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Research Paper

## Geolocators, stable isotopes, and citizen science identify migratory timing, route, and spring molt of Smith's Longspurs

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**ABSTRACT.** Climate change is having a disproportionate impact on the Arctic. For Arctic breeding birds, basic knowledge of their annual cycle, specifically the timing, route, and movement behavior of migration, is needed to understand when and where populations may experience threats. We used a combination of geolocators and stable isotope analysis to identify route and timing of migration in Smith's Longspurs (*Calcarius pictus*) that breed in Alaska's Brooks Range. We trapped males on their breeding grounds from 2011 to 2014 and collected head feathers for stable isotopes of hydrogen ( $\delta^2\text{H}$ ). We deployed 22 geolocators on a subset of individuals and retrieved four, which all overwintered in southern Texas. Individual start dates for fall migration based on geolocators were more variable than for the spring, and individuals were highly mobile while on their wintering grounds. Geolocators and stable isotope values were comparable across years and indicated that birds from the Brooks Range undergo their pre-nuptial molt in central Canada. We compared geocator and stable isotope inferred locations to observations submitted to e-Bird and found that longspurs were distributed farther south during the winter months, but farther north during the spring than most eBird observations. Concurrent deployments of geocator tags across Smith's Longspurs' breeding range would clarify whether migratory behaviors and routes are population-specific or shared widely across breeding locations.

### Utilisation de géolocalisateurs, d'isotopes stables et de science citoyenne pour déterminer les périodes et les voies de migration, et la mue printanière de Plectrophanes de Smith

**RÉSUMÉ.** Les changements climatiques affectent de façon disproportionnée l'Arctique. Pour les oiseaux qui y nichent, une connaissance de base de leur cycle annuel, en particulier les périodes et les voies de migration, ainsi que leur comportement, est nécessaire pour comprendre quand et où les populations font possiblement face à des menaces. Nous avons utilisé une combinaison de géolocalisateurs et d'analyse d'isotopes stables pour déterminer les voies et les périodes de migration chez les Plectrophanes de Smith (*Calcarius pictus*) qui nichent dans la cordillère de Brooks en Alaska. Nous avons capturé des mâles à leur site de nidification de 2011 à 2014 et collecté des plumes de tête pour les isotopes stables de l'hydrogène ( $\delta^2\text{H}$ ). Nous avons fixé 22 géolocalisateurs sur un sous-ensemble d'individus et en avons récupéré quatre, qui étaient sur des oiseaux ayant tous hiverné dans le sud du Texas. Les dates de début de migration d'automne, basées sur les géolocalisateurs, étaient plus variables que celles du printemps, et les oiseaux étaient très mobiles lorsqu'ils se trouvaient sur leur aire d'hivernage. Les données des géolocalisateurs et les valeurs des isotopes stables étaient comparables d'une année à l'autre et indiquaient que les oiseaux de la cordillère de Brooks effectuaient leur mue pré-nuptiale dans le centre du Canada. Nous avons comparé les localisations tirées des géolocalisateurs et des isotopes stables aux observations soumises dans eBird et avons constaté que les plectrophanes étaient répartis plus au sud pendant les mois d'hiver, mais plus au nord pendant le printemps, que la plupart des observations dans eBird. La pose concomitante de géolocalisateurs sur des Plectrophanes de Smith dans l'ensemble de l'aire de nidification permettrait de préciser si les comportements et les voies de migration sont spécifiques aux populations ou s'ils sont généralisés entre divers sites de nidification.

**Key Words:** *Calcarius pictus*; eBird; feather stable isotopes; migration

## INTRODUCTION

Long-distance migrants that breed in the Arctic are facing rapidly changing conditions on their breeding grounds that may affect habitat quality and reproduction (Fossey et al. 2015, Boelman et al. 2017, McFarland et al. 2017), whereas other threats, such as habitat loss or anthropogenic disturbance, may affect survival during their migration and the non-breeding period (e.g., Newton

2006, Yong et al. 2015). For many small-bodied species of bird, e.g., passerines, specific details on migration routes and winter habitat use are lacking. Such details are important to elucidate species' risks and for building management plans. This is particularly the case for passerines breeding in the far northern regions of North America (McKinnon et al. 2016, Hagelin et al. 2021). Here we used a combination of methods to piece together

the route and timing of migration, as well as spring molt locations, for a long-distance Arctic-breeding migrant likely to be impacted by climate change.

The Smith's Longspur (*Calcarius pictus*) is a small polygynandrous passerine identified as one of Alaska's land birds with greatest conservation needs (ADFG 2015) because of threats on the breeding and wintering grounds (Rich et al. 2004, Zack and Liebezeit 2009). Smith's Longspurs breed in tundra or above tree-line areas in Alaska and Northern Canada (Wild et al. 2015, McFarland et al. 2017, Briskie 2020). In the breeding season adults show a relatively high interannual breeding-site fidelity of 88% (Craig et al. 2015). During the non-breeding season, Smith's Longspurs are often found in mixed flocks with Lapland Longspurs (*Calcarius lapponicus*) in highly disturbed agricultural habitats in the southern Great Plains (Dunn and Dunn 1999, Ormston 2000, Holimon et al. 2012, Muller and Ross 2022), which are hotspots for birders (Briskie 2020).

Despite regular sightings of Smith's Longspurs during the non-breeding period, an effort to identify where the Alaskan segment of this population overwinters via band resights was unsuccessful. Between 2007 and 2013, 243 adults and 431 juveniles were banded with unique color-band combinations, but outreach efforts to birders at known wintering areas of Smith's Longspurs did not yield any resights. With 37% and 53% resighting rates for adult females and males, respectively, on the breeding grounds (Craig et al. 2015), this lack of wintering-ground resights is likely not due to mortality.

Our goal was to identify locations and the migratory behavior of Smith's Longspurs breeding in Alaska's Brooks Range. We combined several techniques, e.g., geolocators, stable isotope analysis, and eBird observations, to identify migration routes and wintering areas, the phenology and character of movements, and spring-molt locations of this population of longspurs. We first used compact, lightweight geolocators that measure ambient light levels to track individual birds throughout their migration. Geolocators are a powerful tool in revealing details about small-bird migratory behavior. However, their archival nature, necessitating physical retrieval for data download, combined with technological failures, frequently results in smaller sample sizes (Bridge et al. 2013). Therefore, we supplemented geocator data with location estimates derived from stable isotope analysis of hydrogen ( $\delta^2\text{H}$ ) in head feathers, molted in spring before arrival to the breeding grounds (Jehl 1968). Hydrogen stable isotope values change in relatively predictable patterns with latitude and can be used to broadly identify likely molting locations of feathers (Hobson et al. 2012, Hobson et al. 2015). Whereas this tool is only effective at identifying probable locations for a specific period, it substantially increased our estimate of the timing and location of the pre-nuptial molt. We also compared location estimates from geolocators and stable isotope analysis with community science observations of Smith's Longspurs to see if there were any notable differences between individual tracks from Brooks Range breeding birds and general sightings of longspurs in the non-breeding season. The Cornell Lab of Ornithology hosts an online platform where birders can report bird sightings (<https://eBird.org>), which can be accessed to determine the time, location, and habitat type in which birds have been observed, particularly in areas frequented by birders (Fink et al. 2013).

## METHODS

### Study site

We monitored breeding Smith's Longspurs from late May until the middle of July at two locations in the Brooks Range of northern Alaska: Atigun Gorge (68.278°N, 149.218°W; 2007–2014) and Slope Mountain, 27 km north (68.418°N, 149.408°W; 2011–2014). Both areas (~1060 ha) were accessible from the Dalton Highway and characterized by treeless tundra habitat.

### Field techniques

In 2011 to 2014 we captured Smith's Longspurs using stage-dependent mist-netting techniques that included playback calls and decoys (~28 May to 10 June) and flushing birds into nets set up in a v-formation (~10 June to 4 July). All captured adults were tagged using unique color-band combinations and U.S. Geological Survey (USGS) metal bands under BBL Permit #22662. In 2013 we attached 22 geolocators to the backs of adult males captured at the Atigun Gorge site using a leg-loop harness made of Kevlar thread adjusted to each bird's body size (Naef-Daenzer 2007). During the 2011 to 2014 field seasons, we clipped crown feathers from the black cap of breeding males using a small pair of scissors: nine birds in 2011, 26 in 2012, 29 in 2013, and eight in 2014. For each breeding season, teams of at least two devoted approximately 30 to 40 hours per person, with a minimum of 60 total hours per study site, to resighting. Effort was focused on the first two weeks of the breeding season when birds were the most vocal and visible during their arrival and establishing breeding neighborhoods.

### Stable isotope analysis

After delipidation in methanol (Will et al. 2018) we analyzed feathers for  $\delta^2\text{H}$  at University of Alaska Anchorage's Stable Isotope Laboratory using internal standards of homogenized and lipid extracted chicken and turkey feathers, and homogenized bowhead whale baleen with all samples for in-run calibration of exchangeable H and as quality controls. Stable isotope values are reported in standard  $\delta$  notation of parts per mil (‰) and are referenced to Vienna Standard Mean Ocean Water (VSMOW). Long-term records of internal standards yield an analytical precision of 1.8 ‰ for  $\delta^2\text{H}$ .

### Data analysis

We conducted all data analyses in R (R Core Team 2022), and statistical tests were interpreted using an alpha level of 0.05. We downloaded eBird sightings from the Cornell Lab of Ornithology (eBird 2021) to compare to geocator and stable isotope location estimates. We mapped historical and current sightings of adult birds to make visual comparisons of the migration route and molt locations used by Brooks Range breeding longspurs and observed locations of birds of unknown origin and compared geocator location estimates to the U.S. Environmental Protection Agency's ecoregions to qualitatively characterize non-breeding season habitat use (<https://www.epa.gov/eco-research/ecoregions-north-america>).

### Geocator processing

We converted geocator-recorded light levels to sunrise and sunset times by identifying twilights with R package BASTag (Wotherspoon et al. 2016) using a solar zenith angle of 95 and a

light threshold of 10; following Orben et al. (2014) and Bindoff et al. (2017), twilights were not detectable in our calibration period. We then estimated daily locations using a Hidden Markov Model and particle filter with R package FLIGHTR (Rakhimberdiev et al. 2015, 2017) that did not consider locations in the ocean/Great Lakes and limited the distance between points based on a maximum flight speed (9.2 m/s, Lapland Longspurs; McLaughlin and Montgomerie 1985). We doubly smoothed the resulting tracks by averaging the noon-to-midnight and midnight-to-noon locations, calculating a two-point moving average of those points, following Bräthen et al. (2021) and references therein. Finally, we removed points spanning the fall (8 September to 20 October) and spring (20 February to 3 April) equinoxes to produce the final tracks (Frederikson et al. 2012).

### Migratory behavior

Using the smoothed geolocator positions converted in R package adehabitatLT (Calenge 2006) we calculated net squared displacement (NSD) with R package migrateR (Spitz et al. 2017), the difference in distance between the bird's starting point, and all subsequent locations (Bunnfeld et al. 2011). NSD can be used to identify patterns in large-scale animal movement (Papworth et al. 2012). We calculated break points with R package strucchange (Zeileis et al. 2002) in each individual's migration curve, using the number of breakpoints with the lowest Bayesian Information Criterion score to identify different phases of the non-breeding period. Because our tracks have gaps around the equinoxes, we visually inspected each migration curve at the identified breakpoint and discarded those that were not associated with changes in NSD over time. By late May, birds were far enough north that we could no longer identify twilights, so we lost the final portion of their migration.

To identify core use areas during each non-breeding phase we calculated 25%, 50%, 75%, and 95% utilization distributions of location estimates with R package adehabitatHR using the reference bandwidth, i.e., href, because we were interested in identifying the central concentration of the tracked birds at each time interval (Calenge 2006). To determine times when birds were relatively stationary or moving rapidly, we calculated the probability, i.e., zero to one, with one being a high probability of moving, at each point along the track that the longspur would stay in that same location, or move, with R package aniMotum (Jonsen et al. 2023).

### Stable isotope assignment of head feathers

We used a semi-parametric Bayesian inversion method to estimate locations of molted head feathers based on isotopic  $\delta^2\text{H}$  values using R package assignR (Ma et al., 2020). We used the North American Low Resolution isoscape available in assignR as a base and calibrated it using passerine feather isotope values of known origin ( $F_{1673} = 794.4$ ,  $P < 0.001$ ) collected from the literature and provided as part of the R package. We created a land mask using eBird sightings (eBird 2021) and geolocator locations as a guide 112.5°W to U.S. eastern coastline and 33.4°N to 60°N. We calculated a probability density surface for each bird and selected the cells that encompassed the core 10% of the total density, which we considered the most probable locations for each sample. To determine the timing of the prenuptial molt we visually inspected the smoothed geolocator locations and identified when the track and isotope assigned latitudes were most similar.

## RESULTS

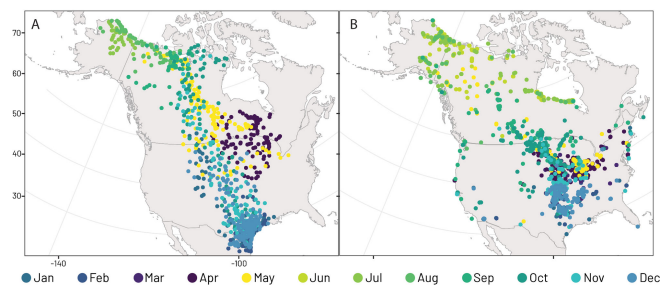
### Geolocator retrieval

In 2014 field crews spent 160 hours, 80 more than the usual re-sighting effort, searching for banded birds at Atigun Gorge, where the geolocators had been deployed in 2013. We successfully located and retrieved geolocators from four individuals. A fifth male was recaptured that had lost its geolocator; it had a scab over its flank suggesting the bird may have removed the device. Two of the four retrieved harnesses were frayed near the O-rings. In total, crews spent over 40 hours in 2014 tracking birds specifically carrying geolocators.

### Migration route

Position estimates from the combined geolocator light level records had an estimated error of  $43.3 \pm 51.5$  km. After the breeding season, the male longspurs moved east in the Alaska and Canadian low Arctic before they began their southward migration through central North America. All four birds overwintered in southern Texas, farther south than most eBird observations; 85.2% of all geolocator positions for the wintering period (December to February) were below 34°N latitude, roughly the southern edge of Oklahoma, compared to only 4.2% of all eBird observations (Fig. 1). By the subsequent April the longspurs had moved into central Canada. From there they completed a rapid spring migration west and north to return to their breeding grounds in Alaska's Brooks Range (Fig. 1). Geolocator tracks and eBird sightings overlapped in August to October, but geolocator birds were farther south in December to March compared to most eBird sightings. Geolocator birds were also farther north than most sightings made in March to May.

**Fig. 1.** (A) The migration route of Smith's Longspurs (*Calcarius pictus*;  $n = 4$ ) carrying geolocators in 2013–2014 (left panel, dates around the equinox have been removed) compared to (B) observations of Smith's Longspurs ( $n = 11,559$ ) reported to eBird (eBird 2021).

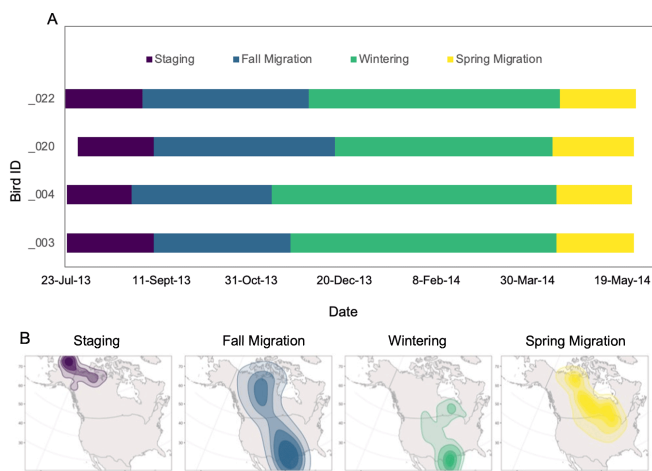


### Migratory timing and spatial extent

The most parsimonious model identified four periods of movement during the non-breeding period based on the breakpoint analysis of each individual's net-squared displacement. These included a pre-migratory period, characterized by slow movement away from the breeding location, two migratory periods, i.e., fall and spring, where the distance covered each day was larger than the other two periods, and a wintering period between the two migratory periods when the distance covered each day was again low and the distance from the breeding location remained relatively constant.

For the four males with geolocators, the start of the fall migration, 4 September (mean)  $\pm$  5.7 days (SD), was more variable than the start of the spring migration, i.e., departure from the pre-nuptial molt location (15 April  $\pm$  1.6 days) and lasted almost twice as long: fall 84.2 days (mean) and 74–98 days (range); spring 42 days (mean) and 41–44 days (range). Birds that departed the breeding grounds early also arrived on the wintering grounds earlier (Fig. 2).

**Fig. 2.** (A) The timing of migratory stages based on net-squared displacement calculations of geolocator location estimates for Smith’s Longspurs (*Calcarius pictus*; n = 4) during the non-breeding season, 2013–2014; and (B) the corresponding utilization distributions of the location estimates by stage including the 50% (darkest), 75%, and 95% (lightest) distributions.



Movement of geolocator-tracked male longspurs was not necessarily restricted while on their wintering grounds (Fig. 2). Although location estimates were centered in southern Texas, longspurs frequently used areas throughout Texas and Louisiana, with occasional forays farther north (Fig. 2). The movement propensity for all four males with geolocators remained relatively high throughout the non-breeding period and consisted of a mix of low and high probabilities of moving to a new location from one day to the next (Fig. 3).

### Pre-nuptial molt

Two of the four birds carrying geolocators also had head feathers sampled and their isoscape latitude estimates (49.0832777°W, 46.0832789°W) were most similar to their geolocator locations in early and late April, specifically 8, 9, 18, 25, and 30 April (Fig. 4). For the rest of the birds for which we had feather samples, we found no difference in  $\delta^2\text{H}$  stable isotope values among the four study years ( $F_{1,65} = 0.463$ ,  $P = 0.5$ ). In April, location estimates based on stable isotope likelihood assignments were generally farther north than eBird sightings.

### DISCUSSION

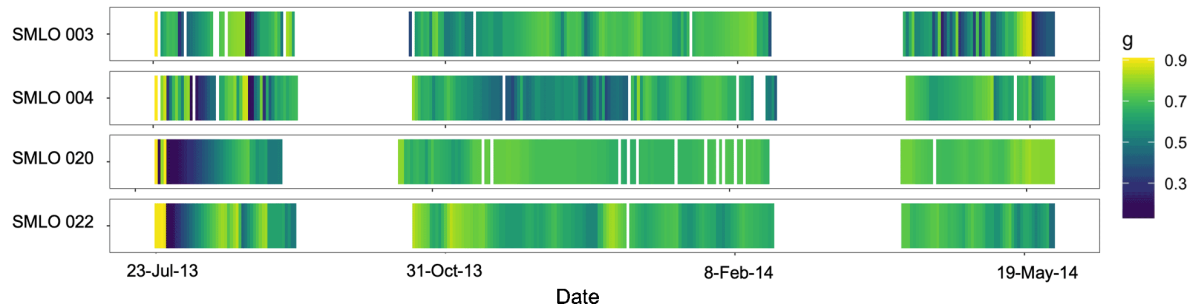
Our study provides the first data on individual migratory behaviors and molt locations of Smith’s Longspurs and provides insight into how discrete sightings of non-breeding longspurs may be linked into a continuous migration path. For example, prior to heading south

during their fall migration Smith’s Longspurs moved east along Alaska and Canada’s coastal plain, indicating that birds sighted in Northern Canada during the fall (Briskie 2020) may include Alaskan breeding birds. Similar to previous reports, longspurs used ecoregions characterized by drier, low-profile vegetation throughout the non-breeding period (Holimon et al. 2012, Briskie 2020 and references therein). The tracks of tagged birds traveled through tundra habitat in northern Alaska and Canada before moving south into taiga, northern forests, then the Great Plains. Birds overwintered along the Texas and Louisiana Coastal Plains. In fall, birds moved north through semi-arid prairies to molt, supported by isotope likelihood location assignments, in the northern forests of Canada, then traveled back through taiga to reach their breeding grounds in the tundra of Alaska. We observed a more synchronous return migration in the spring, which may be indicative of protandry in this species, which may be expected if males benefit from arriving early on the breeding grounds to claim their place in a neighborhood (Tøttrup and Thorup 2008). The timing of migration corresponded to what has been compiled from previous studies (Briskie 2020).

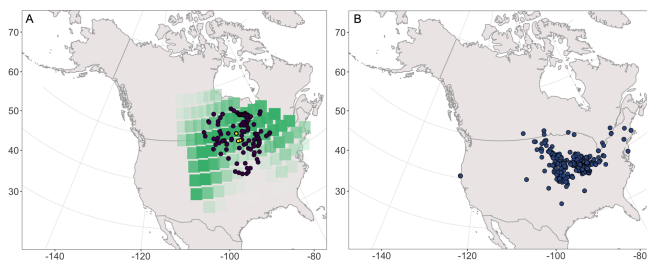
There was overlap in eBird and our geolocator locations, but it was not consistent. For example, longspurs breeding in Alaska’s Brooks Range do not visit breeding areas in the Alaska Range or along Hudson Bay, Canada (eBird data, Briskie 2020), in contrast to some other Arctic breeding birds that have been observed to use lower latitude breeding habitats during their migration (Hagelin et al. 2021). Similarly, most eBird observations of wintering longspurs are made in Oklahoma and Nebraska; however, our tagged birds spent the winter in southern Texas and Louisiana (eBird data, Briskie 2020), farther south than we had expected. Whereas a direct comparison of geolocator location to eBird sighting supports this difference, it may be that Alaska breeding birds are a smaller subset of the population, and so the number of sightings, as represented in eBird as individuals, is indicative of the relative use of that region by the population as a whole. There was also minimal overlap in pre-nuptial molt locations recorded by tags and reported to eBird in April. Concurrent tracking studies from multiple breeding locations are needed to determine whether our data are indicative of population-specific wintering and molt locations or if these differences are a result of birder bias, reflecting human population centers and birding locations (Dickinson et al. 2010, Walker and Taylor 2017). Prior to our study, scant evidence existed linking breeding location to non-breeding location in longspurs because intensive banding efforts on their breeding grounds, in both Alaska and Canada, have yielded no band recoveries of longspurs on their wintering grounds (Briskie 2020).

Our data clearly identified a wintering period, when birds remained a relatively constant distance from their breeding location, but the analysis of their movement during this time indicates that birds were not necessarily staying in one area. They continued to have a relatively high propensity to move locations during their wintering period (Fig. 3), spread over a 500-mile-wide area. Multi-year studies are needed to confirm this observation, because previous accounts of flock movement during the winter reported site fidelity in wintering flocks (Dunn and Dunn 1999), but that movement in winter may be a reflection of food availability, with large movements occurring during cold

**Fig. 3.** The probability that on any given day a male Smith's Longspur (*Calcarius pictus*) will move from one location to the next, calculated for each point throughout the non-breeding period. Lighter colors indicate a higher likelihood of moving. Points for the autumnal and vernal equinox were excluded, and some individual days were excluded during analysis because of time-stamp inconsistencies.



**Fig. 4.** Spring molt locations (A) estimated from  $\delta^2\text{H}$  values in pre-nuptial grown head feathers (green, years 2011–2014 from  $n = 72$  birds), with overlaid geolocator positions (n = 4 birds, blue), with matched locations of geolocator and isotope estimates in yellow (n = 2 birds). (B) sightings of Smith's Longspurs (*Calcarius pictus*) in April reported to eBird (n = 2370 sightings; eBird 2021).



winters after a summer of high grass growth (Grzybowski 1982). The reliance of longspurs on endangered prairie habitats and their potential use of extensive areas during the winter indicates that a network approach to habitat conservation may benefit Smith's Longspurs and buffer them from habitat-related threats during the non-breeding period (see Sanderson et al. 2023 for breeding-season benefits).

The details we present about migratory behavior in this study, specifically the timing, duration, and movement of longspurs during the non-breeding season should be viewed with consideration of the small sample size of our geolocator-marked birds. We cannot definitively attribute poor return rates to any single cause, such as low survival of tagged birds, loss of loggers, and abnormally high rates of relocation among tagged birds. However, we do think that advances in geolocator size, attachment, and functioning, i.e., longer battery life, will improve the ability of future studies to obtain larger sample sizes. Larger sample sizes will help to reduce some of the variability in geolocator location estimates (A, Fig. 4) by increasing the number of birds that kernel density maps (B, Fig. 2) and therefore improving the identification of core-use areas. With these advances, additional geolocation studies at multiple breeding

locations are needed to test whether non-breeding and pre-nuptial molt distributions are structured by breeding location, and to validate the timing and movement behaviors described here.

In conclusion, our results revealed that the Texas coastal plain may be an important wintering area for Smith's Longspurs breeding in northern Alaska. Further studies could expand on these preliminary data and help us understand how experiences during one life stage affects subsequent stages such as whether conditions during molt affect reproduction, i.e., seasonal interactions. This study highlights how detailed understanding of migratory behavior can complement data on habitat use and distribution to provide the basic information needed to assess the impact of non-breeding habitat loss or degradation on breeding populations in long-distance migrants.

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#### Data Availability:

The data that support the findings of this study are openly available at <https://doi.org/10.5066/P9NHNCPL>.

#### LITERATURE CITED

- Alaska Department of Fish and Game (ADFG). 2015. State wildlife action plan. ADFG, Juneau, Alaska, USA. [https://www.adfg.alaska.gov/static/species/wildlife\\_action\\_plan/2015\\_alaska\\_wildlife\\_action\\_plan.pdf](https://www.adfg.alaska.gov/static/species/wildlife_action_plan/2015_alaska_wildlife_action_plan.pdf)
- Bindoff, A. D., S. J. Wotherspoon, C. Guinet, and M. A. Hindell. 2017. Twilight-free geolocation from noisy light data. *Methods in Ecology and Evolution* 9:1190-1198. <https://doi.org/10.1111/2041-210X.12953>
- Boelman, N. T., J. S. Krause, S. K. Sweet, H. E. Chmura, J. H. Perez, L. Gough, and J. C. Wingfield. 2017. Extreme spring conditions in the Arctic delay spring phenology of long-distance migratory songbirds. *Oecologia* 185:69-80. <https://doi.org/10.1007/s00442-017-3907-3>
- Bråthen, V. S., B. Moe, F. Amélineau, M. Ekker, P. Fauchald, H. H. Helgason, M. K. Johansen, B. Merkel, A. Tarroux, J. Åström, et al. 2021. An automated procedure (v2.0) to obtain positions from light-level geolocators in large-scale tracking of seabirds: a method description for the SEATRACK project. Norwegian Institute for Nature Research (NINA) Report 1893, NINA, Trondheim, Norway. <https://brage.nina.no/nina-xmlui/bitstream/handle/11250/2735757/ninarapport1893.pdf?sequence=3&isAllowed=y>
- Bridge, E. S., J. F. Kelly, A. Contina, R. M. Garielson, R. B. MacCurdy, and D. W. Winkler. 2013. Advances in tracking small migratory birds: a technical review of light-level geolocation. *Journal of Field Ornithology* 84(2):121-137. <https://doi.org/10.1111/jfo.12011>
- Briskie, J. V. 2020. Smith's Longspur (*Calcarius pictus*), version 1.0. In A. F. Poole, editor. *Birds of the world*. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://doi.org/10.2173/bow.smilon.01>
- Bunnefeld, N., L. Börger, B. van Mooter, C. M. Rolandsen, H. Dettki, E. J. Solberg, and G. Ericsson. 2011. A model-driven approach to quantify migration patterns: individual, regional, and yearly differences. *Journal of Animal Ecology* 80:466-476. <https://doi.org/10.1111/j.1365-2656.2010.01776.x>
- Calenge, C. 2006. The package “adehabitat” for the R software: a tool for the analysis of space and habitat use by animals. *Ecological Modeling* 197:516-519. <https://doi.org/10.1016/j.ecolmodel.2006.03.017>
- Craig, H. R., S. Kendall, T. Wild, and A. N. Powell. 2015. Dispersal and survival of a polygynandrous passerine. *Auk* 132:916-925. <https://doi.org/10.1642/AUK-15-41.1>
- Dickinson, J. L., B. Zuckerberg, and D. N. Bonter. 2010. Citizen science as an ecological research tool: challenges and benefits. *Annual Review of Ecology, Evolution, and Systematics* 41:149-72. <https://doi.org/10.1146/annurev-ecolsys-102209-144636>
- Dunn, E. H., and R. B. Dunn. 1999. Notes on behavior of Smith's Longspurs wintering in Oklahoma. *Bulletin of the Oklahoma Ornithological Society* 32:13-20.
- eBird Basic Dataset. 2021. Version: EBD\_relNov-2021. Cornell Lab of Ornithology, Ithaca, New York, USA. <https://science.ebird.org/en/use-ebird-data/download-ebird-data-products>
- Fink, D., T. Damoulas, and J. Dave. 2013. Adaptive spatio-temporal exploratory models hemisphere-wide species distributions from massively crowdsourced eBird data. Pages 1284-1290 in *Proceedings of the Twenty-Seventh Association for the Advancement of Artificial Intelligence (AAAI) Conference on Artificial Intelligence (Bellevue, 2013)*. AAAI, Palo Alto, California, USA. <https://doi.org/10.1609/aaai.v27i1.8484>
- Fosøy, F., B. G. Stokke, T. K. Kåsi, K. Dyrset, Y. Espmark, K. S. Hoset, M. I. Wedege and A. Moksnes. 2015. Reproductive success is strongly related to local and regional climate in the Arctic Snow Bunting (*Plectrophenax nivalis*). *Polar Biology* 38:393-400. <https://doi.org/10.1007/s00300-014-1595-6>
- Frederiksen, M., B. Moe, F. Daunt, R. A. Phillips, R. T. Barrett, M. I. Bogdanova, T. Boulinier, J. W. Chardine, O. Chastel, L. S. Chivers, et al. 2012. Multicolony tracking reveals the winter distribution of a pelagic seabird on an ocean basin scale. *Diversity and Distributions* 18:530-542. <https://doi.org/10.1111/j.1472-4642.2011.00864.x>
- Grzybowski, J. A. 1982. Population structure in grassland bird communities during winter. *Condor* 84:137-152. <https://doi.org/10.2307/1367657>
- Hagelin, J. C., M. T. Hallworth, C. P. Barger, J. J. Johnson, K. A. DuBour, G. W. Pendelton, L. H. DeCicco, L. A. McDuffie, S. M. Matsuoka, M. A. Snively, et al. 2021. Revealing migratory path, important stopovers, and non-breeding areas of a boreal songbird in steep decline. *Animal Migration* 8:168-191. <https://doi.org/10.1515/ami-2020-0116>
- Hobson, K. A., S. L. Van Wilgenburg, E. H. Dunn, D. J. T. Hussell, P. D. Taylor, and D. M. Collister. 2015. Predicting origins of passerines migrating through Canadian migration monitoring stations using stable-hydrogen isotope analyses of feathers: a new tool for bird conservation. *Avian Conservation and Ecology* 10:3. <https://doi.org/10.5751/ACE-00719-100103>
- Hobson, K. A., S. L. Van Wilgenburg, L. I. Wassenaar, and K. Larson. 2012. Linking hydrogen ( $\delta^2\text{H}$ ) isotopes in feathers and precipitation: sources of variance and consequences for assignment to isoscapes. *PLoS ONE* 7:e35137. <https://doi.org/10.1371/journal.pone.0035137>
- Holimon, W. C., J. A. Akin, W. H. Baltosser, C. W. Rideout, and C. T. Witsell. 2012. Structure and composition of grassland habitats used by wintering Smith's Longspurs: the importance of native grasses. *Journal of Field Ornithology* 83:351-361. <https://doi.org/10.1111/j.1557-9263.2012.00385.x>
- Jehl, Jr., J. R. 1968. The breeding biology of Smith's Longspur. *Wilson Bulletin* 80:123-149.
- Jonsen, I., W. J. Grecian, L. Phillips, G. Carroll, C. R. McMahon, R. G. Harcourt, M. A. Hindell, and T. A. Patterson. 2023.

- aniMotum, an R package for animal movement data: rapid quality control, behavioural estimation, and simulation. *Methods in Ecology and Evolution* 14:806-81. <https://doi.org/10.1111/2041-210X.14060>
- Ma, C., H. B. V. Zanden, M. B. Wunder, and G. J. Bowen. 2020. assignR: an R package for isotope-based geographic assignment. *Methods in Ecology and Evolution* 11:996-1001. <https://doi.org/10.1111/2041-210X.13426>
- McFarland, H. R., S. Kendall, and A. N. Powell. 2017. Nest-site selection and nest success of an Arctic-breeding passerine, Smith's Longspurs, in a changing climate. *Ornithological Applications* 119:85-97. <https://doi.org/10.1650/CONDOR-16-87.1>
- McKinnon, E. A., C. M. Macdonald, H. G. Gilchrist, and O. P. Love. 2016. Spring and fall migration phenology of an Arctic-breeding passerine. *Journal of Ornithology* 157:681-693. <https://doi.org/10.1007/s10336-016-1333-7>
- McLaughlin, R. L., and R. D. Montgomerie. 1985. Flight speeds of central place foragers: female Lapland Longspurs feeding nestlings. *Animal Behavior* 33:810-816. [https://doi.org/10.1016/S0003-3472\(85\)80014-2](https://doi.org/10.1016/S0003-3472(85)80014-2)
- Muller, J. A., and J. D. Ross. 2022. Fine-scale habitat associations of Oklahoma's longspurs. *Journal of Wildlife Management* 86:e22258. <https://doi.org/10.1002/jwmg.22258>
- Naef-Daenzer, B. 2007. An allometric function to fit leg-hoop harnesses to terrestrial birds. *Journal of Avian Biology*, 38:404-407.
- Newton, I. 2006. Can conditions experienced during migration limit the population levels of birds? *Journal of Ornithology* 147:146-166. <https://doi.org/10.1007/s10336-006-0058-4>
- Orben, R. A., D. B. Irons, R. Paredes, D. D. Roby, R. A. Phillips, and S. A. Shaffer. 2014. North or south? Niche separation of endemic Red-legged Kittiwakes and sympatric Black-legged Kittiwakes during their non-breeding migrations. *Journal of Biogeography* 42:401-412. <https://doi.org/10.1111/jbi.12425>
- Ormston, C. G. 2000. Winter habitat of the Smith's Longspur in Oklahoma. *Bulletin of the Oklahoma Ornithological Society* 33:6-12.
- Papworth, S. K., N. Bunnefeld, K. Slocombe, and E. J. Milner-Gulland. 2012. Movement ecology of human resource users: using net squared displacement, biased random bridges, and resource utilization functions to quantify hunter and gatherer behaviour. *Methods in Ecology and Evolution* 3:584-594. <https://doi.org/10.1111/j.2041-210X.2012.00189.x>
- Paxton, K. L., C. V. Riper III, T. C. Theimer, and E. H. Paxton. 2007. Spatial and temporal migration patterns of Wilson's Warbler (*Wilsonia pusilla*) in the southwest as revealed by stable isotopes. *Auk* 124:162-175. <https://doi.org/10.1093/auk/124.1.162>
- R Core Team. 2022. R: A Language and Environment for Statistical Computing. Version 4.2.1. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>
- Rakhimberdiev, E., D. Winkler, E. Bridge, N. Seavy, D. Sheldon, T. Piersma, and A. Saveliev. 2015. A hidden Markov model for reconstructing animal paths from solar geolocation loggers using templates for light intensity. *Movement Ecology* 3:25. <https://doi.org/10.1186/s40462-015-0062-5>
- Rakhimberdiev, E., A. Saveliev, T. Piersma, and J. Karagicheva. 2017. FLIGHTR: an R package for reconstructing animal paths from solar geolocation loggers. *Methods in Ecology and Evolution* 8:1482-1487. <https://doi.org/10.1111/2041-210X.12765>
- Rich, T. D., C. J. Beardmore, H. Berlanga, P. J. Blancher, M. S. W. Bradstreet, G. S. Butcher, D. W. Demarest, E. H. Dunn, W. C. Hunter, E. E. Inigo-Elias, et al. 2004. Partners in Flight North American Landbird Conservation Plan. Cornell Lab of Ornithology, Ithaca, New York, USA.
- Sanderson, F. J., J. D. Wilson, S. E. Franks, and G. M. Buchanan. 2023. Benefits of protected area networks for breeding bird populations and communities. *Animal Conservation* 26:279-289. <https://doi.org/10.1111/acv.12832>
- Spitz, D. B., M. Hebblewhite, and T. R. Stephenson. 2017. MigrateR: extending model-driven methods for classifying and quantifying animal movement behavior. *Ecography* 40:788-799. <https://doi.org/10.1111/ecog.02587>
- Tøttrup, A. P., and K. Thorup. 2008. Sex-differentiated migration patterns, protandry and phenology in North European songbird populations. *Journal of Ornithology* 149:161-167. <https://doi.org/10.1007/s10336-007-0254-x>
- Wagner, D. N., D. J. Green, J. M. Cooper, O. P. Love, and T. D. Williams. 2014. Variation in plasma corticosterone in migratory songbirds: a test of the migration-modulation hypothesis. *Physiological and Biochemical Zoology* 87:695-703. <https://doi.org/10.1086/676937>
- Walker, J., and P. D. Taylor. 2017. Using eBird data to model population change of migratory bird species. *Avian Conservation and Ecology* 12:4. <https://doi.org/10.5751/ACE-00960-120104>
- Wild, T. C., Kendall, S. J., Guldager, N., and A. N. Powell. 2015. Breeding habitat associations and predicted distribution of an obligate tundra-breeding bird, Smith's Longspur. *Condor: Ornithological Applications* 117:3-17. <https://doi.org/10.1650/CONDOR-14-77.1>
- Will, A. W., E. V. Kitaiskaia, and A. S. Kitaysky. 2018. Red-legged Kittiwake feathers link food availability to environmental changes in the Bering Sea. *Marine Ecology Progress Series* 593:261-274. <https://doi.org/10.3354/meps12509>
- Wotherspoon, S., M. Sumner, and S. Lisovski. 2016. Basic data processing for light-based geolocation archival tags. GitHub Repository. <https://github.com/SWotherspoon/BAStag/tree/master>
- Yong, D. L., Y. Liu, B. W. Low, C. P. Epañola, C. Y. Choi, and K. Kawakami. 2015. Migratory songbirds in the east Asian-Australasian flyway: a review from a conservation perspective. *Bird Conservation International* 25:1-37. <https://doi.org/10.1017/S0959270914000276>
- Zack, S., and J. Liebezeit 2009. New conservation priorities in a changing Arctic Alaska: workshop summary. North America Program, Wildlife Conservation Society, Portland, Oregon, USA.

[https://s3.amazonaws.com/WCSResources/file\\_20110518\\_07335-1\\_New\\_cons\\_priorities\\_changing\\_AK\\_ahgmp.pdf](https://s3.amazonaws.com/WCSResources/file_20110518_07335-1_New_cons_priorities_changing_AK_ahgmp.pdf)

Zeileis, A., F. Leisch, K. Hornik, and C. Kleiber. 2002. strucchange: an R package for testing for structural change in linear regression models. *Journal of Statistical Software* 7:1-38. <https://doi.org/10.18637/jss.v007.i02>

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