year, prompting us to exclude data from most calculations, except for an assessment of inter-annual site fidelity during winter. Occasional recovery of 2-year birds underscores the importance of site visits for at least 2 seasons following deployment. For example, 2 tagged birds returned, but were displaced early in the breeding season by other territorial birds. Consequently, we could not locate, recapture or retrieve tags of displaced birds until the following season. Some banded individuals were re-sighted over 4 consecutive breeding seasons (before and after tag recovery) on the same territory.

In addition to geolocators, we recovered 5 GPS tags and re-sighted one other for a return rate of 21% (6 of 29 deployed, 95% CI: 6, 35%; Table 1). Unfortunately, only 2 GPS tags provided data (both 10-point GPS; 1 male, 1 female) and 3 tags failed (2 10-point GPS, 1 80-point GPS). The two functioning 10-point GPS tags enabled us to determine the southernmost location(s) of each bird during the stationary non-breeding period only. Data from geolocators and GPS tags are available upon request from Movebank.org (ID = 1449428450).

2.4 Light-level geolocation data

We used raw light data collected from geolocators to estimate the geographic coordinates (latitude and longitude) of flycatchers throughout the annual cycle [54]. It is possible to estimate position from observed sunrise and sunset times, because variation in daylength and the time of solar noon across the planet is known [55]. We derived daily location estimates throughout a bird’s annual cycle using the steps below. First, we determined the daily time of sunrise and sunset for each bird using the “findTwillights” function in the TwGeos package (https://github.com/lslovski/TwGeos.git) in program R (version 3.6.3, R Core Team 2021, https://www.R-project.org/) with a user-defined light threshold value of 1.5 to determine the timing of twilight (sunrise or sunset), which occurred when ambient light levels rose above or fell below this threshold. We set a minimum dark period of 10 minutes to help remove spurious twilights, as some individuals bred at high latitudes (Fairbanks and Tetlin), creating very short “dark” durations. Recorded light-levels in these breeding areas sometimes did not fall below our threshold for twilight for multiple days (between late May–late July). We visually inspected, edited and omitted spurious twilights using the “preprocessLight” function from the TwGeos package. Spurious twilights were rare, however, possibly because individuals typically forage from the tops of snags in forest openings [28].

Next, we derived daily location estimates for each bird using the Solar/Satellite Geolocation for Animal Tracking (SGAT) in program R [56, 57]. The SGAT package estimates geographic locations while incorporating the error inherent in light-level geolocation using Markov Chain Monte Carlo simulations. We specified a model for each individual following [54] that included five key components: (1) the raw locations derived from the threshold method, (2) a model that described the error distribution between estimated and known sunrise and sunset times, (3) a behavioral model that described potential flight speeds (km hr⁻¹, Beta distribution: α = 0.7, β = 0.02), (4) a spatial mask that constrained stationary periods to land masses, and (5) a predicted flycatcher abundance surface derived from eBird observations [58] (with spatial resolution = 0.25° x 0.25°) as prior information [3].

Daily position estimates derived using a simple threshold method [59] were used in our modeling process. In addition, we employed the “ChangeLight” function from the GeoLight package [59] to create a migration schedule for each bird’s annual journey, using a minimum (1-day) stopover duration. The migration schedule detailed the dates of a bird’s arrival to and departure from the breeding grounds, each migratory stopover (where a bird was stationary for a minimum 1-day duration), and the stationary non-breeding grounds. We aggregated consecutive stopover locations that occurred within a distance threshold of 250 km with the “mergeSites2” function from the GeoLight package, given the location uncertainty associated with geolocation [59, 60].

The error distribution between estimated and known twilight events followed a log-normal distribution and
was created from light-data recorded when individuals were known to be at their capture location. On-bird calibration data also determined a single sun zenith angle, which we used throughout the year to estimate locations. Our approach yielded similar results to light-data from stationary tags placed within Olive-sided Flycatcher wintering habitat in Latin America, suggesting that zenith angles were like those derived from on-bird calibration (see also: supplemental materials: 6.5 Zenith angle detail for geolocators). We specifically used on-bird calibration data retrieved from the 3 Anchorage geolocators, because those deployed in Fairbanks and Tetlin experienced near-constant light conditions.

The model in SGAT was run 3 times with 5000 iterations on 3 chains. In between each run, the chains were collapsed, and the location estimates summarized. The resulting median daily location estimate was used to initialize the subsequent run. The first 2 runs were discarded and treated as a burn-in. The final run was composed of 5000 iterations and 3 chains. We kept every 10th iteration from the posterior distribution, from which we drew our geographic inference. The posterior distribution of daily geographic coordinates for each individual were summarized into a raster (pixel resolution = 0.25° x 0.25° or ~500km², depending on the exact location on earth) resulting in a distribution surface for each day. R-code is available at: https://github.com/MTHallworth/OSFL_MC/blob/master/Olive-sided-flycatcher-analysis-Jul2021.Rmd.

### 2.5 Migratory routes, phenology, and seasonal patterns

The median location weighted by uncertainty for each stopover (i.e., the underlying raster surface of the posterior distribution) was used to generate the most probable migration route, as well as estimate great circle distances (which account for the earth's curvature) between stopovers of 1-day or more. Summation of distances between stopovers for each individual was used as the total distance traveled. For each bird, we also determined the timing and duration of fall and spring migration, the number of stopovers, time spent at each stopover, and duration of the stationary winter phase. We present all migration data including all available information. A third bird that provided two years of data became injured during its second year. We only used its first (uninjured) migratory cycle in analyses of speed and seasonal patterns.

### 2.6 Identification of “Important Stopovers”

Determining the relative intensity of bird use (i.e., “heatmaps”), while accounting for location uncertainty inherent to geolocators, is relatively new to the migratory literature [e.g., 3, 11]. We created a binary surface for individual stopovers by assigning all locations that fell within the 95% credible interval as “a stopover” [11]. We considered those locations as “used” and assigned the observed duration for the stopover, even though the true use of an individual location was unknown [3, 11].

We next overlaid seasonal routes of all individuals (and the associated location uncertainty of each), then summed the total number of birds per ~500 km² pixel, which we defined as “Birds#,” to clarify that the true number of birds using each pixel within the raster surface is unknown. Pixel values of Birds# were used to generate heatmaps illustrating bird distributions during fall and spring migration, and on the stationary non-breeding by subtracting the sum of fall, spring and winter durations from 365 days (a full annual cycle). We verified accuracy of breeding durations via detailed (biweekly) field observations of nest and post-fledging activity, which we conducted as part of a related effort to document reproductive timing and nest success [61].

We define total speed of migration as (total distance traveled)/(duration of fall + spring migration periods), which provides an overall estimate of migratory travel rate, start to finish, including stopovers, in km day⁻¹ [62]. We also calculated the seasonal differences in duration and speed in terms of the quotient “Q,” which facilitates comparison between Olive-sided Flycatchers and other avian taxa [62]. Negative values of Q indicate slower travel speeds (or longer durations) in spring compared to fall, the reverse for positive values. We used Spearman’s Rho correlations to detect any associations between seasonal variables. We also used this method to correlate migratory distance with breeding latitude, which can reveal evidence of migratory connectivity [3].

Data from most birds represented a single, annual migratory cycle. However, two individuals provided movement data over two consecutive years. For these, we averaged values from the two annual cycles to calculate the aforementioned parameters. This ensured each bird was represented in our migration dataset only once, while still including all available information. A third bird that provided two years of data became injured during its second year. We only used its first (uninjured) migratory cycle in analyses of speed and seasonal patterns.
ing grounds [3,11]. We used a similar method to sum up individual stopover durations at each pixel to determine the total duration of bird use, defined as “BirdDays#.” We then divided BirdDays# by its associated Birds# value to determine a mean BirdDays# per pixel, which created a heatmap highlighting likely places where individuals spent relatively more time [3].

Migratory stopovers where more birds spend longer durations are likely important to consider when prioritizing conservation efforts. Therefore, we used data for stops ≥ 2 days in duration, which provided greater spatial resolution and certainty from geolocator data. We also took the heatmap method a step further by combining the two measures of bird use per pixel (Birds# and BirdDays#) into a new metric, called the “importance score,” rather than analyzing each variable separately. The importance score provides a single, population-level index that quantifies the relative intensity of bird use within a region:

\[
\text{Importance} = \frac{\text{Birds#} \times \sum (\text{BirdDays#})}{\max (\text{Birds#} \times \sum (\text{BirdDays#}))}
\]

From the equation, locations with larger importance scores indicate more intense bird use. The denominator scales the score between 0-1. Compared to other commonly used methods that infer importance, such as migratory networks [e.g., 63], the importance score incorporates location uncertainty associated with light-level geolocation [54]. Unlike other methods, such as migratory connectivity, the importance score does not require users to pre-define regions, nor is it sensitive to the arrangement of pre-defined regions [10]. Consequently, it is an objective, flexible tool to identify high-use bird areas, and can be used in combination with other methods to estimate the strength of migratory connectivity between stationary (breeding/non-breeding) and migratory periods of the annual cycle [64].

We calculated an importance score for each pixel throughout the annual cycle. Scores of 0.2 or greater are biologically meaningful for Olive-sided Flycatchers, because they represented pixels with above-average values of both measures of bird use (estimated bird numbers [Birds#] and total duration \[E(\text{BirdDays#})\]) that comprise the importance score equation (Fig. S2). Evidence for above-average bird use prompted us to set the importance score value to 0.2 per pixel as a threshold value.

We grouped nearby pixels with importance scores ≥ 0.2 into spatially discrete “Important Stopover” regions using the “get_patches” function in the LandscapeMetrics R package [65]. It is not reasonable to consider a single pixel patch (~500 km²) as a unique Important Stopover location, due to the coarse spatial scale of light-level geolocation. Therefore, whenever the “get_patches” function resulted in a single pixel, we merged it with the nearest pixel(s) with importance scores at or above the 0.2 threshold.

We used data from all pixels contained within the spatial extent of each Important Stopover to estimate a median importance score each season and median value of Birds#. These metrics yield relative (rather than absolute) measures, enabling comparisons among sites, despite the coarse spatial resolution of light-level geolocation. For example, if a bird’s estimated location overlapped with more than one Important Stopover (e.g., in Central America), we did not assign it to any single location, since the bird’s exact location was unknown. Instead, we used the entire spatial extent of each bird’s data for every stopover event ≥ 2 days. Overlapping data at the pixel level were then summarized within each Important Stopover raster to compare among sites. We also estimated the median stopover duration for each Important Stopover location, as described below for linear models.

The large spatial extent of Important Stopovers prompted us to generate heatmaps of importance scores for each site at the spatial resolution of modeled geolocator data (0.25° x 0.25°or ~500 km²). The detail of heatmaps enable future field work to target locations within each Important Stopover expected to contain habitat of high value to Alaska-breeding flycatchers (e.g., high-intensity use for extended durations). Heatmaps provide best estimates of bird use to date, given a lack of GPS data during migration.

Since the importance score provides a new method for identifying Important Stopovers, we explored correlations between variables that comprise our approach. We conducted these analyses separately for fall and spring migration. Our first analysis examined the two components that make up the importance score, the number of birds stopping in an area and stopover duration. If these two variables are strongly correlated, then the information each provides to the importance score would be redundant, and the score would not be needed. If, however, the two components are independent of each other, then each contributes unique, rather than duplicative information to the score. We used a general linear model [66] (all analyses done with SAS 9.4, SAS Institute Inc., Cary, NC) with the number of birds as the predictor and stop duration as the response. To calculate the predictor, we generated a probability surface from each bird’s location estimate and calculated the probability (p) that the bird occurred within each Important Stopover or outside of an Important Stopover (1-p), then summed all bird probabil-
ities associated with a given site. If a bird had multiple stops within the same Important Stopover, we generated a single probability to indicate at least one use (e.g., one minus the probability that the bird was never there). Due to multiple observations per bird (e.g., multiple stops of different duration), we estimated all parameters and confidence intervals via bootstrapping [67], where individual birds (including those tagged for 2 years) were selected with replacement for replicate samples. For the GLM, we assessed whether number of birds was related to stopover duration using the small-sample-bias-corrected version of Akaike’s Information Criteria (AICc) [68] by comparing the AICc weight against the weight for a no-predictor model.

In a second evaluation of the importance score method, we examined the association between stopover duration (predictor) and the probability a stop occurred in an Important Area (response). These analyses also used a generalized linear model (binomial error, logit link) [66], with bootstrapping and AICc procedures as described above. We estimated the median difference (and confidence intervals) between stopover durations at Important Stopovers vs. elsewhere using quantile regression [69]. Lastly, we estimated weighted median stopover durations (IQR) and weighted median stop date (IQR) for each Important Stopover. Weights were the probabilities that a bird’s stop occurred in a specific Important Stopover.

2.7 Percent protection of Important Stopovers

We overlaid the Worldwide Database of Protected Areas (WDPA; www.protectedplanet.net) onto the spatial extent of Important Stopovers (areas with importance scores ≥ 0.2; see Methods: 2.6 Identification of “Important Stopovers”). The WDPA, with support from the International Union for the Conservation of Nature (IUCN), provides a single, standardized, global measure of land protection that enables broad comparisons across countries [70]. Our analysis coarsely quantifies the proportion of land area within each Important Stopover that the IUCN currently defines as protected: “A clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” [70] (see Fig. S3 for method). The IUCN recognizes seven land categories as “protected” within the WDPA, including nature areas, national parks, and certain areas of sustainable resource use [71] (see also Table 1.1 in [72]). However, some managed landscapes likely to contain intact wildlife habitats are excluded, such as national forests, where current practices may involve large-scale harvest [71].

Consequently, the percent protection metric yields an initial, quantitative starting point to inform future steps aimed at full annual-cycle conservation. For example, Important Stopovers with minimal percent protection but relatively high intensity bird use could be prioritized for future research to identify immediate human threat(s), if any (e.g., due forest fragmentation, land conversion), and whether flycatchers use habitats that are likely to impacted. Investigators can also use heatmaps of importance scores within an Important Stopover to further refine where future field and conservation efforts may be most fruitful (e.g., areas with relatively high-intensity bird use). This approach assumes that flycatcher habitats in protected areas are less likely to be at risk from human disturbances than those in unprotected habitats.

2.8 Migratory Connectivity

We combined data from both geolocators and GPS tags to estimate the strength of migratory connectivity— the geographic link between populations during two or more phases of the annual cycle [9, 10]. We specifically quantified migratory connectivity between the boreal breeding grounds in Alaska and the stationary non-breeding areas in South America using the package MigConnectivity R [10, 73]. We derived the migratory connectivity metric (MC) from this package by defining each deployment region of Alaska (Anchorage, Fairbanks, Tetlin; Fig. 1) as a “population.” We then estimated the relative abundance of flycatchers at each deployment site by summarizing eBird’s predicted abundance estimates [58] within a 50-km radius. We used international boundaries within the known non-breeding distribution as our target non-breeding regions [e.g., 3, 10].

Additional metrics, such as location bias and location uncertainty, were required to estimate migratory connectivity from light-level data [10]. We derived location bias (longitude: -79.72 km, latitude: 65.05 km) and uncertainty metrics (longitude: 188.80 km, latitude: 103.03 km) with data taken over multiple weeks soon after geolocator deployment (late June–1 August), when birds remained on breeding territories in Anchorage (3 recoveries). Birds with geolocators in other deployment areas (Fairbanks and Tetlin) experienced nearly 24-h daylight during breeding, given proximity to the Arctic Circle, which made similar calculations impossible [59]. We used the median location weighted by the posterior distribution raster surface as the stationary non-breeding location for each individual car-
rying a geolocator [10]. Only the first year of tracking data was used in connectivity analyses, as birds that provided 2 years of data were faithful to stationary non-breeding sites (see Results).

3 Results

3.1 Migratory route and stationary non-breeding locations

Olive-sided Flycatchers tagged in boreal Alaska undertook a median annual migratory journey of 23,555 km (Fig. 2a-e) over a 95-day duration (fall + spring) and travelled at a median total migratory speed (start to finish, including stopovers) of 255 km/day (Table 2). Individuals stopped a median of 34 times for ≥ 1 days at locations spaced 682 km apart (Table 2), which provides an estimate of mean daily travel distance. Annual migration distance correlated positively with number of stopovers (Spearman’s rho = 0.65, P = 0.011).

The stationary non-breeding period lasted a median of 189 days (Table 2) in the following core areas (Fig. 2g): (1) Colombia/Ecuador (5 males, 1 female with geolocators), (2) central Peru (4 birds; 2 males with geolocators, 1 male and 1 female with GPS), and (3) western Brazil/southern Peru (5 males, 1 female with geolocators). Interannual site fidelity during the stationary non-breeding period in South America was high for the three birds that carried geolocators for two consecutive years. Each individual’s estimated non-breeding location in the second winter overlapped with the previous year by >70% (mean [SD]: 72% [0.01], range: 71, 75%, n = 3). The difference between median locations of each bird over consecutive seasons also indicated they wintered in the same area (mean difference: 55km, range: 37, 86km). Finally, we gained some insight into localized movements of a single bird carrying a GPS tag that provided 4 consecutive fixes over a 3.5-month period (mid-November through early March). All points were closely spaced (88–168m apart) in habitat that included both forest patches and clearings.

3.2 Phenology

During fall migration (Fig. 2a,b), birds departed Alaska (median: 4 Aug, IQR = 29 Jul–8 Aug, range = 20 Jul–16 Aug) and travelled south, along the east side of the Rocky Mountains, arriving on stationary non-breeding grounds by 20 Sep (IQR = 15–29 Sep, range = 6 Sep–5 Oct; Fig. 2g; for a larger map, see Fig. S4). The northbound journey in spring (Fig. 2d, e) began on the median departure date of 24 Mar (IQR = 11 Mar–8 Apr, range = 6 Mar–21 Apr) and exhibited a more westerly trajectory through North America.

The most probable migration route indicated most birds (12 of 14) circumnavigated the Gulf of Mexico, rather than crossing it; only 2 (1 in fall, 1 in spring) exhibited a partial, over-water crossing in the southwestern Gulf (Fig. 3).

Median return date to breeding grounds in central and southcentral Alaska was 17 May (IQR = 13–26 May, range = 6–31 May) where the breeding period lasted a median 78 days (Table 2).

3.3 Seasonal patterns

Birds traveled a median of 1,323 km farther and made a median of five more stopovers of ≥ 1-day during spring than fall migration (Table 2). Migration duration also tended to be longer in spring than fall (by a median of 5 days), though the 95% CI of the seasonal difference marginally overlapped 0 (Table 2). Total migration speed, however, was similar in each season, as were stopover durations and distance traveled between stopovers (Table 2). Individuals that traveled faster in spring also traveled faster in fall (Spearman’s rho = 0.63, P = 0.02).

Duration of the stationary non-breeding period and a bird’s subsequent spring migration period were negatively correlated (Spearman’s rho = -0.77, P = 0.0012). Conversely, the stationary non-breeding period and spring migratory speed were positively correlated (Spearman’s rho = 0.62, P = 0.012). Similar patterns were evident for fall (stationary non-breeding vs. fall duration: Spearman’s rho = -0.58, P = 0.03, fall speed: Spearman’s rho = 0.65, P = 0.012). However, duration of the breeding period in Alaska was not related to travel speed in either season or duration of any other migratory period (-0.41 ≤ Spearman’s rho ≤ 0.03, 0.14 ≤ P ≤ 0.89). We also detected no relationship between total migration distance and breeding latitude (Spearman’s Rho = -0.026, P = 0.93).

3.4 Important Stopovers and Percent Protection

We identified a total of 13 “Important Stopovers,” each representing large areas where the importance score was ≥ 0.2 (Fig. 3), ranging in size from 10,796 km² (11 pixels) to 256,204 km² (347 pixels; Table 3), with a median value of 49,174 km². Though some flycatcher activity was
Figure 2a-g: Heatmaps of archival geolocator data illustrating the annual migration path and stationary non-breeding areas of 14 Olive-sided Flycatchers (*Contopus cooperi*) from boreal Alaska. Heatmaps reveal migratory routes during fall (a,b) and spring (d,e), using data summed per pixel to represent the relative number of birds (Birds#; a, d) or mean stopover duration (mean BirdDays#; b,e). A new metric, the importance score (c,f), combines both measures (Birds# and BirdDays#) into a single population-level index to reveal the relative intensity of bird use during migration and highlight Important Stopovers locations. Part (g) illustrates birds on the stationary non-breeding grounds. Black circle and triangle in (g) indicate GPS locations of 2 additional birds obtained during stationary non-breeding months only. A larger map of (g) is provided in supplemental materials (Fig. S4). See also Methods: 2.6 Identification of “Important Stopovers” for more detailed definitions of the variables represented.
Table 2: Seasonal migration summary of 14 adult Olive-sided Flycatchers (*Contopus cooperi*), that bred in boreal Alaska and carried light-level geolocators. Bold text indicates a seasonal difference between spring and fall migratory seasons (e.g., Spring - Fall), where the confidence interval (CI) does not include 0. The last three columns present the quotient “Q,” a metric comparable to other species, in which negative values indicate relatively longer spring durations and slower speeds [62].

<table>
<thead>
<tr>
<th>Variable</th>
<th>Time Period</th>
<th>Median (95% CI)</th>
<th>IQR1 (25, 75%)</th>
<th>Range (Min, Max)</th>
<th>Q² Median (95% CI)</th>
<th>IQR (25, 75%)</th>
<th>Range (Min, Max)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Migration distance (km)</td>
<td>Annual¹</td>
<td>23,555 (22,507, 24,739)</td>
<td>22,515, 24,602</td>
<td>19,387, 27,292</td>
<td>-0.03 (-0.05, -0.01)</td>
<td>-0.05, 0.002</td>
<td>-0.11, 0.04</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>12,918 (12,340, 13,801)</td>
<td>12,003, 14,359</td>
<td>11,065, 15,368</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>11,128 (10,659, 12,027)</td>
<td>10,340, 12,249</td>
<td>9,426, 14,072</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>1,323 (928, 2,527)</td>
<td>492, 2,469</td>
<td>-89, 4,430</td>
<td>-0.11 (-0.20, 0.02)</td>
<td>-0.19, 0.04</td>
<td>-0.46, 0.32</td>
</tr>
<tr>
<td>Migration duration (days)</td>
<td>Annual</td>
<td>95 (92, 110)</td>
<td>88, 114</td>
<td>83, 139</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>53 (47, 59)</td>
<td>43, 63</td>
<td>35, 72</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>47 (44, 52)</td>
<td>43, 52</td>
<td>38, 68</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>5 (0, 11)</td>
<td>-1, 11</td>
<td>-13, 22</td>
<td>-0.30 (-0.39, 0.08)</td>
<td>-0.40, 0.031</td>
<td>-0.73, 0.18</td>
</tr>
<tr>
<td>Total Migration Speed⁶ (km/day)</td>
<td>Annual</td>
<td>255 (219, 260)</td>
<td>197, 268</td>
<td>182, 295</td>
<td>-0.05 (-0.14, 0.06)</td>
<td>-0.20, 0.12</td>
<td>-0.39, 0.21</td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>266 (266, 290)</td>
<td>202, 313</td>
<td>172, 351</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>239 (224, 262)</td>
<td>213, 268</td>
<td>190, 299</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>13 (-11, 41)</td>
<td>-25, 55</td>
<td>-44, 103</td>
<td>-0.30 (-0.39, 0.08)</td>
<td>-0.40, 0.031</td>
<td>-0.73, 0.18</td>
</tr>
<tr>
<td>Total number of stopovers (≥ 1 day)</td>
<td>Annual</td>
<td>34 (31, 35)</td>
<td>31, 34</td>
<td>26, 40</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>19 (16, 20)</td>
<td>15, 21</td>
<td>12, 25</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>14 (13, 16)</td>
<td>13, 15</td>
<td>11, 19</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>5 (1, 7)</td>
<td>0, 6</td>
<td>-3, 13</td>
<td>-0.30 (-0.39, 0.08)</td>
<td>-0.40, 0.031</td>
<td>-0.73, 0.18</td>
</tr>
<tr>
<td>Mean duration (days) per stopover (≥ 1 day)</td>
<td>Annual</td>
<td>3 (3, 4)</td>
<td>2, 4</td>
<td>2, 5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>3 (3, 4)</td>
<td>2, 3</td>
<td>2, 5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>3 (3, 4)</td>
<td>2, 4</td>
<td>2, 4</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>-1 (-1, 0)</td>
<td>-1, 0</td>
<td>-2, 2</td>
<td>0.26 (-0.03, 0.35)</td>
<td>-0.54, 0.62</td>
<td>-0.11, 0.41</td>
</tr>
</tbody>
</table>
Table 2 continued: Seasonal migration summary of 14 adult Olive-sided Flycatchers (Contopus cooperi), that bred in boreal Alaska and carried light-level geolocators. Bold text indicates a seasonal difference between spring and fall migratory seasons (e.g., Spring - Fall), where the confidence interval (CI) does not include 0. The last three columns present the quotient “Q,” a metric comparable to other species, in which negative values indicate relatively longer spring durations and slower speeds [62].

<table>
<thead>
<tr>
<th>Variable</th>
<th>Time Period</th>
<th>Median 95% CI</th>
<th>IQR (25, 75%)</th>
<th>Range (Min, Max)</th>
<th>Q² Median 95% CI</th>
<th>IQR (25, 75%)</th>
<th>Range (Min, Max)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Number of Important Stopovers</td>
<td>Annual</td>
<td>8 (7, 9)</td>
<td>8, 9</td>
<td>7, 10</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>4 (4, 5)</td>
<td>4, 4</td>
<td>3, 6</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>4 (3, 5)</td>
<td>4, 4</td>
<td>2, 5</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>0 (-1, 1)</td>
<td>0, 0</td>
<td>-2, 4</td>
<td>-0.02 (-0.55, 0.001)</td>
<td>-0.53, 0.15</td>
<td>-1.50, 0.37</td>
</tr>
<tr>
<td>Mean duration (days) per Important Stopover</td>
<td>Annual</td>
<td>9 (7, 11)</td>
<td>8,10</td>
<td>6, 13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>8 (7, 10)</td>
<td>8, 9</td>
<td>5, 15</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>9 (8, 10)</td>
<td>9, 10</td>
<td>6, 13</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>-1 (-3, 1)</td>
<td>-2, 0</td>
<td>-5, 7</td>
<td>-0.06 (-0.48, 0.04)</td>
<td>-0.49, 0.15</td>
<td>-1.50, 1.02</td>
</tr>
<tr>
<td>Total Duration (days) spent at Important Stopovers</td>
<td>Annual</td>
<td>63 (58, 88)</td>
<td>60, 75</td>
<td>41, 107</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>35 (27, 46)</td>
<td>31, 43</td>
<td>23, 57</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>34 (28, 45)</td>
<td>32, 37</td>
<td>17, 42</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>1 (-16, 12)</td>
<td>-7, 4</td>
<td>-17, 21</td>
<td>-0.04 (-0.39, 0.08)</td>
<td>-0.27, 0.14</td>
<td>-1.07, 0.54</td>
</tr>
<tr>
<td>Mean distance (km) between all stopovers ≥ 1 day</td>
<td>Annual</td>
<td>682 (671,724)</td>
<td>662,740</td>
<td>634,786</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>667 (636,733)</td>
<td>624,737</td>
<td>561,867</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>724 (673,776)</td>
<td>670,776</td>
<td>571,947</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>-41 (-120, 40)</td>
<td>-172,86</td>
<td>-251,239</td>
<td>-0.06 (-0.17, 0.06)</td>
<td>-0.24, 0.12</td>
<td>-0.37, 0.32</td>
</tr>
<tr>
<td>Mean distance (km) between Important Stopovers</td>
<td>Annual</td>
<td>1,012 (950, 1,128)</td>
<td>927,1,107</td>
<td>810,1,431</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring</td>
<td>1,042 (988, 1,174)</td>
<td>956,1,146</td>
<td>871,1,521</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Fall</td>
<td>1,098 (984, 1,358)</td>
<td>855,1,484</td>
<td>669,1,772</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Spring - Fall</td>
<td>-56 (-307, 127)</td>
<td>-412,128</td>
<td>-701,680</td>
<td>-0.051 (-0.24, 0.15)</td>
<td>-0.32, 0.14</td>
<td>-0.56, 0.59</td>
</tr>
</tbody>
</table>

1IQR = inter-quartile range
2For duration, Q = log₁₀(fall duration/spring duration), but the quotient is reversed for speed (Q = log₁₀[spring speed/fall speed]) [62]. We also present values of Q for other variables in table, as calculated for duration.
3Median of annual migration values (fall + spring).
4Stationary non-breeding phase in Latin America.
5Stationary breeding phase in central or southcentral Alaska.
6Overall migratory rate, start to finish, including stopovers. This is not a measure of bird speed during active flight; see also: “Mean distance between stopovers (≥ 1 day)”
7Locations where importance score ≥ 0.2. Whenever the coarse spatial resolution of geolocator data overlapped with more than one Important Stopover simultaneously, only a single location was included in an individual’s tally. Estimate of mean distance traveled during the day when birds were actively moving.
recorded at the 13 stopovers each season, 3 were primarily used in fall, 7 in spring, and 3 during both seasons (Fig. 3, Table 3). The largest (Stopover 6 in Central America; Fig. 3) showed greatest sustained use in both migratory seasons, as indicated by relatively large importance scores (Table 3). During fall migration, Stopover 3 (Guatemala/Mexico) exhibited the highest median importance score, whereas Stopover 12 (northeastern California) had the highest in spring (Fig. 3, Table 3).

On average, 17.3% of the land area in the 13 Important Stopovers was in areas defined by the IUCN as protected (95% CI: 9.6%, 25.0%; Table 3). Greatest percent protection (49.3%) was in Important Stopover 5 (Yucatan region; Fig. 3, Table 3). The least protection (3.8%) was in Important Stopover 12 (northeastern California; Fig. 3, Table 3). Individuals made, on average, 8 of 34 stops (24%) at Important Stopovers, each lasting a median duration of 8–9 days (Table 2). Cumulatively, individuals spent a median of 63 days at Important Stopovers annually (Table 2). The 63-day duration equates to approximately 66% of a birds’ 95-day median migratory duration (Table 2).

We provide heatmaps of importance scores within each of the 3 Important Stopovers most-used during both migratory seasons, because they are large (Fig. 4). Pixels with the greatest importance scores indicate highest-intensity bird use, which can inform future field work aimed
Table 3: Summary data for 13 Important Stopovers of Olive-sided Flycatchers (Contopus cooperi) presented in Figure 3. Three sites were principally used during Fall migration, 7 in Spring, and 3 during both migratory seasons. Bold text highlights the maximum and minimum percent area currently under full protection (as defined by the IUCN [70]), as well as the greatest importance scores during fall only, spring only and during both migratory seasons.

<table>
<thead>
<tr>
<th>Important Stopover</th>
<th>Season</th>
<th>Area (km²)</th>
<th>Protected Area (km²)</th>
<th>Percent Protected</th>
<th>Importance Score²</th>
<th>Days stopped per bird¹</th>
<th>Dates used (IQR)¹</th>
<th>Median Latitude (Centroid)</th>
<th>Median Longitude (Centroid)</th>
<th>Country/Countries</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Fall</td>
<td>52,477.4</td>
<td>4,193.6</td>
<td>8.0</td>
<td>0.25 (0.24, 0.29)</td>
<td>4 (3, 4)</td>
<td>8 (7, 9)</td>
<td>22Aug (16-30Aug)</td>
<td>24.62 (19-26)</td>
<td>Mexico</td>
</tr>
<tr>
<td>2</td>
<td>Fall</td>
<td>12,855.1</td>
<td>2,151.4</td>
<td>16.7</td>
<td>0.26 (0.24, 0.30)</td>
<td>4 (3, 5)</td>
<td>9 (8, 10)</td>
<td>22Aug (16-30Aug)</td>
<td>21.89 (20-23)</td>
<td>Mexico</td>
</tr>
<tr>
<td>3</td>
<td>Both</td>
<td>143,983.0</td>
<td>15,431.3</td>
<td>10.7</td>
<td>Fall: 0.58 (0.50, 0.70)</td>
<td>Spring: 0.26 (0.24, 0.30)</td>
<td>3 (3, 4)</td>
<td>8 (8, 10)</td>
<td>25Aug (15Aug-8Sep) 21Apr (8-30Apr)</td>
<td>17.31 (15-20)</td>
</tr>
<tr>
<td>4</td>
<td>Fall</td>
<td>16,031.9</td>
<td>5,839.9</td>
<td>36.4</td>
<td>0.38 (0.34, 0.43)</td>
<td>4 (4, 4)</td>
<td>15 (13, 16)</td>
<td>6Sep (27Aug-19Sep)</td>
<td>18.75 (13-23)</td>
<td>Guatemala, Mexico</td>
</tr>
<tr>
<td>5</td>
<td>Both</td>
<td>49,173.5</td>
<td>24,257.9</td>
<td>49.3</td>
<td>Fall: 0.30 (0.34, 0.50)</td>
<td>Spring: 0.42 (0.34, 0.47)</td>
<td>3 (3, 4)</td>
<td>10 (8, 12)</td>
<td>6Sep (26Aug-19Sep) 14Apr (29Mar-25Apr)</td>
<td>17.48 (12-22)</td>
</tr>
<tr>
<td>6</td>
<td>Both</td>
<td>256,203.7</td>
<td>59,339.2</td>
<td>23.1</td>
<td>Fall: 0.42 (0.34, 0.50)</td>
<td>Spring: 0.42 (0.32, 0.54)</td>
<td>5 (3, 6)</td>
<td>10 (9, 10)</td>
<td>8Apr (26Mar-20Apr)</td>
<td>12.23 (10-14)</td>
</tr>
<tr>
<td>7</td>
<td>Spring</td>
<td>11,503.4</td>
<td>1,533.3</td>
<td>13.3</td>
<td>0.25 (0.21, 0.25)</td>
<td>2 (1, 3)</td>
<td>10 (8, 12)</td>
<td>7Apr (31Mar-12Apr)</td>
<td>-4.54 (0.5-3)</td>
<td>Ecuador, Peru</td>
</tr>
<tr>
<td>8</td>
<td>Spring</td>
<td>49,577.6</td>
<td>8,382.4</td>
<td>16.9</td>
<td>0.39 (0.32, 0.46)</td>
<td>3 (2, 4)</td>
<td>11 (8, 16)</td>
<td>24Mar (11Mar-18Apr)</td>
<td>7.45 (4-10)</td>
<td>Colombia, Panama</td>
</tr>
<tr>
<td>9</td>
<td>Spring</td>
<td>94,216.98</td>
<td>13,353.5</td>
<td>14.2</td>
<td>0.58 (0.47, 0.66)</td>
<td>7 (6, 8)</td>
<td>10 (7, 10)</td>
<td>16Apr (3-28Apr)</td>
<td>15.37 (12-18)</td>
<td>Belize, El Salvador, Guatemala, Honduras, Mexico</td>
</tr>
<tr>
<td>10</td>
<td>Spring</td>
<td>10,796.2</td>
<td>721.5</td>
<td>6.7</td>
<td>0.23 (0.22, 0.29)</td>
<td>4 (4, 5)</td>
<td>6 (5, 8)</td>
<td>25Apr (10Apr-1May)</td>
<td>20.74 (19-21)</td>
<td>Mexico</td>
</tr>
<tr>
<td>11</td>
<td>Spring</td>
<td>77,608.2</td>
<td>7,295.8</td>
<td>9.4</td>
<td>0.35 (0.25, 0.46)</td>
<td>5 (3, 6)</td>
<td>7 (5, 9)</td>
<td>24Apr (10-30Apr)</td>
<td>17.90 (15-19)</td>
<td>Mexico</td>
</tr>
<tr>
<td>12</td>
<td>Spring</td>
<td>31,903.3</td>
<td>1,209.9</td>
<td>3.8</td>
<td>0.68 (0.57, 0.86)</td>
<td>12 (10, 13)</td>
<td>7 (7, 8)</td>
<td>6May (28Apr-14May)</td>
<td>39.91 (30-40)</td>
<td>United States (California)</td>
</tr>
<tr>
<td>13</td>
<td>Spring</td>
<td>44,070.2</td>
<td>7,132.1</td>
<td>16.2</td>
<td>0.39 (0.31, 0.47)</td>
<td>8 (6, 10)</td>
<td>8 (8, 9)</td>
<td>2May (12Apr-10May)</td>
<td>44.35 (40-48)</td>
<td>United States (Oregon, Washington)</td>
</tr>
</tbody>
</table>

¹Protected: “A clearly defined geographical space, recognized, dedicated and managed, through legal or other effective means, to achieve the long-term conservation of nature with associated ecosystem services and cultural values” [70].

²A population-level metric indicating intensity of bird use, as defined in Methods. Value provided represents the median of each Important Stopover raster.

³IQR: Inter-quartile range (25-75% quantiles)

⁴Summed number of birds per pixel, defined as “Birds#,” to clarify that the true number of birds using a pixel is unknown, given associated uncertainty of geolocation (see Methods).

⁵Calculated by applying a bird’s stopover duration to its most probable stopover site, as determined from a probability surface (see Methods: 2.6: Identification of “Important Stopovers”).

⁶Median date that birds used their most probable Important Stopover. IQR for this metric provides a time span of use (25% quantile of arrivals-75% quantile of departures).
at locating flycatcher habitats and assessing threats. Similar heatmaps for the remaining Important Stopovers are provided in Fig. S5–S7, and seasonal raster data for all Important Stopovers are provided in Appendix 1 (as a geotiff file) in supplementary materials.

Finally, we report on the exploratory analysis we ran for each season to determine whether the two measures that comprise the importance score (number of birds and stopover duration) contribute independent or redundant information. During fall, we detected a weak positive relationship between the estimated number of birds that used an Important Stopover and relatively longer individual stay durations (AICc weight = 0.797), as the 95% CI of the slope marginally overlapped 0 (Table 4: Model 1). By comparison, there was no relationship in spring, for which the AICc weight was 0.52 and the 95% CI of the slope broadly
3.5 Migratory Connectivity

Olive-sided flycatchers exhibited weak migratory connectivity (MC) between the boreal breeding grounds in Alaska and their stationary, non-breeding locations in South America (MC [SE] = 0.13 [-0.07, 0.33]). Birds from the three deployment regions overlapped during the stationary non-breeding period. Anchorage birds wintered in both the northern- and southernmost core areas of Fig. 2g and Fig. S4 (2 in western Colombia/Ecuador, 1 in western Brazil/southern Peru). Fairbanks birds were fairly evenly distributed across all 3 core wintering areas (4 in western Colombia/Ecuador, 4 in central Peru [includes 2 GPS tags], 3 in western Brazil/southern Peru; Fig. 2g and Fig. S4), and two birds from Tetlin wintered in the southernmost area (western Brazil/southern Peru).

Our primary goal was to quantify the first data on the annual life-cycle movements of Olive-sided Flycatchers, by assessing places that birds use most, providing an essential step toward understanding factors that may limit populations of this steeply declining aerial insectivore and informing future efforts aimed at reducing losses. Individuals breeding in boreal Alaska exhibited a median 23,555 km annual journey in 95 days (Fig. 2a-g, Table 2). Birds followed a clockwise, looped migration pattern, characteristic of many passerines [40, 74], in which the spring route is longer and more coastal than fall (Fig. 2a-d, Table 2). Looped migration of insectivores is hypothesized to be an adaptive behavior to track arthropod emergence coincident with spring green-up [74] and

Birds tagged in Fairbanks further illustrate variation in migratory routes, in that they accounted for both the minimum and maximum migratory distances (Table 2). Furthermore, members of a single Fairbanks breeding pair wintered in the northern- and southern reaches of the wintering range, with the median location of the male 1,820 km north of the female. By contrast, the 2 other Fairbanks birds (each carrying a functional GPS tag) nested and wintered in remarkable proximity (3 km between nests in Alaska, 70 km between stationary non-breeding locations [Fig. 2g]).

4 Discussion

4.1 Migratory trajectory, stationary non-breeding locations and migratory connectivity

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is restricted to lower elevations than fall [5]. Long-distance migration imposes substantial energetic demands, often resulting in higher mortality risk to individuals en-route than during stationary breeding and non-breeding periods [e.g., 13-17]. However, deforestation and land conversions in Latin America, are also considered high-level threats to Olive-sided Flycatchers during the stationary non-breeding season [28, 75]. Conservation actions for this species are therefore more likely to be successful, when both migratory route and stationary non-breeding locations are known, in addition to the threats and limiting factors occurring within these locations that are likely to have the greatest impact on populations [3, 4, 76].

The stationary non-breeding ranges of birds from boreal Alaska (Fig. 2g, Fig. S4) overlapped with the western portion of the species’ winter range in South America (see Fig. 3 in [28]), including the Columbian Andes where the Olive-sided Flycatcher reaches its highest non-breeding abundance [28]. Tagged birds also exhibited concentrated areas of use in Colombia, Ecuador and south along the Andes (Fig. 2g, Fig. S4), where there has been a recent surge in mining concessions [77]. Co-occurrence of flycatchers with resource extraction provides an important mitigation opportunity, not only for Alaskan populations, but also for more than 10% of the Olive-sided Flycatcher’s global population and several other species of steeply declining migratory songbirds [77]. Similarly, portions of the stationary non-breeding range in northwestern Colombia and Darién Gap (spanning the Panama-Columbia border in this study; Fig. 2g) have also been noted as important wintering areas for other migratory insectivores [8]. Thus, conservation actions in flycatcher areas could potentially benefit many migratory species. It is currently unknown whether a limited degree of land use can result in a level of habitat disturbance that might benefit non-breeding individuals, which are commonly found near clearings, along forest edges [28]. Future investigations comparing abundance, feeding rates, and survival in disturbed versus undisturbed habitats are needed to understand whether human forest use creates an ecological trap in non-breeding areas, as hypothesized for breeding [e.g., 47]. Comprehensive analyses of habitat loss in breeding and non-breeding areas are also necessary to determine vulnerable periods of the life cycle, when habitat reduction is associated with decline [76].

The strength of migratory connectivity in our study was weak; birds originating from the three study regions in boreal Alaska largely overlapped across the western portion of the species’ winter range in South America (Fig. 2g, Fig. S4, [9, 10]). However, we only tracked birds breeding at the northwestern extent of a much broader breeding range [28], which currently limits our understanding. Breeding populations that we did not study likely migrate to other parts of the known winter range that Alaskan birds do not use. For example, the subspecies C. c. majorinus breeds in southern California and northern Baja California and is thought to winter in southern Mexico [28]. Weak connectivity is nonetheless common in long-distance migrant groups, including aerial insectivores, and may provide resilience against some stressors, such as climate change, if negative impacts are diffuse across the species’ range [e.g., 78, 79]. Resilience may be limited, however, if significant land conversion or habitat loss occurs over broad areas [28], and particularly if individuals throughout the range experience significant negative impacts [78].

Finally, geolocator data collected for 3 individuals over 2 consecutive years suggests that Olive-sided Flycatchers return to their stationary non-breeding locations. Species with high non-breeding site fidelity are more vulnerable to habitat loss or other stressors, which can carry-over to negatively affect future breeding [e.g., 80, 81]. Further, the fine spatial resolution of GPS data collected from 1 non-breeding bird suggested territorial behavior, which appears consistent with field observations, but unusual relative to other migrant passerines [28]. More data on non-breeding site fidelity and from GPS tags would greatly improve knowledge of non-breeding habitat associations and behavior.

4.2 Identification of Important Stopovers

The importance score we developed here objectively delineated 13 Important Stopovers of Olive-sided Flycatchers that breed in boreal Alaska (Fig. 3, Table 3). This provides a critical first step toward identifying locations that may be associated with limiting factors that contribute to the loss of this steeply declining species [e.g., 2, 3]. Unlike existing methods [3, 11], the importance score approach combines two parameters at once—numbers of birds (Birds#) and numbers of bird days (BirdDays#)—to characterize the relative intensity of bird use by season. The index, therefore, provides a population-level metric that is broadly applicable to any species with tracking data and can be used alongside methods that measure strength of migratory connectivity [64].

For Olive-sided Flycatchers, setting the importance score to a threshold to ≥ 0.2 enabled us to identify locations with above-average bird numbers and stopover durations each season (Fig. S2). More Important Stopovers near the equator and fewer at higher latitudes (Fig. 3, Table 3) suggest that birds concentrate, and importance
scores increase, where land is limited in Central America due to a geographic “funnel effect” [8]. Likewise, broader dispersal across North America may have contributed to fewer continental stopovers (e.g., in fall; Fig. 2c), suggesting it may be reasonable to reduce the importance score threshold in this region to delineate areas of less-intense use (e.g., in northern Idaho; Fig. 2a, c). However, neither continental geography or GLM evidence (of seasonal migratory dispersion) inhibited detection of two stopovers in western North America with high importance scores in spring (northeastern California and Oregon; Fig. 3, Table 3). Future research is needed to assess the reliability, ecological relevance, and application of the importance score metric, which aims to provide an objective starting point to quantify the population-level use of stopover areas during the migratory period.

In addition to the importance score, we also calculated percent protection based on IUCN data, which coarsely characterizes human land use at Important Stopovers (Table 3). This makes it possible to identify Important Stopovers with minimal protection but high intensity bird use for future investigations of immediate human threat(s), if any (e.g., due forest fragmentation, land conversion; Table 3). In combination, the two metrics provide an initial means of objectively comparing among stopover locations over a trans-hemispheric spatial extent, with the goal of identifying, prioritizing, and targeting conservation actions [4, 16, 82, 83].

### 4.3 Conservation implications for Olive-sided Flycatchers

Focused conservation, management and research efforts at Important Stopovers provide an opportunity to impact relatively high numbers of birds making prolonged stops during migration, when individual mortality can be greatest [e.g., 13-16]. For example, Important Stopovers 3, 5, and 6 comprised areas of greatest importance during both migratory seasons for birds that breed in boreal Alaska (Fig. 4, Table 3). Our data suggest, however, that only a limited amount of land area across all Important Stopovers, < 18% on average, is fully protected or managed for long-term conservation goals, as defined by IUCN (Table 3), despite birds spending over half of the annual migratory period at these locations in a small subset of stops (Table 2). We hypothesize that Olive-sided Flycatchers are engaged in multi-day refueling activities [8] or “prolonged stopovers” [84] of 8-9 days (Table 2), though further study is necessary to quantify bird behavior and habitats used. Additional tracking data are also needed from populations outside of boreal Alaska to identify stopovers of range-wide importance and gain further insight into the strength of migratory connectivity between breeding and wintering areas [10, 79, 82].

Several Important Stopovers we identified appear to overlap with areas recently described as important for other Nearctic-Neotropical migratory species [8]. During fall, many avian species pass through areas in southeastern Mexico/Yucatan, including Stopovers 3, 4, and 5 (Fig. 3), relatively quickly [e.g., 8, 85, 86]. However, the birds we studied stopped for comparatively longer periods (a median of 8-15 days; Table 3), consistent with fall behavior of Willow Flycatchers (Empidonax traillii) [87]. Important Stopover 6 is also notable for its large size and sustained, high levels of activity (Fig. 3, Table 3); it includes portions of northern Central America, where investigators have highlighted a lack of stopover data for fall migratory birds [8].

During spring, we detected two Important Stopovers in western North America (12 and 13; Fig. 3), which include montane, forested regions of northeastern California and portions of the Willamette River Valley in Oregon. Both stopovers show minimal overlap with existing “Important Bird Areas” recognized by the National Audubon Society [88], although some riparian areas can be diverse migratory corridors [5]. Our example highlights a basic lack of understanding as to whether these or other stopovers are important to large numbers of migratory landbirds. Therefore, we recommend future studies use additional metrics like those in [89] to estimate the proportion of bird populations moving through an Important Stopover. This approach can assess the conservation value of Important Stopovers for Olive-sided Flycatchers and other declining migratory landbirds.

Unexpectedly, Important Stopover 12 in northeastern California exhibited both the highest median importance score and the lowest percent protection of all stopover locations (Table 3). The area falls within national forest lands, which the global database we used excludes from its definition of a “protected area,” because management practices can include large-scale industrial timber harvest [71]. We see significant opportunities for Olive-sided Flycatcher conservation in national forests and other locations managed for natural resources, where large areas of intact habitat likely occur. However, notable data gaps exist for migratory and stationary non-breeding periods. For example, we know relatively little about habitat selection of individuals, the impacts of forest fragmentation or management practices on non-breeding populations [28], compared to breeding areas [e.g., 90]. Data taken during migration/non-breeding are needed to inform land man-
agement plans at Stopovers 12 and 13, as required under the National Forest Management Act of 1976 [e.g., 91-94], and for mitigation efforts on mining concessions in South America [77] or other types of publicly managed lands [e.g., 95]. Future fieldwork should also target areas with the highest importance scores (Fig. 4, Fig. S5-S7, Appendix 1) and assess imminent threats (e.g., of land conversion) where percent protection is low.

Finally, we were surprised that approximately half (6 of 13) of the Important Stopovers we identified overlapped with distinctive portions of the species’ stationary non-breeding and breeding ranges. For example, Stopovers 3, 5, 9, and 11 (Fig. 3) supported tagged birds migrating through southern Mexico and northern Central America, but these same areas also sustain overwintering populations, as part of an isolated segment of the species’ stationary non-breeding range outside of South America (see Fig. 2 in [28]). A similar pattern occurred at Important Stopovers 12 and 13 in spring, where birds enroute to Alaska refueled in regions well-known for abundant western breeding populations (Fig. 3, [28]). Characteristics of Olive-sided Flycatcher breeding and wintering habitat are similar (montane, forest edge [28]). Therefore, we hypothesize that habitats along migratory routes that also coincide with known breeding or wintering areas may be predictive of migratory use.

4.4 Climate change challenges: habitat and migratory timing

Long-distance migrants like Olive-sided Flycatchers are not only impacted by human land-use, but also stressors from climate change, which vary in both space (e.g., habitat alteration) and time (phenology) [e.g., 24, 27, 96]. We did not directly measure flycatcher response to climate, but recent studies in relation to our geolocator data reveal new insights. Forest loss is predicted in temperate montane areas of western North America (Important Stopovers 12, 13; Fig. 3), due to increased fire frequency, intensity, and reduced tree growth [e.g., 38, 97, 98, 99; see also 100]. Flycatcher abundance often increases after fire, but the relationship is complex [e.g., 46, 101, 102], and study is needed to quantify any positive impacts at stopovers, such as increased feeding rate or condition. Finally, the rate of climate change is relatively lower in temperate, montane forests of both hemispheres (e.g., Cascades, Andes) than in boreal biomes [96], but upslope shifts in birds and habitat are detectable at temperate elevations where flycatchers occur [e.g., 37, 103]. Broad-scale analyses of habitat change along migratory routes and in wintering areas, like those in boreal breeding locations [e.g., 90, 104] are necessary to understand climate-driven threats [105], future scenarios and refugia [104], and synergistic effects with land-use change [106].

Regarding migratory timing, looped migration synchronizes migratory movement (and breeding) of bird populations with food emergence during green-up [40, 74]. Our geolocator data indicate this pattern is adaptive at the individual level. Spring routes were longer and required more stopovers than fall, yet birds achieved a “time-minimization” strategy [e.g., 107] by maintaining similar travel speeds each season (Table 2). Flycatcher behavior differed, however, from a general avian pattern, in that tagged birds did not travel faster to breeding areas [62] via reduced spring stopover duration [108] (Table 2). Instead, a lack of rapid northward movement suggests that insect availability during green-up may limit spring travel speeds, or inclement weather may compromise success of early-arriving breeders [109, 110]. We note, however, that geolocators only represent a subset of surviving, tagged birds; many others failed, perhaps due to ill-suited migratory responses [111].

Climate change creates further timing challenges between bird arrival and spring green-up, a problem known as “phenological mismatch” [e.g., 25, 112, 113], which can impact long-distance more than short-distance migrants [e.g., 25, 26, 111-114, but see 115]. Our geolocator data revealed a capacity for migratory adjustment in flycatchers, although the extent to which phenological mismatch impacts individuals is unclear [104, 116]. We detected a spring travel pattern of “early and slow vs. late and fast,” hypothesized to reflect low vs. high quality wintering habitats, respectively [117]. Faster travel speeds enabled late-departing flycatchers to compensate (i.e., catch up) in spring without compromising breeding duration, which remained independent of other periods in the annual cycle. Spring migration was also spatially more dispersed than fall (Table 4: Model 2), suggesting that birds capitalized on scattered patches of spring resources [e.g., 118, 119], or alternatively, poor spring weather dispersed birds to suboptimal feeding sites. Weather-caused dispersion appears less likely, as birds encounter relatively stronger head winds in the Pacific Flyway during fall migration, rather than spring [120].

Even if birds can compensate temporally and spatially, rapid climate-change may still outpace the rate at which individuals can adjust. Phylogeny is predictive migratory timing [26], making it informative to consider recent patterns in spring arrival of two congeners [39]. Western Wood-Pewees (Contopus sordidulus) arrived progressively later in North America (0.34 days/year),
coincident with a western cooling trend that delayed forest green-up. Eastern Wood-Pewees (*Contopus virens*), however, arrived earlier (-0.39 days/year), coincident with Atlantic warming, but failed to keep pace with the accelerated rate of green-up (-0.94 days/year), resulting in a phenological mismatch. We therefore hypothesize that Olive-sided Flycatcher populations following a western migratory path are better aligned with climate trends and spring phenology than eastern populations. However, accelerated change at the northern extent of the breeding range [90, 96], such as boreal Alaska, will nonetheless pose phenological challenges for nesting adults, if spring timing at high latitudes advances faster than the rest of the migratory pathway [e.g., 39, 121].

5 Conclusions

Boreal breeding birds have suffered some of the greatest losses in North America [1], and yet little is known about the important non-breeding areas for most migratory species. To inform future conservation and management actions of an aerial insectivore in steep decline, we identified the migratory route and 13 Important Stopovers of Olive-sided Flycatchers that breed in boreal Alaska and overwinter in western South America, revealing details of one of the longest migrations of any Nearctic-breeding passerine. Habitat loss due to land conversion in non-breeding areas is considered a critical threat [28]. Each bird spent, on average, 34% of its migratory time at Important Stopovers annually, yet the extent of protected habitat at these sites (as defined by IUCN) ranged from 3.8%-49.3%. Collectively, our method for identifying Important Stopovers enables investigators to refine focus over vast spatial extents and to facilitate future studies aimed at characterizing key habitats, ground-truthing threats, assessing change, and prioritizing conservation actions during periods of the annual migratory cycle that will have greatest impact on declining populations. GPS technology, compared to the coarse spatial scale of geolocators in this study, stands as a promising method to reveal data on habitat selection during non-breeding, which is virtually unknown. Finally, climate change poses spatial and temporal threats to migratory birds with regard to habitat loss, compositional shifts, and changes in phenological timing. Our geolocator data suggest flycatchers have a capacity to compensate in space and time during migration, but the extent to which birds can or must adjust is unknown. Accelerated green-up and habitat change at high latitudes may be particularly challenging for populations breeding in boreal habitats.

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References


Migration and important stopovers of Olive-sided Flycatchers


Migration and important stopovers of Olive-sided Flycatchers


