Research Article

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Migration and winter distribution of the Chestnut-collared Longspur

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Abstract: The Chestnut-collared Longspur (*Calcarius ornatus*) is one of five grassland songbirds, endemic within North America, with populations that have declined >65% since the 1960s. These species breed and winter in the northern and southern Great Plains, respectively. Identifying migration routes, wintering sites, and the timing of their habitat use is key for understanding the relative magnitude of threats across the annual cycle and effectively targeting habitats for conservation. We tracked migratory movements of seven Chestnut-collared Longspurs with light-level geolocators deployed in Canada. Individuals wintered up to 112-1,200km apart. All followed the Central Flyway, circumvented high-elevation terrain, and traveled east of the breeding location. Unlike most songbirds, the durations of spring and fall migrations were similar; on average 42 ± 7d and 41 ± 5d during fall and spring migrations, respectively, for an approximately 2,000km migration; this highlights the need to better understand habitat requirements during migration for grassland songbirds. Using geospatial habitat data, we assessed winter distribution overlap with four other endemic grassland songbirds; wintering range overlapped 63-99%. Future studies should use more precise devices (e.g., archival GPS units), programmed for data collection dates from this study, to identify specific migratory sites for better conserving this and associated grassland species.

Keywords: cropland; geo-logger; grasslands; migration rate; northern Great Plains; songbird

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1 Introduction

As a group, North American obligate grassland birds have declined more than any other since the 1960s [1,2]. Extensive cultivation of grasslands for annual crops, throughout the North American Great Plains (> 1,577,485km^2 or 32%, [3]), has been implicated in the population declines of 23 species of grassland-dependent birds [see 1,4,5). Other contributors to the declines include habitat degradation, fragmentation [6], and the widespread use of pesticides [7, but see 4]. Climate change has also been raised as a threat to the suitability of breeding and wintering areas [8-10], with analyses suggesting that over half of current climatic ranges would be lost by 2050 without potential for gains elsewhere [8]. Despite the imperiled status of several species of grassland songbirds, information on their migrations is limited in scope (limited to dates of departures and arrivals) and geography (single location or area) to purely observational records and little is understood about the relative importance of habitats at the areas used for breeding, migration, and wintering throughout migration [11].

Several of the bird species of greatest conservation concern are endemic within the grasslands of the North American Great Plains [see 12, reviewed in 13], breeding and wintering in the northern (Canada and U.S.) and southern (U.S. and Mexico) Great Plains, respectively [11], Figure 1. Five of these species have undergone dramatic (>65%) population losses since the 1960s: Sprague's Pipit *Anthus spragueii*; Chestnut-collared Longspur *Calcarius ornatus*; McCown's Longspur *Rhyncophanes mccownii*; Lark Bunting *Calamospiza melanocorys*; and Baird's Sparrow *Ammodramus bairdii* (Table 1) [2]. The Chestnut-collared Longspur has declined by an estimated 87% over the period between 1966-2015 [2], has undergone contractions on both its breeding and wintering distributions [11], and is a species of international conservation priority (Table 1). The declines are associated with the loss of grasslands at both ends of its annual cycle, inferred because the species is a strong indicator of grassland integrity in breeding areas [11,14] and its winter presence is positively associated with grass cover [15].

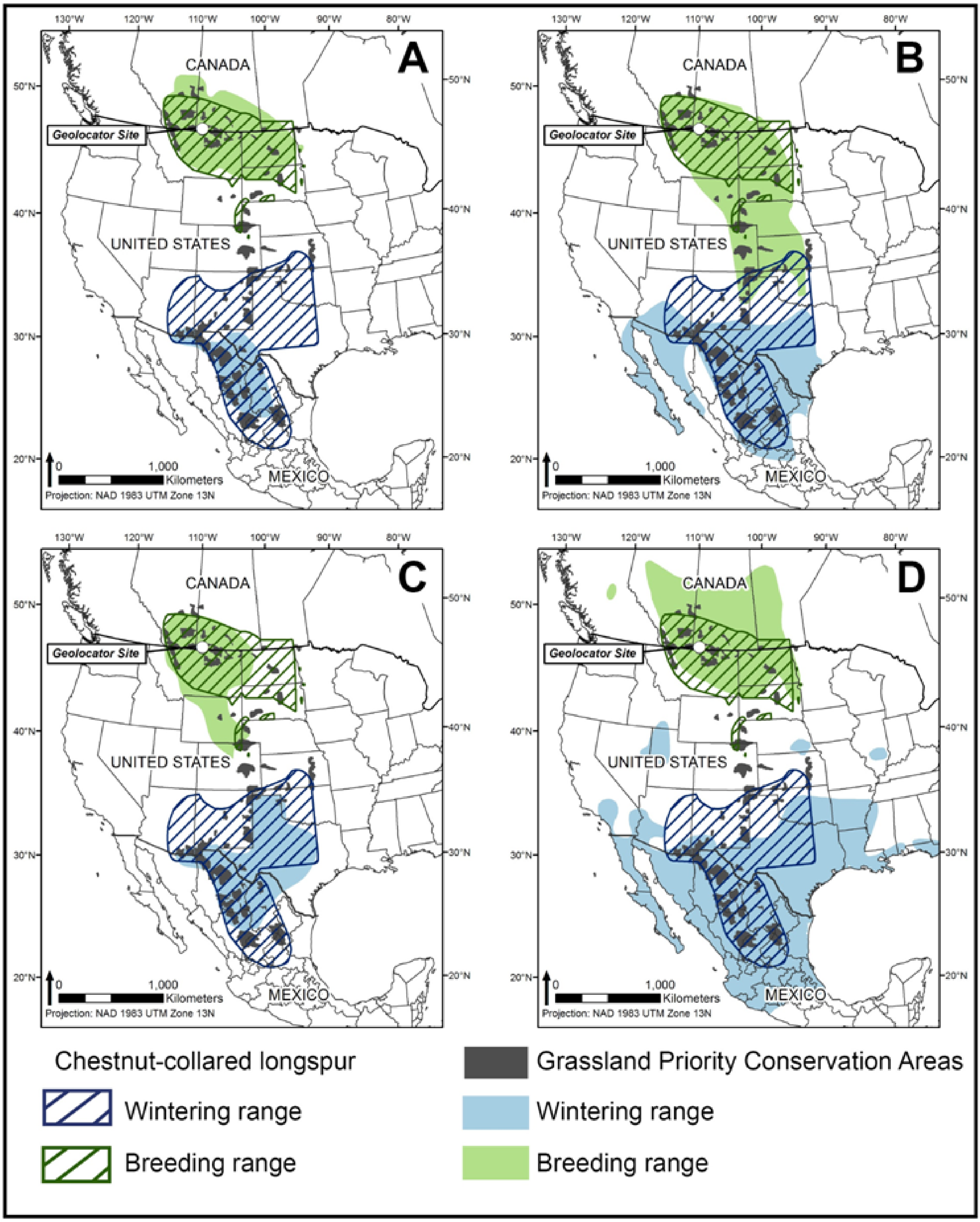

Figure 1. Breeding and wintering distributions of the four songbirds endemic to the Great Plains that co-occur with breeding distribution of the Chestnut-collared Longspur (cross-hatched in each) [40]: A. Baird's Sparrow; B. Lark Bunting; C. McCown's Longspur; and D. Sprague's Pipit. The species distributions show a high degree of overlap and the relative importance of the Grassland Priority Conservation Areas [41]. Geolocator deployment site within breeding distribution denoted by white circle.

Table 1. Status and degree of wintering distribution overlap among the five endemic, migratory breeding songbirds of the northern Great Plains.

Species	BBS trend 1966-2013 (Sauer et al. 2014)	Species conservation status†
Sprague's Pipit *Anthus spragueii*	-80%	Threatened (COSEWIC, SARA) Vulnerable (IUCN)
Chestnut-collared Longspur *Calcarius ornatus*	-87%	Threatened (COSEWIC, SARA) Near-threatened (IUCN)
McCown's Longspur *Rhyncophanes mccownii*	-88%	Threatened (COSEWIC) Special Concern (SARA) Least Concern (IUCN)
Lark Bunting *Calamospiza melanocorys*	-83%	Least Concern (IUCN)
Baird's Sparrow *Ammodramus bairdii*	-73%	Special Concern (COSEWIC) Least Concern (IUCN)

†Sources: Committee on the Status of Endangered Wildlife in Canada (COSEWIC) and Species At Risk Act (SARA) [61]; and International Union for Conservation of Nature [62].

Information on the parameters of migration (timing of movements, durations of movements and habitat use within an area, and geographic locations) can provide insight for refining conservation efforts [16]; in this case identifying grassland bird conservation funding priorities among the three North American countries. Also, migration strategies for a species endemic to the North American Great Plains may be quite different from those of songbirds migrating longer distances to Central and South America, where large barriers (e.g., Gulf of Mexico, western deserts) shape migration strategy [17,18] and/or molt-migrations may be undertaken [19]. Therefore, tracking migration of Chestnut-collared Longspurs can improve our understanding of the migration strategies of grassland birds of the Great Plains in general.

Both intrinsic [20] and extrinsic [21] markers have been used to infer migration routes and measure the strength of migratory connectivity [20]; however, there are limitations to these methods. For some species, band recoveries can provide enough information to reconstruct population-level patterns of breeding-wintering connectivity and approximate migration routes [21]. However, not enough individuals of many grassland species are marked annually to obtain recapture data. For example, among 3,672 records for banded Chestnut-collared Longspurs, only five band returns were recorded, all of which were at the sites where they were originally banded (Danny Bystrack, USGS Bird Banding Lab, unpubl. data). Likewise, records of returns at breeding sites are limited for Sprague's Pipit (< 1%, N=404; [22, 23, K. Ellison unpubl. data]), Lark Bunting (< 1%, N=4,880; [24]), Baird's Sparrow (5%, N=164; [25, 22]), and McCown's Longspur (< 1%, N=796; [26]) and no recoveries have been recorded from elsewhere other than breeding sites. Thus, banding data alone are not able to provide information on migration for these species. Stable isotope analysis of feathers has been used for determining spatial connections between moulting and capture locations for many species [20]. This requires isotopic variability in the landscape experienced by moulting birds, which, given the restricted breeding range of longspurs in the northern Great Plains, is unlikely to be present. Furthermore, longspurs do not undergo a complete winter moult [11]. Therefore, extrinsic tracking devices such as light-level geolocators, currently provide the best means for delineating migration routes and wintering sites for specific breeding populations of this declining species.

Our objectives were: 1. To quantify migration behavior and winter locations for Chestnut-collared Longspurs, and 2. Provide a context for the impacts of habitat loss on the wintering grounds by using habitat classification data to refine the wintering range distributions for the Chestnut-collared Longspur and the four endemic grassland songbird species with which it commonly co-occurs. We analyzed data recorded by geolocators to characterize migratory and winter movements, including departure and arrival dates, approximate migration routes, and winter locations. A relatively slow migration would entail the need for more stop-over habitat along migration routes than a long-distance migrant would require; long-distance migrants move much farther and depend on energy stored as fat across a few days whereas birds making a relatively protracted 1-2 month migration would require multiple stops or make 'hops' in migration *sensu* [27], thus being more dependent on feeding during migration, see [28]. Because grassland species travelling along the Central North American flyway [29] have no habitat barriers to contend with, and thus, no need to stop-over and build up endogenous energy supplies for crossing inhospitable barriers as quickly as possible, we predicted a relatively slow (mean daily travel speed circa 50 km/d), less energy-limited migratory strategy [30] for the Chestnut-collared Longspur. Existing characterizations of wintering ranges were extremely basic and based on distributional records rather than habitat; therefore we refined potential wintering areas based on land classification data. To help prioritize conservation of remaining habitats to the longspur and the other endemic grassland songbirds, we overlaid the Chestnut-collared Longspur wintering range with those of four other endemic grassland songbird species and analyzed grassland conversion to cropland and other human impacts within these areas using existing geospatial data.

2 Methods

2.1 Study sites

We attached geolocator tags to male Chestnut-collared Longspurs at Nature Conservancy Canada's Old Man on His Back Reserve near Claydon in southwestern Saskatchewan, Canada (49.203° N, 109.121° W) April-July, 2012-2015. Birds were captured, banded, and re-sighted for in four sampling areas of 50-200ha in 50-2490ha pastures, each 0.5 km apart, separated by other pastures with less optimal habitat (wetlands and taller and/or non-native crested wheatgrass [*Agropyron cristatum*]). The pastures ranged from ungrazed (50ha pasture), grazed by cattle (50 and 194ha pastures), and grazed by plains bison (*Bison bison bison*) (2,390ha pasture). Vegetation was typical of arid mixed-grass prairie, dominated by grasses (*Stipa* spp. [*richardsonii, viridula,* and *curtiseta*, *Poa* spp. [*pratensis* and *canadensis*], crested wheatgrass, and western [*Pascopyrum smithii*], northern [*Agropyron dasystachyum*], and awned [*A. subsecundum*] wheatgrasses,) and up to 10-15% shrubs, primarily big sagebrush (*Artemisia tridentata*).

2.2 Data Collection

2.2.1 Capture techniques

We used mist nets with stereo playback of conspecific song, as well as walk-in traps at nests with young, to capture and re-capture male Chestnut-collared Longspurs. Individuals were banded with three colored Darvic leg bands for identification and each bird was weighed to determine if the geolocator would represent < 3% body mass and only birds heavy enough (> 18.3g) were tagged.

Re-sighting surveys for birds banded in prior years were conducted between April-May, 2013-2015. Each season, upon confirmation that Chestnut-collared Longspurs had returned, two surveyors systematically searched for banded individuals by walking through focal areas in parallel at 50-100m distant. All individuals encountered were observed through a spotting scope to verify the presence or absence of leg bands. Upon re-sighting a color-banded bird, we recorded the location with a hand-held GPS.

Re-sighted longspurs were then monitored to facilitate recapture and retrieval of geolocator tags. Because territorial behavior among breeding Chestnut-collared Longspurs decreases with the onset of nesting [31], we attempted mist-netting only prior to nesting or for unpaired males. If a longspur was not captured using a mist net, we monitored the territory until the male was feeding young. We then used walk-in traps over the nests to capture these males.

2.2.2 Geolocators

We used three types of geolocators throughout this study. The nature of geolocator technological development is such that rapid advances are made and the device designs continue to evolve. For deployments in 2012, we used MK20S British Antarctic Survey (BAS) geolocators (0.7g; 15mm; 13°-angled light-stalk). In 2013, we used MK6740 geolocators made by Biotrack/Lotek (0.7g; 22mm; 13°-angled light-stalk). In 2014, we used Intigeo P50B1-7 geolocators (0.6g; 7-mm light pipe) from Migrate Technology. The geolocators used in 2012 and 2013 recorded ambient light levels at 2-minute intervals, whereas the tags deployed in 2014 recorded at 5-minute intervals. We deployed geolocators as follows: 7 in 2012, 6 in 2013 and 20 in 2014.

We used a Rappole-Tipton [32] harness to attach geolocators, with simple knots sealed with commercially-available cyanoacrylate glue. We used a flat tubular Teflon tape for harnesses, except for 2014, when we used net repair nylon from the British Trust for Ornithology. The shift in harness material was necessitated by the smaller diameter of attachment tubes in the Intigeo geolocators. Recaptured longspurs were inspected visually upon geolocator recovery for any abrasions or injuries from the tag.

2.3 Analysis

2.3.1 Light-level data processing

We analyzed the light data using custom geolocator-analysis software packages in R. Sunrise and sunset times were determined from raw light data by using the threshold method with the package SGAT [33]. Extensive shading of the tags by feathers and/or habitat precluded using the template fit (i.e. FlightR) analysis for position estimates [34]. The light threshold was set slightly above baseline value, i.e. total darkness, at 1 lux for the Intigeo tags or 1 unit for the British Antarctic Survey tag). We visually inspected the light data by using the R package TwGeos [35], and removed any false sunrises and sunsets. We calculated a sun elevation angle (a.k.a. zenith angle) by using functions 'solar', 'refracted', and 'zenith' in the package SGAT [33], based on input of light data from dates when individual birds were re-sighted at their breeding sites post-tag deployment, or until the end of July (on average, 52 d, range 21-79 d). Breeding site calibration indicated an average zenith angle of 95 (range 94.3 to 95.5). There were no significant differences in breeding area-calibrated sun elevation between tag models. Sunrise and sunset times ('twilight times') were then transformed into latitude and longitude estimates using the thresholdPath function (similar to the coord function in the R package GeoLight [36]). We disregarded latitudes for a period of 15 days prior to and after the autumnal and vernal equinox; however, we still examined patterns in longitude to infer movements during these times [37].

The tags deployed in 2012 (BAS tags) gave winter site location estimates within the expected range for Chestnut-collared Longspurs when using the breeding-site calibrated sun elevation. However, initial analysis of data from the Intigeo tags (7mm light 'pipe') produced latitude estimates >10° N of known winter range. Given that sun elevation angles can be dramatically affected by shading of habitat, weather, and bird behavior/feathers, we determined a winter-site sun elevation by deploying two Intigeo tags in Chestnut-collared Longspur overwintering habitat near Janos, Chihuahua, Mexico (30.844024° N, 108.470051° W) 17 January-31 March, 2016. One tag was attached to a fence post (fully exposed) and one was tied to a wire pin flag (partial vegetation shading). These tags experienced similar weather and habitat (i.e. tall grass) to that which overwintering Chestnut-collared Longspurs would experience, and the zenith angles calculated from these tags produced much lower values (91.7) than the breeding site calibration. We used these Mexico-calibrated sun elevations to calculate wintering sites and fall migration locations for all subsequent analyses, and obtained latitudes that were within the expected range for this species. We used consistent shifts in longitude of >2° to infer movement away from stationary sites and calculate time spent at winter sites and on migration. Winter locations were calculated as average latitudes and longitudes for the entire winter period (excluding equinox periods). Kernel densities of wintering points were plotted by using the kde2d function from the MASS package in R [38], using the normal (Gaussian) reference bandwidth. Analyses were conducted using R version 3.3.1 [39].

2.3.2 Assessment of wintering ranges of endemic grassland songbirds

We assessed the amount of overlap among species wintering distributions by overlaying species distribution maps. These were then refined by habitat classification, removing areas classified as unsuitable habitats. To generate a minimum estimate for remaining habitat for the Chestnut-collared Longspur and co-occurring endemic grassland songbird species, we refined the species range data provided by the "Seasonal" attribute in the BirdLife International data set of NatureServe [40] and a map of the Commission for Environmental Cooperation's definition of the Chihuahuan Desert biome [41]. These species maps are very generalized and include broad areas linking distant observations with little consideration for vagrancy. To add consideration for habitats, we excluded sub-ecoregions (and portions thereof to keep borders simple) that were not predominantly grassland or desert. Specifically, we clipped the following sub-ecoregions: Arizona/New Mexico Mountains, Sierra Madre Occidental with Conifer, Oak, and Mixed Forests, and the Sierra Madre Oriental with Conifer, Oak, and Mixed Forests [42]. We repeated this process for the other four endemic grassland songbirds that co-occur with the longspur (Sprague's Pipit, McCown's Longspur, Lark Bunting, and Baird's Sparrow). We verified range use by inspecting 2004-2014 observation records from the Breeding Bird Survey [2] and eBird [43]. We also further refined the estimated range for the Sprague's Pipit by deleting isolated pockets of winter range separated from the contiguous block by 100-500km. These areas (see Figure 1, Utah, Nebraska, Illinois, South Carolina, and Florida) were included by [40] due to low, but semi-regular records of vagrancy with very low densities, see [23].

We then examined the impacts of land conversion on longspur habitat within the refined species winter ranges by expanding the Plowprint [3], an annually updated accounting of cropland assembled from satellite-derived data collected by the US Department of Agriculture (USDA) and Agriculture and AgriFood Canada, to include the portion of Arizona within the Chestnut-collared Longspur winter habitat and added cropland data for Mexico. For Mexico, we extracted all agriculture land cover types from the Instituto Nacional de Estadística y Geografía's layer of Land Use and Vegetation (Uso del Suelo y Vegetación - Serie V) [42]. Though this layer certainly under-represents the extent of area that has been historically impacted by agricultural conversion, it presents a minimal estimate for the amounts, densities, and locales of cropland.

We also assessed overlap of the overwintering distributions of Chestnut-collared Longspurs with the four at-risk endemic grassland songbirds and the existing areas identified as Grassland Priority Conservation Areas (GPCAs) by the Commission for Environmental Cooperation (Figure 1), including Marfa, Valles Centrales, Janos, New Mexico Bootheel, and Otero Mesa [41]. GPCAs range from those with near complete (Cuatro Cinegas) to zero protection. In all, the GPCAs comprise nearly 16.5 million ha, of which only 5% or 816,358 ha is protected [41]. As the primary remaining areas of intact grassland habitat, the GPCAs support a high abundance of wintering grassland bird species [41]. Other lands with suitable habitat occur in the wintering range; these have variable protections, ranging from none, to partial (e.g., US Federal lands that allow leases for energy extraction), to complete (e.g., Organ Mountains-Desert Peaks National Monument), but are generally more fragmented and smaller than the GPCAs.

3 Results

3.1 Returned birds

Fourteen (33%) of the 43 banded (10 birds had bands only) and geolocator-tagged (33 birds) Chestnut-collared Longspurs returned. From a sample of 33 tagged males (three were tagged again after recapture in a subsequent year), 11 birds were re-sighted between years. Eight of the 11 tagged and re-sighted birds were recaptured, however one bird lost its tag and we retrieved a total of seven tags (one BAS tag in 2013, two Lotek tags in 2014, and four Intigeo tags in 2015). Some Intigeo tag batteries failed while the birds were at their wintering sites (n=2) and during spring migration (n=1), thus winter site occupancy and spring migration data were only available for five and four of seven individuals, respectively (Table 2, Figure 2). No birds exhibited obvious ill-effects associated with geolocators other than the areas along the upper thighs were missing several feathers.

3.2 Migration phenology

Birds remained at the breeding site post-deployment, and departed on fall migration on average Oct 3 ± 2.5d (Table 2, Figures 3-4). Geolocator estimates of location when birds were still at the breeding site averaged 72km away from the deployment site (range of 12-120km). Fall migration duration averaged 41 ± 5.0d and ranged between range 26-56d (Table 2). Birds generally traveled east before heading south and all individuals migrated east of elevational barriers such as mountains and high elevation areas (Figure 2). Birds arrived at their overwintering sites between 1 Nov and 4 Dec, and remained at winter sites 123 ± 6.1d until departure on spring migration on average by Mar 15 ± 7.3d (n=4). Birds returned to their breeding sites between Apr 22 and May 15, with an average migration duration of 42 ± 6.6d. One individual that left relatively early, on Feb 22, spent about two weeks longer on spring migration (59d vs. 27-42d).

3.3 Migration routes

Most birds travelled along the Central Flyway, east of their breeding sites then south during fall. Equinox black-out periods for latitudes and poor-quality data due to light sensor shading, a known limitation to geolocation, obscured routes for individual 2014-15A. All six birds with clear fall migration locations flew west to their wintering location such that each bird flew an arc-shaped path between breeding and wintering locations (Figure 2). For birds where spring data were available, it appears that they reversed their fall route in spring, travelling northwards up the Central Flyway and west to their breeding site. There was no obvious pattern of loop migration. The bird with the clearest data (from the stalked BAS tag) showed almost complete overlap between spring and fall routes through the US portion of the Central Flyway (i.e. south

Table 2. Migration timing and duration for seven male Chestnut-collared Longspurs *Calcarius ornatus* tracked using geolocators. NA indicates that data were not available due to tag failure before initiation of spring migration or poor quality light data.

Bird ID (tag)	**Fall depart**	**Fall duration (d)**	**Winter arrival**	**Winter duration (d)**	**Spring departure**	**Breeding return**	**Spring duration (d)**
2012-13 (BAStrak)	30 Sep	36	4 Nov	136	21 Mar	2 May	42
2013-14A (Lotek)	5 Oct	56	30 Nov	115	26 Mar	5 May	39
2013-14B (Lotek)	8 Oct	26	3 Nov	112	22 Feb	22 Apr	59
2014-15A (MigrateTech)	3 Oct	NA	NA	NA	NA	NA	NA
2014-15B (MigrateTech)	2 Oct	30	1 Nov	NA	NA	NA	NA
2014-15C (MigrateTech)	22 Sep	46	7 Nov	130	18 Mar	15 Apr	27
2014-15D (MigrateTech)	13 Oct	52	4 Dec	NA	NA	NA	NA
Mean (SE)	3 Oct (2.5)	41 (5.0)	8 Nov (7.3)	123 (6.1)	15 Mar (7.3)	26 Apr (4.6)	42 (6.6)

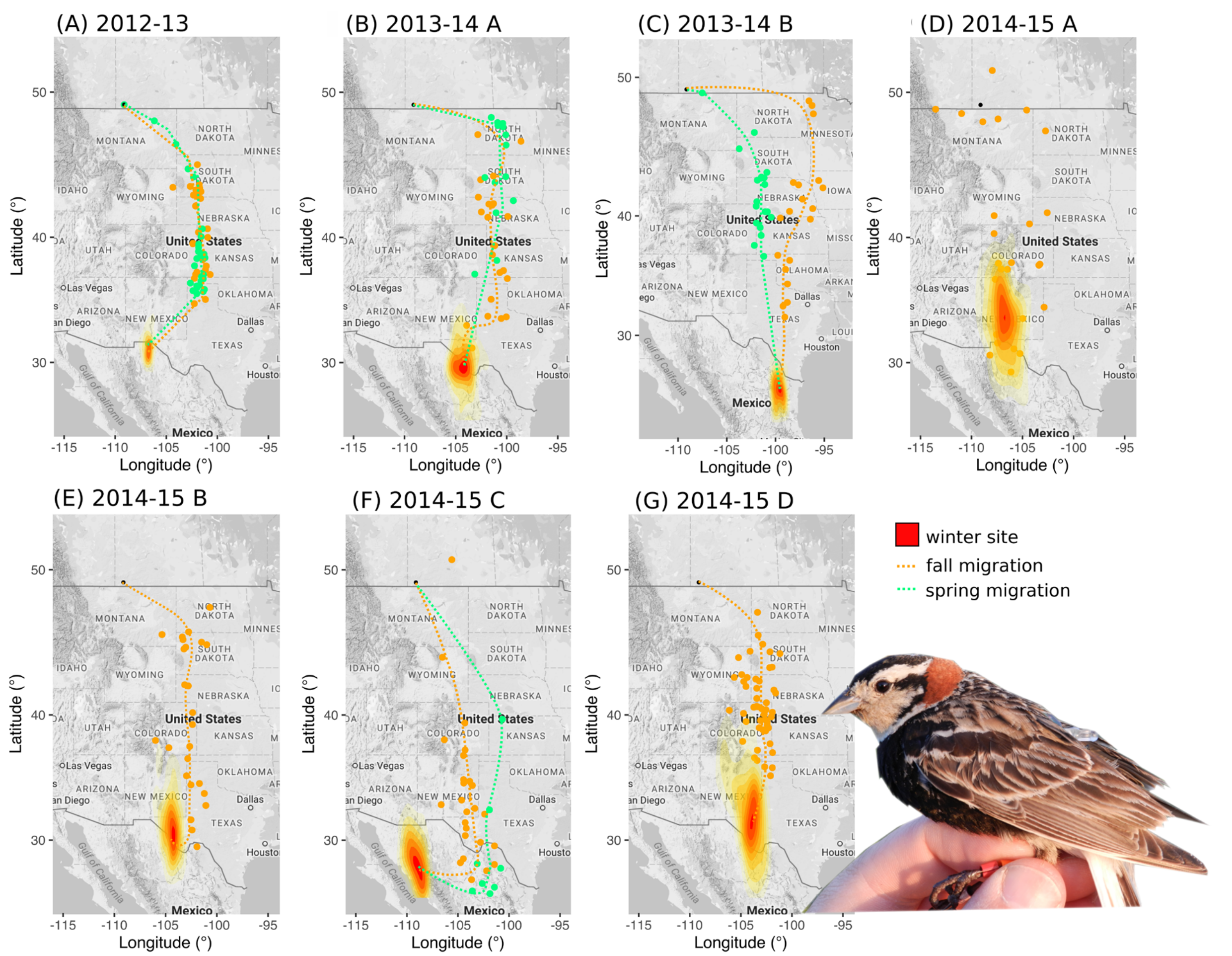

Figure 2. Individual maps (A-G) of migration and wintering locations for seven male Chestnut-collared Longspurs captured as breeding birds in southern Saskatchewan, Canada, 2011-2014. Locations were derived using the threshold method (see text for details) and routes are estimated based on locations (circles) during the migratory period, not including the equinox blackout period when latitudes could not be estimated. Winter sites are shown as kernel densities of estimated locations. Inset photo shows a male Chestnut-collared Longspur harnessed with a light-pipe archival geolocator tag. Please note that map C is slightly zoomed out relative to the other maps, due to a wider range of locations estimated for this individual.

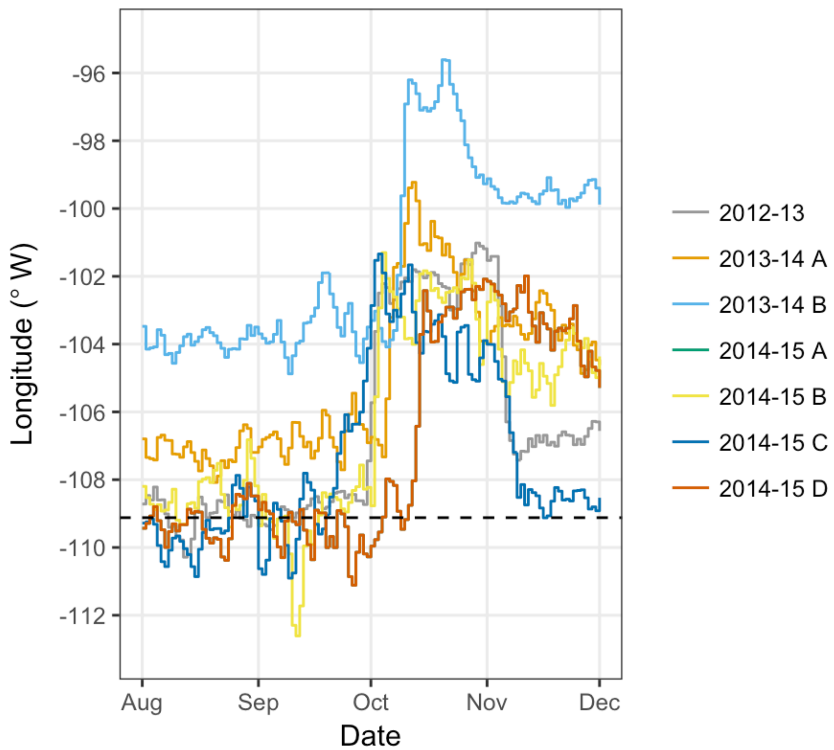

Figure 3. Longitudinal movements during fall migration of seven male Chestnut-collared Longspurs captured as breeding birds in southern Saskatchewan, Canada, 2012-2014. Dashed line depicts longitude of breeding location. All birds migrated along the US-portion of the Central Flyway, east of their breeding site.

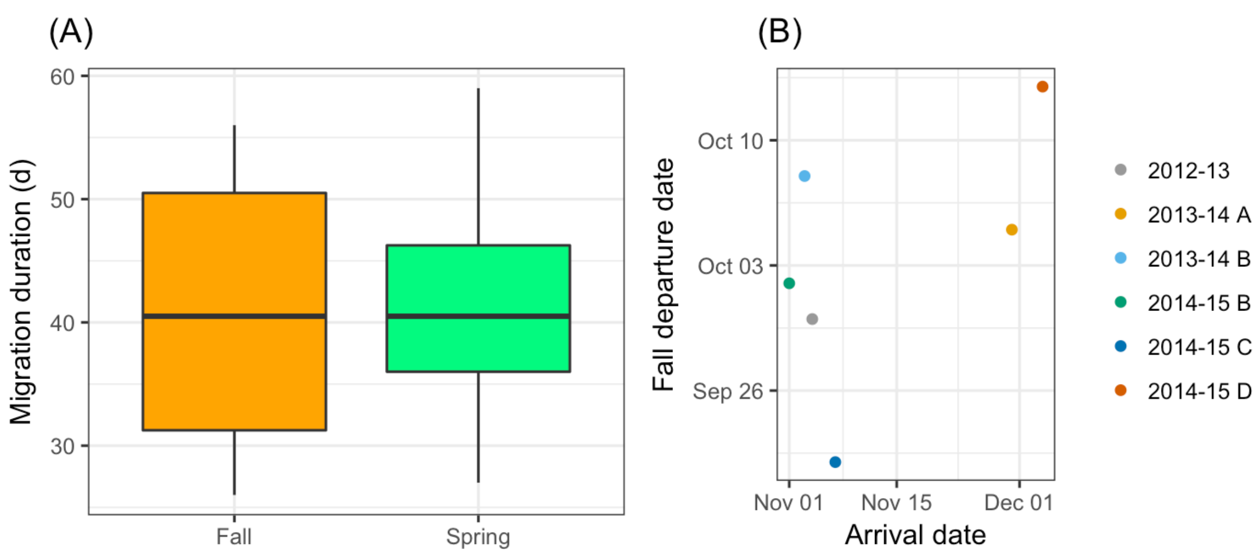

Figure 4. Migration timing of seven male Chestnut-collared Longspurs captured as breeding birds in southern Saskatchewan, Canada, 2012-2014: (A) durations of fall and spring migrations and (B) fall departure dates relative to winter site arrival dates.

through the Dakotas, Nebraska, Colorado, and Texas). Birds appeared to stopover at 3-5 distinct sites in fall, and 2-4 sites in spring, although we were not able to pinpoint the exact locations of stopovers, a limitation with continental light-level geolocation.

3.4 Winter sites

All birds overwintered in the southwestern US (New Mexico, Texas, and one bird possibly in southern Colorado) or northern Mexico (states of Chihuahua, Coahuila, and, for one bird each, possibly Sonora or Sinaloa, and Tamaulipas) (Figure 5). Overall, the winter sites for these seven males were spread over the entire wintering range (Figures 1-2 and 5), although 3 birds wintered at around -109°W (2013-14A, 2014-5B, 2014-15D) and two at around -107°W (2012-13 and 2014-15A). Birds 2014-15C and 2013-14B wintered distinctly west and east of the others, respectively (Figure 5). Wintering locations were based on an average of 109d (range: 80-122d) of recorded light data. Variation in readings occurred with average standard deviations of +2.95°N (range: 1.47-3.69°N) latitude and +0.931°W (range: 0.494-1.34°W) longitude.

3.5 Wintering ranges relative to other grassland songbirds

Through refining estimates for the Chestnut-collared Longspur winter range by reducing the range estimate to potentially suitable habitat, we found a difference of 99,852km^2 (Figure 6). Using this refined area estimated for Chestnut-collared Longspur winter range (1,338,650km^2), we calculated extensive overlap with the wintering ranges of the Baird's Sparrow (99%) and McCown's Longspur (88%) (Figure 7). Wintering ranges for the Lark Bunting (69%) and Sprague's Pipit (63%) exhibited considerably less overlap with the Chestnut-collared Longspur (Figure 7). Applying agriculture data to the refined estimate for Chestnut-collared Longspur winter range, we found that, since 2013, an estimated 258,040km^2 (19%) of potential habitat was planted into agricultural row-crop production.

4 Discussion

4.1 Winter sites

We documented the year-round locations of a migratory songbird endemic to the Great Plains, the Chestnut-collared Longspur (Figure 2). All seven male Chestnut-collared Longspurs migrated along the US-portion of the Central Flyway and wintered in the southern Great Plains, consistent with the expected wintering range for this species [39] (Figure 2).

While tracking birds from only one breeding population does not allow us to make any conclusions

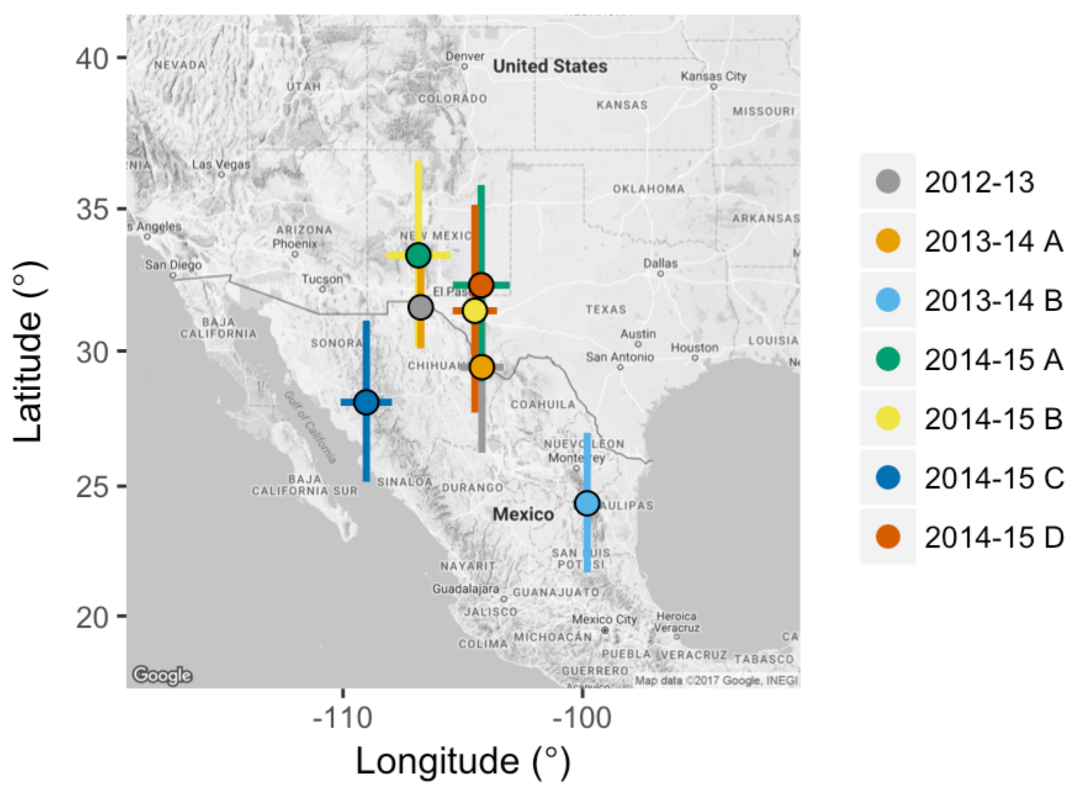

Figure 5. Wintering sites of seven male Chestnut-collared Longspurs in the southern USA and northern Mexico. Points show mean locations, with lines extended to standard deviation for latitdue and longitude, respectively.

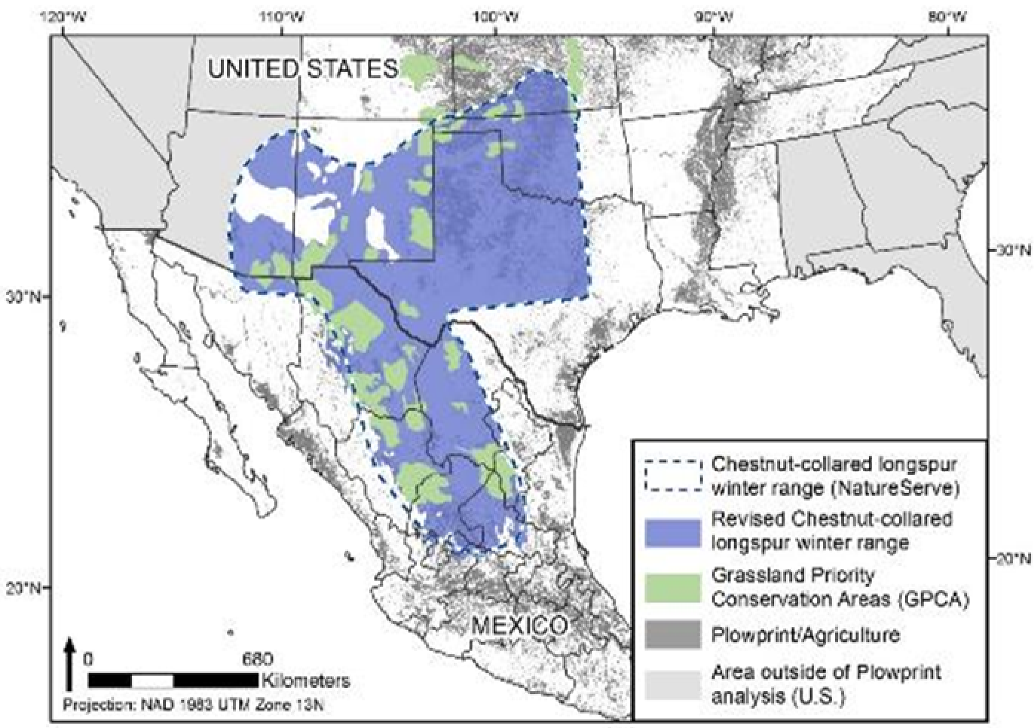

Figure 6. Map of estimated Chestnut-collared Longspur winter range [40], refined estimated range considering habitats [42], Grassland Priority Conservation Areas [41], and agricultural land cover; Mexico: [41]; USA: [3].

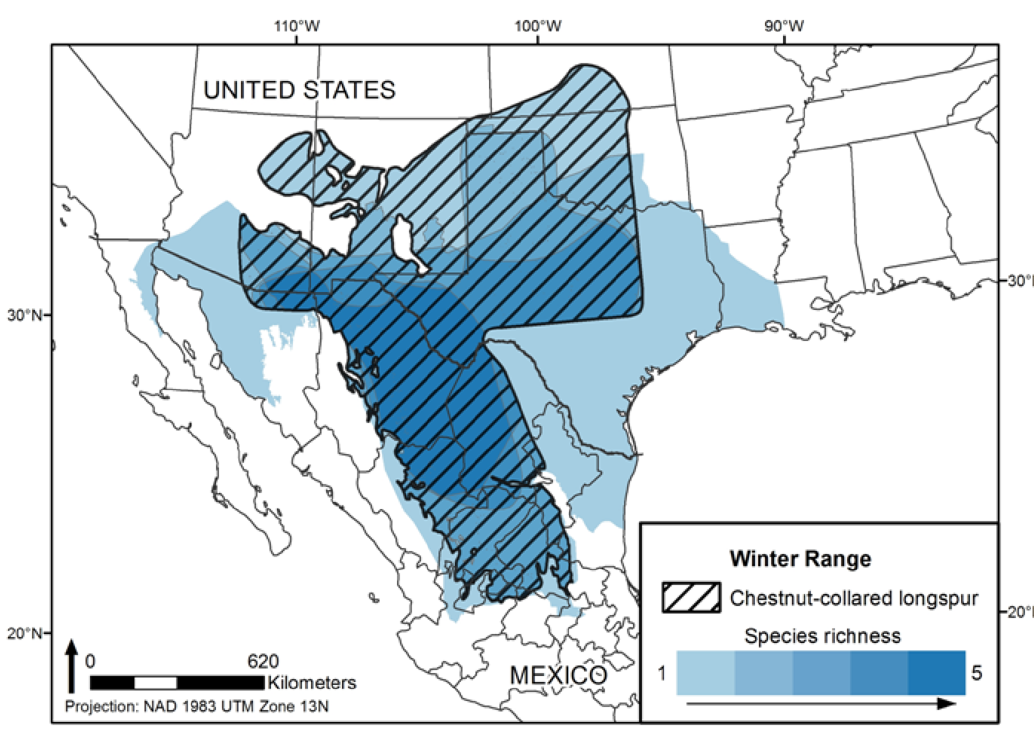

Figure 7. Species richness map of the wintering distributions of the four songbirds endemic to the Great Plains that co-occur with breeding Chestnut-collared Longspurs [40], with ranges as refined in this study (excluded inappropriate sub-ecoregions).

about migratory connectivity, we did find that the individuals we tracked wintered in geographically disjunct areas up to > 1,200km apart (Figures 2 and 5). This can be defined as high population spread, *sensu* [44], and often promotes inter-population mixing on the nonbreeding grounds, and thus, weak migratory connectivity. Given that the overall migration distance of this species is only about 2,000km, the distances among wintering birds suggests a biologically meaningful difference in wintering areas. Chestnut-collared Longspurs did not overwinter in any one political or biogeographic region: three (43%) of the seven centroids for individual winter range estimates were in the U.S., two (29%) were along the U.S.-Mexico borderlands, and two (29%) were well within Mexico (Figure 5). Five (71%) of the seven estimates were within the Chihuahuan Desert.

This complicates efforts to prioritize areas for conservation of this species, because birds from breeding populations in Canada and the US likely overwinter in widely dispersed locations (Figures 1 and 5). Thus, areas of wintering habitat are relatively equal in potential conservation value to population-level genetic diversity because birds from multiple breeding populations are intermingled. Combined with the apparent mobility of large flocks on wintering grounds [11] and climate based projections for habitats [10], we recommend that both the US and Mexico should act to maintain grasslands in wintering areas. Wintering areas in both countries are largely unprotected through a lack of public policy [45] and enforcement of grassland conservation policies [5, 46]. Moreover, Mexico should review the political and socio-economic importance of these species, and consider federal protection for them, as the US and Canada already impose domestic restrictions associated with any legal status for these species in their breeding areas (Table 1, federal and provincial status in Canada and state species of concern and US FWS Candidate Conservation Agreements in the US). In Mexico, precedent already exists as several species occur only as non-breeding migrants and are federally protected [47]. Moreover, some of these species have population sizes similar to or greater than those for the endemic grassland songbirds (e.g., Sandhill Crane [*Grus canadensis*], Tundra Swan [*Cygnus bewickii*], and several *Buteo* species).

Since 2013, at least 258,040km^2 (19%) of intact habitat in the winter range of the Chestnut-collared Longspur (Figure 6) has been planted with annual crops. Solely within the Valles Centrales GPCA, 692.4km^2 of land was converted, as determined via remote sensing, exceeding the amount of land that had been permitted for land-use change to cropland, according to government records, by > 2,000% [5]. Based on the rate of land conversion, Pool et al. [5] projected that the ongoing expansion of ground-water irrigated cropland could eliminate the remaining low-slope valley bottom grasslands from the Valles Centrales region by 2025. Therefore, more efforts to maintain intact habitat and to enforce the protected status of GPCAs, where applicable, are needed to facilitate conservation of the Chestnut-collared Longspur and associated imperiled grassland bird species, see also [46].

4.2 Pace of migration

Chestnut-collared Longspurs tracked with geolocators initiated fall migration in Sept-Oct, similar in timing to observed departure dates for the species departing the Canadian prairies [48-50] and the northern US [51]. Our findings suggest that western grassland bird migration timing may be slower than the more commonly tracked eastern songbird species [52,53], and that more information is needed on habitat requirements during this understudied period. This is particularly so as a slow migration would entail the need for more stop-over habitat along their migration routes than a long-distance migrant would require; long-distance migrants move much farther and depend on energy stored as fat across a few days whereas a 2-month migration, making multiple stops or makes ‘hops’ in migration *sensu* [27], is more dependent on feeding during migration, see [28]. The slow pace of spring migration in this species (Table 2, Figure 3), appears atypical compared to other migratory songbirds [52].

Both fall and spring migration were similar in duration for Chestnut-collared Longspurs, although our spring data were limited to only four birds with complete migration. The pace of fall migration is often relatively slow in migratory songbirds, while spring migration is usually considerably faster [52,53, but see 54]. This is presumably because of fitness benefits of early arrival at breeding sites [52]. However, longspurs took more than a month to cover ~2,000km, averaging < 50km/d. We know little about migration for western grassland species, but it may be that a slower pace in spring is more typical of this group and/or the species may be capable of migrating at a faster pace under certain conditions [52]. Frequent harsh weather in the northern prairies can cause stronger selection against arriving too early at breeding sites, resulting in a slower spring migration pace overall. Indeed, such conditions are what migrants avoid through migration and even part-time exposure can be detrimental [17,55]. Further research into migration strategies of western grassland birds may provide insight into the ubiquity of this pattern, as well as causal mechanisms. We note that the Chestnut-collared Longspur is a part of a lineage that survived climate extremes of the Pleistocene [56] and that further studies of the impacts of climatic variation, both past and present, are needed. Our research on this population from Saskatchewan, toward the northern limit of the species range, should be complemented with future studies of more southern breeding populations such as those in Wyoming and Colorado.

4.3 Implications for conservation

The use of multiple stop-over sites and different sites between and likely within winters complicates grassland bird conservation as no subset of GPCAs will provide for all the species across multiple years (Figures 1 and 7) [41]. GPCAs within the Chestnut-collared Longspur wintering range vary in size from the 2.7 million ha Valles Centrales to the 153,098ha Cuatro Cienegas [57]. This scale of habitat need exceeds that provided under traditional forms of land protection [58]. We suggest that programs (e.g., U. S. Department of Agriculture Natural Resources Conservation Service, Quivira Coalition, World Wildlife Fund's Sustainable Ranching Initiative, National Audubon Society's Conservation Ranching Program, etc.) that can help ranching families continue to graze cattle and, thus, keep land in grass, are a more cost-effective long term strategy for maintaining grassland bird habitat in the region. Among grassland birds, population densities are generally higher on wintering grounds [5] and great variation in habitat occurs (depending on grazing, fires, and precipitation); therefore we cannot create effective demographic models nor assess the relative importance of breeding, migration, and wintering areas without identifying population-level migratory connectivity [59] and completing full annual cycle models [*sensu* 60]. For these reasons, we encourage further study of grassland bird migrations and, in particular, point to how GPS-based devices [*sensu* 34], programmed to record precise locations based on dates of migration identified by this study, can provide the resolution of data required to help guide conservation efforts for these rapidly declining species.

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