Department of Defense

Legacy Resource Management Program

PROJECT 16-764

Migratory connectivity of At-Risk grassland birds

Final Report

Jason Hill and Rosalind Renfrew

Vermont Center for Ecostudies

Table of Contents

Migratory Connectivity of At-Risk Grassland Birds

Final Report

Executive Summary

Elucidating movement patterns throughout the annual cycle of migratory birds offers avenues for Department of Defense (DoD) installations charged with managing these species to share the responsibility of protecting populations. The research and conservation communities have acknowledged that effective management must extend beyond the breeding grounds of migratory birds, yet our understanding of movement patterns and space use throughout their annual cycle has been limited. To investigate the little-known migratory patterns of three At-Risk migratory grassland bird species, we used new technologies to track movements of individuals breeding on DoD installations across the U.S. throughout the year, supported by the DoD Legacy Program (Project 16-764, Agreement number HQ0034-16-2-0008).

We deployed 180 light-level geolocators on Grasshopper Sparrows (*Ammodramus savannarum*), 29 and 11 Argos-GPS tags on Eastern Meadowlarks (*Sturnella magna*) and Upland Sandpipers (*Bartramia longicauda*), respectively, and 4 Argos-satellite tags on Upland Sandpipers at a total of seven DoD installations distributed across the species' breeding ranges. We retrieved and analyzed location data from 34 light-level geolocators, 11 Argos-GPS tags from Eastern

Meadowlarks, 5 Argos-GPS tags from Upland Sandpipers, and 4 Platform Transmitting Terminals (PTTs) from Upland Sandpipers.

Grasshopper Sparrows remained on their breeding grounds at installations until Oct, and then migrated on average approximately 2500 km for about 30 days to their wintering grounds in the southern U.S. They made brief flights with many stops along their migratory routes. Grasshopper Sparrows exhibited strong migratory connectivity at a continental scale, with the North American Great Lakes region serving as a migratory divide for Midwest and East Coast breeding populations. Our data from Eastern Meadowlarks provided evidence for a diversity of stationary and short- and mid-distance migration strategies, consistent with their status as a “partial migrant”. Upland Sandpiper migration was characterized by relatively long flights over land and water, with stops lasting from a few days during spring to up to four weeks in the fall. Within South America, migration routes were elliptical and usually clockwise. Connectivity between breeding and wintering locations was weak, and some sandpipers remained in the same location throughout winter, while others made multiple movements of up to hundreds of kilometers. Some Upland Sandpipers wintered in eastern Brazil or along the Amazon River, a region not traditionally considered to be part of their wintering range.

In addition to addressing our primary objective of describing the migratory patterns for these At-Risk grassland birds, we collected grassland bird relative abundance data for each participating installation and assessed efficacy of the location technologies we used for our study; results for those objectives are provided in other Legacy products (Renfrew and Hill, 2015a - 2015f, Hill and Renfrew, 2017).

We gathered data to help installations to identify potential conservation partners for full annual cycle conservation of these At-Risk species, based on their migratory routes and wintering locations. We provide a complete list of DoD installations and U.S. non-military landholders of conserved lands along the U.S. pathways and wintering grounds for each species. For Upland Sandpiper conservation, we also determined potential international partners and provide their contact information in Mexico and in each of the South American countries where Upland Sandpipers occur during the non-breeding season.

Using this first examination of individual nonbreeding movement ecology for these three North American grassland bird species, we provide a basis for a migratory grassland bird conservation strategy that considers the full annual cycle of migratory bird species. We refine information gaps and provide a basis for expanding grassland bird conservation to include migration paths and wintering sites elucidated in our study.

Background

The quantity and quality of grassland bird habitat has declined in North America during the last half century, and concurrently, grassland bird population declines have been among the steepest of all North American landbirds. More than 70% of grassland bird species declined significantly between 1966 and 2012, while only 7% increased. Upland Sandpiper (*Bartramia longicauda*), Grasshopper Sparrow (*Ammodramus savannarum*), and Eastern Meadowlark (*Sturnella magna*) are three At-Risk migratory grassland bird species that commonly occur on military installations supporting substantial grasslands. Populations of Grasshopper Sparrow, a DoD Partners In Flight (PIF) priority bird species, have dropped by 78% in the last four decades. Many states, particularly in the Northeast, have listed Grasshopper Sparrows as Threatened or Endangered. Upland Sandpiper populations have decreased substantially in some regions, including parts of the Midwest (IL, WI, MN, and MI), and in NY and other eastern states. It is Endangered, Threatened, or of Special Concern in five of eight Midwestern states and in most eastern states. The U.S. Fish and Wildlife Service considers Upland Sandpiper to be of national conservation concern due to population declines during the last century, and the U.S. Shorebird Conservation Plan lists Upland Sandpiper as a Species of High Concern. Eastern Meadowlark populations have experienced some of the most dramatic declines of any grassland bird species. Their long-term population decline has resulted in a loss of 80% of the population since 1966, and this sharp decline has continued unabated even in recent years.

The effect of ecological factors on populations are expected to vary with the strength of migratory connectivity – the spatial-temporal coupling between different periods of an organism's annual cycle (Syroechkovski and Rogacheva, 1995; Fraser et al., 2012; Palacín et al., 2017). Breeding populations with weak migratory connectivity diffuse across the species' wintering range, effectively mixing in the winter (Fraser et al., 2012; Finch et al., 2017). As a result, the influences of localized processes on survival and condition during the wintering period are buffered across many breeding populations. In contrast, strong connectivity (Cormier et al., 2013; Hahn et al., 2013) occurs when most individuals from a breeding population overwinter in a geographic area separate from wintering areas of other breeding populations. High relative isolation during any part of the annual cycle potentially subjects a greater proportion of the species to negative population processes (McFarland et al., 2013; Cooper et al., 2017).

Monitoring changes in bird migration routes and timing, wintering areas, or migratory connectivity over time can yield important insights into the effects of habitat disturbance and climate change and inform conservation measures (Jenni and Kéry, 2003; Martin et al., 2007; Visser et al., 2009; Sheehy et al., 2010; Palacín et al., 2017). Management actions can be hindered, however, by a lack of basic data on songbird migratory routes and wintering areas (e.g., migratory routes and wintering areas; Sherry and Holmes, 1996; Faaborg et al., 2010; Hostetler et al., 2015).

An understanding of migratory patterns and wintering areas for grassland birds is needed to help address their continental population declines over the past 50 years. Despite an intensive conservation focus—largely on the breeding grounds (Askins et al., 2007) – grassland bird population declines continue, and are thought to be due to habitat loss and degradation resulting from intensification and expansion of agricultural activities on the breeding and wintering grounds (Askins et al., 2007; Hill et al., 2014; Pool et al., 2014). Basic information about migratory connectivity and key wintering areas could facilitate collaborative conservation efforts and identify factors limiting population growth throughout their annual cycle.

Until now, the understanding of migration and wintering ecology of most migratory songbirds has been extremely difficult, if not intractable, and linking breeding, migration, and wintering locations has not been possible. Radar technology is useful for tracking broad migration patterns and timing at fixed locations for birds in general (e.g., Fischer et al., 2012), but species or individuals cannot be discerned, limiting inferences. Managers have necessarily managed breeding populations with sparse, if any, knowledge of the limitations imposed on those populations during the rest of the year. Powerful tools have emerged in the last decade that allow researchers to track movements of birds throughout the year. Miniaturized light-level geolocators (hereafter geolocators) and Global Positioning System (GPS) tags provide new means of revealing migration corridors and wintering grounds for specific breeding populations (Bächler et al., 2010; DeLuca et al., 2015). For a bird as small as a Grasshopper Sparrow, geolocators are the only currently available option for obtaining year-round movements of small passerines, and provide latitude and longitude estimates for each day. Larger birds like Eastern Meadowlark can carry GPS tags that provide accurate (within 500 m) location fixes for a limited number of programmable dates each year, downloaded via satellite onto a computer. For a species as large as Upland Sandpiper, location data can now be obtained every 2 to 3 days throughout the year using solar-powered satellite technology.

The data provided by geolocation technologies can provide DoD installation managers insight into the regions used throughout the year by the birds they manage during the breeding season. Managers and other conservation practitioners operating on the breeding, migration, and wintering regions can then partner to coordinate and reinforce their collective conservation efforts to address the full range of habitat needs for migratory birds.

Military Mission Benefits

Conservation of natural resources on DoD lands fulfills the military training mission by ensuring the long-term availability of training lands in appropriate habitat conditions. In addition to serving the mission, conservation fulfills the DoD’s obligation, as required by the Migratory Bird Treaty Act, Executive Order 13186 (“Readiness Rule”), and the Sikes Act, to protect and conserve migratory birds on installations through research, habitat management, partnerships, and education. Managers can use their resources more effectively if they are equipped with an understanding of the events that affect migratory birds during their entire life cycle, rather than only during the 3-4 month-long breeding season. More specifically, they can communicate to the public an appreciation for the full life cycle of the species they are managing for, and they can partner with other entities, including other installations, that support the birds during other times of the year.

Upland Sandpiper, Grasshopper Sparrow, and Eastern Meadowlark are top DoD priority species in part because they are rare and of high responsibility for DoD, and classified as DoD Species At Risk (SAR). Their status is in part because their occurrence in open areas and on airfields make them likely to affect or to be in conflict with training and airfield activities--further underscoring the need to understand their year-round ecology. Without an understanding of the ecology of these species outside of the breeding season, the weight of responsibility falls entirely on land managers on the breeding grounds, such as DoD, for maintaining populations. Knowledge of the non-breeding ecology of these species is a starting point for spreading the weight of responsibility to partners, present and future, at migration stopover sites and wintering grounds. For example, threats to wintering Grasshopper Sparrows may differ between coastal Mexico versus inland Florida, and the partnerships required would involve different entities. The insight from geolocators provides direction for DoD partnership priorities, and indicate where additional research is needed. Most importantly, identifying and addressing threats to these species on non-breeding grounds will help the DoD maximize the benefits and efficacy of breeding season management. Finally, by working to sustain populations of SAR, DoD can help prevent species from declining to the point of being listed as Threatened or Endangered, which can interfere with mission-related activities.

Methods

Study sites

In 2015 and 2016, we conducted field work at six DoD installations: Camp Grafton, ND (47.700°N, -98.665°W), Fort Riley, KS (39.207°N, -96.824°W), Camp Ripley, MN (46.090°N, -94.358°W), Fort McCoy, WI (43.967°N, -90.660°W), Joint Base Cape Cod (JBCC), MA (41.658°N, -70.521°W), and Patuxent River Naval Air Station (NAS), MD (38.286°N, -76.408°W). We also captured Upland Sandpipers at one nature preserve (Konza Prairie, KS; 39.100°N, -96.608°W) as an alternative to Fort Riley, KS after we were unable to locate birds to capture at Fort Riley. We compare movement patterns of grassland birds between the five sites in the Midwest (KS, ND, MN, and WI) and the two sites on the East Coast (MD and MA). All necessary DoD installation, state and federal permits for wildlife research were obtained prior to field work, and our research protocols followed the Ornithological Council's Guidelines to the Use of Wild Birds in Research (Fair et al., 2010).

Geolocator and tag deployment and geolocator retrieval

Between 11 May and 18 Jun 2015, we deployed a total of 180 light-level geolocators (model Intigeo-P50B1-7-dip, Migrate Technology Ltd., Cambridge, UK, hereafter geolocators) on adult male Grasshopper Sparrows – 30 at each of six installations: Fort Riley (KS), Camp Grafton (ND), Fort McCoy (WI), Camp Ripley (MN), and JBCC (MA). We captured Grasshopper Sparrows on their territories using mist nets and audio playback. Each captured sparrow received a unique combination of leg bands: three colored plastic and one aluminum. To construct geolocator harnesses, we passed an 81-mm section of Stretch Magic jewelry cord (0.7 mm) through the geolocator tubes, and then melted the jewelry cord ends together to form a single circular loop divided by the geolocator (Figure 1a, inset). A geolocator (~ .52g) and harness together weighed ≤ 3.0% of each sparrow's body mass, and were held onto the lower back via a leg loop harness. We assessed harness fit by ensuring that approximately 2mm of vertical play occurred when we gently lifted the geolocator from a bird's back, or else we replaced the harness.

Individuals wearing geolocators must be recaptured to obtain the stored data. In 2016, we systematically searched for color-banded Grasshopper Sparrows wearing geolocators over the approximately same time period as our visits in 2015. We concentrated our searches on the territorial locations of males captured in 2015, and then expanded our search area outward as time permitted. We passively recaptured male sparrows with mist nets deployed within flight lanes, or used audio playback when passive netting was unsuccessful. We relocated 36 color-banded Grasshopper Sparrows at five of the installations and successfully recaptured all but one. Return rates varied widely (overall = 0.19, range = 0.00-0.40) across sites (see Appendix A: Table 1). At two installations (Fort Riley, KS and Fort McCoy, WI), military training exercises or unexploded ordinances prevented us from thoroughly searching our 2015 study area and likely reduced the number of recovered geolocators. We did not recover any geolocators from Camp Ripley, MN, and only one geolocator from Camp Grafton, ND. Recaptures at Eastern sites were higher, possibly a result of higher return rates due to limited available breeding habitat for this species.

In Apr 2016, we deployed 4.0-g PinPoint Argos-GPS tag (Lotek Wireless, Canada, hereafter GPS tag, Figure 1b) on 29 Eastern Meadowlarks and 11 Upland Sandpipers. Meadowlarks were captured with mist nets and audio playback. Roosting Upland Sandpipers were captured at night soon after arrival to the breeding grounds and before nesting commenced. We used spot-lights from the back of moving vehicles (trucks or gators) or (rarely) from the ground to locate the upland sandpipers, then approached them on foot and netted them with handmade long-handled dip nets. We captured 29 male Eastern Meadowlarks on their breeding territories in 2016 between 21 Apr and 11 Jun at four DoD installations (Fort Riley [n = 5], Fort McCoy [n = 10], JBCC [n = 7], and Patuxent River NAS [n = 4]) and Konza Prairie (n = 3). We captured 11 Upland Sandpipers on their breeding territories in 2016 between 24 Apr and 25 May at three DoD installations (Westover Air Reserve Base (ARB) [n = 4], JBCC [n = 1], Fort Riley [n = 2], and Konza Prairie [n = 4]). We constructed leg loop harnesses out of a continuous piece of Stretch Magic jewelry cord (1.0 mm) to affix a GPS tag with an 18-cm antenna reinforced at the base to guard against bird-inflicted damage. Harnesses were constructed on the bird and finished with a single double-overhand knot next to the GPS tag; the knot was also covered in a thin film of Loctite super glue (Henkel Corporation, Connecticut, USA). We assessed harness fit as we did for Grasshopper Sparrows. A GPS tag and harness together weighed ≤ 4.0% and ≤ 3.0% of each meadowlark's and sandpiper's body mass, respectively.

GPS tags have the memory capacity to store 30 GPS fixes (i.e., location estimates) with an accuracy of approximately 10m, and an approximate battery life of one year. We programmed these tags to attempt weekly fixes Sep-Nov and Feb-Apr and once per two weeks for the rest of the period between 15 Jul, 2016 and 15 Apr, 2017 (see Hill and Renfrew [2017] for complete list of dates). GPS fixes attempts were set for 12:00 UTC. GPS data were stored onboard the tags until a pre-programmed date (15 Apr, 2017) when all data were uploaded in mass to the Argos satellite system and transmitted to us via email. A GPS tag would not have transmitted any data, therefore, if the tag malfunctioned or became damaged prior to 15 Apr, 2017.

In Apr 2016 we deployed four 5-g solar-powered Argos PTTs (Microwave Telemetry, Inc., hereafter PTT, Figure 1c) on Upland Sandpipers at Westover ARB, MA on 5 May and at JBCC, MA on 25 May, and at the Konza Prairie Biological Station, KS on 23 Apr and 4 May. A PTT and harness together weighed ≤ 3.0% of each sandpiper's body mass. These PTTs provide location estimates that are captured and immediately transmitted every two or more days with less precision (1 SD from the mean location = <2.5 – 94 km, depending on the quality of the satellite fix) than accuracy (0.1-5.0 km; Nicholls et al., 2007).

Geolocator Light-level Data Processing

All data from geolocators were downloaded by Migrate Technology Ltd, and we discarded light-level data once the units started consistently recording maximum light values, which indicate that the battery is near the end of life (J. Fox, pers. comm.). Data from one geolocator were lost prior to data analysis. We used package BAStag (with a light threshold value of 1.0) within program R to estimate daily twilight times from geolocator light level data (Hill and Braun, 2001; Wotherspoon et al., 2016). Following Cooper et al. (2017), we edited twilight times in egregious examples, such as when BAStag estimated that a twilight event occurred during the middle of the day or night (n = 9 out of 18,952 twilight events). BAStag rarely (< 10 times) estimated two twilight events within minutes of each other; in those instances we visually selected a twilight event closest to the threshold value. Unedited geolocator data are available at Movebank (Hill and Renfrew, 2017; Wikelski and Kays, 2018).

We converted the timing of estimated twilight events into estimates of latitude and longitude using package FLightR (Rakhimberdiev and Saveliev, 2016). FLightR uses a particle filter algorithm within a Bayesian framework to combine a random walk movement model (with two states: sedentary or migrating), a hidden Markov model that probabilistically estimates unobserved animal locations, and an optional user-defined spatial probability mask based on a 50-km x 50-km grid (Rakhimberdiev et al., 2015). We ran FLightR with 1 million particles, the outlier routine turned on, and a prior of 0.05 for migration probability. We chose a migration direction prior of 180° (i.e., due south) for dates May-Dec, 2015 and 0° (i.e., due north) for dates Jan - May, 2016. We constrained the movement model to allow up to 810-km flights based on a maximum 15-hour flight between twilights at an assumed maximum flight speed of 54.0 km/hr (Pennycuick et al., 2013).

Our spatial probability mask bounded location estimates from 49.0°N south to the equator, and between –110.0°W and –60.0°W. We allowed sparrows to migrate over water and fly up to 1500 km from shore, because Grasshopper Sparrows are regular vagrants to Bermuda (Vickery, 1996). To accommodate for the coarseness of the FLightR spatial grid, we treated nearshore areas (≤ 25.0 km from the coastline) as land, and allowed Grasshopper Sparrows to remain stationary over offshore waters (> 25.0 km from the coastline) with only a 5% probability (Cooper et al., 2017). In preliminary analyses, the FLightR model results suggested that some birds moved frequently (often back-and-forth) between Caribbean Islands and Florida; similar patterns of unlikely movement behavior had been previously reported for Kirtland Warbler (*Setophaga kirtlandii*) in the Caribbean based on geolocator data (Cooper et al., 2017). To avoid similar model behavior, we treated 300 km around the Cayman Islands, Cuba and Jamaica as nearshore areas (Cooper et al., 2017). For offshore location estimates (e.g., equidistant between ≥ 2 islands), such an approach does not coerce location estimates onto land. The resulting estimates of migration routes, flight speed, and timing of migration were nearly identical to our preliminary analyses, except that winter utilization distributions were smaller in our preliminary models for birds overwintering in the Caribbean and southern Florida.

We used an in-habitat calibration period to account for the environmental conditions experienced by each sparrow (Fudickar et al., 2012; Lisovski et al., 2012). For each bird, we used a calibration period spanning from the day after it was banded through 1 Aug, 2015 (median = 57 d, 44-80 d). Geolocators attached to three sparrows remained functional until shortly after they returned to their breeding grounds in 2016, which allowed us to use a second calibration period. For these three sparrows, we reran the FLightR model with a second calibration period (medium = 6 d, range = 5-10 d) representing the time period when the birds were back on their breeding grounds in 2016 with functioning geolocators. Including a second calibration period for these three birds allowed us to account for the decreased sensitivity of the light sensor that occurs over time.

Statistical Analysis of Processed Geolocator Data

To identify stationary (≥ 2 consecutive twilights) and movement periods throughout the year for each bird we used the stationary.migration.summary function in FLightR, with a 5% minimum movement probability. Following Hahn et al. (2013) and Jacobsen et al. (2017), we combined stopover sites during migration that were < 45 km apart. We identified the onset of fall migration as the first movement of at least 45 km south of the breeding grounds. We considered arrival on the wintering grounds to have occurred when a bird stopped moving in a southerly direction consistent with fall migration (Fraser et al., 2012). We measured the correlation (rB) between breeding and wintering longitude with the BayesianFirstAid package in R. We identified the start of spring migration by identifying the movement period that carried the bird > 45 km northward from its wintering grounds, after which the bird continued to move northward.

We measured the length of migration routes by connecting consecutive median twilight location estimates between FlightR-identified stationary periods with a great-circle path between the breeding and first stationary period on the wintering grounds (fall migration) or ultimate wintering stationary period location and breeding grounds (spring migration). For each sparrow we calculated median migration speed (km-day; migration distance traveled divided by total days) and median traveling rate (km-day; migration distance traveled divided by number of days when the bird was non-stationary). For sparrows whose geolocator functioned until the onset of spring migration, we created 50% and 90% kernel utilization distributions (UD) for the complete wintering periods in FlightR and calculated their area (km2) in ArcGIS (ESRI, 2016). Our approach explicitly incorporates wintering location uncertainty in the estimation of the UD.

Grasshopper Sparrow Migration Connectivity

We used two approaches to assess the strength of migration connectivity. First, we calculated the Mantel correlation coefficient (rM) (ade4 package in R) with 10,000 random permutations (Dray et al., 2007; Ambrosini et al., 2009). The Mantel test uses a matrix populated with distances between individuals on the breeding and wintering grounds. It is often used to assess migration connectivity, but it is sensitive to the relative size of the non-breeding range, and of limited value on its own (Trierweiler et al., 2014). Therefore, we also report the distances (km) between individuals from the same population during the wintering period (Finch et al., 2017), and the Mantel correlation coefficient calculated from Midwest and East Coast populations separately. Second, we calculated migratory connectivity (MC) with the MigConnectivity package in R which uses small sample size correction and a matrix populated with distances between wintering and breeding areas (Cohen et al., 2017). We combined Florida and the Caribbean in this analysis, because location errors for most birds in this wintering region overlapped (see Results). To compare MC to the Mantel test results, we calculated an overall MC and an estimate of MC for the Midwest populations; an MC estimate for the East Coast populations was not possible because all East Coast birds overwintered within Florida or the Caribbean.

Location Accuracy and General Statistical Analysis

As a measure of location accuracy, we measured the distance between each bird's territory and the FLightR model's location estimates throughout the calibration period in 2015. FLightR location estimates of sparrows through the end of the calibration period were a median of 21.80 km (SD = 35.64 km) from the sparrows' known territory locations, suggesting high precision of locations during the breeding season. Likewise, we calculated the half-width of the 95% credible interval (CRI) for locations during Jan as a measure of wintering location precision; interval half-widths are commonly used to measure uncertainty of intervals (e.g., Phillips and Gregg, 2001). We created error polygons during fall and spring migration to visually demonstrate location uncertainty, with two steps: 1) we created twilight-specific minimum convex polygons (MCPs) using the ends points of the 95% CRIs for latitude and longitude of each twilight, and 2) then we combined all MCPs during both migratory periods. Results are presented as median (±SD, range [min-max]) unless otherwise noted.

Compiling potential partners for full life cycle conservation of At-Risk grassland birds

We used the location data to determine DoD and non-military partners with the greatest likelihood of hosting the individuals we tracked. For Upland Sandpipers and Eastern Meadowlarks, point locations were not recoded at frequent (e.g., daily) intervals, and the paths were often not the actual routes of the birds, but represent an approximation. Even when exact migration paths are known in a given year, individuals vary their routes from year to year. We therefore constructed 100-km buffers around the geodesic paths between point locations from GPS and PTT tags as approximations of where the bird may have traveled. To determine potential military partners, we overlaid the buffers with 654 U.S. military installations, including ranges and training areas (ArcGIS REST Services Directory version 10.51; thom7739@esri.com, 16 Dec 2015), and extracted all installations within the buffers. We added columns in the dataset to denote whether potential partners were associated with routes of meadowlarks, sandpipers, or both species. To determine potential non-military partners, we performed the same procedure using the U.S. Geological Survey GAP Protected Areas Database (PAD-US) conserved lands database (USGS GAP, 2016) and a combined buffer that included the meadowlark buffers, and the GPS and PTT sandpiper buffers.

To determine potential international partners for conservation of Upland Sandpipers, we compiled a list of organizations and individuals from the countries in South America and in Mexico where tracked Upland Sandpipers traveled or stopped. When possible we refined our recommendations to within-country states, departments, or regions. We chose individuals or organizations as potential partners based on: 1) existing professional connections whose programmatic work aligns with conservation of habitats that support Upland Sandpiper; 2) authors of published research on related topics such as grasslands and co-occurring species that share similar habitats; and 3) searches for conservation organizations within the countries where the sandpipers occurred.

Results

Grasshopper Sparrow Fall Migration

The 34 geolocators with data that we retrieved from recaptured Grasshopper Sparrows provided usable data for a median of 287 days (± 53.1 d, 19-338 d, n = 34). The median date of fall departure was 5 Oct, 2015 (± 9.6 d, 16 Sept - 25 Oct, 2015, n = 33) and lasted a median of 30.0 d (± 15.2, 8.5-58.5 d) (Figures 2-3). Sparrows traveled a median of 2491.73 km (± 895.80, 1147.71-6291.29 km) to their wintering grounds (Figure 3). Individuals made a median of four stopovers (± 2.02, 1.00-9.00) during fall migration, and stopover durations were a median of 3.0 d (± 4.7, 1.5-31.5 d). Median fall migration speed was 82.27 km-d (± 62.29, 32.42-314.11 km-d), and median travel rate was 153.27 km-d (± 152.14, 33.21-748.16 km-d). Fall migration routes were almost entirely over land for all but five Grasshopper Sparrows (from the MA and MD study populations) that likely wintered in the Caribbean via passage through southern Florida (see Appendix B). Sparrows from Midwest populations commenced fall migration approximately two weeks before sparrows from the East Coast (Figure 4). See Appendix A: Table 1 for individual-level data.

Grasshopper Sparrow Wintering Areas, Wintering Habitat, and Population Connectivity

Grasshopper Sparrows from Midwest populations wintered in Mexico (n = 10), Texas (n = 2), or in one case, the Florida panhandle (n = 1), whereas East Coast sparrows (n = 20) wintered in

Florida, the Greater Antilles, or possibly the Bahamas (Figures 5-7). The 95% CRI half-width of locations during Jan equated to approximately 165 km (latitude) and 50 km (longitude). Results from the Mantel and MigConnectivity tests were nearly identical. When all breeding populations were included, results from both tests suggested strong migratory connectivity at the continental scale between breeding and wintering areas (rM = 0.80, $P < 0.001$; MC = 0.81, n = 33). However, individuals from same breeding population wintered a median of 473.05 km apart (± 425.97, 39.74-1942.71 km), and Midwest birds were farther apart from each other than East Coast birds (see Appendix A: Table 2). When only sparrows from the Midwest (rM = 0.10, P = 0.245; MC = -0.02, n = 13) or East Coast (rM = -0.04, P = 0.704, n = 20) populations were considered, both tests suggested no regional population connectivity. However, breeding and wintering longitude were highly correlated (rB = 0.92, 95% CRI: 0.86-0.97).

Despite the inherent uncertainty in wintering locations derived from light-level geolocator data, the general habitats in wintering areas can be described, especially where location estimates are more precise because the bird remained in the same location for months (e.g., Figure 8), similar to what has been found in research on Grasshopper Sparrow wintering grounds elsewhere (Macías-Duarte et al., 2017). In general, Grasshopper Sparrow wintering locations suggest that they remained in open habitats in winter. The speciifc land use cannot be determined remotely, but they did not include croplands, and the landscape composition appeared to be predominantly fallow/natural grasslands and ranchlands.

Grasshopper Sparrow Spring Migration

Twelve sparrows with functioning geolocators started spring migration on a median date of 8 Mar, 2016 (± 22.16 d, 15 Jan to 30 Mar, 2016; Figure 9); three geolocators were still functioning when birds arrived at the breeding grounds on 17 Apr, 20 Apr, and 2 May, 2016, respectively. Three sparrows followed a counter-clockwise elliptical loop migration pattern: spring paths were farther east than fall migration paths (see Appendix B). Cumulative annual migration distance (fall + spring) for the three birds was a median of 5196.93 km (± 1644.88, 3325.11-6603.90 km).

Grasshopper Sparrow Annual Time Budget

Fall migration spanned 8.22% (± 4.17, 2.33-16.03%) of the total annual cycle for the 33 sparrows that completed fall migration; between 9 and 28 Oct, >75% of these sparrows were engaged in fall migration (Figure 4). Twelve sparrows carrying geolocators that functioned until the start of spring migration spent a median of 34.93% (± 6.37, 23.01-42.19%) of the annual cycle on their wintering grounds. The 50% kernel UDs for the entire wintering period covered a median of 9231.97 km2 (± 16581.10, 6106.40-57572.04 km2, n = 12), including the uncertainty of location estimates. Sparrows were largely stationary at the wintering grounds, spending a median of only 1.94% (± 6.72, 0.00-24.02%, n = 12) of twilights on the move. Of the three sparrows that completed spring migration with functioning geolocators, they spent a median of 9.59% (± 7.79, 4.93%-20.14%) and 44.11% (± 2.28, 40.55%-44.79%) of their annual cycle on spring migration and the breeding grounds, respectively (Figure 10).

Eastern Meadowlark Partial Migration, Movements, and Wintering Areas

We obtained location data from 11 of 29 GPS tags deployed on Eastern Meadowlarks (Hill and Renfrew, 2017). Five GPS tags provided location estimates of meadowlarks throughout the reporting period (Figure 11): 1) two meadowlarks from Patuxent River NAS were year-round residents of the airfield, 2) one meadowlark from JBCC migrated approximately 556 km in early

Nov and early Mar to and from MD, 3) one meadowlark from Fort Riley migrated approximately 328 km in mid-Oct and mid-Mar to and from southeast KS via a clockwise loop, and 4) one meadowlark from Fort McCoy migrated 1201 km to southeast AR in late Oct and mid-Mar via a counter-clockwise loop. As assessed via aerial photography, Eastern Meadowlarks predominantly used agricultural grasslands such as hayfields or pastures throughout their migration and wintering periods (Hill and Renfrew, 2017).

Of the remaining six tags that reported any data, one malfunctioned soon after deployment and provided no useable data. Three tags reported data from a likely stationary location (± 10 m), suggesting that they were on the ground throughout the Jul - Apr reporting period. Another tag provided only five locations, and another tag provided three location estimates followed by 21 stationary location estimates. For tags that transmitted from a stationary location, crews searched ground cover on multiple occasions for carcasses or tags at the stationary location during the summer of 2017, but were unable to locate any tags.

Upland Sandpiper Movements During Breeding Season

We obtained Upland Sandpiper location data from 5 GPS tags (Figure 12; see Appendix C for maps of each individual's movements) and 4 PTTs (Figure 13). One sandpiper captured at Fort Riley, KS in Apr was still migrating north, and GPS tranmissions in Jun and Jul showed the bird in northern SD, on its presumed breeding grounds. At the time of writing, one PTT is still transmitting data from its breeding grounds in Kansas.

Within the breeding season, Upland Sandpipers in KS moved off of the initial breeding grounds where they were captured. Data from three breeding seasons (2016, 2017, and 2018) shows the bird rotating between three sites within 50km of one another (Figure 14). We cannot know whether some of these movements occurred after failed nesting attempts, but the bird did not appear to spend enough time in any one area to indicate that it successfully reared young. Another bird was tagged at Konza Prairie, KS on 5 May and remained in that location until 12 Jun, then moved approximately 70 km to the west, where it remained until 31 Aug. Although it stayed in the second location long enough for renesting, it would have been breeding outside documented nesting dates (Houston et al., 2011). In contrast, the two sandpipers with PTT tags in MA stayed on their breeding sites, where they were captured, throughout the breeding season.

Upland Sandpiper Migration

Upland Sandpipers followed regional flyways north of South America. Individuals breeding in the eastern U.S. followed the East Coast and traveled through the Caribbean, while sandpipers from Midwest breeding grounds followed a fairly narrow route through KS, OK, and TX, and continued south through Mexico and Central America (Figures 12, 13). Within South America, migration routes were elliptical and clockwise, with southbound migration easterly and northbound migration westerly, except one Kansas bird with a counter-clockwise pattern.

Data from the four PTT tags we deployed on Upland Sandpipers allowed us to track the timing of migration events for parts or all of the year. Migration included lengthy flights between stopovers of days or weeks, with longer stops during southbound migration. The long flights enabled sandpipers to bypass major ecological barriers; for example, southbound birds from the eastern U.S. flew over the Gulf of Mexico and Caribbean Sea, and some of the Midwest birds flew over the Andes and the Pacific Ocean. Stops during southbound migration lasted up to four weeks (Table 1). Stops during the northbound migration were usually less than a few days and lasting up to 2 weeks, with the exception of a stop by the JBCC (MA) sandpiper in Venezuela 14 Mar – 9 Apr.

Migration timing varied dramatically among individuals breeding and wintering in different parts of the country or continent, with different migratory routes. A sandpiper breeding in KS left its breeding grounds between 7 and 9 Jul in one year and between 2 and 4 Jul the next year, while another left Kansas between 31 Aug and 2 Sept. A bird breeding at JBCC (MA) left breeding grounds between 21 and 23 Aug in one year and between 20 and 22 Aug the next year. A sandpiper at Westover ARB (MA) left breeding grounds between 19 and 21 Jul. All sandpipers arrived on wintering grounds in Sept and Oct. Based on two years of data, fall migration lasted more than 14 to 16 weeks for a bird that left KS breeding grounds in the first half of Jul to winter in Uruguay, versus less than 3 weeks to more than 5 weeks for a bird leaving MA breeding grounds in late Aug and flying over the Atlantic Ocean to winter in Brazil. Birds migrated north in Mar and Apr and Spring migration took 3 – 6 weeks or more. A bird from Konza Prairie (KS) left Uruguay 23 Mar and arrived on its breeding grounds 24 Apr or later (last transmission 535 km south of breeding grounds) in one year, and migrated 11 Mar - 30 Apr or later (no transmissions until 18 May) the next year. The sandpiper from JBCC (MA) began migrating from Brazil 7-9 Apr and arrived on breeding grounds 27-29 Apr.

Migration speed could be approximated during specific legs of the journey when satellite data from PTT tags were transmitted frequently. For example, part of an oceanic flight of a KS bird in its second year one bird 27 -29 Mar was estimated to be 40 mph, and before this leg it flew overland at 30 - 45mph. Multiple transmissions from a single day in 2016 and from two days in 2017 showed the JBCC (MA) sandpiper flying 29 mph southbound over the Atlantic Ocean, but speed may be underestimated. The Westover ARB bird carrying a PTT tag flew at least 28.5 mph over the ocean from the Baltimore-Washington International (MD) airport to north of Puerto Rico, and several transmissions from that location on 14 Sept likely more accurately depict flight speed, estimated at 32 mph over the course of 8 hours 40 minutes.

Upland Sandpiper Wintering Areas and Connectivity

We found weak connectivity between breeding and wintering Upland Sandpiper populations, based on winter location data from five Midwest and two East Coast birds. Of these, three sandpipers from the Midwest wintered in the Pampas of Argentina or Uruguay, and two of the Midwest birds and both of the East Coast birds wintered in Brazil (Figures 12, 13). Of the four sandpipers that wintered in Brazil, three wintered along the southeastern edge of the Amazon Basin, and one wintered along the Amazon River (for both winters the bird was tracked). The wintering locations in Brazil are north of what has been considered to be the wintering range of this species (Vickery et al., 2008). That the other three sandpipers flew to the traditional Argentina and Uruguay wintering grounds suggests that the tags did not limit migration distance for at least some individuals. Within-season movements of Upland Sandpipers to locations hundreds of kilometers apart during winter were common but not universal among the individuals we tracked (Table 1, Figure 15).

Repeatability of Upland Sandpiper Routes and Wintering Areas

Two of the PTT tags transmitted data for 1.5 - 2 years, allowing a comparison of migration patterns between years for the two individual Upland Sandpipers. Each individual followed the same general route in each year, occasionally mirroring the previous year closely. In both years, northbound and southbound, an Upland Sandpiper from Konza Prairie (KS) flew through a fairly narrow band in southern Texas, crossed the Gulf of Mexico, and crossed the Pacific Ocean. Within South America, in both years the bird first stopped within about 100 km of the same location and on the same date (9 Sept) in western Colombia after a flight over the Pacific Ocean, and from there flew an eliptical route to the wintering grounds and north in spring. Its southbound migration path crossed the Amazon from Colombia to eastern Bolivia, then continued through northeastern Argentina or Paraguay to Uruguay. In the first year it stayed in Uruguay from 7 Dec until 6 Feb and then moved up to 650 km to Buenos Aires Province, Argentina. In year two, however, it remained in Uruguay, although it moved considerably within the country. Its northbound migration route therefore started from different locations in each year, but in both years its spring migration proceeded on a similar bearing, maintaining a flight path southwest of the southbound route (Figure 13). The second Upland Sandpiper, from JBCC (MA), took the same oceanic route south to Venezuela in both years, and from there took slightly different routes to arrive at the same wintering site in both years.

Upland Sandpiper Migration and Wintering Habitat

The Upland Sandpipers we tracked avoided forested and urban areas, and were able to move great distances to reach inland, open habitats for stopovers. The Andes did not pose an ecologcial barrier for Upland Sandpiper, but valleys within the range were sometimes used after long flights. A bird from Konza stopped in a valley between the Cordillera Occidental and the Cordillera Central within the Andes in Colombia during both of the years we recorded its southbound migration. This was its first stopover after a nonstop oceanic flight of more than 2,000 km over the Pacific Ocean. Another bird from the Konza was located on 8 and 15 Sept in an agricultural valley between Medellin and Bogota.

We were able to determine finer-scale habitat use from GPS tag data, and from PTT tag data at multi-day or longer stops. Upland Sandpipers used a variety of open lands during migration and winter that included natural and agricultural habitats. Grazed and/or natural grasslands were used, but crops were used most frequently. Collaborators from Asociación Calidris in Colombia drove to the latitude/longtitude transmitted by a PTT tag for several days and did not locate the bird but verified that it was in an area of sugar cane production. Most grassland habitat on Uruguay wintering grounds consists of extensive ranchlands, while the bird that wintered along the Amazon River used open, presumably grassy islands. The JBBC (MA) sandpiper spent 6 Feb – 7 Mar in open habitats of the southeastern corner of the state of Bolívar, Venezuela, just outside the Canaima National Park. Upland Sandpiper stops in Cuba, El Salvador, Mexico, western Colombia, Bolivia, and Paraguay were in crops, identified in Google Earth. Sandpipers also used crops during the wintering period in western Bahia (Figure 15) and Mato Grosso, Brazil, and in the province of La Pampa, Argentina.

Fate of Birds, GPS and PTT Tag Performance

We learned of the fate of two birds carrying GPS tags. A lone hunter witnessed and reported a group of hunters who shot and killed a GPS-tagged meadowlark on 23 Oct 2016, at Crane Wildlife Area, adjacent to JBCC (MA). The lone hunter recovered the carcass and reported its band number, but the GPS tag was missing. An Upland Sandpiper was found dead on 17 May 2017 by Westover ARB (MA) operations staff, still with its GPS tag (#158662) attached, on a runway where it had been captured the previous year during breeding season. Its tag had reported 18 locations in South America before it returned to its breeding grounds.

Hill and Renfrew (2017) detail the methods and performance (including functioning and data quality) of geolocators, GPS tags, and PTT tags used in this study. The evaluation includes the return rates of birds, costs and benefits of each technology, and guidelines for future use of the technologies to evaluate movements of grassland birds. The study was not designed to evaluate the effects of the technology on the birds, but we detected no serious injuries nor weight loss in recaptured Grasshopper Sparrows. Opportunistic resightings of Eastern Meadowlarks and Upland Sandpipers indicated no major problems, but was limited to within two weeks of deployment; our protocol required that we move on to the next study site immediately after tags were deployed.

Since Hill and Renfrew (2017), more data from the PTT tags we deployed have been reported via satellite, and here we report the tag outcomes for all four Upland Sandpipers carrying PTT tags in the tudy. When PTT tags stop reporting data, the cause cannot be known unless the bird or tag are relocated. A PTT deployed at Westover ARB (MA) stopped reporting in the first fall in Venezuela, but we cannot know whether the bird died or the tag stopped functioning. In another case, the tag started reporting low-quality data from Texas in the fall (data quality is included in satellite feed) every few weeks, and eventually stopped altogether. That the tag kept reporting from Texas for several months indicates that the bird dropped the tag or died there, or the bird wintered there but the tag was not functioning properly. A PTT tag deployed at JBCC stopped transmitting in its second year on the wintering gounds. The fourth PTT tag continues to report satellite data at the time of writing. It is important to note that it stopped reporting for several weeks during spring migration, but began reporting regularly again after the bird had reached its Kansas breeding grounds. This indicates that there may be factors such as weather or bird posture or behavior that shields the tag from transmitting or from recharging, and if a tag stops transmitting it should continue to be monitored until breeding season is well underway.

Partnerships for Full Annual Cycle Conservation

For Upland Sandpiper and Eastern Meadowlark, 108 DoD installations were within 100 km of the movements paths and stops of the birds we tracked (Appendix D: Table 1). Some installations were within the migration path of both species, while others were potential hosts for only one of the species. Our inferences are constrained by the accuracy and precision of the location technology, and the inherent variability in the routes and stops chosen by the birds among years requires a flexible approach. Regardless, we present potential partners for each breeding population that have the greatest probability of resulting in beneficial outcomes, based on location data suggesting that they may host the same individuals. Further filtering is needed, however, to determine the installations within this list that support open habitat. Undoubtedly, some of the installations listed are small, forested, urban, and/or dominated by infrastructure that would make them inhospitable to grassland birds. Our research on international entities to collaborate with for full life cycle conservation of Upland Sandpiper resulted in 76 potential international partners; Mexico and possibly Cuba partners may also apply to Grasshopper Sparrow conservation, although research is needed to confirm and spatially refine their locations.

Most grasslands are on private lands, and ownership is not readily discerned from maps. However, we were able to identify airfields that birds with tracking tags used outside of the breeding season. Despite the location uncertainty associated with PTT tags, several transmissions in one area increases confidence in the location of the bird. An Upland Sandpiper that nested at Westover ARB (MA) flew south to the Baltimore-Washington International airport (BWI) in

MD around 21 Jul and remained there until 11 Sept, before it continued southward (Figure 16a). Another sandpiper stopped at Allen Perkinson Blackstone Army Airfield, VA 24-27 Apr during spring migration on its way to JBCC (MA) to breed (Figure 16b). This was the only stopover north of FL that we detected for this bird during spring migration, suggesting it was an important location for refueling.

Thousands of non-military holders of conserved lands in the U.S. were identified along the probable migratory routes for meadowlarks and sandpipers. We provide a database of landholdings that intersect with the migratory routes we documented for each species (Appendix E). Users may select their own search criteria among the characteristics associated with these holdings in order to identify the potential partners they are interested in working with. For example, users may choose spatial criteria (eg., state), owner type or name, type of holding (e.g., Refuge), or search for specific names of conserved areas.

Discussion

Revelations about the non-breeding movements of At-Risk migratory birds that breed on military lands enables DoD to be a leader in transforming approaches to the conservation of migratory bird species. Here, we provide the first complete migratory routes for individual Upland Sandpipers, Grasshopper Sparrows, and Eastern Meadowlarks to inform conservation of these species throughout their annual cycle.

Grasshopper Sparrows

Grasshopper Sparrows in our study exhibited strong migratory connectivity at a continental scale, which may be bolstered by an apparent migratory divide, and weak migratory connectivity within regions. Breeding and wintering longitudes were highly correlated, similar to other migrant songbird species such as American Robins (*Turdus migratorius*, Brown and Miller, 2016) and American Redstart (*Setophaga ruticilla*, Norris et al., 2006). Our data suggests that the Great Lakes region serves as a migratory divide (Salomonsen, 1955) between Midwest and East Coast populations of Grasshopper Sparrows, and routes on either side of the region generally parallel each other. The differences in the annual range of these two populations correspond approximately with the ranges of two migratory Grasshopper Sparrow subspecies *A. s. pratensis* (East Coast population) and *A. s. perpallidus* (Midwest population), although the two subspecies' breeding ranges overlap in the Midwest (Vickery, 1996).

Migratory divides are common among migrant songbird populations (Finch et al., 2017). In North America, divides separating eastern and central North American migratory populations have been documented for Ovenbird (*Seiurus aurocapilla*; Hallworth et al., 2015), American Redstart (Norris et al., 2006), and Snow Buntings (*Plectrophenax nivalis*; Macdonald et al., 2012), among others. In particular, the migratory patterns of American Robins, elucidated through band recoveries, closely resemble those of Grasshopper Sparrows in our study. American Robins west of the (approximately) Mississippi River predominantly migrated to TX, while robins (approximately) east of the Mississippi River mostly migrated to the Southeast U.S. Furthermore, robins that overwintered in FL were largely from coastal breeding populations, whereas robins breeding in Wisconsin wintered in Texas and the Southeast U.S. (Brown and Miller, 2016).

The Grasshopper Sparrows in our study utilized a strategy of delayed fall migration by remaining on or near the breeding grounds until early Oct even though fledging from nests typically occurs by early Aug (Sutter and Ritchison, 2005; Hovick et al., 2011; Hill and Diefenbach, 2013). Our findings differ from the Birds of North America account for the species, which used anecdotal reports to estimate that northern populations predominantly migrated in Aug and Sept (Figure 4 in Vickery, 1996). Bird species of open habitat (e.g., Grasshopper Sparrow, Savannah Sparrow [*Passerculus sandwichensis*], and Scissor-tailed Flycatcher [*Tyrannus forficatus*]) may delay fall migration longer (into Oct) and spend a greater proportion of the year (>40%) on the breeding grounds than bird species of other habitats (this study; Jahn et al., 2013; reviewed in McKinnon et al., 2013; Woodworth et al., 2016).

Midwest Grasshopper Sparrows commenced migration earlier compared to East Coast sparrows (Figure 4), but we do not know whether a difference in timing between the two regions occurs consistently across years. Macdonald et al. (2012) used geolocators to monitor the migration of 13 Snow Buntings from Nunavut, CA in two consecutive years. Buntings departed from the breeding grounds between 23 Sept and 6 Oct in the first year, and between 8-10 Oct in the second year. Similarly, Wood Thrush (*Hylocichla mustelina*) fall migration characteristics (e.g., departure date and duration) are highly variable from year to year (Stanley et al., 2012). Fall migration timing is likely related to favorable weather (surface air pressure and wind direction) and local declines in ecological productivity (La Sorte et al., 2015; Schmaljohann et al., 2017).

The Grasshopper Sparrows in our study wintered at a wide range of elevations and habitats from Caribbean Islands, to the Chiapas coast of Mexico, to the Southern Sierra Madre and Central Plateau of Mexico. Our 50% winter UDs of Grasshopper Sparrows were large despite the sedentary nature of this species on the wintering grounds (Grzybowski, 1983; Vickery, 1996; Gordon, 2000). We captured Grasshopper Sparrows in grasslands with few woody shrubs, but during the wintering period they also use shrubby to near-woodland habitat (Dunning and Pulliam, 1989; Hutto, 1992; Igl and Ballard, 1999). Differences in habitat use and the frequencies of some behaviors (e.g., singing from exposed perches on territories) between the breeding and wintering seasons would affect the amount of sunlight reaching the geolocator and reduce location precision during the wintering period (Lisovski et al., 2012). The UDs we calculated were large also because we properly incorporated the twilight-specific location uncertainty. Calculating UDs without error reduced the UD size by more than an order of magnitude (JMH unpub. data).

Eastern Meadowlarks

Our year-round location data from Eastern Meadowlarks depicted the partial migration behavior of the species. Some individuals were year-round residents and others short-distance migrants. Partial migration is a widespread characteristic of animal migration where populations consist of resident and migratory individuals (Lack, 1943), and has been documented in species such as Blue Tits (*Cyanistes caeruleus*), Northern Flicker (*Colaptes auratus*), and American Robins (Smith and Nilsson, 1987; Gow and Wiebe, 2014; Brown and Miller, 2016). Multiple factors (e.g., competition for resources or mates and predation risk) have been linked to partial migration, but the decision to stay or migrate is largely dependent on individual condition

(Chapman et al., 2011). Due to the poor performance of the GPS tags on meadowlarks, we obtained data from too few individuals to assess population connectivity.

Upland Sandpipers

Upland Sandpipers exhibited weak migratory connectivity between breeding and wintering populations. Migratory routes were regional-specific and followed the major migratory bird flyways, with Midwest breeding populations flying through Mexico and Central America, and East Coast breeding populations passing through the Caribbean to Venezuela. The pattern mimics the migratory divide we found for Grasshopper Sparrow that follows major migratory bird flyways. These two migratory pathways tend to place Midwest versus East Coast sandpiper breeding populations in western versus eastern parts of South America, respectively, at least during their migration within the continent, and sometimes throughout the winter.

The lengthy stops of Upland Sandpipers during their migration are typical of other shorebirds, and increasingly, geolocator studies are revealing they are common across a diversity of long-distance migratory songbird species (reviewed in Bayly et al., 2018). Upland Sandpipers overlap spatially and temporally with Buff-breasted Sandpipers, and are found in some of the same regions of Colombia (C. Ruiz, pers. comm.) and Bolivia (T. Boorsma, pers. comm.) during southbound migration, and have been observed using different habitats within less than a kilometer of each other on a regular basis (T. Boorsma, pers. comm.).

The wintering areas of Upland Sandpipers fell into one of two geographic categories: 1) east of the Amazon Basin in Brazil, and 2) Uruguay and Argentina. Upland Sandpipers wintered in eastern Brazil were far north of what was previously considered their wintering range. Some birds dropped into the first open habitat encountered beyond or within the Amazon rainforest, and then remained there for the winter. These wintering habitats included non-forested (presumably grass-dominated) islands on the Amazon River and agricultural lands just east of the forested Amazon Basin. Some of the Upland Sandpipers we tracked spent their wintering period at two or more distinct locations. Recent research using geolocation technologies suggests that movements during the winter are common across species and families of migratory birds that do not maintain winter territories (e.g., Jahn et al., 2013).

Small sample sizes and temporal irregularity of location points limited our statistical analysis on Upland Sandpiper movement data. However, Upland Sandpiper location estimates were more accurate, especially from GPS tags, and PTT tag data were more precise at stops where many data points were acquired. GPS tags yielded relatively accurate locations, but the tags we used could acquire only up to 30 location points per year due to battery limitations, resulting in very coarse temporal resolution. Methods have been developed recently that better incorporate error from satellite data like those obtained via PTT tags. Although these methods are an improvement, they yield movement maps that do not (falsely) depict exact migration paths. We are conducting analyses that model uncertainty for Upland Sandpiper data, and writing a manuscript based on this analysis for submission to a professional journal.

Management Implications and Recommendations

The migration pattern we documented for Grasshopper Sparrow, with short but frequent flights, was not surprising given their repute for short flights and their ground-foraging behavior (Vickery, 1996). Excluding stops, Grasshopper Sparrows we tracked moved as little as 33 km per day during their fall migration, and a median of only 153 km per day. They are not strong fliers and may not migrate over ecological barriers. Habitat for migrating Grasshopper Sparrows during migration may be best as corridors of closely-spaced open, grass or perhaps even shrub habitat patches within north-south corridors. Small or linear patches of grass or shrub may provide adequate habitat as long as they contain adequate food resources. The vulnerability of Grasshopper Sparrows to predators or other threats in linear versus non-linear habitats are unknown, however, and could affect survival probability. Ensuring that migration corridors are populated with patches of grassland or (less ideally perhaps) shrubland that are connected by open lands is recommended to facilitate Grasshopper Sparrow migration.

Research on winter survival in the Chihuahuan Desert in Mexico of Grasshopper Sparrows that breed in the western Great Plains is beginning to yield insights into the importance of wintering habitat. Winter survival there appears to be low, and may be limiting populations (Macías-Duarte and Panjabi, 2011, Macías-Duarte et al., 2017). The researchers propose the possibility that birds might be tracking favorable habitat conditions, and moving around from one winter to the next in order to occupy higher quality sites. The variability found in the few studies of grassland bird winter survival (e.g., Thatcher et al., 2006) suggests that survival rates from one wintering area cannot be extrapolated to other wintering populations, including those in this study. However, the results from the research in Mexico suggest that installations supporting wintering populations of Grasshopper Sparrows could play an important role in maintaining viable populations if they provide quality habitat.

Some installations provide habitat during both breeding and non-breeding periods for any or all of the three species in this study, and therefore must manage beyond the breeding season. For example, Fort Riley (KS) supports breeding populations of Upland Sandpiper, and our data showed that it also served as a spring migration stop for a sandpiper that was on its way to breeding grounds in SD. Until more is known about the fine-scale distribution of grassland birds during migration, installations with grassland habitat located along the flight paths presented here may want to assume that they provide habitat during migration.

General management recommendations for DoD installations in the U.S.:

- **Identify and prioritize installations that support migrating or wintering Grasshopper Sparrow or Eastern Meadowlark populations** based on surveys during the non-breeding season at installations within migration and wintering corridors that contain open habitats.

- **Extend the period of breeding season management for Grasshopper Sparrows** to account for their entire stay at installations. Our data show that Grasshopper Sparrows remain on breeding grounds longer than previously assumed. Nesting activities are completed by mid-Aug (Vickery, 1996), but birds do not migrate until the end of Sept. During this post-breeding period, food resources and predator avoidance are presumably their primary needs. Consideration of the species should extend until 1 Oct, and we recommend that military and management activities such as trainings, intensive grazing, or fire be avoided on at least half of the area used by Grasshopper Sparrows for breeding.

- **Manage breeding Upland Sandpipers in the Midwest at a landscape scale**. Biologically, and even for the largest grasslands at installations, Upland Sandpiper populations are defined at a broader scale than a single installation. Our data show that individuals are mixing at distances of at least 75km during the breeding season, and therefore their populations need to be managed cooperatively at this scale, rather than in isolation. Establishing partnerships with this fact in mind is discussed further below, in *Building a Network of Conservation Partners.*

- **Identify and prioritize installations and other grasslands in Upland Sandpiper staging areas** before and after their oceanic flights. Staging areas with abundant resources are critical for fat loading and recovery before and after lengthy flights in fall and spring, respectively. Partnering in these relatively discrete areas within the U.S., based on our findings, is more feasible than coordination across South American countries visited by sandpipers, and management efforts have a greater probability of positively impacting populations. Managers at installations along the sandpipers' travel corridors indicated by this study can monitor during the appropriate dates based on findings in this study within their region.

- **Actively manage at installations known to support migrating or wintering populations of grassland birds.** Management entails preventing shrub encroachment and providing adequate grass cover. Macías-Duarte et al. (2017) found Grasshopper Sparrow winter survival was lower where shrub height was higher, presumably because they provide perches for predators such as raptors and Loggerhead Shrikes (*Lanius ludovicianus*). We recommend that areas used by wintering grassland birds be kept free of shrubs, especially those greater than 50 cm, based on findings from their findings and other research (e.g., Rango et al., 2005). Habitat with greater grass height, density, volume, and cover has been associated with greater densities of Ammodramus sparrows in Chihuahuan Desert (Macıas-Duarte et al., 2009, Panjabi et al., 2010), and we encourage management on wintering grounds to promote grass cover.

- **Extend the period of management for any of the three At-Risk species beyond the breeding season at installations that may also support or are known to support non-breeding (migrant or wintering) populations.** The data we present can be used to determine the approximate dates when monitoring and management should be conducted, depending on the location of the installation.

Recommended Research

Our research more narrowly defines information gaps outside of the breeding season. The migratory connectivity of Grasshopper Sparrow populations in the Upper Midwest and beyond our study region still remain largely unknown. Grasshopper Sparrow return rates were relatively low at Upper Midwest sites in our study, resulting in a limited number of retrieved geolocators. Return rates tend to increase from the Midwest (Kaspari and O'Leary, 1988) to the East Coast (Small et al., 2009). Obtaining year-round location data via light-level geolocators for Grasshopper Sparrow populations breeding in the Upper Midwest may require more extensive search efforts to recover geolocators, or perhaps tagging sparrows on the wintering grounds (e.g., Hallworth et al., 2015) if they show greater site fidelity to wintering areas.

Grasshopper Sparrows require grasslands throughout the year, but they are more flexible in the habitats they use during migration and winter (Vickery 1996). Identifying the breadth of the habitats used by Grasshopper Sparrows during migration and winter, especially in the Caribbean, is a research priority to help determine threats and guide conservation and management actions.

Research and conservation on wintering grassland birds in Mexico have been focused on the Chihuahuan desert (e.g., Macías-Duarte et al., 2017), but the birds breeding in KS wintered further south. Given the conservation concerns that have arisen from research in the Chihuahuan Desert, research is needed to determine whether grassland birds face similar threats in other regions.

As for many small migratory songbirds, research into Grasshopper Sparrow seasonal survival during migration and winter is needed, but is logistically challenging. Technological advances may allow for tracking more individuals at finer spatial scales to determine habitat use, seasonal survival, and finer-scale interseasonal connectivity. Motus towers detect birds wearing nanotags that pass within approximately 100m, and a small array of towers erected at an installation can detect birds carrying tags that have been deployed during another part of the annual cycle.

Given the variation of individual migration strategies for Eastern Meadowlarks, future studies should explore the links between migratory strategy and other characteristics such as individual condition, social status, and reproductive performance (Chapman et al., 2011). A larger sample size is needed to determine connectivity and degree of partial migration among breeding populations of Eastern Meadowlarks, especially given the diversity of migratory strategies we documented. We recommend testing geolocator tag durability and persistence on Eastern Meadowlarks, perhaps using different units or attachment methods. In our study, two meadowlarks were observed aggressively picking at the antenna immediately following deployment, and at least three meadowlarks appeared to have removed tags. The GPS tag models we used may have also failed to function properly. Scarpignato et al. (2016) also experienced difficulties with 3.4 g PinPoint GPS tags deployed on three shorebird species; only four of 38 tags (10.5%) communicated data. GPS tag technology has since advanced, however, and can now transmit accurate location data for 100 pre-programmed dates per year. Furthermore, the data are transmitted to the user as they are collected, so the tag does not need to survive the entire year for the user to obtain any data.

More data are needed on the migratory routes of Upland Sandpipers that breed in the East. Our limited data suggest that they may fly an oceanic route in the fall and an inland route from Florida in spring. In the fall, breeding populations may differ in their coastal departure point, with inland birds first following the East Coast southward before beginning their transoceanic flight. These patterns are based on data from one individual from each of two breeding sites in MA, and cannot be assumed to represent populations.

We obtained wintering location data for only two Upland Sandpipers breeding in the eastern U.S., and both wintered just east of the Amazon Basin. More data are needed to determine whether some East Coast birds winter in Argentina or Uruguay, considered the core of the species' wintering range. Still unknown are the movement patterns of breeding populations in Alaska and the Yukon (Miller et al., 2014) that are spatially disjunct from the rest of the North American breeding populations. Research is needed to compare their movements with those found in this study in order to determine whether these disjunct breeding populations experience different threats and require different conservation tactics during the nonbreeding season.

Survival during migration and winter can be included within a modeling framework to develop a more complete picture of a species' annual cycle. Using both productivity and seasonal survival data, and understanding the connectivity between breeding, migration, and wintering populations, we can parameterize models that determine what is limiting populations and therefore where conservation efforts are most needed. Our results represent the first step in providing the spatial relationships among populations that are essential for full life cycle modeling.

Adequate data now exist for Upland Sandpiper full annual cycle modeling, and many of the pieces needed for modeling Grasshopper Sparrow populations are in place. Years of Upland Sandpiper mark-recapture data from research at Konza Prairie (KS) and within-season resight data from Uruguay wintering grounds (B Sandercock, pers. comm.) provide seasonal and annual survival estimates for these populations. Combining this survival data, existing fecundity estimates, and connectivity information from this study, a life cycle model can be developed for that population. In addition, our work complements DoD Legacy Program funded work that assessed the breeding productivity of grassland birds on two of the same military airfields (Legacy projects #10-381 and #11-408). Westover ARB (MA) and Patuxent NAS (MD) obtained productivity data for Grasshopper Sparrow, and Westover ARB also collected data on Upland Sandpipers. Models developed from these breeding season studies have helped to guide management practices, and our data is a first step in incorporating factors outside of the breeding season that contribute to population viability at the installations. Combining this information with survival estimates would enable the development of a full life cycle model. Breeding and annual survival estimates may be able to be used form studies on these species elsewhere under various assumptions, but research is needed to determine winter survival for Grasshopper Sparrows.

Building a Network of Conservation Partners

We provide a foundation for DOD, through its alliance with PIF, to forge or enhance partnerships that can maximize positive management impacts on grassland bird populations that breed on installations. Partnerships guided by these data on migration patterns are a major step towards sustaining the military training mission through a more collaborative approach to conserving migratory grassland birds throughout their annual cycle. The potential partners we compiled based on the location data from this study for three At-Risk grassland birds provide a starting point for DoD to develop a network with military and non-military stakeholders. Although coordination across states and countries must occur at the national and international levels, installation managers can coordinate with military and non-military grasslands landholders within their state and even in their region.

Our finding that all three At-Risk grassland bird species in this study exhibit region-specific characteristics in their migratory paths within the U.S. indicates that other installations hosting breeding populations within a region may make inferences from our results. For example, Hanscom AFB (MA), Fort Devens Army Base (MA), Massachusetts Military Reservation (MA), and Fort Drum (NY) may coordinate with Westover ARB (MA) and JBCC (MA) to address non-breeding conservation needs of grassland birds that migrate along the East Coast. Installations such as Fort Indiantown Gap (PA) that may host migrating individuals for brief periods and also support breeding populations should be included in partnerships in both capacities. Similarly, McConnell AFB (KS) and Fort Leavenworth (KS) could not only host migrating individuals from Fort Riley and Konza Prairie in KS, but host breeding populations that follow similar migration routes within the U.S. Inference for an installation such as Fort Campbell (KY/TN) is less clear, given it is located too close to the (not yet defined) divide between Midwest and East Coast regions.

To narrow the list of potential DoD installations partners, we recommend that the list of installations we provide be reduced to those containing grassland habitat. If a database of installations supporting grasslands exists, we recommend intersecting it with the installations in the dataset provided here. From the database we provide of potential non-military partners in the U.S., we recommend that installations determine criteria for prioritizing the types of entities they can best coordinate with to manage grassland bird populations. Once types are prioritized, there may be associated databases that provide habitat information to filter to local potential partners.

Opportunities to conserve grassland birds in the eastern U.S. are more limited yet potentially more straightforward compared to the Midwest. The fewer, more isolated grasslands in the East limit the possibilities of where grassland birds may occur. Individuals and populations are more likely to be linked between grasslands in the East, and there is a greater probability of a direct benefit from partnering with other grassland holders. In the Midwest where habitat is relatively extensive, return rates of birds is lower, and benefits to a given installation from partnering, and even benefits from managing, are likely to be difficult to measure, and dispersed among a larger network of grassland landowners in the Midwest.

Within the U.S., the migratory routes used by birds and some direct connections we found between breeding and stopover sites provide a basis for more specific partnership recommendations. Given the variable migration paths among individuals and small sample sizes, our priority recommendations are based on the strongest connections between breeding and non-breeding sites or regions based on the location data we collected. We recommend:

- **Installations supporting breeding Upland Sandpipers collaborate with military and non-military grasslands landholders in their area.** The sandpipers we tracked in KS moved up to 70 km during the breeding season, and we recommend that Midwest installations coordinate among landholders within at least this distance; our database provides landholders of up to 100 km within all locations. On the East Coast, grasslands are more isolated and Upland Sandpiper movements off of installations were limited or non-existent during the breeding season. Based on the recovery of a dead Eastern Meadowlark and resightings of Grasshopper Sparrows, at least some individuals of these species are using grasslands adjacent to installations between and/or within years, and nearby grasslands should be treated as part of the grassland complex that is managed whenever possible.

- **East Coast installations coordinate with airfields along the eastern migratory routes documented in this study.** Airfields near the coast should be prioritized for Upland Sandpiper. Grassland habitat is generally rare along the East Coast, limiting options for grassland bird stopover and wintering habitat. In a landscape dominated by forest and developed areas that includes few grasslands that are fragmented and isolated, the relatively large acreages of open lands provided by airfields may often be the best and sometimes the only option for grassland bird species such as Eastern Meadowlark and Upland Sandpiper that select large grasslands with open viewsheds. This limitation also presents an opportunity for partnering with a relatively high likelihood of benefitting eastern grassland bird populations. As with DoD airfields, FAA regulations or management protocols at civilian airfields often entail animal control intended to prevent air strikes. By coordinating with military and non-military airfields along migratory routes on the East Coast, DoD installations can enhance year-round protection of the birds they manage on the nesting grounds.

- **Coordination between upper and lower Midwest/Great Plains states.** An Upland Sandpiper that was captured at Fort Riley (KS) continued north to apparent breeding grounds in northern SD, indicating a direct north-south link between breeding and migration sites. This provides direct evidence for the logical connection between northern and central states along this flyway, and suggests that installations farther north with grassland habitat such as Grand Forks AFB (ND) and Minot AFB (ND) may also pass through KS.

- **Focus efforts on grasslands landholders along central (longitudinally) OK and central TX.** This north-south corridor serves as migratory habitat for Upland Sandpipers and Grasshopper Sparrows, and as wintering habitat for some Grasshopper Sparrows that breed in the Midwest and northern Great Plains. Eastern Meadowlarks also winter in TX (Jaster et al., 2012), and their habitat choice can be robust among various management practices (Saalfeld et al., 2016). Upland Sandpipers are in TX mostly during Aug and the first half of Apr. Coordination with TX landholders will benefit migratory and wintering populations in the region for all three At-Risk species in thus study. Furthermore, some of these regions are important for other migratory and wintering bird species, including the At-Risk Henslow's Sparrow.

Internationally, conservation of Upland Sandpipers through partnerships in the Caribbean and South America is potentially an enormous task. The lengthy, complex, and varied migration routes make it difficult for international conservation measures to realize direct, measurable benefits to a breeding population at a given installation. However, focusing efforts on a few, specific regions increase the potential efficacy of migration and wintering grounds conservation for the species. Despite apparent weak connectivity between breeding and wintering sandpiper locations, our results indicate that conservation during the non-breeding season should focus on different regions of South America for Midwest versus East Coast breeding populations.

- During migration periods, Midwest breeding populations will benefit from conservation in Mexico and Colombia, while grassland birds breeding on the East Coast are more likely to use habitats in Venezuela. In both cases, our data suggest that the window of conservation during migration should focus on Sept and the first week of Apr.

- More data are needed, however results from this study suggest that Midwest and East Coast populations will benefit most from conservation in Uruguay/Argentina and in Brazil, respectively, during the wintering period (Nov – Mar).

- Previously unknown wintering areas in Brazil warrant further investigation and should be included as potential regions for full annual cycle conservation of Upland Sandpiper.

Regional, national, and international conservation across the annual cycle of the three At-Risk grassland birds in this study must be carried out in concert with conservation of other landbird species for which DoD is responsible. Coordination across taxa is an efficient means to address conservation needs, and a practical necessity, given the limited resources and the broad geographic scales required for full annual cycle conservation. For example, Fort Polk (LA) is included in our list of potential partners for Upland Sandpiper conservation, and major migratory bird exodus events have been documented via radar at this installation (Fischer et al., 2012).

Internationally, Colombia serves as an important "bottleneck" for several species of migratory birds, and there are calls for coordination of research and conservation of the many bird species occurring in the country during migration and wintering periods (Bayly et al., 2018).

Through its Natural Resources Program, the DoD protects SAR by coordinating with other entities, implementing management guidelines, and developing partnerships for implementation. The species in this study overlap temporally and spatially with other migratory bird species, providing opportunities to identify the role of installations and the partners to prioritize to maximize the efficacy and efficiency of conservation efforts. This study is the first step in identifying potential partnerships and guidelines for conserving migratory birds that use DoD habitats during their entire annual cycle.

Acknowledgments

Funding and support was provided by the DoD Legacy Program (Project 16-764, Agreement number HQ0034-16-2-0008). Our success was made possible by the assistance of DoD and other staff: Sue Vos, Tim Wilder, Doug Westbrook, Jim Hubbard, David Beckmann, and Carol Tester (Fort McCoy); Shawn Stratton, Mike Houck, and the biology crew (Fort Riley); Steve Miller, Kent Belland, and Joel Cichos (Camp Grafton); Nancy Dietz, Tim Notch, Brian Dirks (Camp Ripley); Jake McCumber, Elizabeth Kirkpatrick, Marc Robert, Commander Hernaez, Peter Jamieson, Lt. Gary Kuehn, and Mary-Ellen Wilczynski (JBCC); DoD Airfield Manager Jack Moriarty and Joe Rogers of USDA APHIS (Westover ARB); and Kyle Rambo (NAS Patuxent River). Crew leaders Clay Graham, Dr. Dan Kim, Alison Nevins, and Dan Inserillo were instrumental to our success. Special thanks to the Fire Desks, Air Traffic Controls, and Range

Controls that kept us safe. We thank Juan Carlos Martinez for his research on international conservation partners. B. Sandercock and J. Lloyd provided valuable comments on sections of this report. Maps throughout this report were created using ArcGIS® software by Esri. ArcGIS® and ArcMap™ are the intellectual property of Esri and are used herein under license. Copyright © Esri. All rights reserved. For more information about Esri® software, please visit www.esri.com.

Appendices

Appendix A: R code used for processing light-level geolocator data for Grasshopper Sparrows.

Appendix B: Movement results for all Grasshopper Sparrows contained in ESRI shapefiles.

Appendix C: Location data from individual Upland Sandpipers wearing GPS tags.

Appendix D: Potential military partners for full annual cycle conservation of three At-Risk grassland bird species.

Appendix E: Potential non-military partners for full annual cycle conservation of three At-Risk grassland bird species.

Literature Cited

Ambrosini, R., Møller, A.P., and Saino, N. (2009) A quantitative measure of migratory connectivity. Journal of Theoretical Biology, 257, 203–211.

Askins, R.A., Chávez-Ramírez, F., Dale, B.C., Haas, C.A., Herkert, J.R., Knopf, F.L., and Vickery, P.D. (2007) Conservation of grassland birds in North America: understanding ecological processes in different regions: "Report of the AOU Committee on Conservation." Ornithological Monographs, 64, iii–Viii, 1-46.

Bächler, E., Hahn, S., Schaub, M., Arlettaz, R., Jenni, L., Fox, J.W., Afanasyev, V., and Liechti, F. (2010) Year-round tracking of small trans-Saharan migrants using light-level geolocators. PLOS ONE, 5, e9566.

Bayly, N. J., Rosenberg, K.V., Easton, W.E., Gómez, C., Carlisle, J., Ewert, D.N., Drake, A., and Goodrich, L. (2018) Major stopover regions and migratory bottlenecks for Nearctic-Neotropical landbirds within the Neotropics: a review. Bird Conservation International, 28, 1-26.

Brown, D. and Miller, G. (2016) Band recoveries reveal alternative migration strategies in American Robins. Animal Migration, 3, 35–47.

Chapman, B.B., Brönmark, C., Nilsson, J.-Å., and Hansson, L.-A. (2011) The ecology and evolution of partial migration. Oikos, 120, 1764–1775.

Cohen, E.B., Hostetler, J.A., Hallworth, M.T., Rushing, C.S., Sillett, T.S., and Marra, P.P. (2017) Quantifying the strength of migratory connectivity. Methods in Ecology and Evolution, 9, 513–524.

Cooper, N.W., Hallworth, M.T., and Marra, P.P. (2017) Light-level geolocation reveals wintering distribution, migration routes, and primary stopover locations of an endangered long-distance migratory songbird. Journal of Avian Biology, 48, 209–219.

Cormier, R.L., Humple, D.L., Gardali, T., and Seavy, N.E. (2013) Light-level geolocators reveal strong migratory connectivity and within-winter movements for a coastal California Swainson's Thrush (Catharus ustulatus) population. The Auk, 130, 283–290.

DeLuca, W.V., Woodworth, B.K., Rimmer, C.C., Marra, P.P., Taylor, P.D., McFarland, K.P., Mackenzie, S.A., and Norris, D.R. (2015) Transoceanic migration by a 12 g songbird. Biology Letters, 11, 20141045.

Dray, S., Dufour, A.B., and Chessel, D. (2007) The ade4 package-II: two-table and K-table methods. R News, 7, 47–52.

Dunning, J.B. and Pulliam, W.M. (1989) Winter habitats and behavior of Grasshopper Sparrows near Athens, Georgia. Oriole, 54, 51–53.

ESRI (2016) ArcGIS Desktop Release 10.4. Environmental Systems Research Institute, Redlands, California, USA.

Faaborg, J., Holmes, R.T., Anders, A.D., Bildstein, K.L., Dugger, K.M., Gauthreaux, S.A., Heglund, P., Hobson, K.A., Jahn, A.E., Johnson, D.H., Latta, S.C., Levey, D.J., Marra, P.P., Merkord, C.L., Nol, E., Rothstein, S.I., Sherry, T.W., Sillett, T.S., Thompson, F.R., and Warnock, N. (2010) Recent advances in understanding migration systems of New World land birds. Ecological Monographs, 80, 3–48.

Fair, J.M., Paul, E., Jones, J., Clark, A.B., Davie, C., and Kaiser, G. (2010) Guidelines to the Use of Wild Birds in Research. Third edition. Washington, D.C.: Ornithological Council.

Finch, T., Butler, S.J., Franco, A.M.A., and Cresswell, W. (2017) Low migratory connectivity is common in long-distance migrant birds. Journal of Animal Ecology, 86, 662–673.

Fischer, R. A., Guilfoyle, M. P., Valente, J., Gauthreaux Jr., S. A., Belser, C. G., Blaricom, J. W., Donald, V., Cohen, E., and Moore, F. R. (2012) The identification of military installations as important migratory bird stopover sites and the development of bird migration forecast models: a radar ornithology approach. Engineer Research and Development Center Vicksburg MS Environmental Lab, No. ERDC/EL-TR-12-22.

Fraser, K.C., Stutchbury, B.J.M., Silverio, C., Kramer, P.M., Barrow, J., Newstead, D., Mickle, N., Cousens, B.F., Lee, J.C., Morrison, D.M., Shaheen, T., Mammenga, P., Applegate, K., and Tautin, J. (2012) Continent-wide tracking to determine migratory connectivity and tropical habitat associations of a declining aerial insectivore. Proceedings of the Royal Society of London B: Biological Sciences, 1–6.

Fudickar, A.M., Wikelski, M., and Partecke, J. (2012) Tracking migratory songbirds: accuracy of light-level loggers (geolocators) in forest habitats. Methods in Ecology and Evolution, 3, 47–52.

Gordon, C.E. (2000) Movement Patterns of Wintering Grassland Sparrows in Arizona. The Auk, 117, 748–759.

Gow, E.A. and Wiebe, K.L. (2014) Males migrate farther than females in a differential migrant: an examination of the fasting endurance hypothesis. Royal Society Open Science, 1, 140346.

Grzybowski, J.A. (1983) Patterns of space use in grassland bird communities during winter. The Wilson Bulletin, 95, 591–602.

Hahn, S., Amrhein, V., Zehtindijev, P., and Liechti, F. (2013) Strong migratory connectivity and seasonally shifting isotopic niches in geographically separated populations of a long-distance migrating songbird. Oecologia, 173, 1217–1225.

Hallworth, M.T., Sillett, T.S., Van Wilgenburg, S.L., Hobson, K.A., and Marra, P.P. (2015) Migratory connectivity of a Neotropical migratory songbird revealed by archival light-level geolocators. Ecological Applications, 25, 336–347.

Hill, J.M. and Diefenbach, D.R. (2013) Experimental removal of woody vegetation does not increase nesting success or fledgling production in two grassland sparrows (Ammodramus) in Pennsylvania. The Auk, 130, 764–773.

Hill, J.M., Egan, J.F., Stauffer, G.E., and Diefenbach, D.R. (2014) Habitat availability is a more plausible explanation than insecticide acute toxicity for U.S. grassland bird species declines. PLoS ONE, 9, e98064.

Hill, J. and R. Renfrew (2017) Efficacy of location technologies used to track grassland birds. DoD Legacy Program Research Report, Project 16-764. 20 pp.

Hill, R.D. and Braun, M.J. (2001) Geolocation by Light Level. Electronic Tagging and Tracking in Marine Fisheries. Pp. 315-330 IN J.R. Sibert, J. R. and J. L. Nielsen, eds. Proceedings of the Symposium on Tagging and Tracking Marine Fish with Electronic Devices, February 7-11, 2000, East-West Center, University of Hawai'I. Springer, USA.

Hostetler, J.A., Sillett, T.S., and Marra, P.P. (2015) Full-annual-cycle population models for migratory birds. The Auk, 132, 433–449.

Houston, C. S., C. Jackson, and D. E. Bowen Jr. (2011) Upland Sandpiper (*Bartramia longicauda*), version 2.0. In The Birds of North America (A. F. Poole, Editor). Cornell Lab of Ornithology, Ithaca, NY, USA. https://doi.org/10.2173/bna.580

Hovick, T.J., Miller, J.R., Dinsmore, S.J., Engle, D.M., Debinski, D.M., and Fuhlendorf, S.D. (2011) Effects of fire and grazing on Grasshopper Sparrow nest survival. Journal of Wildlife Management, 76, 19–27.

Hutto, R.L. (1992) Habitat distributions of migratory landbird species in western Mexico. Ecology and conservation of Neotropical migratory birds. (ed. by J.M. Hagan, III and D.W. Johnson), pp. 221–239. Smithsonian Institution Press, Washington, D.C.

Igl, L.D. and Ballard, B.M. (1999) Habitat associations of migrating and overwintering grassland birds in southern Texas. The Condor, 101, 771–782.

Jacobsen, L.B., Jensen, N.O., Willemoes, M., Hansen, L., Desholm, M., Fox, A.D., Tøttrup, A.P., and Thorup, K. (2017) Annual spatiotemporal migration schedules in three larger insectivorous birds: European nightjar, Common Swift and Common Cuckoo. Animal Biotelemetry, 5, 4.

Jahn, A.E., Cueto, V.R., Fox, J.W., Husak, M.S., Kim, D.H., Landoll, D.V., Ledezma, J.P., Lepage, H.K., Levey, D.J., Murphy, M.T., and Renfrew, R.B. (2013) Migration timing and wintering areas of three species of flycatchers (Tyrannus) breeding in the Great Plains of North America. The Auk, 130, 247–257.

Jaster, L.A., Jensen, W.E., and Lanyon, W.E. (2012) Eastern Meadowlark (Sturnella magna), version 2.0. In The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America: https://doi.org/10.2173/bna.160.

Jenni, L. and Kéry, M. (2003) Timing of autumn bird migration under climate change: advances in long–distance migrants, delays in short–distance migrants. Proceedings of the Royal Society of London B: Biological Sciences, 270, 1467–1471.

Kaspari, M. and O'Leary, H. (1988) Nonparental attendants in a north-temperate migrant. The Auk, 105, 792–793.

La Sorte, F.A., Hochachka, W.M., Farnsworth, A., Sheldon, D., Fink, D., Geevarghese, J., Winner, K., Van Doren, B.M., and Kelling, S. (2015) Migration timing and its determinants for nocturnal migratory birds during autumn migration. Journal of Animal Ecology, 84, 1202–1212.

Lack, D. (1943) The problem of partial migration. British Birds, 37, 122-130 and 143-150.

Lisovski, S., Hewson, C.M., Klaassen, R.H.G., Korner-Nievergelt, F., Kristensen, M.W., and Hahn, S. (2012) Geolocation by light: accuracy and precision affected by environmental factors. Methods in Ecology and Evolution, 3, 603–612.

Macdonald, C.A., Fraser, K.C., Gilchrist, H.G., Kyser, T.K., Fox, J.W., and Love, O.P. (2012) Strong migratory connectivity in a declining Arctic passerine. Animal Migration, 1, 23–30.

Macías-Duarte, A., and Panjabi, A. O. (2013) Association of habitat characteristics with winter survival of a declining grassland bird in Chihuahuan Desert grasslands of Mexico. The Auk, 130, 141-149.

Macías-Duarte, A., Montoya, A.B., Mendez-Gonzalez, C.E., Rodriguez-Salazar, J.R., Hunt, W.G., and Krannitz, P.G. (2009) Factors influencing habitat use by migratory grassland birds in the state of Chihuahua, Mexico. The Auk, 126, 896–905.

Macías-Duarte, A., Panjabi, A. O., Strasser, E. H., Levandoski, G. J., Ruvalcaba-Ortega, I., Doherty, P. F., & Ortega-Rosas, C. I. (2017) Winter survival of North American grassland birds is driven by weather and grassland condition in the Chihuahuan Desert. Journal of Field Ornithology, 88, 374-386.

Martin, T.G., Chadès, I., Arcese, P., Marra, P.P., Possingham, H.P., and Norris, D.R. (2007) Optimal Conservation of Migratory Species. PLOS ONE, 2, e751.

McFarland, K.P., Rimmer, C.C., Goetz, J.E., Aubry, Y., Wunderle, J.M., Sutton, A., Townsend, J.M., Sosa, A.L., and Kirkconnell, A. (2013) A winter distribution model for Bicknell’s Thrush (Catharus bicknelli), a conservation tool for a threatened migratory songbird. PloS One, 8, e53986.

McKinnon, E.A., Fraser, K.C., and Stutchbury, B.J.M. (2013) New discoveries in landbird migration using geolocators, and a flight plan for the future. The Auk, 130, 211–222.

Miller, V., Nol, E., Nguyen, L. P., and Turner, D. M. (2014) Habitat selection and nest success of the Upland Sandpiper (Bartramia longicauda) in Ivvavik National Park, Yukon, Canada. The Canadian Field-Naturalist, 128, 341-349.

Nicholls, D. G., C. J. R. Robertson, and Murray, M.D. (2007). Measuring accuracy and precision for CLS: Argos satellite telemetry locations. Notornis, 54, 137-157.

Norris, D.R., Marra, P.P., Bowen, G.J., Ratcliffe, L.M., Royle, J.A., and Kyser, T.K. (2006) Migratory connectivity of a widely distributed songbird, the American Redstart (Setophaga ruticilla). Ornithological Monographs, 61, 14–28.

Palacín, C., Alonso, J.C., Martín, C.A., and Alonso, J.A. (2017) Changes in bird-migration patterns associated with human-induced mortality. Conservation Biology, 31, 106–115.

Panjabi, A., Levandoski, G., and Sparks, R. (2010) Wintering bird density and habitat use in Chihuahuan Desert grasslands. Rocky Mountain Bird Observatory, Brighton, CO.

Pennycuick, C.J., Åkesson, S., and Hedenström, A. (2013) Air speeds of migrating birds observed by ornithodolite and compared with predictions from flight theory. Journal of The Royal Society Interface, 10, 20130419.

Phillips, D.L. and Gregg, J.W. (2001) Uncertainty in source partitioning using stable isotopes. Oecologia, 127, 171–179.

Pool, D.B., Panjabi, A.O., Macías-Duarte, A., and Solhjem, D.M. (2014) Rapid expansion of croplands in Chihuahua, Mexico threatens declining North American grassland bird species. Biological Conservation, 170, 274–281.

R Core Team (2017) R: A Language and Environment for Statistical Computing. Version 3.4.2. R Foundation for Statistical Computing, Vienna, Austria.

Rakhimberdiev, E. and Saveliev, A. (2016) FLightR: SSM for solar geolocation. R package version 0.4.6, http://github.com/eldarrak/FLightR.

Rakhimberdiev, E., Winkler, D.W., Bridge, E., Seavy, N.E., Sheldon, D., Piersma, T., and Saveliev, A. (2015) A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. Movement Ecology, 3, 25.

Rango, A., Huenneke, L., Buonopane, M., Herrick, J.E., and Havstad, K.M. (2005) Using historic data to assess effectiveness of shrub removal in southern New Mexico. Journal of Arid Environments, 62, 75–91.

Renfrew, R. and Hill, J. (2015a) Migratory connectivity of At-Risk grassland birds: Camp Grafton 2015. Research Report to DoD Legacy Program. 34 pp.

Renfrew, R. and Hill, J. (2015b) Migratory connectivity of At-Risk grassland birds: Camp Ripley 2015 Research Report to DoD Legacy Program. 26 pp.

Renfrew, R. and Hill, J. (2015c) Migratory connectivity of At-Risk grassland birds: Fort McCoy 2015 Research Report to DoD Legacy Program. 26 pp.

Renfrew, R. and Hill, J. (2015d) Migratory connectivity of At-Risk grassland birds: Fort Riley 2015 Research Report to DoD Legacy Program. 29 pp.

Renfrew, R. and Hill, J. (2015e) Migratory connectivity of At-Risk grassland birds: JBCC 2015 Research Report to DoD Legacy Program. 29 pp.

Renfrew, R. and Hill, J. (2015f) Migratory connectivity of At-Risk grassland birds: Naval Air Station Patuxent River 2015 Research Report. 22 pp.

Saalfeld, D.T., Saalfeld, S.T., Conway, W.C. and Hartke, K.M. (2016) Wintering grassland bird responses to vegetation structure, exotic invasive plant composition, and disturbance regime in coastal prairies of Texas. The Wilson Journal of Ornithology, 128, 290-305.

Salomonsen, F. (1955) The evolutionary significance of bird migration. Danish Biologiske Meddelelser, 22, 62.

Scarpignato, A.L., Harrison, A.-L., Newstead, D., Niles, L.J., Porter, R.R., van den Tillaart, M., and Marra, P.P. (2016) Field-testing a new miniaturized GPS-Argos satellite transmitter (3.5 g) on migratory shorebirds. Wader Study, 123, 1–8.

Schmaljohann, H., Lisovski, S., and Bairlein, F. (2017) Flexible reaction norms to environmental variables along the migration route and the significance of stopover duration for total speed of migration in a songbird migrant. Frontiers in Zoology, 14, 17.

Sheehy, J., Taylor, C.M., McCann, K.S., and Norris, D.R. (2010) Optimal conservation planning for migratory animals: integrating demographic information across seasons. Conservation Letters, 3, 192–202.

Sherry, T.W. and Holmes, R.T. (1996) Winter habitat quality, population limitation, and conservation of Neotropical-Nearctic migrant birds. Ecology, 77, 36–48.

Small, D.M., Parks, J., Gruber, J.G., and Gill, D.E. (2009) Grasshopper Sparrow (Ammodramus savannarum) longevity record. North American Bird Bander, 33, 186–187.

Smith, H.G. and Nilsson, J.-Å. (1987) Intraspecific variation in migratory pattern of a partial migrant, the Blue Tit (Parus caeruleus): An evaluation of different hypotheses. The Auk, 104, 109–115.

Stanley, C.Q., MacPherson, M., Fraser, K.C., McKinnon, E.A., and Stutchbury, B.J.M. (2012) Repeat tracking of individual songbirds reveals consistent migration timing but flexibility in route. PLOS ONE, 7, e40688.

Sutter, B. and Ritchison, G. (2005) Effects of grazing on vegetation structure, prey availability, and reproductive success of Grasshopper Sparrows. Journal of Field Ornithology, 76, 345–351.

Syroechkovski, E.E. and Rogacheva, H.V. (1995) Bird conservation in Siberia: a summary. Ibis, 137, S191–S194.

Thatcher, B. S., Krementz, D.G. and Woodrey, M.S. (2006) Henslow's Sparrow wintersurvival estimates and response to prescribed burning. Journal of Wildlife Management, 70, 198–206.

Trierweiler, C., Klaassen, R.H.G., Drent, R.H., Exo, K.-M., Komdeur, J., Bairlein, F., and Koks, B.J. (2014) Migratory connectivity and population-specific migration routes in a long-distance migratory bird. Proceedings of the Royal Society of London B: Biological Sciences, 281, 20132897.

U.S. Geological Survey (USGS), Gap Analysis Program (GAP). (2016) Protected Areas Database of the United States (PAD-US), version 1.4 Combined Feature Class.

Vickery, P.D. (1996) Grasshopper Sparrow (Ammodramus savannarum), version 2.0. In The Birds of North America (P. G. Rodewald, Ed.). Ithaca: Cornell Lab of Ornithology; Retrieved from the Birds of North America. https://doi.org/10.2173/bna.239.

Vickery, P.D., Blanco, D.E., and López-Lanús, B. (2008) Conservation plan for the Upland Sandpiper (*Bartramia longicauda*). Version 1.0. Manomet Center for Conservation Sciences, Manomet, Massachusetts.

Visser, M.E., Perdeck, A.C., Van Balen, J.H., and Both, C. (2009) Climate change leads to decreasing bird migration distances. Global Change Biology, 15, 1859–1865.

Wikelski, M. and Kays, R. (2018) Movebank: archive, analysis and sharing of animal movement data. Hosted by the Max Planck Institute for Ornithology. www.movebank.org.

Woodworth, B.K., Newman, A.E.M., Turbek, S.P., Dossman, B.C., Hobson, K.A., Wassenaar, L.I., Mitchell, G.W., Wheelwright, N.T., and Norris, D.R. (2016) Differential migration and the link between winter latitude, timing of migration, and breeding in a songbird. Oecologia, 181, 413–422.

Wotherspoon, S.J., Sumner, M.D., and Lisovski, S. (2016) BAStag. Basic data processing for light based geolocation archival tags. Version 0.1.3.

Tables and Figures

Table 1. Dates and locations of major fall stops and wintering areas of Upland Sandpipers wearing GPS and PTT tags in 2015-16 (Year 1 for birds with two years of data) and 2016-17 (Year 2 for birds with 2 years of data).

Tag Type and ID	No. GPS locations	Breeding Location	Fall stop > 3 wks	Min. fall stop dates	Wintering location	Winter 1 lat/long	Winter 1 Min. Dates	Winter 2 lat/long	Winter 2 Min. Dates	Distance Winter 1 & 2
GPS 146682	25	Fort Riley KS	OK, USA 34.376605° -98.990017°	1 Aug - 1 Sept	State of Bahia, Brazil	-12.378207° -46.233076°	15 Oct - 22 Jan	-12.480934° - 45.366653°	1 Feb - 1 Apr	100
GPS 146690	24	Fort Riley KS	None	N/A	San Jose, southern Uruguay	-34.151302° -56.920083°	22 Oct - 15 Dec	-37.165860° - 58.765241°	1 Jan - 23 Mar	375
GPS 146702	27	Konza Prairie KS	None	N/A	Mato Grasso, Brazil	-13.118149° -57.799849°	15 Oct - 15 Dec	-13.277657° - 52.789929°	1 Jan - 15 Mar	540
GPS 158662	18	Westover	No Data	N/A	Mato Grasso, Brazil	-11.688142° -55.532871°	15 Oct - 1 Dec	a	15 Dec - 15 Mar	
GPS 146694c	30	Konza, KS	Beni, Bolivia -13.479127° -65.673898°	1 - 22 Sept	Mato Grasso do Sul, Pantanal, Brazil	-23.012585° -55.573222°	15 Oct - 15 Nov	b		
PTT	N/A	Konza KS Year 1			Uruguay	Many locations	18 Oct - 15 Mar			
PTT	N/A	Konza KS Year 2			Uruguay	Many locations	23 Oct - 15 Mar			
PTT	N/A	JBCC MA Year 1			Pará, Brazil	-2.171° -55.564°	28 Sept - 2 Feb	4.758° -61.311°	10 Feb - 8 Mar	488
PTT	N/A	JBCC MA Year 2			Pará, Brazil	-2.179° -55.386°	16 Sept - 28 Jan [d]			

[a] Moved up to 400 km every 2-3 weeks in central and western Mato Grasso, Brazil

[b] Moved up to 260 km every 2-4 weeks in Cordoba and La Pampa, Argentina

[c] Traveled 4800 km between 23 Mar and 1 Apr. Last transmissions (1, 8, 15 Apr) in El Salvador, within 0.1 km.

[d] Transmissions stopped 28 Jan

Figure 1. Grassland bird species wearing tracking units used in this study prior to release: a) a Grasshopper Sparrow (geolocator; communication wires for turning on the unit via a laptop software connection were trimmed prior to deployment (inset; photo by Alex Lehner and Inez Hein); b) Eastern Meadowlark (GPS tag); and c) Upland Sandpiper (PTT).

a) b) c)

Figure 2. Median latitude (dark line) and interquartile range (shaded area) from the onset of fall migration onwards for all Grasshopper Sparrows that were initially fitted with a geolocator in Massachusetts (*n* =10, panel A), Maryland (*n* = 10, panel B), Kansas (*n* = 8, panel C), and Wisconsin (*n* = 4) and North Dakota (*n* = 1, panel D), 2015-2016. Sample sizes refer to maximum sample size for that population, as sample size changed on a daily basis.

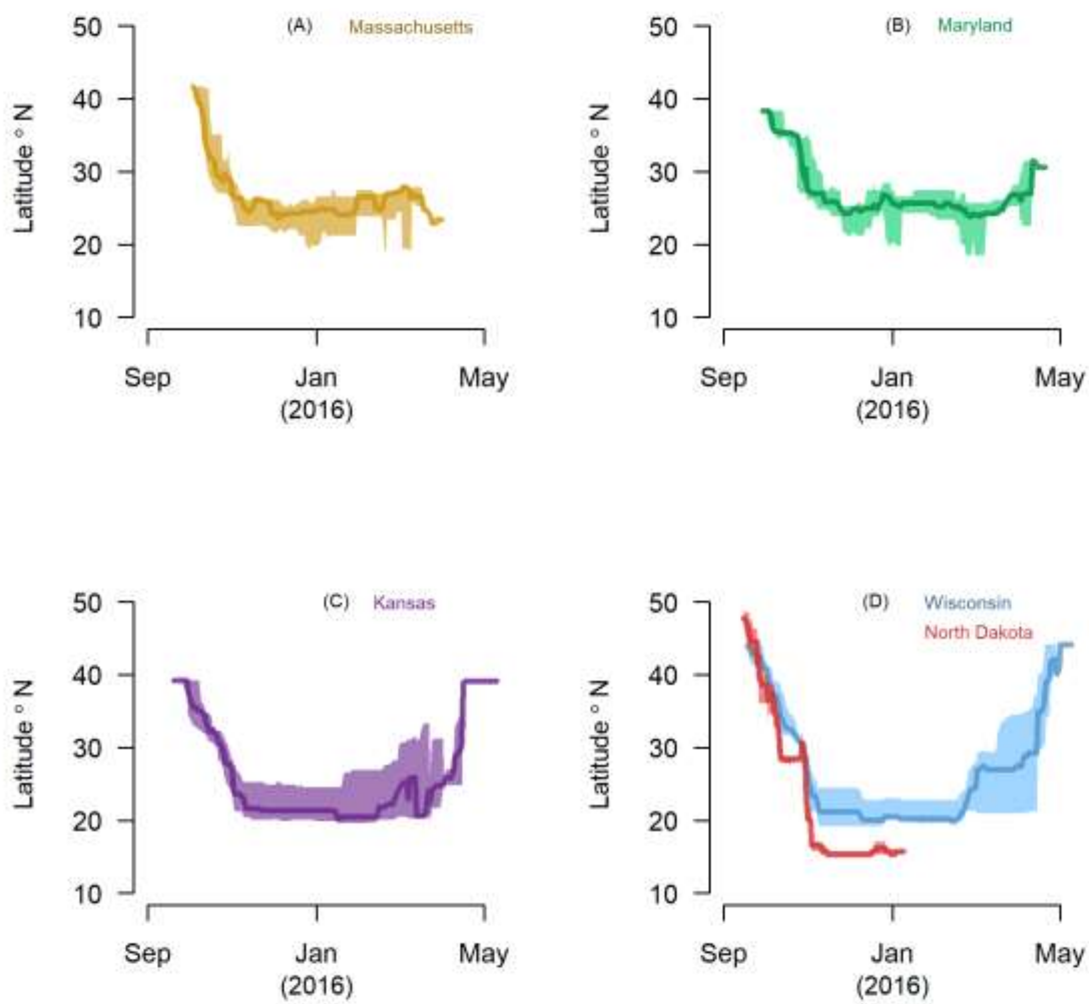

Figure 3. Median (dark line) and interquartile range (shaded area) of cumulative distance travelled (km) during fall migration for Grasshopper Sparrows with geolocators in Massachusetts (*n* = 10, panel A), Maryland (*n* = 10, panel B), Kansas (*n* = 8, panel C), and Wisconsin (*n* =4) and North Dakota (*n* = 1, panel D), 2015-2016. Sample sizes refer to maximum sample size for that population, as sample size changed on a daily basis.

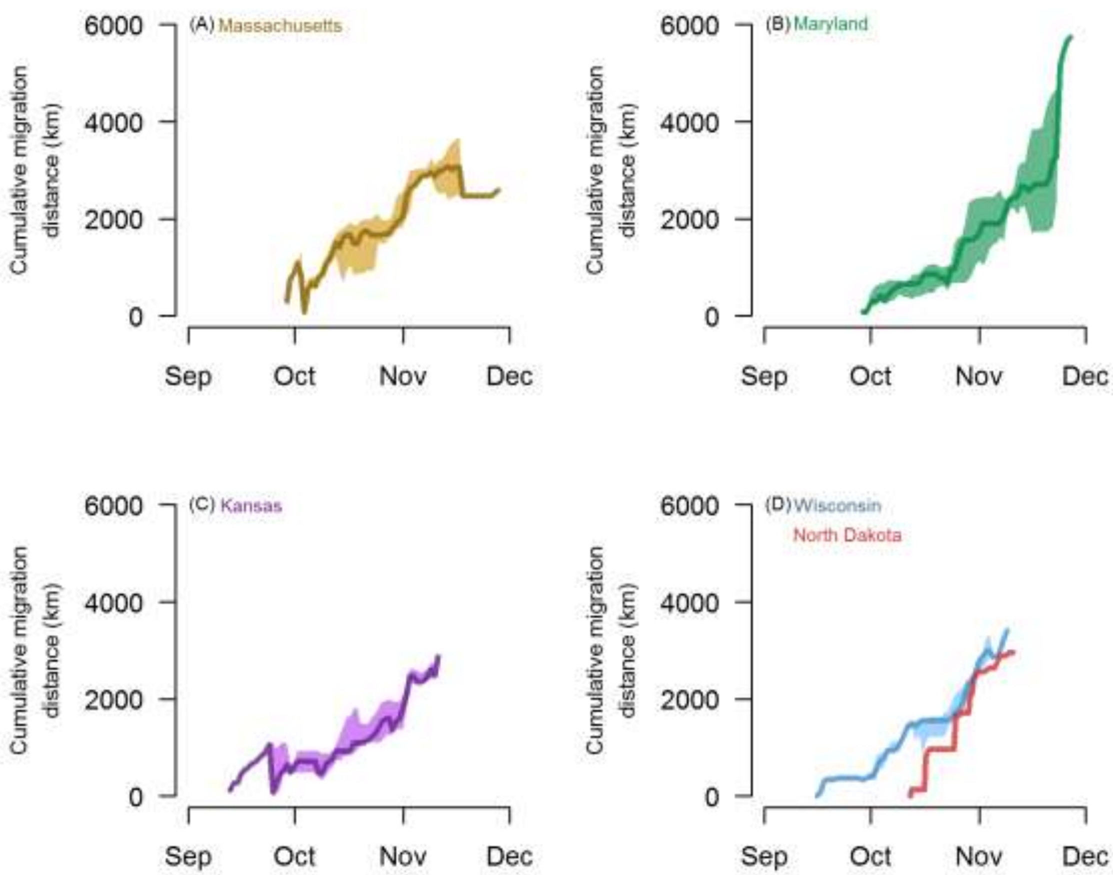

Figure 4. Cumulative proportion of Grasshopper Sparrows that had started fall migration (migration onset) and reached the wintering grounds (migration cessation), by date and breeding population: Midwest (brown: Kansas, North Dakota, and Wisconsin, *n* = 13 sparrows) and East Coast (blue: Maryland and Massachusetts, *n* = 20 sparrows).

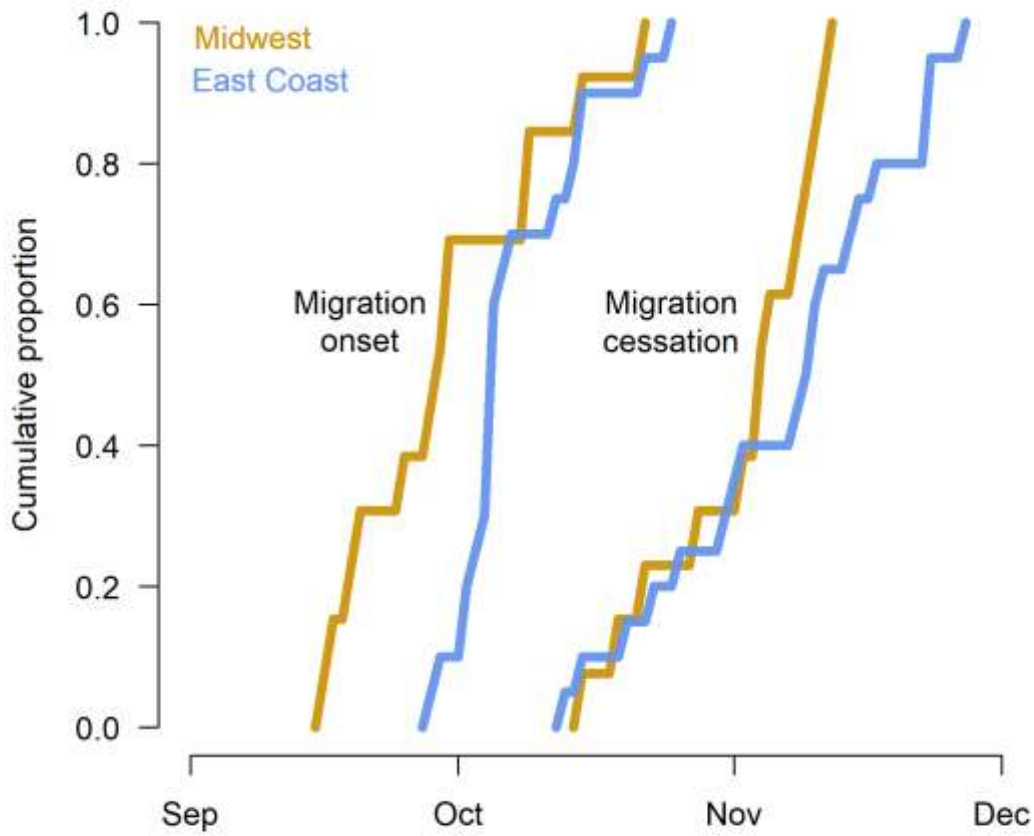

Figure 5. Breeding locations (triangles) and wintering 50% kernel UDs (which resemble a series of ovals) for Grasshopper Sparrows (uniquely identified with a four-digit alphanumeric code) fitted with geolocators in Kansas (purple, *n* = 6), Maryland (green, *n* = 3), and Wisconsin (blue, *n* = 3). Latitudinal errors were typically greater than longitudinal errors (See Appendix B). Birds with geolocators that ceased functioning prior to spring migration (e.g., all birds from North Dakota and Massachusetts, black triangles) are not shown. No geolocators were recovered from the Minnesota breeding population (black triangle). See Appendix B for UDs for all birds.

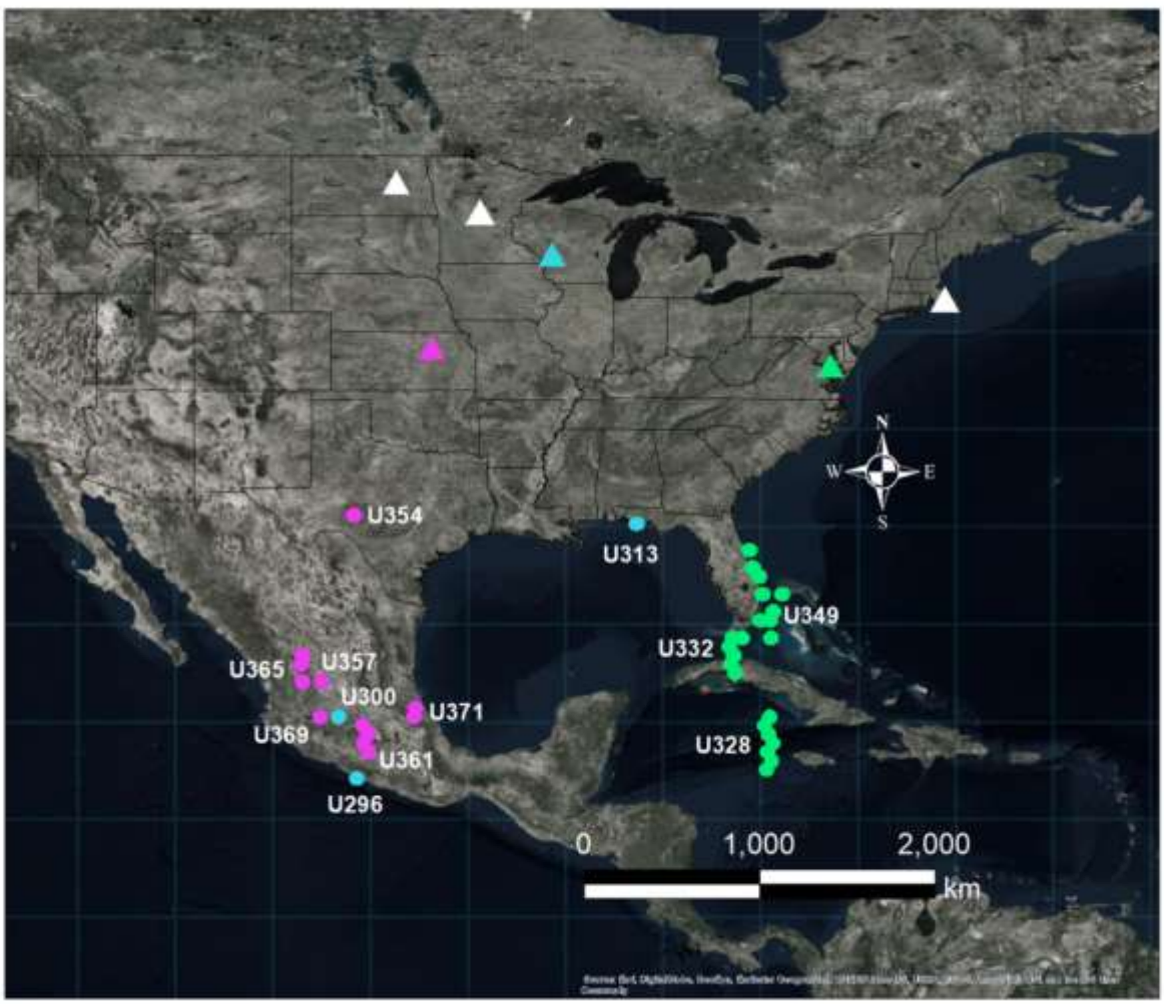

Figure 6. Probable fall migration routes for Grasshopper Sparrows from breeding populations in Kansas (purple, *n* = 8) and Maryland (green, *n* = 10) [left panel] and North Dakota (red, *n* = 1), Wisconsin (blue, *n* = 4), and Massachusetts (orange, *n* = 10) [right panel]. Routes were created by connecting consecutive twilight location estimates with orthodromic lines. See Appendix B for utilization distributions and uncertainty estimates for all birds.

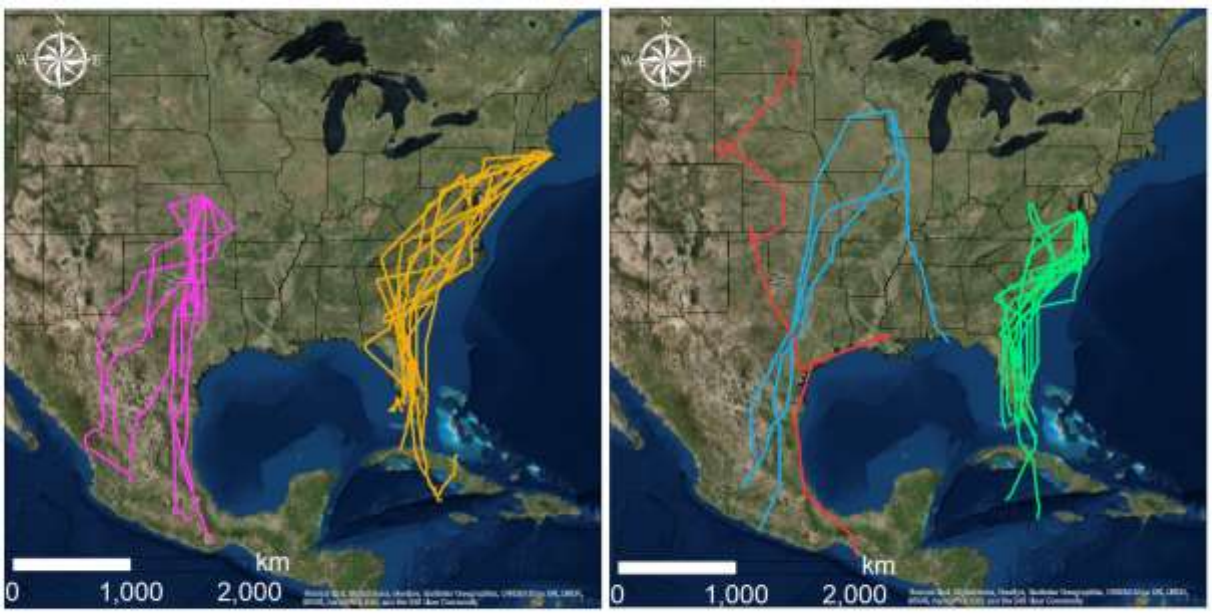

Figure 7. Examples of probable fall migration routes (dark lines) and the uncertainty of location estimates (shaded regions) for three Grasshopper Sparrows fitted with geolocators in North Dakota (red), Wisconsin (blue), and Maryland (orange), respectively. Routes were created by connecting consecutive twilight median location estimates with orthodromic lines. Error polygons (shaded regions) were created by overlaying twilight-specific 95% CRIs during fall migration (see methods). See Appendix B for utilization distributions and uncertainty estimates for all birds.

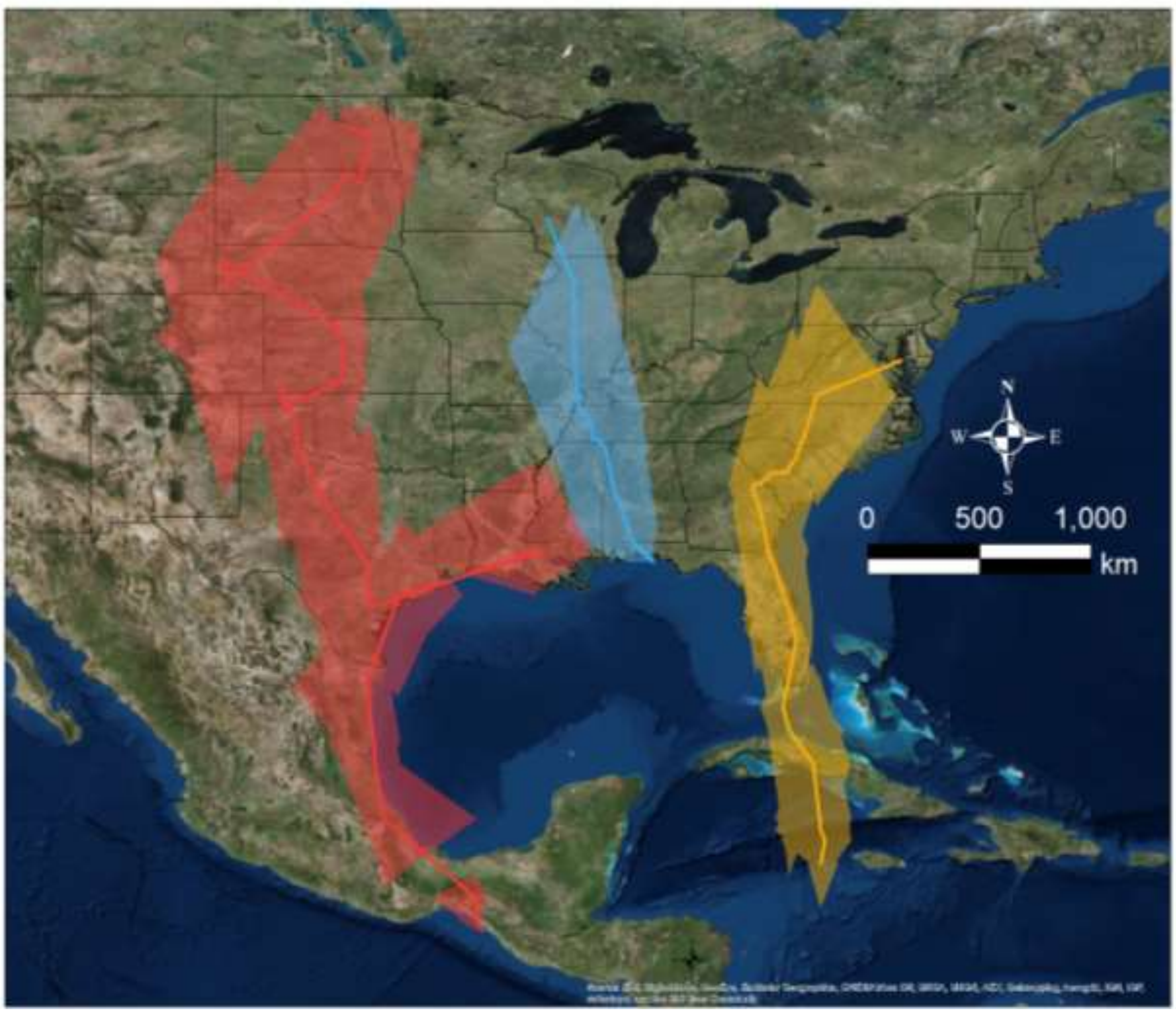

Figure 8. Examples of wintering habitat for Grasshopper Sparrows a) breeding in North Dakota and overwintering in coastal agricultural areas in southern Mexico, and b) breeding in Kansas and overwintering in the Sierra Madre foothills. Photos shared under Creative Commons license via Google Earth Pro (2017).

a)

b)

Figure 9. Estimated cumulative distance traveled (km) during spring migration for 12 Grasshopper Sparrows that started spring migration with functioning geolocators and who were initially fitted with a geolocator in Maryland (panel A), Wisconsin (panel B), or Kansas (panel C). Each line represents one sparrow's cumulative travel distance (km). Most of these geolocators (9) ceased recording useable data during spring migration, but three birds completed their spring migration (indicated by a colored-dot at the line terminus) with functioning geolocators.

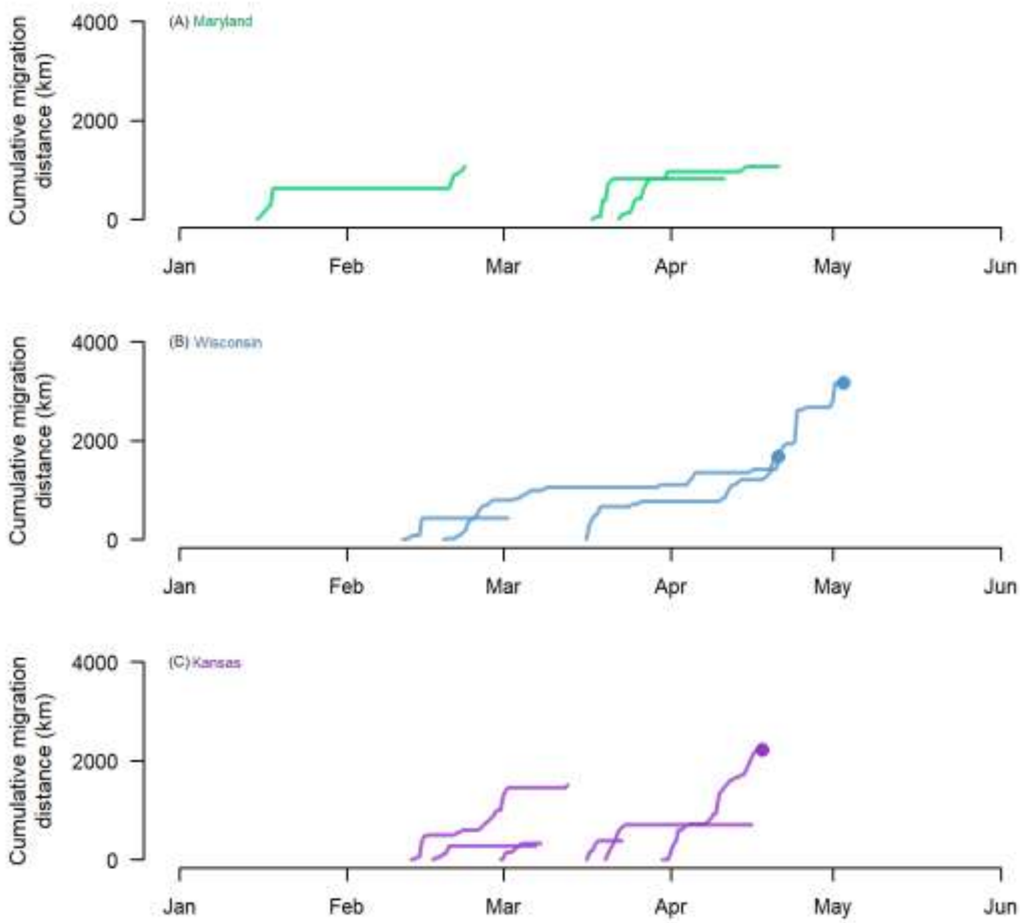

Figure 10. Annual cycle of Grasshopper Sparrows (n = 33), as estimated from geolocator data. Each color represents a period of the annual cycle, and the data for each period is presented by three arcs (from thickest to thinnest) drawn from the median to median, 25^{th} to 75^{th} percentile, and minimum to maximum date, respectively. Sample size varies throughout the annual cycle.

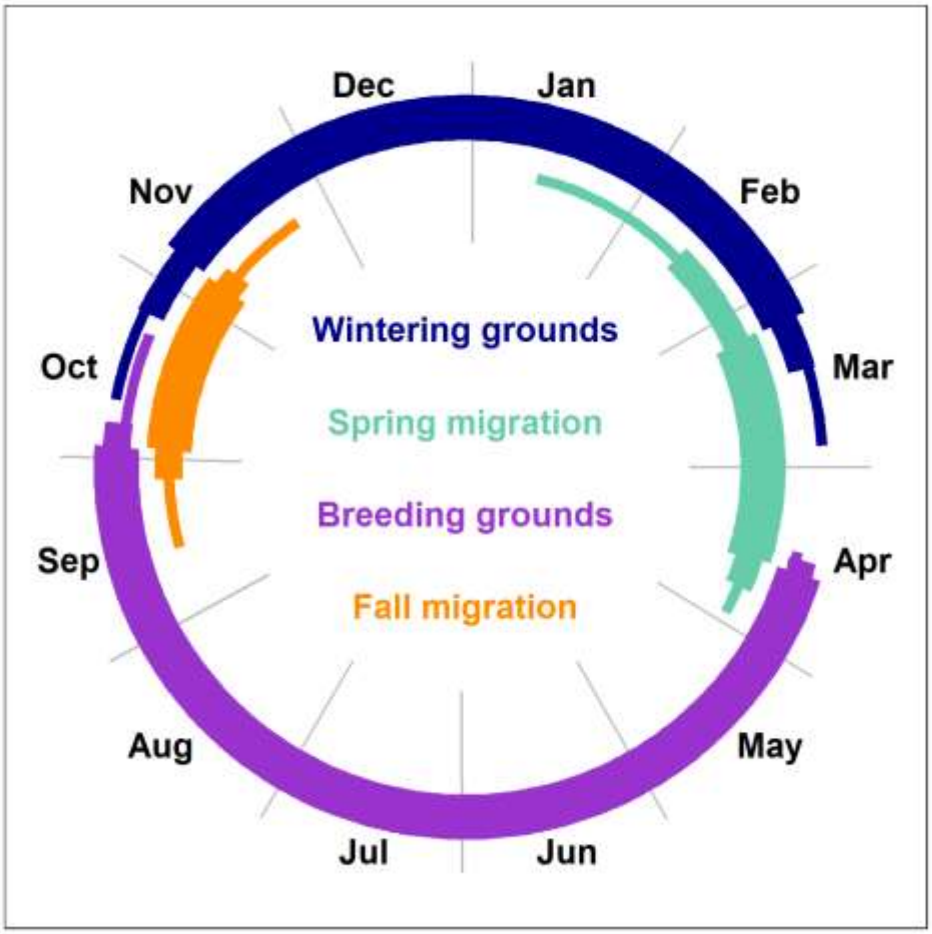

Figure 11. GPS tag locations (circles) during fall (orange) and spring (green) migration, and the wintering period (blue) from Eastern Meadowlarks originally tagged at DoD installations (triangles) in KS and WI (main panel), and MA (inset). Colored lines are orthodromic lines between consecutive (~7-14 d apart) locations. Location estimates were obtained for the meadowlark tagged in MA on the breeding (29 Ap - 22 Oct, 2016 and 15 Mar - 15 Apr, 2017) and wintering (15 Nov, 2016 - 1 Mar, 2017) grounds, and during spring migration (8 Mar, 2017). Not shown are two meadowlarks tagged in MD that were non-migratory year-round residents.

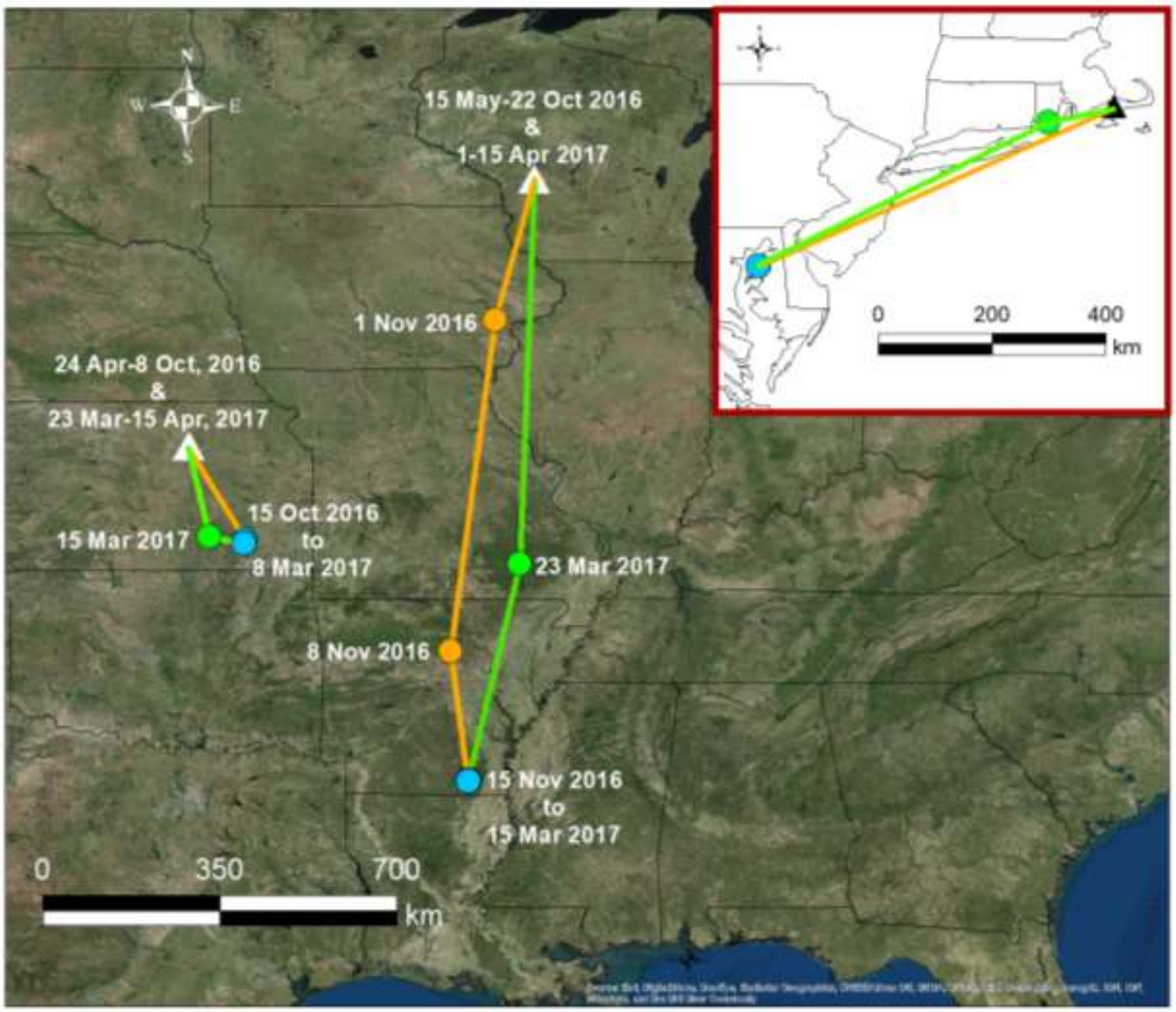

Figure 12. GPS locations (circles) with colored geodesic lines between consecutive (~7-14 d apart) locations (not necessarily the actual migration path) from five Upland Sandpipers with GPS tags deployed at DoD installations in 2016. Location data were transmitted for up to one year. The bird represented in green was tagged at Westover ARB (MA) but its tag transmitted only 1 Oct – 8 Apr, and two other tags (red and light blue) stopped transmitting before they returned to the breeding grounds in 2017. See Appendix C for individual details.

Figure 13. Migration routes of 4 Upland Sandpipers wearing Argos-satellite PTTs beginning in Apr or May 2016. Orange shades and blue shades represent two years of data from the same birds from KS and MA breeding grounds, respectively. PTTs in yellow and purple stopped transmitting on 21 Sept and 30 Nov, respectively.

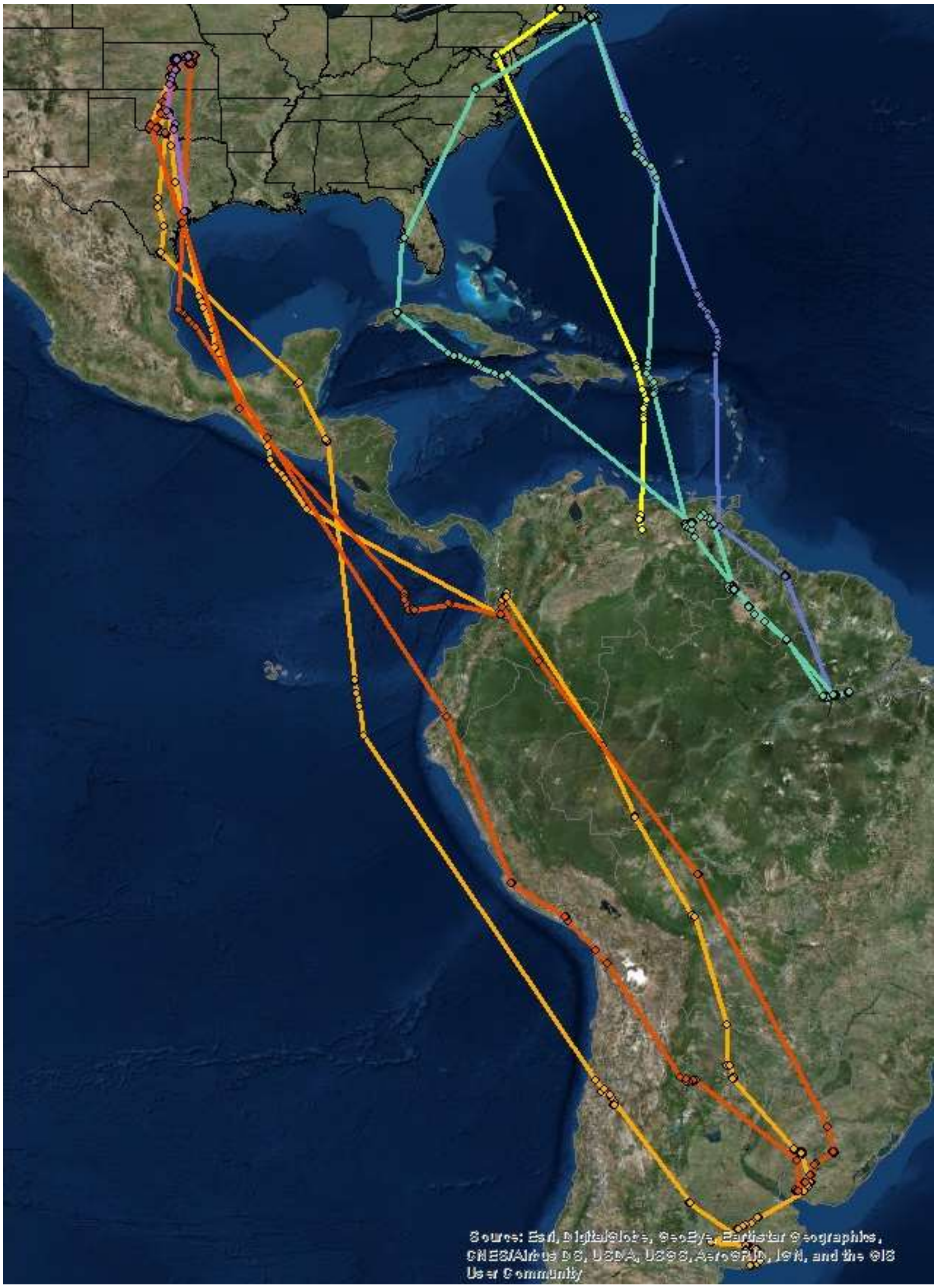

Figure 14. Movements of an Upland Sandpiper in Kansas during three breeding seasons (2016, 2017, and 2018) color-coded by year. Movements were between Konza Prairie (upper left), agricultural crop fields outside the town of St. Mary's (upper right), and grasslands just east of the town of Council Gove (bottom).

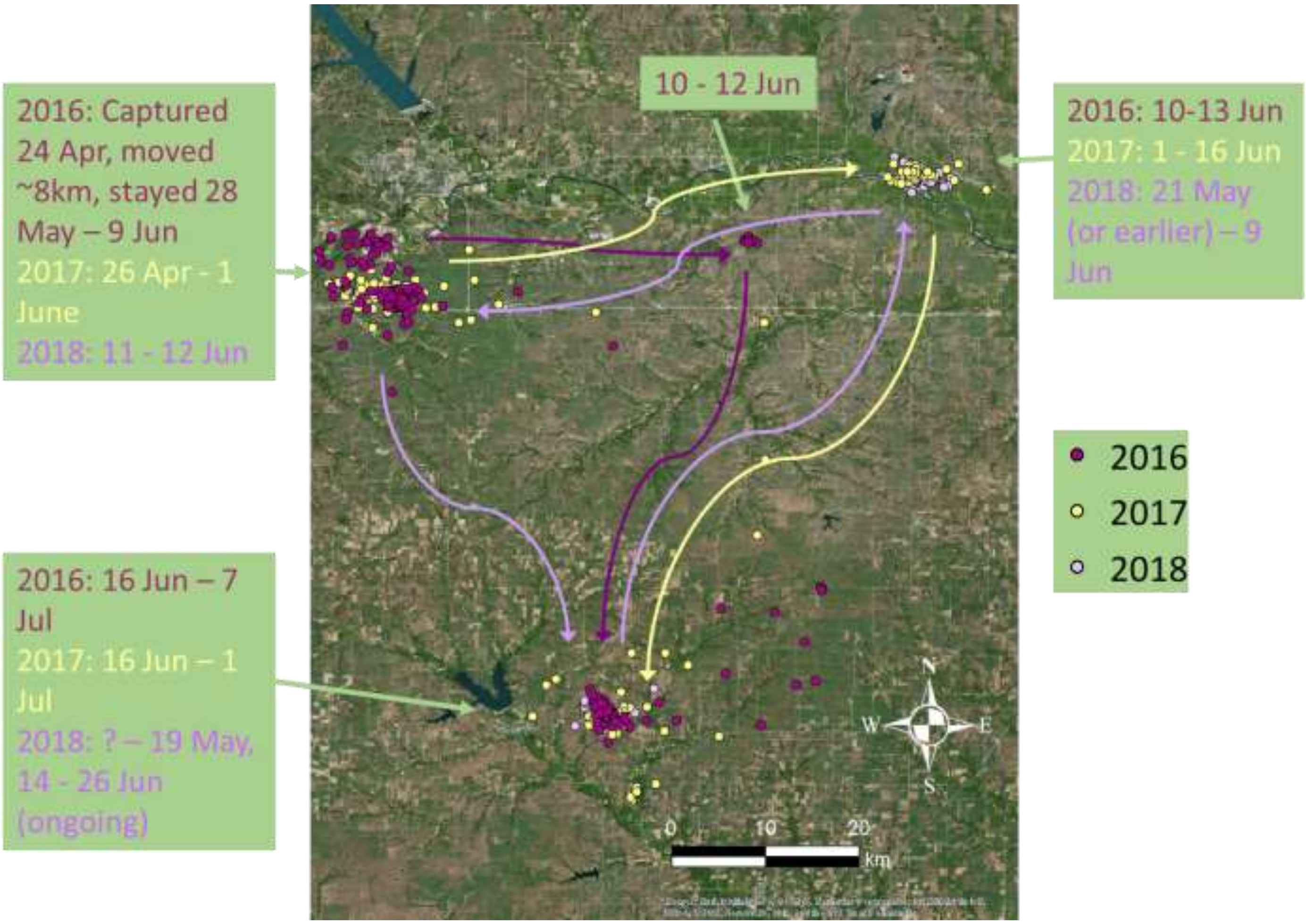

Figure 15. Wintering locations and dates of an Upland Sandpiper in western Bahia, Brazil for a) the first wintering area used and b) the entire wintering period, based on data from a GPS tag deployed on the breeding grounds at Fort Riley, Kansas.

a)

b)

Figure 16. Migration stopovers of two Upland Sandpipers at airfields based on PTT tag data: a) a stop during southbound migration at the Baltimore-Washington International airport (BWI) in MD, 21 Jul until 11 Sept, after the bird had left the breeding grounds at Westover ARB (MA); and b) a stop at Allen Perkinson Blackstone Army Airfield, VA on 24-27 Apr on the way to JBCC (MA) to breed.

a) b)