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# A TALE OF FOUR SPURS: HABITATS, DISTRIBUTION, ABUNDANCE AND MOVEMENTS OF OKLAHOMAS WINTERING LONGSPURS AND THEIR CO-OCCURING SPECIES

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By

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# A TALE OF FOUR SPURS: HABITATS, DISTRIBUTION, ABUNDANCE AND MOVEMENTS OF OKLAHOMAS WINTERING LONGSPURS AND THEIR CO-OCCURING SPECIES

A DISSERTATION APPROVED FOR THE
DEPARTMENT OF BIOLOGY

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**Abstract**

Grasslands are the most threatened ecosystem in North America and have been consistently reduced since the settlement of Euro-Americans through the conversion to farmland. This drastic loss in habitat is why grassland birds have suffered worse population declines over the past fifty years compared to other bird guilds. There is growing evidence that survival during the nonbreeding season has a strong influence on the population trends of migratory species. Therefore, understanding winter survival of migratory grassland bird species may be central to their conservation. Chestnut-collared ((*Calcarius ornatus*): hereafter CCLO) and Thick-billed Longspur ((*Rhynchophanes mccownii*): hereafter TBLO) are extreme examples of recent population reduction with an 89% and 86% population reduction from 1966-2017. Though prior studies and first-hand expert knowledge exists about longspur wintering ecology, there remain some major research gaps. In Oklahoma and the entire Great Plains there are fundamental unknowns concerning the habitat needs, mortality risks, flocking behavior, and seasonal movements of at-risk longspur species.

This dissertation focuses on answering several baseline questions about the wintering ecology of longspurs and their co-occurring grassland bird species. These questions include: *What are the distributions of wintering grassland birds in Oklahoma and the Texas Panhandle (i.e., Southern Great Plains)? How do the densities of the most common grassland birds differ across different sites? How do those densities change throughout and between winters?* W*hat landscape level variables affect distributions and predict species richness and diversity.* To answer these questions, I use multiple techniques including surveying for all grassland bird species using distance sampling walking transects spread out across 14 field sites in Oklahoma and the Texas Panhandle. Using points collected with distance sampling I was able to map the

distributions of potentially suitable habitat. I also sought to determine: *What fine-scale habitats longspurs use? How those habitats change across different study sites?* W*hat management actions could be beneficial to longspurs to improve their wintering habitat?* To answer these questions, I used the longspur point locations to sample the horizontal, vertical, and species composition characteristics of the vegetation that longspurs were actively using and compared those characteristics to the vegetation characteristics that was available. Additionally, I sought to address: *How do individual CCLO use space throughout the winter?* W*hat are the sex and age ratios that CCLO have in Southwestern Oklahoma?* For this I captured and tracked individual CCLO with VHF radio-transmitters at the Wichita Mountains Wildlife Refuge.

The first Chapter aims to quantify the recent disparity and to explain why there is one in the number of publications between the seasonality of avian research with regards to breeding and non-breeding. I analyzed publication disparity over the last decade (2010-2020), and expanded on the quantification of seasonal bias using two approaches: 1) a traditional literature review of the avian research published in multiple North American ornithological journals, and 2) various text analyses to automate and explore the literature. I found that the disparity between studies of the breeding and non-breeding grounds has not changed within the last decade, and that the publication of studies on breeding continues to far outpace that of studies on non-breeding. Wintering research emphasized more rudimentary and less involved topics such as species distributions, compared to breeding research, which often included predation rates and nest success. I also proposed various reasons for this bias and proposed potential solutions for overcoming those biases.

Chapter 2 addresses the need to understand the distribution and densities of grassland birds within the Southern Great Plains. I used distance sampling walking transects across 14

different sites for three winters (2018-19, 2019-20, 2020-21), throughout the three major grassland ecotypes (shortgrass, mixed-grass, and tallgrass prairies) in Oklahoma and Texas Panhandle. I used this data to determine the density and distribution of grassland birds across space and time. I detected 27,166 individuals of 69 species of grassland bird over the three years of the study. I found that many grassland birds exhibit both inter- and intra-seasonal variance in their densities at various sites. At landscape levels most species were negatively associated with shrubs and positively associated with percent of grassland on the landscape, and several species of longspur, including CCLO and TBLO, were positively associated with wider diurnal temperature ranges. My findings can improve management and conservation of critical grassland areas within the Southern Great Plains and will increase the amount of important non-breeding habitat for many declining grassland bird species.

For Chapter 3, I quantified the fine-scale habitat characteristics that the four species of longspur use during winter. The Southern Great Plains is an excellent region for studying the habitat differences between the species as the non-breeding ranges of all four longspur species overlap in this region. My study encompassed large, representative tracts of the three major types of prairie ecosystems (i.e., shortgrass, mixed-grass, and tallgrass prairies) that intersect within the Southern Great Plains. I evaluated the relationship between wintering longspur occupancy and the fine-scale habitat characteristics using a combination of standardized bird surveys and paired occupied-random vegetation plot sampling. Using both randomization tests and classification trees, I characterized longspur habitats and compared associations across the three prairie ecosystems. Habitat use varied among all species, departed at very fine scales, and species' associations shifted across grassland types. These findings can be applied to the

management of grasslands to help develop full-life cycle conservation plans for CCLO and TBLO.

The final Chapter focuses on CCLO, as they are the most rapidly declining species of grassland bird in North America, experiencing an 89% population decline during the last five decades. I determined the spatial scale at which management would need to occur to properly manage for the species. I captured and tracked individuals during the winters of 2018-19 and 2019-20 at the Wichita Mountains Wildlife Refuge and calculated their home ranges as both Minimum Convex Polygons (MCP) and Fixed Kernel Density Estimates (KD). Across the two years I captured and banded 116 CCLO (roughly 75% male) and fitted 90 of these with VHF radio transmitters. The winter (December 5 through March 8) home ranges defined by MCP averaged 128.8 ha, while the 95% KD indicated a mean of 29.87 ha. Wintering CCLO used larger areas and displayed higher nomadism than what has been reported for other co-occurring grassland bird species. Therefore, management for this species scales beyond the relatively small areas that longspurs aggregate into flocks within, and will require landscape-level coordination to maintain habitat adequate for effective winter population.

# Chapter 1: Quantifying and Explaining Bias in the Seasonality of Ornithological Publications

John A. Muller and Jeremy D. Ross

*Formatted as a "Perspectives" article for submission to Ornithology*

**Abstract**: Information about the full annual and life cycles of birds is necessary to mitigate the decline of threatened species and develop comprehensive conservation strategies. to develop these strategies, we must overcome seasonal biases in which the stages of bird annual and life cycles are represented in the published research. Because of the need for full life cycle research, there is a problematic disparity in the amount of research conducted, and therefore in the amount of accumulated knowledge, about birds between the breeding and non-breeding seasons, with a much greater prevalence of breeding biology studies in the literature. We updated the previously established extent of this disparity by evaluating seasonal biases in ornithological research published between 2010-2020, and expanded on the quantification of seasonal bias using two approaches: 1) a manual review of the literature published in top ornithological journals, and 2) automated text analyses to explore literature reviews. We found that the disparity between studies of breeding and non-breeding grounds has not changed within the last decade, and that the publication of breeding studies continues to outpace that of non-breeding studies. Wintering research emphasized less involved topics, such as species distributions which often only requires presence data, while breeding research, often included rates of predation and nest success which requires more in-depth research following individual birds. We also explored various causes and potential solutions for why this disparity exists, including ecological, institutional, and social explanations, such as the conduciveness of breeding behaviors to bird detection, the constraints of the academic calendar, and the impacts of Seasonal Affective Disorder, respectively. Our

study demonstrates the utility of text analysis, a tool that is infrequently used in ecological research, for exploring trends and disparities in publications our findings underscore the need for more research on the wintering and migratory periods of the annual cycle, either through *in situ* field studies or remotely through indirect methods.

**Patterns of seasonal bias?**

The complex annual cycles of migratory birds are divided among several phases (e.g. breeding, migration, and overwintering), each with its own potential hazards and benefits. Studies that focus on breeding or the breeding season make up the majority of the published literature on migratory birds, even though most of the birds' life cycles are allotted to the non-breeding phases (Herkert et al. 1996, Marra et al. 1998, Igl and Ballard 1999, Sillett and Holmes 2002, Newton 2004).

The extent of the disparity between breeding and wintering avian research has been calculated before by Marra et al. (2015), whose literature review found that there were just over 4 times as many peer-reviewed journal articles about breeding ecology as wintering ecology, and about 2.5 times as many breeding as non-breeding (winter + migration) articles. Although there have been calls for more non-breeding studies (Faaborg et al. 2010, Marra et al. 2015), and many studies have shown the importance of the non-breeding periods on the population trends of migratory species (e.g., Morrison et al. 2013, Rushing et al. 2016, Macías-Duarte et al. 2017, Woodworth et al. 2017, Akresh et al. 2019), the majority of avian research is still biased towards studies of the breeding period. Both the Faaborg (2010) and Marra et al. (2015) papers have hundreds of citations, therefore we attempt to see if these papers affected the trend in seasonal bias and changed the bias towards more wintering studies per breeding study.

We performed a literature review of three top North American avian journals: Ornithology (formerly Auk), Ornithological Applications (formerly Condor), and Journal of Field Ornithology (JFO). We reviewed all published research articles, excluding review articles, from 2010-2020 to determine the avian life cycle stage in which the studies were conducted (breeding, migration, or wintering). For example, an article exploring metabolism of females during incubation would qualify as a "breeding" study, whereas research on the wintering distribution of a species, even if dataloggers were deployed and retrieved on the breeding grounds, would be considered a "winter" study. Some studies spanned multiple life stages and were therefore counted towards each represented category. Publications describing methods applicable to breeding, migration, and winter were included, but those that were cross-applicable were not. Articles that did not fall into these categories (e.g., those using museum specimens, fossils, genetics, and community science data) were not included in the analysis.

Between 2010-2020, Ornithology, Ornithological Applications, and JFO averaged 3.6, 2.9, and 2.6 times as many breeding articles as non-breeding articles, and 9.1, 6.3, and 5.0 times as many breeding articles as winter articles, respectively. We performed a linear regression on the breeding:nonbreeding ratios to determine whether the bias ratio decreased across the decade, but trendlines were generally flat and the $R^2$ values were insignificant (Figure 1).

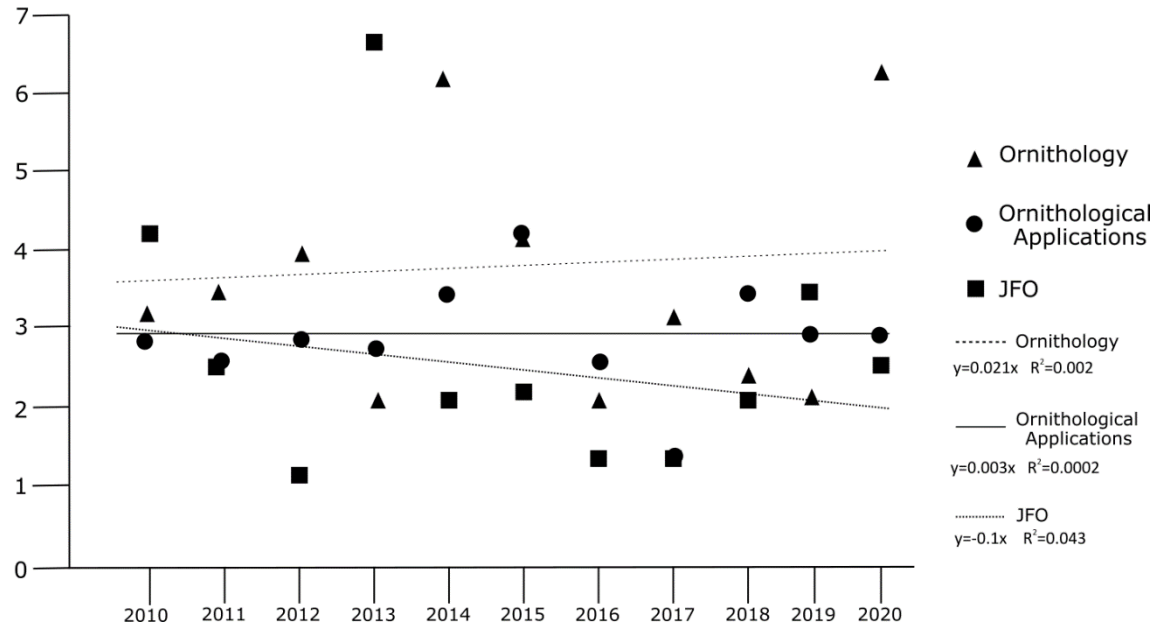

Figure 1. The ratio of breeding to non-breeding papers published in the three Journals (Ornithology, Ornithological Applications, and the Journal of Field Ornithology). Trendlines across the decade were derived from linear regression.

Text Analysis: In December 2020, we used Web of Science to search and download all of the abstracts of articles pertaining to a certain general search (e.g. “grassland bird”, “California bird”). All abstracts were combined to create a collection of words, generally referred to as a “corpus”. We then cleaned the corpus by removing punctuation, numbers, extra spaces, and stop words. Then combined synonyms relating to one season or another, for example we changed (breeds, breed, nest, nestling) to “breeding”. We used various text analysis packages on those abstracts including both the tm (Feinerer 2008) and topicmodels packages (Grun et al. 2011) in Program R Version 3.5.1 (r core team 2018). We did simple analyses including how many abstracts contained the word “breeding” or “wintering”, as well as which terms were most frequently found within the corpus. We also conducted various Topic Model analyses (Blei 2012). Topic models is a text mining method used to determine correlations and associations within a corpus. We tested to see what words are associated with a selected target words (i.e. breeding, winter). The topicmodels package can also be used for basic displays of information such as wordclouds and histograms of the most common words occurring within the corpus (Figure 2).

Text analysis has been used to discover trends in publications and research gaps (Westgate et al. 2015, Busch et al. 2020). In order to keep the amount of data manageable, we limited our abstract downloads to just six US states. The states we choose have large state

universities that span a broad spatial area of the US (Alaska, California, Colorado, Florida, Ohio, and Texas). Of the 16,089 abstracts there are 2.7 times as many breeding papers as wintering papers. Our analysis also showed that among breeding publications the most common subjects were those dealing with fecundity (e.g., success (36%), predation (27%), survival (22%)) whereas the most common topics in wintering studies were those investigating distribution (e.g., grounds (27%)). Fecundity requires measuring many various aspects of breeding success which requires extensive field work, whereas distribution studies often requires point locations and remote data, which can be extracted from existing data. This implies that wintering research is still in a more basic research stage than breeding studies. We used text analysis to reveal a comparable discrepancy in publication bias when compared to manual literature reviews, and unexplored biases in the most commonly studied topics in breeding and winter studies, proving again the usefulness of Text Analysis in ecological work.

**How does seasonal bias potentially impact our understanding of carryover effects and conservation needs?**

Studying all life-history segments is crucial to conservation efforts not only because each segment contributes to an individual's survival and reproduction, and because circumstances in one segment may 'carry over' to affect survival and reproduction in the next (Harrison et al. 2011, Morrison et al. 2013, Rushing et al. 2016, Macías-Duarte et al. 2017, Woodworth et al. 2017, Briedis 2018). As more and more evidence points to the importance of carry over effects, full life cycle conservation planning has become a priority (Hostetler et al. 2015, Marra et al. 2015, Somershoe 2018). However, despite calls by Ornithologists and Ornithological organizations for more research into non-breeding periods (Faaborg et al. 2010, Marra et al.

2015), we continue to have a large disparity in the seasonality of research on migratory birds, with a disproportionate emphasis in the literature on breeding biology.

All 5 of the fastest declining birds in North American (Sauer et al. 2017) would benefit from increased research on their wintering life stage, as basic life history information is lacking for these critically declining species. For example, the wintering distribution of northern King Rail (*Rallus elegans*) is unknown (Pickens and Meanley 2020). Little is known about the wintering ecology of Black Swifts (*Cypseloides niger*) (Lowther et al. 2020); a Web of Science search showed only a single winter period paper (Beason et al. 2012) that was on wintering distribution. Bank Swallows (*Riparia riparia*) despite being one of the most studied swallow species in the world due to their circumpolar distribution, have very little basic winter life history is known (Garrison and Turner 2020). For Chestnut-collared Longspur (*Calcarius ornatus*), there are fundamental unknowns about winter habitat, migration stopovers, population connectivity and wintering social behavior (Bleho et al. 2020). The need for full life cycle conservation plans is great, and as we ornithologists continue to pursue research, we must include more full life cycle conservation strategies. To implement full life cycle conservation, we must conduct more research on the wintering and migratory periods either through *in situ* studies or remotely through alternative methods, as currently the insufficiency of wintering and migratory knowledge is inhibiting effective full-life cycle management of these species.

**Case Study (Grassland Birds)**

We chose grassland birds for a case study as they are the guild undergoing the highest rates of decline and are in high need of conservation and additional research (Brennan and Kuvlesky 2005, Rosenberg et al. 2019). Currently, the wintering knowledge of several rapidly declining species of grassland birds are lacking and, to adequately implement effective

conservation and management programs, increased knowledge from the wintering grounds is needed. Species such as Chestnut-collared and Thick-billed Longspur (*Rhynchophanes mccownii*), Sprague's Pipit (*Anthus spragueii*) and Lark Bunting (*Calamospiza melanocorys*) all have rapidly declining populations and limited knowledge of the wintering period (Sauer et al. 2017, Somershoe 2018), and have threats affecting them on the wintering grounds (Phillips 1964, Stotz et al. 1996, Desmond et al. 2005, Hill et al. 2014, Pool et al. 2012). But, there are fundamental unknowns (i.e., site fidelity, survival, habitat associations) about their wintering ecology that are affecting management (Somershoe 2018, Bleho et al. 2020).

A Web of Science search for "grassland birds" resulted in 3741 abstracts. Text analysis resulted in roughly 3.7 times as many abstracts containing the word breeding compared to wintering abstracts (Figure 2). Breeding season specific words such as "nest" (818) and "reproduction" (94), also occurred far more often than non-breeding season specific words like "migration" (102), or "stopover" (34) (Figure 2). The results of our Topic Models word association again showed that most associated words with the term "breeding" were fecundity related such as "success" (47%), "survival" (39%) and "predation" (36%), while the most associated words with the term "winter" were, "grounds" (28%) and "migratory" (18%). These results were very similar to the analysis for the six states, only with an even larger discrepancy, implying that wintering knowledge of grassland birds is even further behind with regards to seasonal bias than birds in general.

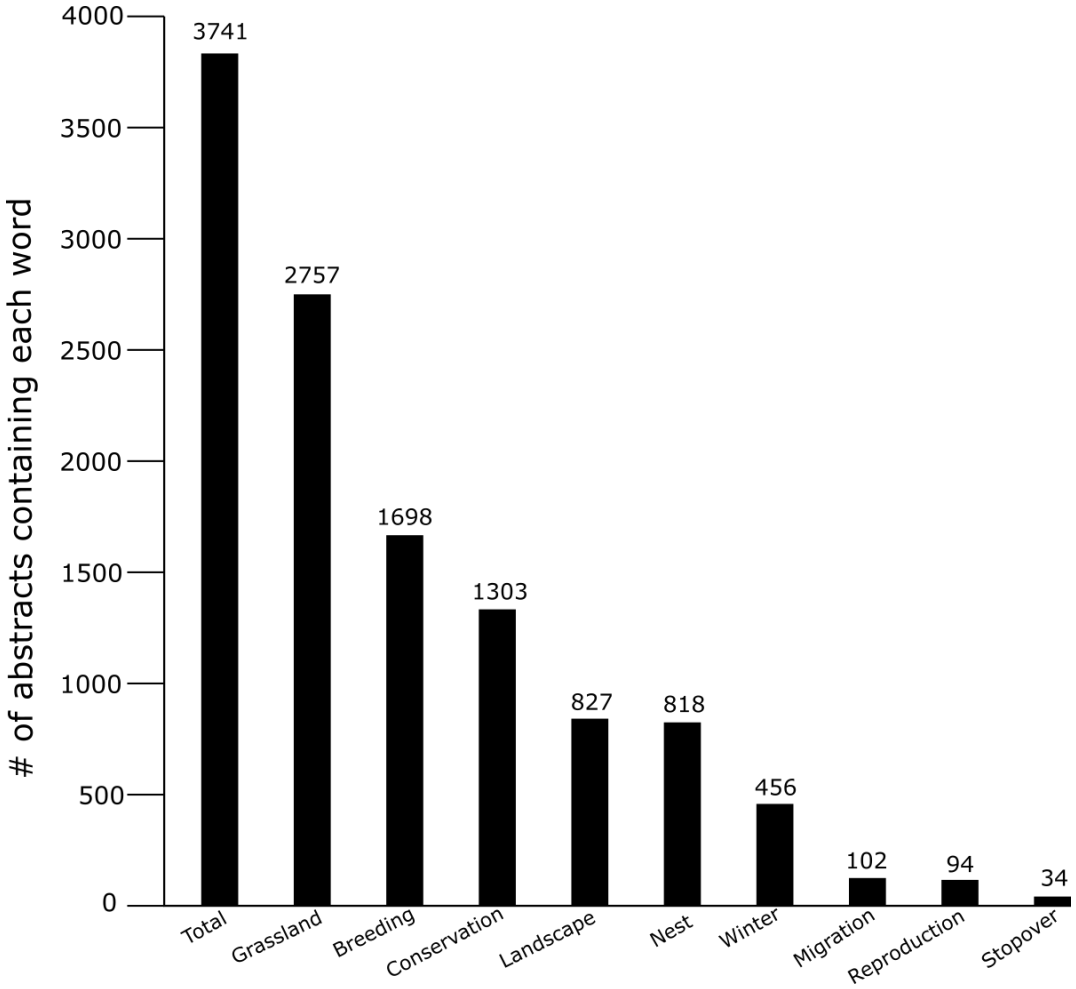


Figure 2. Histogram of the number of abstracts containing some of the most common terms contained in the grassland bird abstracts. The most common "breeding" specific terms ("nest" and "reproduction") compared to non-breeding specific terms ("migration" and "stopover") and the two terms of interest ("Breeding" and "Winter"). Also, included are general terms that showed high frequency ("conservation" and "landscape") from a Web of Science search for "Grassland Birds".

**What are the potential causes of seasonal biases?**

Although there are many possible explanations as to why the disparity and bias of seasonal publications exists, they are often only mentioned briefly or are poorly explored, if at all. We categorized these biases into the three categories we believe are most descriptive (institutional, ecological, or social in origin). None of these explanations were not explicitly

tested and are merely speculation on our part. We believe there are multiple institutional reasons contributing to the seasonal bias: First the academic calendar can play a major role in the discrepancy in seasonal studies due to the fact that there are typically many more days outside the classroom during the summer months when compared to the winter months. In the Northern Hemisphere universities using the semester system there are roughly three times as many days in between spring and fall (summer break) as the fall and spring (winter break) semesters. Winter seasons also include several holidays in an already time limited season. Conducting a field season, completing all required travel, and collecting sufficient data within the span of a month (duration between fall and spring semesters) is impractical for many projects. Academic freedom and flexibility are often touted as major selling points for academic careers, but academic institutions are lacking flexibility when it comes to the academic calendar to account for winter studies.

Second, species with different conservation statuses in different countries can provide incentive for studying the species in one country, but not in another. This potentially biases which season a species is studied if that species occurs in different countries. For example, Chestnut-collared Longspur, Thick-billed Longspur and Sprague's Pipit are all listed as threatened in Canada (COSEWIC 2019), with a large portion of their breeding range occurring within the country. But all three are unlisted in the United States and Mexico where their entire wintering range exists. This results in incentives such as research grants existing in the Canadian breeding range but not on the wintering grounds of the United States and Mexico. International "State" ownership also exists in countries and States where priorities for research and conservation may exist for resident or breeding birds but not for migrants or wintering species, as

there can be the belief that migratory and wintering species are other countries birds (Faaborg et al. 2010).

Various ecological reasons can also contribute to the bias: (1) Breeding behavior can be more conducive to research than non-breeding behavior. Birds that sing and defend territory on the breeding grounds are more detectable than silent birds on the wintering grounds. Nests don't move meaning individual birds and young can be re-found and easily tracked throughout the breeding season, whereas on the wintering grounds all birds are mobile adults. (2) Breeding biology has more established topics than non-breeding biology, including brood parasitism, development and growth, mating systems and sexual selection, and parental care. (3) In most areas across the US and Canada, there are more species occurring during the summer breeding season than during the winter (Sullivan et al. 2009). This could contribute to the research bias in that there are more species available and therefore more opportunities to study during breeding seasons. There is also far more research conducted in the United States than in Central and South America (Ciocca and Delgado 2017). Therefore, species that breed in the US but winter or migrate through Central or South America are more likely to be studied on the breeding grounds. (4) In temperate climates there is also more time in the day during the summer breeding season, allowing researchers more opportunities to collect data.

Finally, there are various social reasons that potentially contribute to the research bias. (1) According to the American Psychiatric Association (2013), Seasonal Affective Disorder, also commonly referred to as the "Winter Blues" is a seasonally driven depression typically starting late in the fall and ending in the early spring. Symptoms can include low interest and energy, hypersomnia and difficulty concentrating; with risk factors including living farther from the equator and being female (Melrose 2015). Lower levels of sunlight and lower temperatures have

been shown to have a negative effect on mood and increase in tiredness (Denissen et al. 2008, Ettema et al. 2017). Because of the lower light levels and cold, researchers in temperate zones may have negative physiological responses during winter and not want to work as much as they do during summer. (2) There can be the belief that breeding season is more important and therefore warrants more attention (Pulliam and Millikan 1982).

**What can potentially be done to reduce such biases?**

There are many possible reasons and explanations for why there is a discrepancy between breeding and non-breeding studies (i.e., Ecological, Institutional, or Social), but all of these reasons have solutions to which we can implement.

Academic institutions can provide more flexibility to graduate students wishing to conduct research during non-breeding seasons, by adjusting degree requirements and allowing for more research hours and less in-class time. Another possibility to increase flexibility within academic institutions is to switch to the quarter system and away from the semester system. Roughly 83% of Doctoral awarding research institutions in the United Stated are on the semester system and there are 5.6 times as many graduate degree awarding universities on the semester as compared to the quarter system in the six states we looked at above (NCES 2021). Quarter systems provide more flexibility than semester systems for graduate students in that it is easier to conduct a field season and miss a three month quarter over a five month semester, it is also easier for PI's to fund a three month assistantship over a five month one. Institutions that are already on the quarter system could take advantage of this flexibility and focus more on non-breeding studies. Universities could also increase flexibility by allowing students to enroll in online versions of classes. Due to the Covid-19 pandemic many new policies were put in place to allow distance learning, continuing these policies would allow students to be in the field and still active

in coursework. If the seasonal calendar for academic researchers does not have the flexibility to allow more time during winter, non-academic institutions that do have more flexibility can take the lead on non-breeding studies. Institutions, and state governments in the southern US where there are more species during winter compared to northern states and provinces (Sullivan et al. 2009), can focus on projects involving wintering ecology as they have easier access. Finally, Ornithological societies and funding agencies could also create winter and non-breeding specific grants to incentivize studies and alleviate graduate students from teaching and class time during winter.

Changing the inherit systematic biases involved in seasonal field studies (i.e. political boundaries or academic calendar) is often outside the reach of researchers. Instead of attempting to change these biases researchers can circumvent them by conducting non-breeding research during the breeding season. By taking advantage of new technologies such as GPS trackers (Ng et al. 2018), Geolocators (Ellison et al. 2017), Stable Isotopes (Akresh et al. 2019), or widespread automated receivers such as the MOTUS network (Taylor et al. 2017, Mckinnon et al. 2019), data on wintering distributions, movement, and habitats can be collected without ever stepping foot on the wintering grounds. Current researchers can also exploit vast amounts of citizen science and publicly available data such as eBird (Muller et al. 2018, Long et al. 2019, Martín et al. 2020). Luckily, this kind of research is being done and is a hopeful sign that these research gaps are being filled despite the barriers in place (Danielsen et al. 2014, Sullivan et al. 2017).

The insufficiency of wintering and migratory knowledge is inhibiting effective full-life cycle management of declining species. The need for full life cycle conservation plans is great, and as we ornithologists continue to pursue research, we must include more full life cycle

conservation strategies. But, in order to implement full life cycle conservation, we must have more information about what factors are affecting birds during the wintering and migratory periods. Therefore, we must overcome the biases that exist against wintering studies and increase the amount of research being done during winter and migration either through on the ground field studies or remotely through alternative methods.

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## Chapter 2: Grassland Bird Species Density and Distribution across Oklahoma and the Texas Panhandle

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*Formatted along the guidelines for the Journal of Wildlife Management*

**ABSTRACT** Drastic loss of grassland habitat is likely why grassland birds have suffered worse population declines over the past fifty years compared to other bird guilds. Along with habitat loss there are life history unknowns hampering conservation efforts. Winter ecology of grassland birds in the southern Great Plains is very poorly understood, despite the region comprising a substantial portion of many species' winter range. This lack of knowledge of wintering ecology contributes to the lack of full life cycle conservation planning. We used distance sampling across 14 different sites during three winters (2018-19, 2019-20, 2020-21), across the three major grassland ecotypes in Oklahoma and Texas panhandle in order to adequately sample the full range of environmental variability across the region. We used this data to determine the density and distribution of grassland birds both spatially and across temporal time frames. We had a total and 27,166 individuals of 69 species, detected using grasslands across the three years of the study. We found that many grassland birds exhibit both inter- and intra-seasonal variance in their densities at various sites. At landscape levels most species were negatively associated with shrubs and positively associated with percent of grassland on the landscape. Several species of longspur including Chestnut-collared (*Calcarius ornatus*) and Thick-billed (*Rhynchophanes mccownii*) were positively associated with wider diurnal temperature range. Proper management and conservation of critical grassland areas within the region should be a priority as the area has the potential and ability to serve as important non-breeding habitat for many declining grassland bird species.

**KEY WORDS** Grassland, Great Plains, landscape, Species Distribution Model, habitat management, winter ecology

## INTRODUCTION

Grasslands are critically important ecosystems, providing ecological value as water catchments, carbon sinks, and habitat for wildlife, while also serving as an economic resource via cattle grazing, agriculture, and energy development (Samson et al. 2004, Grand et al. 2019). Grasslands are the most threatened ecosystem in North America (Blancher 2003) and economic exploitation has been a leading cause for the reduction of ecologically functional grasslands historically. Even though we know that grasslands are threatened across North America, they continue to have a high rate of decline (Gage et al. 2016, Olimb and Robinson 2019, Homer et al. 2020). Tallgrass, Mixed-grass, and Shortgrass Prairie — the three major grassland ecosystems in North America—have been reduced from their historic sizes by 98%, 76%, and 46%, respectively (Comer et al. 2018). Grasslands are among the most dynamic ecotypes in the world, as they are highly susceptible to varying amounts of rainfall, fire, grazing pressure, timing and compounding or offsetting effects of all of these factors (Collins et al. 1998, Knapp et al. 1999, 2002, Griffin-Nolan et al. 2018). Drastic habitat loss is likely why North American grassland birds have suffered worse population declines over the past fifty years compared to other bird guilds (Vickery et al. 1999, Sauer et al. 2017, Rosenberg et al. 2019) as a conservation crisis continues to unfold in the region (Brennan and Kuvlesky 2005).

Winter ecology of migratory grassland birds in Oklahoma and North Texas [i.e., the South-Central Great Plains (SGP)] is poorly understood, which is unfortunate given that the region encompasses a substantial portion of many species' winter range. There is growing evidence that survival during the non-breeding season has a strong influence on the population

trends of migratory species (Calvert et al. 2009, Morrison et al. 2013, Macías-Duarte et al. 2017). Therefore, understanding winter survivorship of migratory grassland bird species may be central to their conservation. There are several at-risk grassland species that winter in the SGP, including: Loggerhead Shrike (*Lanius ludovicianus*; LOSH), Thick-billed Longspur (*Rhynchophanes mccownii;* TBLO), Chestnut-collared Longspur (*Calcarius ornatus*; CCLO), Western Meadowlark (*Sturnella neglecta*; WEME), Eastern Meadowlark (*S. magna*; EAME), Savannah Sparrow (*Passerculus sandwichensis*; SAVS), and Vesper Sparrow (*Pooecetes gramineus*; VESP). By identifying and conserving high quality habitats for these rapidly declining species in the region, we may be able to develop conservation and management strategies across the SGP that can sustain grassland bird populations.

As study areas increase in size, habitat richness (number of different types of habitats) typically also rises due to their heterogeneous nature (Hanski 1999). Such increases in habitat richness should, in turn, increase bird species richness (Williams and Others 1964, Connor and McCoy 1979). Moreover, landscape-level factors, including temperature, precipitation, seasonality of rainfall, habitat fragmentation, topography, tree canopy cover/ shrub encroachment, and amount of grassland within the landscape, have been shown to affect species distributions and abundances (Renfrew and Ribic 2002, Davis 2004, Thogmartin et al. 2006, Greer et al. 2016, Gorzo et al. 2016, Muller and Veech 2018). The SGP has a high amount of variation in environmental gradients (i.e. precipitation and temperature) and many various habitats and ecotypes including multiple grassland systems such as the Tallgrass Prairies of the Flint Hills, Mixed-grass prairies of the Central Great Plains and Crosstimbers, and Shortgrass prairies of the High plains and Southwestern Tablelands (Omernik 1987). Oklahoma, for example, is roughly 850 km from the southeast to the northwest corner spanning average annual

temperatures from 18° C- 13° C, and yearly precipitation accumulations of 142 cm- 43 cm, respectively (McPherson et al. 2007). This variety of habitats and environments makes the SGP ideal for sampling along environmental gradients. By sampling across the wide environmental gradients found in the SGP, we should also see an increase in overall species richness due to varying environmental niches across the area. We hypothesize that because Oklahoma and North Texas have such a high diversity of both grassland habitat types and environmental gradients, the region should support a high diversity of non-breeding grassland birds.

Many grassland bird species exhibit high levels of area sensitivity, such that relative abundance increases with patch size (Ribic et al. 2009, Muller and Veech 2018). Relative abundance of individuals is often considered a proxy for habitat quality (Fretwell and Lucas 1970). If we assume that areas of relatively high density or abundance of individuals of a species is due to high habitat quality (Jones 2001, MacKenzie 2005), then locating areas with high densities of specific species should provide a good indicator of high quality habitat for the species. *Partners In Flight* has argued that identification and conservation of high quality habitats a high research priority for conservation of migratory birds (Donovan et al. 2002). So, as we attempt to identify and conserve suitable habitats for at-risk species, we should continue to prioritize areas that host high relative densities of at-risk species.

Ecological Niche Models (ENMs) along with Species Distribution Models (SDMs) are useful tools to visualize species' environmental requirements within a focal area and have been applied to a wide range of ecological issues (Guisan and Zimmermann 2000, Guisan and Thuiller 2005, Raxworthy et al. 2007, Lozier et al. 2009, Veloz 2009, Fernandes et al. 2018). For example, SDM's can be used to identify potential areas of occupancy for focal species (Trudeau

et al. 2012, Funk et al. 2013), as well as to identify areas that are best suited for additional management (Zhang et al. 2012, Bellamy et al. 2013).

We sampled protected grassland areas across the state of Oklahoma and Texas Panhandle for wintering grassland bird species in order to determine the distribution and relative abundances of species within the grassland bird community. Our questions included: 1) What are the distributions of grassland birds in the SGP? 2) What areas of the state of Oklahoma would be beneficial for state agencies or NGOs to focus land acquisition or adaptive management for grassland birds? 3) What are the relative densities of grassland birds at various protected areas across Oklahoma and the Texas Panhandle and how do these sites contribute potentially critical non-breeding habitat for species of conservation concern? 4) What landscape level factors (e.g. area of field site, precipitation, topography) affect the distribution and diversity of grassland birds in the SGP? 5) How prevalent is inter-seasonal transience, evinced by changes in relative densities of the most common birds throughout the winter?

**STUDY AREA**

We sampled from 14 different sites during the three winters (2018-19, 2019-20, 2020-21) (descriptions found in Appendix A). Study sites were dispersed across the three major grassland ecotypes in Oklahoma and Texas panhandle (Fig. 1), in order to adequately sample across the full range of environmental variability available in the SGP.

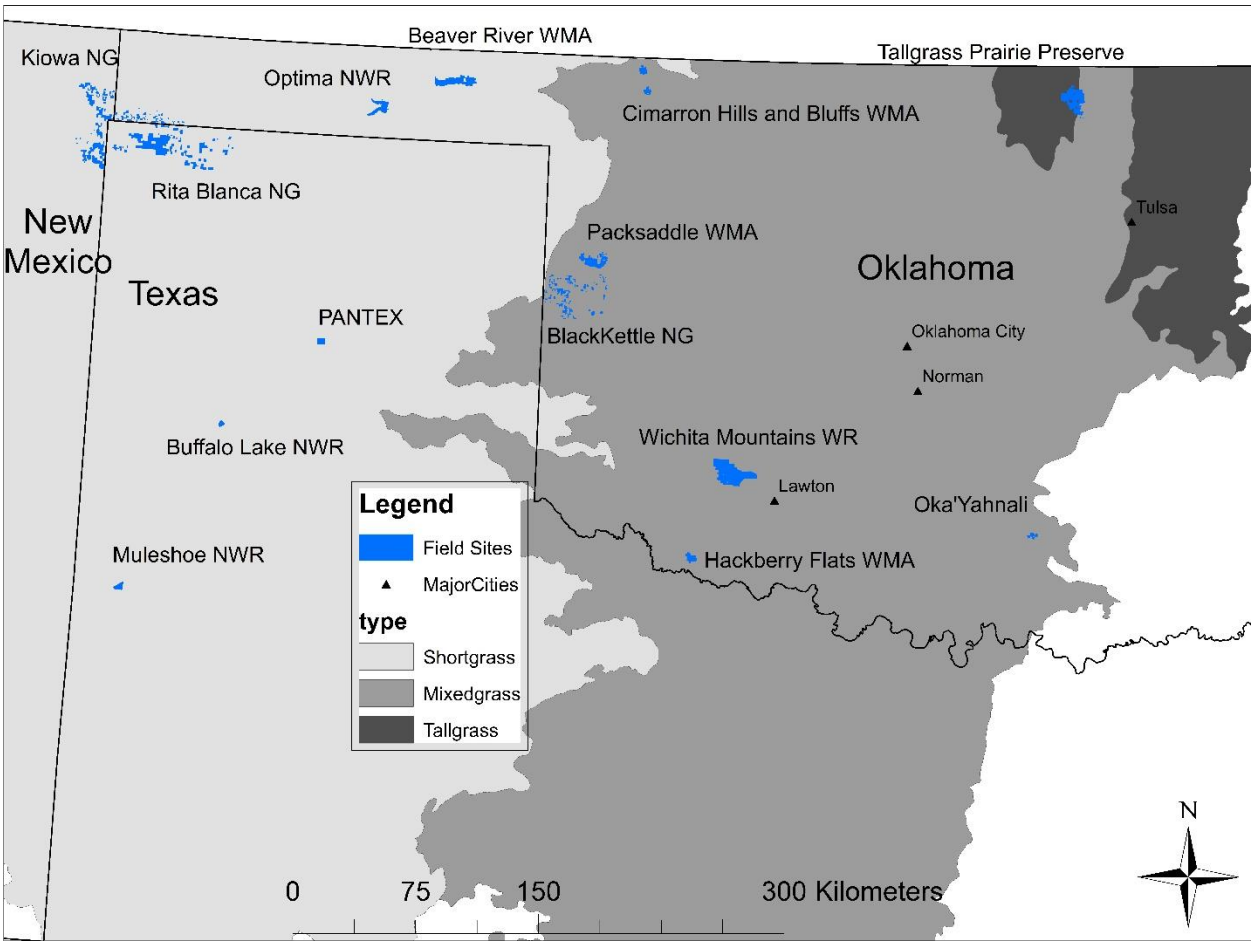


Figure 1. Map showing the distribution of the field sites used for distance sampling. Shortgrass, Mixed-grass and Tallgrass prairie boundaries were taken from Omernik (1987) and are generalized ecotypes.

## METHODS

### Density

*Bird Sampling*: Our field crew surveyed for all species of wintering grassland birds along transects using a distance-sampling framework (Buckland et al. 2001, Pool et al. 2012). Field crews were trained by the same person for the first two weeks of each field season. We selected sites to get an adequate sample of the various grassland types throughout our study range and to sample a sufficient number of points from across the state of Oklahoma and Texas Panhandle for Distribution Modeling (Fig. 1). We used ArcGIS to generate a pool of random points (size of pool depended on size of field site) within available grassland habitat on each property. From

each of those points, we generated transects varying in length from 1- 5 km at randomly selected bearings. Length of transects depended on the size of the accessible grassland patch, with smaller sites receiving shorter transects. Transects that fell substantially outside a study site boundary or outside of grassland habitat were eliminated. For each study site, we randomly selected 3 to 22 of the remaining transects, depending on the size of the property and availability of grassland habitat. The first winter we surveyed 9 sites (Rita Blanca and Black Kettle National Grasslands, Wichita Mountains and Optima National Wildlife Refuges, Beaver River, Packsaddle, and Hackberry Flats Wildlife Management Areas, and Oka'Yanahli and Tallgrass Prairie Preserves). During the second field season we added 6 sites (Kiowa National Grasslands, Muleshoe and Buffalo Lake National Wildlife Refuges, Cimarron Hills and Cimarron Bluffs Wildlife Management Areas, and the PANTEX Nuclear plant) while dropping Black Kettle National Grassland. For our third season we had to additionally drop Oka'Yanahli Preserve, Optima National Wildlife Refuge, Hackberry Flats, Beaver River, Cimarron Hills and Bluffs WMA's, as well as the PANTEX plant due to travel limitations induced from the Covid-19 pandemic.

We attempted to survey each transect at least three times per winter at approximately 4-week intervals, typically once in December, January and February. Due to weather and time constrictions, not all sites were surveyed three times. During surveys, observers used laser rangefinders to measure radial distance to each bird or cluster of birds. We recorded the angle and means of detection (e.g. call, visual, singing) for all detections of birds actively using grassland habitat, as well as basic weather information (cloud cover, temperature, wind speed and direction). Birds that traveled through the grassland, such as woodpeckers flying from forest patch to forest patch, were not counted, but birds flying over but actively using grassland patches, such as hunting Northern Harriers (*Circus hudsonius;* NOHA), were counted. We did

not conduct surveys during high winds (>8 m/s; i.e., 29 kph or 18 mph) or when precipitation was more than light rain/snow. We recorded GPS locations of all birds that flushed from grass as well as opportune sightings of focal species (e.g., longspurs that flushed while driving roads or walking to or from survey transects). Opportunistic sightings were only used in Distribution Modeling and not used in Density or Species Diversity analysis.

**Distribution, Density, and Diversity Analysis**

*Density Analysis*: Perpendicular distances to all flush points were calculated from distance sampling transects. Points were truncated to cut off the 5% largest distances, which is suggested if there are no obvious outliers so long as the detection probability is above g(x)>=0.15 (Buckland et al. 2001). Various detection curve models were tested to determine the best fit model. The detection curve models included various key functions (e.g. uniform, half-normal, and hazard-rate), all models included the potential for adjustment terms (cosine), and various co-variables (observer, year, detection type, field site, and various weather variables). DeltaAIC were used for model selection and if multiple models were within 2 ΔAIC, the model with the highest p-value (Cramer-von Mises goodness of fit) was selected. We included only species for which there were at least 60 detections (Buckland et al. 2001).

*Distribution modeling*: We generated 23 response surfaces using the 19 Bioclim variables from CHELSA (Karger et al. 2017) (response layer descriptions can be found in Appendix B). We included 3 land-cover response surfaces derived from the National Land Cover Database (NLCD), which consists of several land-cover products created by the Multi-Resolution Land Characteristics Consortium (MRLC), a partnership of federal agencies led by the U.S. Geological Survey (USGS) (Homer et al. 2020). We also included the tree canopy cartographic data layer created by the U.S. Forest Service using the same satellite imagery as used by the

NLCD (Homer et al. 2015). The final response-layer surface was derived from the difference in the highest and lowest point from the digital elevation model data downloaded from The National Map USGS at ⅓ arc sec (Archuleta et al. 2017).

Distribution models were generated with Maxent (Phillips et al. 2006) is a program used to model species distributions and is the most popular "presence only" method (Yackulic et al. 2013). Maxent does not model occurrence probability (Yackulic et al. 2013), instead it models responses to environmental variables. Because Maxent uses "presence only" data it is ideal for species for which there is limited occurrence data. Even though Maxent cannot estimate relative abundances (Yackulic et al. 2013), it does a good job at estimating suitable environments and produces easily interpretable maps. Maxent is also the highest performing method for datasets with low <75 occurrence points (Hernandez et al. 2006). For our Maxent analyses we incorporated all the points for each species, including both transect-based and incidental detections. In order to reduce psuedoreplication, we spatially rarefied points by removing spatially autocorrelated points that were within 1km of each other (Boria et al. 2014). One kilometer was chosen because the response layers were at a resolution of 1km. After reducing spatial autocorrelation, we used model calibration and model selection for species in which there were at least 20 points.

Maxent models were spatially jackknifed (geographically k-fold cross-validation) into 3 groups for model calibration (Peterson et al. 2011, Boria et al. 2014, Radosavljevic and Anderson 2014). After calibration we tested 20 candidate models that were a combination of 4 regularization multipliers (0.5,1,1.5, and 2) as well as 5 combinations of feature classes (1, linear; 2, linear and quadratic; 3, linear, quadratic, hinge; 4, hinge; 5, linear, quadratic, hinge, product and threshold). We used omission rates and AUC to evaluate models, and the model

with the lowest omission rate were selected. If models had similar omission rates, then the model with the highest AUC was selected.

We calculated four diversity variables. Simplest among them is species richness, the number of species detected on surveys at each site. We also kept track of species that were seen at a site but were not detected on surveys (Appendix B). Because of uneven sampling effort, we calculated the rarified richness (expected number of species based on random subsamples of the community), by using the "rarefy" function in the r package "vegan" (Oksanen 2020). We estimated the rarefied richness by randomly resampling each location with a sample size equal to the site with the lowest number of individuals. Then the mean number of species from the resampling was calculated. We also calculated Shannon-diversity indexes (H' (Krebs 1999)) and species evenness (J' (Zar 1999)) using relative abundances, of how many individuals were seen on transects (Table 2). We used generalized linear models ("glm" function) in R, to test the relationships between various diversity metrics (species richness, H', J'), which we treated as the independent variable and, effort and environmental variables (e.g. number of transects, area of field site, average annual temperature) which we treated as the dependent variables. We then used a forward stepwise AIC model selection in R ("step" function), starting with a null model ($H_0$=Y~1) to determine which variables would best predict a selected dependent variable (i.e., species richness, H', J') at a field site.

## RESULTS

### Surveys and diversity

We had a total and 27,166 individuals of 69 species detected on 1230.6 km of transects for an average of 22.1 individuals per km of transect (Table 1 shows the 20 most abundant species while Appendix B has all species). The field site with the lowest number of individuals detected

per kilometer was Muleshoe NWR with 3.23 birds/km whereas PANTEX had the highest with 130.37 birds/km (Table 2). The most abundant species detected across all sites were the CCLO, Horned Lark (*Eremophila alpestris*; HOLA) and SAVS with 7645, 5292 and 2981 individuals respectively. The most widespread species were SAVS and WEME, which was found at all 14 field sites, while NOHA were found at 13.

The Wichita Mountains had the highest number of species with 44, while Muleshoe NWR and Pantex had the least with only 10 species each (Table 2). Packsaddle WMA had both the highest H' and J', while Kiowa NG had the lowest J'. Tallgrass had the highest rarified richness with 20.2 species, while Kiowa had the lowest with 5.8. CCLO made up 64.1% of all individuals detected at the Wichita Mountains, and SAVS made up 62.8% of individuals at Oka'Yahnali. Flock dynamics varied greatly between species as well, CCLO averaged 17.9 (SD 20.7) and 31.2 (SD 46.7) individuals per flock at the Wichita Mountains during years 1 and 2, whereas SAVS only averaged 2.7 (SD 3.03) and 2.8 (SD 3.1) individuals per flock at Oka'Yanahli in years 1 and 2.

Table 1. The 20 species for which there were enough detection points for distribution analysis and the number detected at each of the 14 sites (Tall (Tallgrass Prairie Preserve), Oka (Oka'Yahnali Preserve), WMWR (Wichita Mountains Wildlife Refuge), Hack (Hackberry Flats WMA), BK (Black Kettle National Grasslands), Pack (Packsaddle Wildlife Management Area), CHCB (Cimarron Hills and Cimarron Bluffs Wildlife Management Areas), Optima (Optima National Wildlife Refuge and Wildlife Management Area), Beav (Beaver River Wildlife Management Area), Kiowa (Kiowa National Grasslands), Rita (Rita Blanca National Grasslands), Mule (Muleshoe National Wildlife Refuge), Buff (Buffalo Lake National Wildlife Refuge), Pant (PANTEX Nuclear Site)), across all three years of effort. Species are listed using the 4-letter alpha code used by the U.S. Bird Banding Laboratory (https://www.pwrc.usgs.gov/bbl/manual/speclist.cfm). Species seen at the site by us but were not detected on a survey are denoted with an *.

| Species | Tall | Oka | WMWR | Hack | BK | Pack | CHCB | Optima | Beav | Kiowa | Rita | Mule | Buff | Pant |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AMKE | 6 | 5 | 11 | 7 | 3 | 1 | * | 4 | * | 1 | 4 | 4 | * | 1 |
| AMTS | 48 | | 10 | 1 | 8 | 57 | 42 | 9 | 14 | | | | | |
| CCLO | 1 | * | 5851 | 8 | | | * | | | 303 | 1440 | 32 | 10 | |
| DEJU | * | 4 | 334 | * | 185 | 101 | 26 | | | | | | | |
| EABL | 5 | 2 | 30 | | 13 | 13 | | | | | | | | |
| EAME | 78 | 170 | 886 | 1239 | 21 | 75 | 3 | | 23 | | * | 1 | | |
| FISP | 7 | 35 | 101 | | 48 | 81 | * | 2 | 10 | | | | | |
| HOLA | 39 | 16 | 46 | 82 | 5 | 37 | | 440 | 13 | 652 | 3669 | | 21 | 272 |
| LALO | 19 | | * | 381 | 6 | | | 38 | 16 | 26 | 1279 | | | 12 |
| LCSP | 22 | 130 | 92 | 10 | 2 | 3 | | | 1 | | | | | |
| LOSH | 2 | * | 2 | 6 | 4 | * | * | | | 2 | * | 6 | * | |
| MCLO | | | 1 | 7 | | 3 | | | | 2 | 136 | | | 79 |
| NOFL | 22 | 2 | 8 | | 4 | 5 | 3 | 1 | | | | | 1 | |
| NOHA | 82 | 13 | 13 | 30 | * | 7 | 10 | 3 | 3 | 6 | 8 | 2 | 3 | 4 |
| SAVS | 122 | 848 | 998 | 806 | 6 | 41 | 2 | 2 | 34 | 2 | 14 | 15 | 11 | 17 |
| SMLO | 252 | * | 107 | | | | | | | | | | | |
| SOSP | 26 | 81 | 212 | 75 | 26 | 41 | 10 | | 52 | | | | | |
| VESP | | 1 | 22 | 5 | 1 | 1 | | | | | 1 | | | |
| WCSP | | | 1 | 87 | 4 | 74 | 1 | 4 | 37 | * | 1 | 8 | | 1 |
| WEME | 1 | 1 | 146 | 201 | 7 | 21 | 8 | 126 | 180 | 29 | 187 | 57 | 74 | 169 |

Table 2. The diversity metrics including number of species (#), Rarified Diversity (Rare), Shannon Diversity (H'), Evenness (J'), total number of individuals (Total), and individuals per kilometer (I/K). Also lists effort metrics including number of kilometers walked (KM), years surveyed (Years), number of survey trips (Trips), and Area of the field site in $km^2$ (Area). Also included is selected environmental means Average annual temperature in °C (Temp), Average annual Precipitation in mm (Precip), Percent of field site that's Grass (Grass), Mean Diurnal temperature Range in °C (Range), Average temperature during the coldest quarter in °C (Cold), Average Tree Canopy cover for the field site (Tree), across the 14 field sites.

| Location | # | Rare | KM | Total | I/K | H' | J' | Area | Temp | Precip | Grass | Tree | Range | Cold | Years | Trips |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Tallgrass | 33 | 20.2 | 156 | 910 | 5.8 | 2.5 | 0.73 | 160 | 14.9 | 989.6 | 86.4 | 7.8 | 9.8 | -3.4 | 3 | 9 |
| Oka | 27 | 10.6 | 50 | 1350 | 27.0 | 1.4 | 0.42 | 15 | 17.1 | 1035.0 | 85.5 | 16.6 | 9.4 | -0.2 | 2 | 5 |
| WMWR | 44 | 12.1 | 211 | 9125 | 43.2 | 1.4 | 0.38 | 81 | 15.9 | 833.6 | 80.1 | 14.7 | 10.6 | -2.3 | 3 | 10 |
| Hack | 30 | 11.9 | 37.5 | 3160 | 84.3 | 1.8 | 0.54 | 29 | 17.6 | 688.9 | 43.4 | 0.11 | 10.8 | -0.6 | 2 | 5 |
| BK | 31 | 18.7 | 47 | 661 | 14.1 | 2.2 | 0.63 | 127 | 14.9 | 601.9 | 57.4 | 4.3 | 11.3 | -3.8 | 1 | 3 |
| Pack | 29 | 19.4 | 47 | 786 | 16.7 | 2.7 | 0.80 | 80 | 14.8 | 635.2 | 79.9 | 2.85 | 11.2 | -3.9 | 3 | 7 |
| CHCB | 14 | 14 | 12 | 115 | 9.6 | 1.9 | 0.74 | 14 | 14.7 | 619.1 | 98.2 | 0.08 | 11.2 | -4.5 | 1 | 2 |
| Optima | 14 | 7.4 | 24 | 636 | 26.5 | 1.0 | 0.38 | 50 | 14.5 | 442.2 | 21.8 | 0.24 | 12.1 | -4.4 | 2 | 4 |
| Beaver | 21 | 11.8 | 30 | 1229 | 40.9 | 1.4 | 0.45 | 15 | 14.3 | 500.0 | 4.8 | 0.24 | 11.9 | -4.7 | 2 | 5 |
| Kiowa | 13 | 5.8 | 123 | 1029 | 8.4 | 0.9 | 0.37 | 202 | 12.6 | 389.7 | 70.9 | 0.08 | 12.5 | -5.3 | 2 | 6 |
| Rita | 22 | 6.5 | 401 | 6837 | 17.1 | 1.3 | 0.41 | 376 | 13.4 | 397.9 | 83.2 | 0.0007 | 12.4 | -4.8 | 3 | 9 |
| Mule | 10 | 9.7 | 44 | 142 | 3.2 | 1.7 | 0.75 | 26 | 15.5 | 435.8 | 18.2 | 0.07 | 12.1 | -1.9 | 2 | 5 |
| Buffalo | 12 | 11.4 | 40 | 130 | 3.2 | 1.5 | 0.59 | 31 | 14.8 | 429.4 | 70.5 | 0.14 | 12.1 | -3.1 | 2 | 5 |
| Pantex | 10 | 6.3 | 8.1 | 1056 | 130.4 | 1.4 | 0.59 | 1 | 14.2 | 502.3 | 21.7 | 0.0 | 12.1 | -4.1 | 1 | 3 |

**Models predicting richness**

Our stepwise GLM showed two variables each in the best model for dependent variable of species richness and H'. For species richness the first variable selected was annual precipitation and second was kilometers walked, for H' the first variable was diurnal range and then the second was percent tree canopy cover. The single factor analysis of H' and diurnal temperature range showed a negative relationship and the trend was slightly insignificant ($p=0.08$). Species richness showed a positive association with precipitation, and the trend was significant ($p=0.005$). For rarified species richness the GLM showed three variables, first was diurnal range followed by average daily temperature during the coldest quarter and annual precipitation. The single factor analysis of rarified and diurnal range shows a significant negative trend ($p=0.03$, Fig. 2).

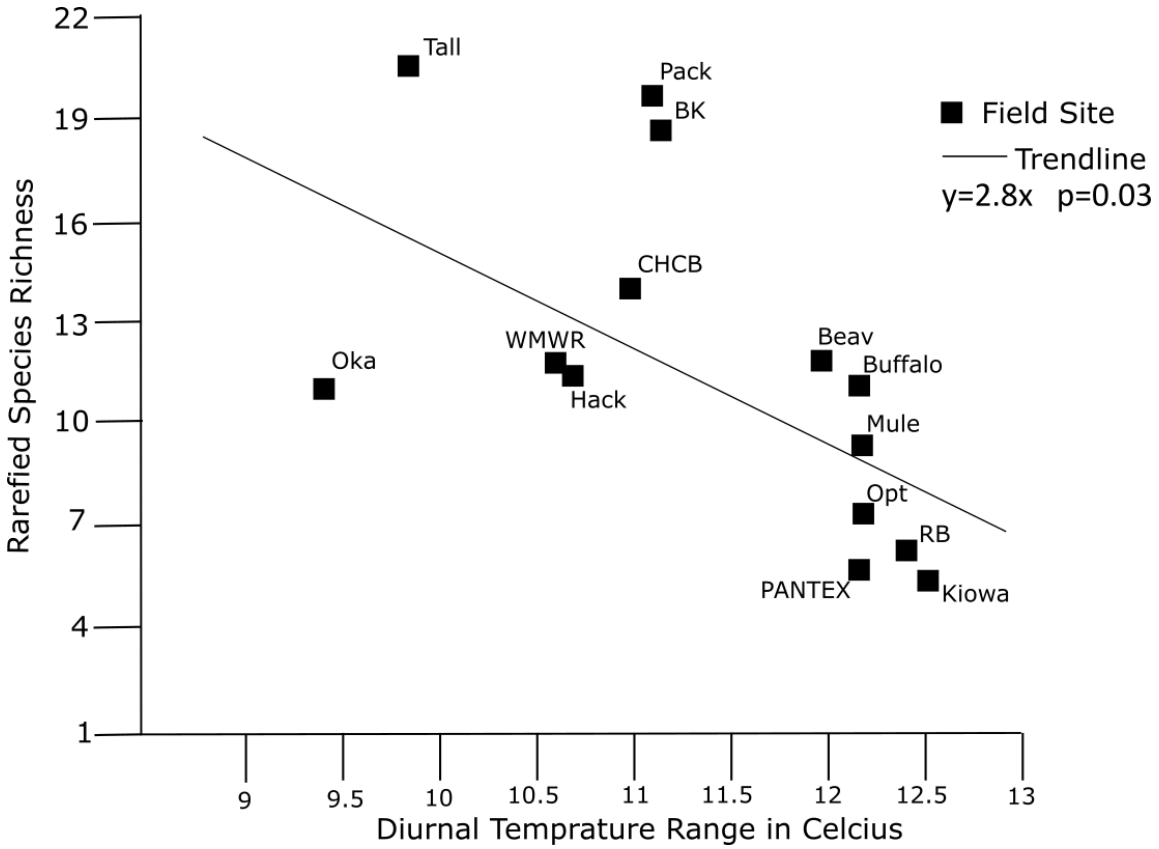


Figure 2. The negative association between rarefied species richness and Diurnal Temperature Range. (Tall (Tallgrass Prairie Preserve), Oka (Oka'Yahnali Preserve), WMWR (Wichita Mountains Wildlife Refuge), Hack (Hackberry Flats WMA), BK (Black Kettle National Grasslands), Pack (Packsaddle Wildlife Management Area), CHCB (Cimarron Hills and Cimarron Bluffs Wildlife Management Areas), Opt (Optima National Wildlife Refuge and Wildlife Management Area), Beav (Beaver River Wildlife Management Area), Kiowa (Kiowa National Grasslands), RB (Rita Blanca National Grasslands), Mule (Muleshoe National Wildlife Refuge), Buffalo (Buffalo Lake National Wildlife Refuge), PANTEX (PANTEX Nuclear Site)

**Detection Curves**

There were 11 species with which there were at least 60 detections. No weather variables were selected in the detection function models, but Observer and Detection type (e.g. Call or Visual) were frequently selected. Detection range varied widely from a low of 10.1 m with LeConte's Sparrow (*Ammospiza leconteii*; LCSP) (Table 3), to a high of 199.1 m with NOHA (Table 3). Detection probability also varied widely, from a low of 25% for CCLO to a high of 54% for NOHA (Table 3).

Table 3. The 11 species with which there were enough detections to develop detection curves. The species are listed using the 4-letter alpha code used by the U.S. Bird Banding Laboratory (https://www.pwrc.usgs.gov/bbl/manual/speclist.cfm). The detection probability is listed (p), the detection range in meters (Range), the number of detections (n) and the model that was selected (Model). Model selection used either Half-Normal (hn), Hazard Rate (hr) or Uniform (un) distributions, as well as Observer and Detection type.

| Species | p | Range | n | Model |
|---|---|---|---|---|
| CCLO | 0.25 | 0-82.3 | 433 | hr+Detection+Observer |
| LCSP | 0.49 | 0-10.1 | 227 | hn |
| SAVS | 0.39 | 0-40.1 | 1162 | hr+Detection |
| WEME | 0.32 | 0-141.3 | 374 | hr+Detection |
| EAME | 0.37 | 0-132.5 | 362 | hr+Detection |
| SOSP | 0.4 | 0-69.4 | 327 | hr+Detection |
| FISP | 0.43 | 0-57.1 | 82 | hn+Detection |
| HOLA | 0.52 | 0-78.8 | 532 | hr+Detection+Observer |
| NOHA | 0.54 | 0-199.1 | 133 | $un+cos^2$ |
| SMLO | 0.41 | 0-52.1 | 71 | hn+Detection |
| LALO | 0.29 | 0-106.7 | 199 | hr+Detection+Observer |

**Distribution Models**

We had 20 species for which there were at least 20 detections after removing psuedoreplicated points. The results from the Maxent modeling showed that 18 out of the 20 species had Percent Grassland as a top three factor for the model, several other common variables included Tree Canopy coverage and various precipitation values (Table 4). There were several areas of Oklahoma that were repeatedly highlighted as being suitable for many species including: 1. Tallgrass Prairie west of Bartlesville, 2. the grasslands of Cimarron Co. and western Panhandle, 3. The Southwest portion of the state including Camanche, Caddo and Grady Co., 4. The area south of Tulsa near Mcintosh Co., and western Oklahoma near the towns of Cheyenne and Arnett (Fig. 3). These areas varied in suitability depending on species, with widespread species such as White-crowned Sparrow (*Zonotrichia leucophrys*; WCSP) and NOHA having more suitable areas highlighted compared to rarer species such as CCLO and Smith's Longspur (*Calcarius pictus*; SMLO) (Fig. 4) (individual Maxent Models can be found in Appendix F).

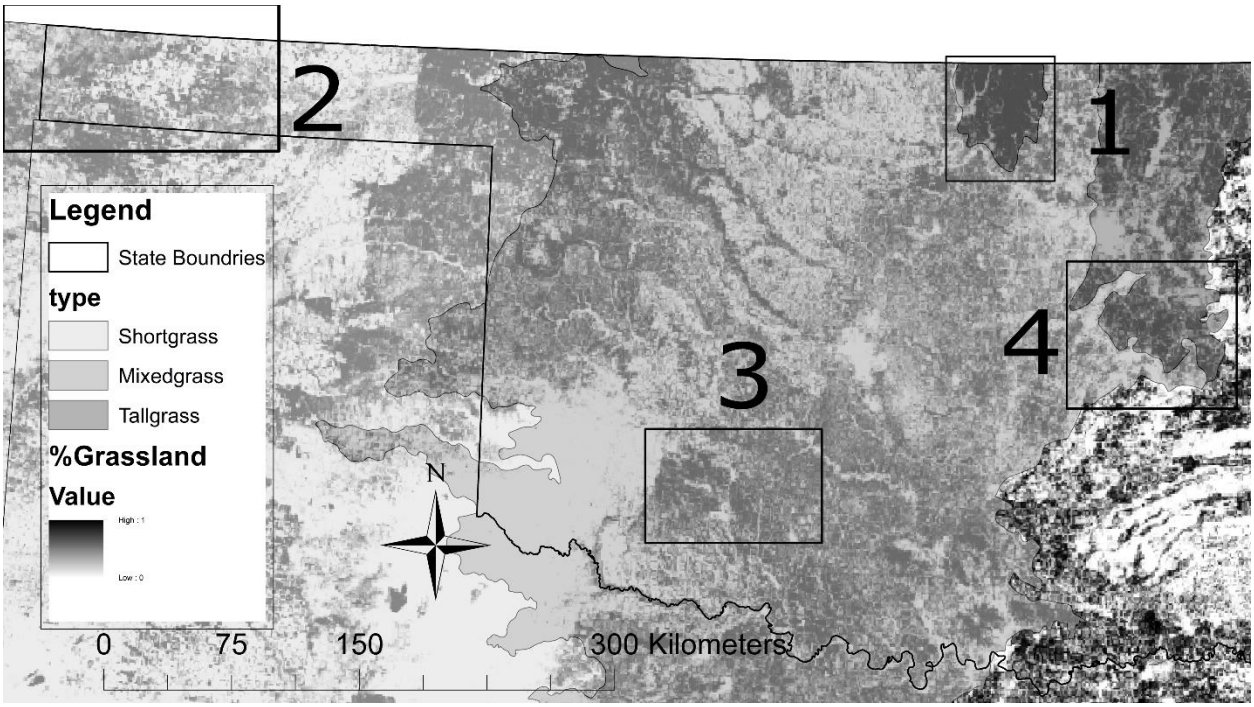

Figure 3. Map of Oklahoma and Texas Panhandles where the Maxent Species Distribution Models repeatedly highlighted areas that were “suitable” for the 20 Maxent models produced.

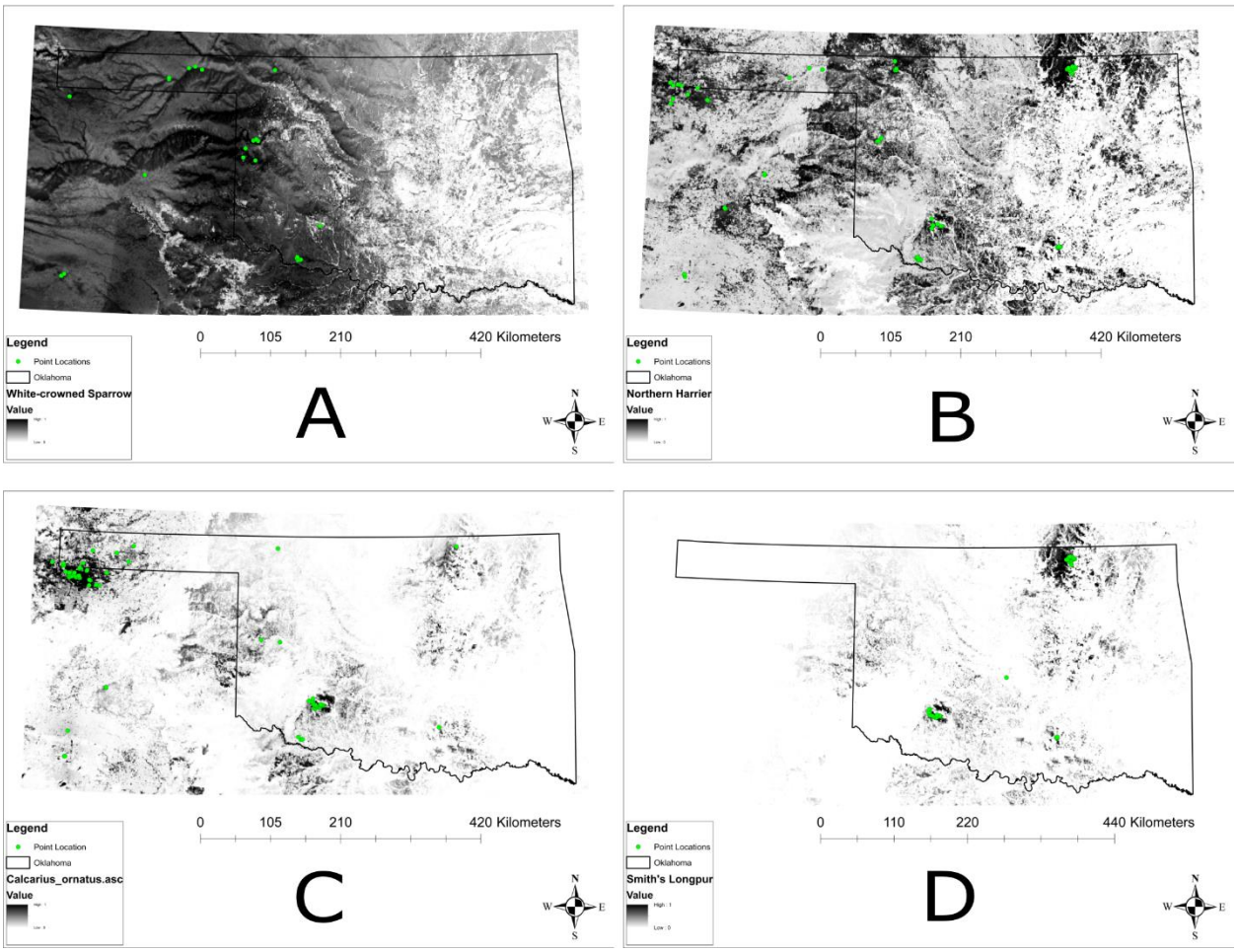


Figure 4. Four of the species Maxent Model results. Two Widespread Species White-crowned Sparrow (Panel A) and Northern Harrier (Panel B), and 2 rarer species Chestnut-collared (Panel C) and Smith's Longspur (Panel D).

Table 4. Showing the 20 species with which there were enough points to make Maxent Models. As well as the 2-3 most important variables determined by maxent. + means a positive relationship, - means a negative relationship, and -+ means that there was a positive relationship at small percentages but negative at large percentages. Variables include Percent of landscape that is grassland (%Grass), Mean Daily Diurnal Temperature Range (Range), Annual Precipitation (Annual Precip), Variability between the wettest quarter and driest quarter (Precip Seasonality), Average Daily Temperature of the coldest quarter (Winter Temp), Mean Tree Canopy Cover (Tree Canopy), Percent of landscape that is an "open" land cover type (Openness), and the difference in the highest and lowest elevation point (Topography). Species are listed using the 4-letter alpha code used by the U.S. Bird Banding Laboratory (https://www.pwrc.usgs.gov/bbl/manual/speclist.cfm).

| | %Grass | Range | Annual Precip | Precip Seasonality | Winter Temp | Tree Canopy | Openness | Topography |
|---|---|---|---|---|---|---|---|---|
| HOLA | + | + | | + | | | | |
| NOFL | + | | | | | -+ | | |
| EAME | + | | + | | | - | | |
| WEME | + | - | | + | | | | |
| CCLO | + | + | - | | | | | |
| SMLO | + | | + | | | | | |
| TBLO | | + | | + | | | + | |
| LALO | + | + | | + | | | | |
| AMKE | + | | | | | -+ | | + |
| NOHA | + | | | + | | -+ | | |
| LOSH | + | | | | - | -+ | | |
| RTHA | + | | | | | -+ | | |
| SOSP | + | | + | | | | | + |
| SAVS | + | | - | | | - | | |
| VESP | + | | | | | -+ | | |
| LCSP | + | | + | | | | | |
| WCSP | | | - | | | -+ | | |
| FISP | + | | - | | | | | + |
| ATSP | + | | | | | -+ | | + |
| EABL | + | | | | | | | + |

**Densities**

Individual densities varied widely from field site to field site as well as across species (complete density table in Appendix). For example, SAVS had a density of 263.4 birds/ $km^2$ (CI 182.4-380.2) at the Wichita Mountains (Fig. 5) but only 15.3 birds/ $km^2$ (CI 6.5-36.1) at Tallgrass Prairie Preserve in year 1. In year 2 CCLO had a density of 406.2 birds/ $km^2$ (CI 222.3-742.1) at

the Wichita Mountains and a much lower density of 21.8 birds/ $km^2$ (CI 7.4-64.9) at Rita Blanca NG (Fig. 5). Among species with enough points for density analysis at the Wichita Mountains WR; densities varied from the most common CCLO, 1109.3 birds/ $km^2$ (CI 626.8-1963.5) to 0.7 birds/ $km^2$ (CI 0.1-4.4) with SMLO in year 3 even though these two species occupied very similar fine scale habitats (Chapter 3).

Many species also had variable densities across years and even months within years. For example, at the Wichita Mountains Wildlife Refuge SAVS had a density of 263.4 birds/ $km^2$ (CI 182.4-380.2) and 168.4 birds/ $km^2$ (CI 116.8-242.8) between years 1 and 2 respectively, in year 3 they varied from a density of 105.2 birds/ $km^2$ (CI 57.1-193.9) in December to 4.9 birds/ $km^2$ (CI 1.7-14.3) in January (Fig. 6). While CCLO varied from 152.9 birds/ $km^2$ (CI 79.4-294.4) in Year 1 to 1109.3 birds/ $km^2$ (CI 626.8-1963.5) in Year 3, while varying in Year 2 from 990.1 birds/ $km^2$ (CI 503.2-1948.1) in December to 160.4 birds/ $km^2$ (CI 56.1-458.6) in January (Fig. 6). LCSP varied from 68.1 birds/ $km^2$ (CI 42.7-110.3) and 15.5 birds/ $km^2$ (CI 7.3-32.7) across years 1 and 2 at the Wichita Mountains (Fig. 6) (a full table of all densities can be found in the Appendix).

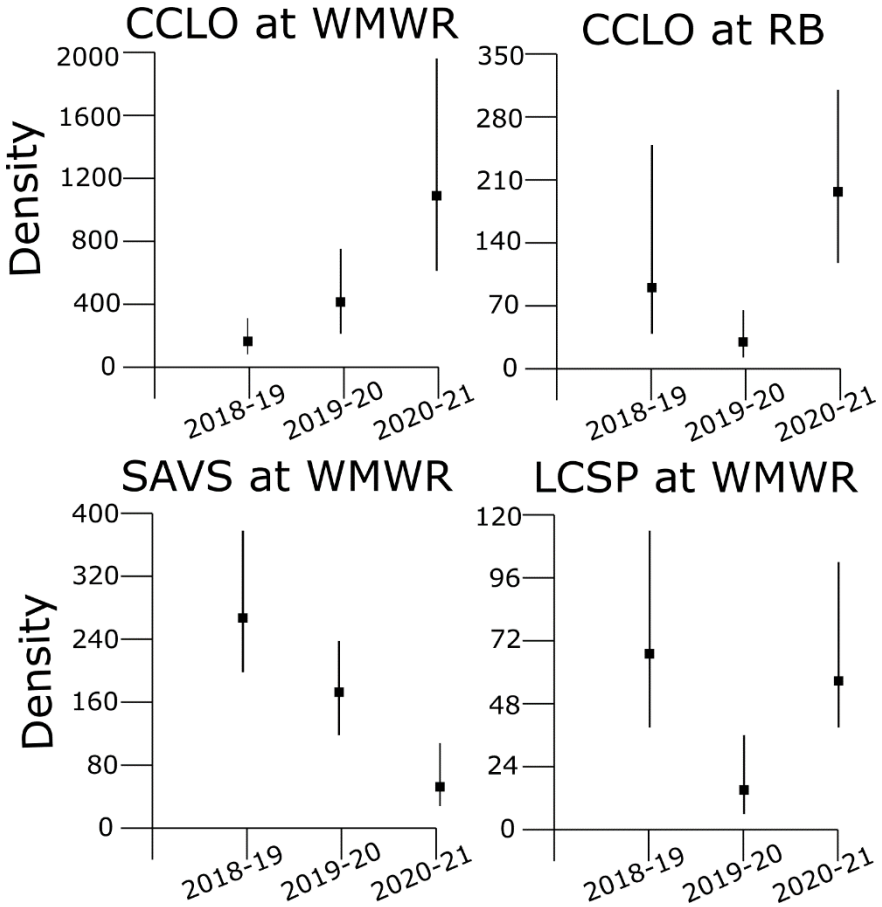


Figure 5. Estimate of the mean winter (December-February) density of Grassland species (Chestnut-collared Longspur (CCLO), Savannah Sparrow (SAVS) and LeConte's Sparrow (LCSP) at the Wichita Mountains Wildlife Refuge (WMWR) and Rita Blanca National Grasslands (RB) for the three winters surveyed. Density Estimate is presented along with the 95% Confidence interval.

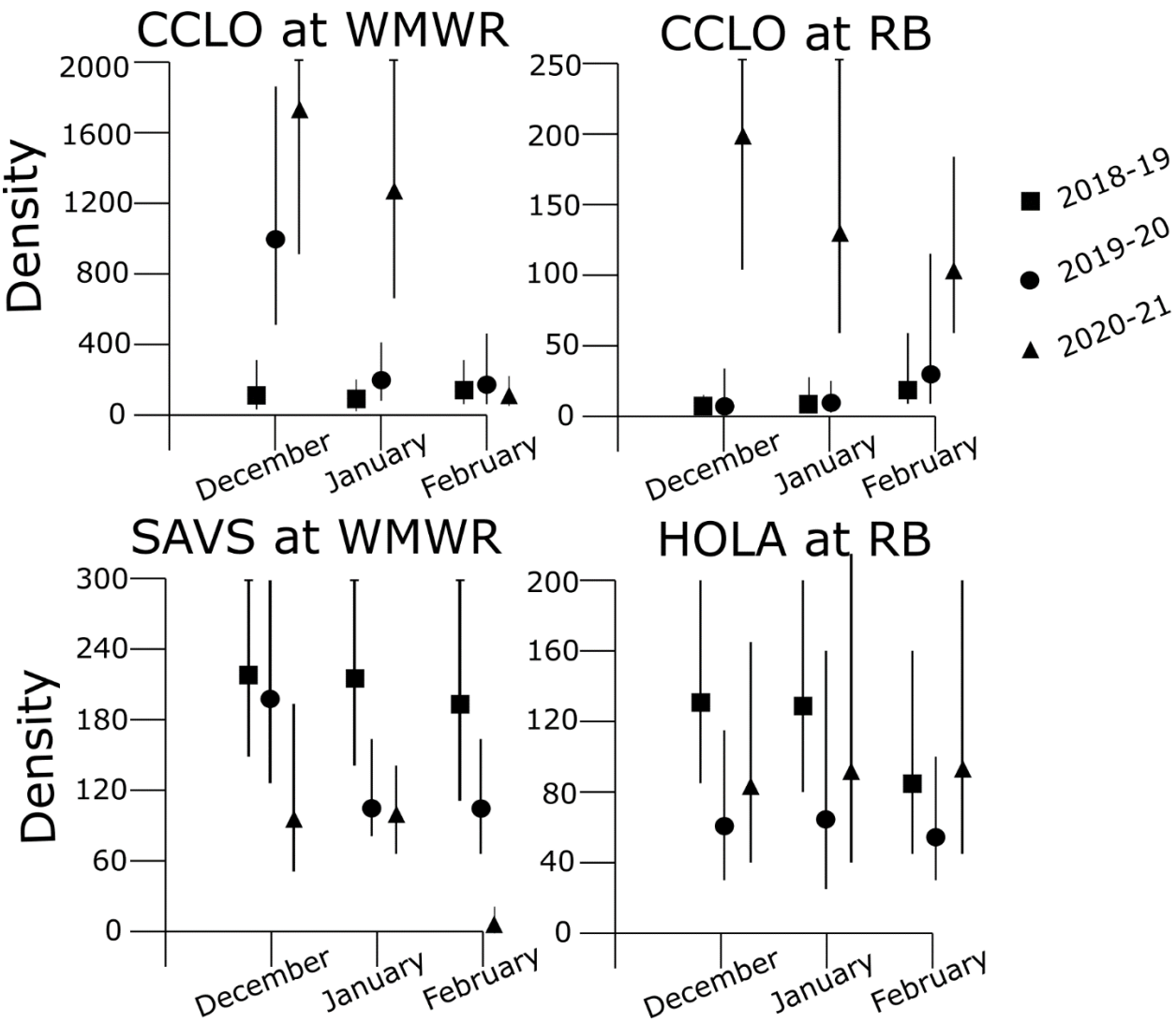


Figure 6. Densities of Chestnut-collared Longspur (CCLO), Savannah Sparrow (SAVS) and Horned Lark (HOLA) during the winter 2018-19 (black square), winter 2019-20 (black circle), and winter of 2020-21 (black triangle). At the Wichita Mountains Wildlife Refuge (WMWR), and Rita Blanca National Grassland (RB). Density estimates are presented along with the 95% Confidence interval.

**DISCUSSION**

Our study found multiple new discoveries about the wintering ecology of grassland birds within the SGP. Our SDM analysis found multiple hotspots for grassland birds within the state of Oklahoma that would be a priority for State and NGO's to pursue land acquisition and fine-scale management. We also found that many species that winter within the SGP, exhibit high levels of both inter- and intra-seasonal variability, implying that individual birds are moving large

distances between both between and within the same season. For species in which we had enough points, most associated with areas that had high amounts of grassland within the landscape and that were relatively devoid of shrubs. We also found that precipitation and diurnal temperature range were the strongest environmental variables predicting species diversity across the SGP. The overall grassland bird diversity in the SGP is high, we found 69 species using grasslands. The high diversity and abundance of birds within the SGP means that the SGP is an important area for grassland bird conservation especially for the multiple species that are undergoing major population declines (e.g., CCLO and TBLO).

Species Distribution Models (SDM) are effective tools for identifying areas of suitable habitat. Our SDM showed widespread suitability for many common species including WCSP and NOHA (Fig. 4), while the model identified fewer suitable areas for rarer species such as CCLO and SMLO (Fig. 4). For a few infrequent species the SDMs highlighted some areas as potential habitat despite our surveys not producing any detections at those areas, such as CCLO at Packsaddle WMA and Four Canyon Preserve or SMLO at Oka'Yanahli Preserve. This is likely because although the habitats and environments are seemingly suitable at the landscape level, this may not extend to habitat characteristics at the fine scale. Longspurs have specific fine-scale habitat requirements (see Chapter 3) that are selected at a resolution higher than 25 m. Areas such as Packsaddle WMA and Oka'Yanahli would likely contain longspurs if local management changed to select for finer scale habitats (i.e., management at the plot or individual field level) suitable for imperiled longspur species, such as the introduction of periodic, intensive cattle grazing to reduce vegetation height and density. The SDM repeatedly highlighted several locations across the SGP as having high suitability for various species (Fig. 3). Hence, our

analysis provides a guideline for suitable locations if state agencies or NGOs decide to pursue land acquisition or adapt current management practices of existing properties.

The non-breeding grassland bird species community of the SGP has a large overlap with the species community of the Chihuahuan desert and south Texas grasslands. The density estimates varied widely among years and sites for several species, which is a common finding across the wintering range for these species (Grzybowski 1982, Pool et al. 2012, CEC 2013). While CCLO were only detected on seven of our sites, density for the two most populous sites, WMWR and RB, ranged from 153-1109 birds/ $km^2$ at WMWR and 22-193 birds/ $km^2$ at Rita Blanca. This wide range of densities between sites and years for CCLO has been found in other studies as well. Grzybowski (1982) showed CCLO densities ranging from 5-166 birds/$km^2$ in Oklahoma. Pool et al. (2012) found an atypical high density of 1289.9 birds/$km^2$ at Llano Las Amapolas in the Chihuahuan Desert while typical estimates ranged from 248-595 birds/$km^2$ (CEC 2013). Such differences across sites are also found for other species; SAVS in South Texas display densities of 62-1580 birds/$km^2$ depending on site and year, while in Central Oklahoma their densities ranged from 5-1060 birds/$km^2$ (Grzybowski 1982). Macias-Duarte et al. (2018), found that SAVS had a density of 37.52 birds/$km^2$ in the Chihuahuan Desert, while we found densities ranging from 370-818 birds/$km^2$ at Hackberry Flats to 0.22- 2.6 birds/$km^2$ at Rita Blanca. At one site in south Texas (Grzybowski 1982) found densities of LCSP ranging from 67 - 1888 birds/$km^2$ over a three year period (the high year was considered an "exceptional year" with above average precipitation and tall, dense grass), whereas in central Oklahoma he found much lower densities of 22-43 birds/$km^2$. During our study we found Oklahoma sites such as Oka'Yanahli that had very high densities of LCSP (208-283 birds/$km^2$). This high degree of variation between years and sites shows the challenge of conserving these declining grassland

birds, as from one year to the next their populations can fluctuate greatly. Although we were able to track these highly variable densities across sites, we did not test for possible explanations for the high amounts of variability.

At the individual sites, we found large differences in abundance between years for several species including CCLO and SAVS (Fig. 5). Wintering grassland birds have shown an ability to alter their fine-scale winter distributions based on resource availability (Pool et al. 2012, Kristensen et al. 2013, Macías-Duarte et al. 2018), also known as the Theory of Ideal Free Distribution (Fretwell 1972). Because these species are able to shift their wintering areas to follow optimal resources, they likely can adapt to the effects of climate change better than other species as long as adequate amounts of suitable grassland are maintained across the wintering range of species. This has important implications for conservation. First, environmental changes on an annual basis (e.g., precipitation and seasonal phenological changes) affect the distribution and abundance of wintering species (Macías-Duarte et al. 2018). As a result, factors outside of managers' control can shift species abundances and distributions. However, this also means that grassland birds are adaptable and able to move into previously un-occupied areas if proper fine-scale management occurs. This gives confidence that local management actions in areas that are suitable at the landscape level can fulfill the habitat needs of focal species once the fine-scale management has been adjusted accordingly.

The transience of non-breeding grassland birds also has other management implications. If birds are moving across the landscape at distances larger than a single field site, there is a need for coordinated, landscape-scale management. Incorporating multiple stakeholders, including public land managers, private landowners, governments and NGO's (Drum et al. 2015), will be essential for conserving rapidly declining grasslands and the species they support. Habitat

fragmentation is a major driver in the downward population trends of many grassland birds (Koper and Schmiegelow 2006, Winter et al. 2006, Haddad et al. 2015, Wimberly et al. 2018). This fragmentation complicates the management of species such as longspurs, as unfragmented landscapes are rare. Effective management for these at-risk populations, even at the site level, will require management approaches across spatial scales. Future research into what factors drive this inter-seasonal transience (e.g. weather, resource depletion, predation, hormonal), is necessary.

At landscape levels all 20 species for which we completed SDMs, were positively associated with grassland amount. Not only were they positively associated, but for 18 of the species, grassland amount was one of the three most important response surfaces. The two species that did not include grassland amount in the top three still displayed a positive relationship with grassland amount. This could be an artifact of our sampling design. By sampling areas that contained large grassland tracts we are potentially biasing our surveys for species that like large grassland tracts. We attempted to rectify this potential bias by sampling areas that did not have large grassland tracts, such as shrub encroached tracts at Black Kettle NG, Beaver River WMA, and several transects at the Wichita Mountains WR; as well as agricultural transects at Hackberry Flats WMA, Optima NWR, PANTEX and Packsaddle WMA. We believe this rectification of potential bias was successful as species typically more associated with large expanses of grasslands, such as CCLO and SMLO (Ribic et al. 2009), had the strongest response curves to Grassland amount. Therefore, we believe our results show that increasing the amount of grassland on the landscape will be a benefit to all grassland species. But, future studies will be needed to determine how landscape level management affects the abundance and distribution of grassland birds in the SGP.

Many wintering grassland birds display a negative association to shrubs and woody vegetation (Pool et al. 2012, Ferrato et al. 2021), and multiple studies show that grassland birds are affected by shrub encroachment at various hierarchical scales (Thompson et al. 2014, Muller and Veech 2018). Our results indicate that many species show similar negative associations to shrubs and tree canopy cover at the landscape scale (Table 4). However, several grassland species (including multiple with declining populations) (Sauer et al. 2017), show positive associations to shrubs and tree cover at low densities (VESP and LOSH, Table 4). Because of this differing habitat preference of multiple species of concern, and for general conservation of avian biodiversity; if land managers are interested in conservation of biodiversity, grassland management should prioritize a heterogeneous mosaic of grasslands ranging from large shrub free areas to areas of relatively high shrub density.

While area amount is a common predictor of species richness (Williams and Others 1964, Connor and McCoy 1979, Hanski 1999), we found no relationship between field site area and either species richness metric. The number one predictor for species diversity (H') was Diurnal Temperature range, with more extreme temperature swings from daytime highs to nighttime lows associated with lower diversity. On the other hand, the top predictor for species richness was annual precipitation, with increasing aridity linked to lower richness. The association between higher precipitation and higher avian abundance and diversity has been linked many times (Macias-Duarte et al. 2009, 2018; Liang et al 2020), although this association has not been documented in the SGP as of yet. Kilometers surveyed were a secondary predictor for H' implying the need to continue site surveys to increase the reliability of the models. We detected decreasing species richness along the east-west gradient of the SGP region. Several environmental variables also show a trend along the east-west gradient, including precipitation

and diurnal temperature range. Annual precipitation is strongly tied to plant species richness and plant biomass in grasslands (Adler and Levine 2007, Yan et al. 2015). This increase in plant species and biomass likely leads to the increase in bird species richness that we witnessed (Li et al. 2013). Thermal tolerance has been an explanatory variable in determining the extent of species ranges (Gaston and Spicer 2001, Calosi et al. 2010, Khaliq et al. 2017). Even though we detected a decrease in species richness and diversity with increased temperature range we found a strong positive relationship between increased diurnal temperature range and species such as CCLO and TBLO (Table 4). These findings suggest that these species have a higher thermal variability tolerance thus allowing them to exploit a wide breadth of "exposed prairie" environmental niche space. Although, it is still unknown as to whether or not longspurs are being outcompeted and forced into these environments through competition or whether longspurs are genetically predisposed to be able to physiologically utilize the environment where other species cannot and are preemptively choosing to settle in highly temperature variable environments.

Of the 69 species detected on surveys, 11 species had at least 60 detections. The detectability of grassland bird species was highly variable. The detection curve for LCSP showed that only 49% of birds were detected within 10.1 m of the transect, whereas for NOHA 54% of individuals were detected up to 199.1 m from the transect. This means that to properly survey for and track species such as LCSP during winter when they are silent will require covering large distances of transects. Other species such as NOHA can be adequately surveyed with more traditional low-effort methods such as point counts. Because detection probability is so variable between species, relative abundance is a much better metric of true diversity.

Some individual wintering grassland birds have shown a high level of transient behavior throughout a single winter season (Gordon 2000, Muller et al. in review, Muller et al.

unpublished). We found changing densities for multiple common species throughout the winter. December typically had the highest density compared to January and February. This result implies that the population in December was composed of both winter resident and migratory individuals. In addition to this transience throughout the winter, species such as CCLO also show large confidence intervals and Standard Errors in their density estimates. This is due to the variability in abundance between sites (alpha diversity), the large variability between transects, and large variation of flock size (beta diversities). It was not uncommon for us to observe flocks on the same transect vary between 0-10 individuals to over hundred, as well as adjacent transects ranging from devoid of longspurs to having hundreds. Because of this flocking and highly social behavior resulting in uneven distributions, and the inter-seasonal variability throughout each winter, estimating true densities for species such as CCLO is difficult.

Oklahoma has a high diversity of wintering grassland birds. We detected over 69 species during the winter. This high level of diversity signifies the importance of Oklahoma as habitat for many rapidly declining grassland species. Even sites with relatively low H' and J', such as the Wichita Mountains WR and Oka'Yanahli, displayed extreme abundance of a few species. This can be explained by the extreme abundance of a few species, such as CCLO which made up 64.1% of all individuals detected at the Wichita Mountains. CCLO are a critical species for conservation displaying the fourth fastest population decline of any bird species in the United States and Canada (Sauer et al 2017). Therefore, the Wichita Mountains having a low H' is not necessarily a negative if it means that CCLO are being adequately conserved.

**NEXT STEPS**

Multiple questions have arisen from our study including 1) looking into the thermal variability tolerance of longspurs, that allows them to seemingly thrive in the highly variable environment

of the western plains that other species cannot, 2) tracking the inter and intra-seasonal movement of wintering grassland bird populations to see the true scale of movement as well as the potential drivers of that movement (i.e., is it facilitated by weather, resources, predation, or some other factors), 3) responsiveness of wintering populations to landscape management, and 4) the specific environmental factors affecting seasonal changes to distributions. Investigations into any of these questions will provide information that will assist in the conservation of these rapidly declining species. Sites such as the Wichita Mountains WR which are on the periphery of the wintering range of LCSP, CCLO and TBLO, will become more important as western grasslands and aridity push westward in the coming decades due to changes in rainfall patterns and phenology (Wilsey et al. 2019). If conservation of rapidly declining species is deemed a priority, proper management and conservation of critical grassland areas within the state should become a priority even if those management practices are contrary to other species of interest. Oklahoma has the potential and the ability to become a sanctuary for many of these declining grassland bird species and become a critical area for the persistence and recovery for these species, if proper management is enacted (i.e., removing shrubs, increasing the amount of grassland on the landscape by converting unsuitable habitats to grasslands). Specific site level management actions are described in more detail in chapter 3.

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## Appendix

Appendix A. Description of the 14 field sites used during the 3-year study.

| Site | Ecosystem | Size ($km^2$) | Description |
|---|---|---|---|
| Tall | Tallgrass | 160 | The Joseph H. Williams Tallgrass Prairie Preserve in northeastern Oklahoma. Owned and managed by the Nature Conservancy is the largest protected remnant of Tallgrass Prairie left on earth. It employs a "patch-burn" model using 2,500 free-ranging American Bison (*Bison bison*) designed to mimic the natural wildfire disturbance regime (Fuhlendorf and Engle 2001). The preserve is located in the Flint Hills region of Kansas and Oklahoma, where rocky rolling hills protected the preserve from the plow and development. |
| Oka | Mixedgrass | 15 | Located in Johnston County, Oklahoma and owned by The Nature Conservancy the Oka'Yanahli Preserve is composed mostly of Cross-timbers Mixedgrass prairie. The preserve was purchased in 2015 and is not grazed, although there has been invasive species management. |
| WMWR | Mixedgrass | 81 | The Wichita Mountains Wildlife Refuge is located in southwestern Oklahoma just north of the city of Lawton and Fort Sill Military Base. The refuge contains a variety of habitats including Mixedgrass prairie as well as substantial scrubland areas dominated by blackjack (*Quercus marilandica*) and post oak (*Q. stellata*). The rocky soil of these grasslands helped spare the Wichita's from agricultural development. The area was designated a national game reserve in 1905 and was added to the national refuge system in 1936, making it one of the oldest wildlife refuges in the US. In 1907 the refuge introduced 15 bison from the New York Zoological Society, and in 1927 a herd of longhorn cattle (*Bos taurus*) was introduced to reflect the cultural history of the region. These "free ranging" bison and cattle provide a grazing regime while the refuge actively manages both the cattle and bison populations through roundups and auctions. |
| Hack | Mixedgrass | 29 | Established in 1995, and located near Frederick in southwestern Oklahoma, Hackberry Flats Wildlife Management Area provides wildlife recreational opportunities. Owned and managed by the Oklahoma Department of Wildlife Conservation, the site was restored to wetland, and created a vast mosaic of wetland habitats for prairie waterfowl, shorebirds and other wetland-dependent birds. Upland areas contain units of native sunflowers and cultivated fields. |
| BK | Mixedgrass | 127 | Black Kettle National Grasslands were established in 1960, the site is open year-round and offers camping, picnicking, hiking, fishing, and wildlife viewing. Managed by the National Forest Service it contains mixed grass prairie, forested river bottomland, and colorful red sand hills. |

| | | | |
|---|---|---|---|
| Pack | Mixedgrass | 80 | Packsaddle Wildlife Management Area is a mixture of rolling sand hills and wooded bottoms with the Canadian River as its southern boundary. Uplands sites are vegetated with mixed grass species including Big Bluestem, Indiangrass, Little Bluestem, Side-oats Grama, and Buffalo Grass and brush species like Shinnery Oak, Sagebrush, and Sand Plum |
| Beav | Shortgrass | 13 | Located in the Panhandle of Oklahoma, and along the Canadian river. Beaver River Wildlife Management Area includes uplands of shortgrass prairie dominated by sagebrush and buffalo grass, with interspersed sand plums and mixed grass prairie grasses. |
| Opt | Shortgrass | 30 | Located in the Panhandle of Oklahoma, Optima National Wildlife Refuge and Wildlife Management Area, includes uplands of shortgrass prairie dominated by sagebrush and buffalo grass, with interspersed sand plums and mixed grass prairie grasses. Also, includes a large Impoundment with a seasonal lake |
| Cimarron | Mixedgrass | 14 | Consisting of both Cimarron Hills and Cimarron Bluffs Wildlife Management Areas, the sites consist primarily of rolling hills with high bluffs overlooking the west side of the Cimarron River. Area is dominated by mixed-grass prairie vegetation with isolated pockets of sand sagebrush, sand plum, and sumac occurring on red clay and gypsum soils. |
| RB | Shortgrass | 376 | Located across both Texas (Dallam County) and Oklahoma (Cimarron County), Rita Blanca National Grasslands is 37,632 ha of shortgrass prairie. Both Rita Blanca and Kiowa National Grasslands are administered together by the U.S. Forest Service and consist of a patchwork of public land interspersed among private agriculture and ranchland. |
| Kiowa | Shortgrass | 202 | Adjacent to Rita Blanca NG in Union County New Mexico is the Eastern section of Kiowa National Grasslands. |
| Buffalo | Shortgrass | 31 | Containing one of the best remaining plots of shortgrass prairie and a designated National Natural Landmark, Buffalo Lake National Wildlife Refuge is just South of Amarillo in the Texas Panhandle |
| Mule | Shortgrass | 26 | Known for its three major playa lakes which house a wintering population of Sandhill cranes and as a migratory stopover site for waterfowl, the majority of Muleshoe National Wildlife Refuge is shortgrass prairie interspersed with mesquite shrubs |
| PANTEX | Shortgrass | 1 | Located just northeast of Amarillo Texas, Pantex Plant is the primary Nuclear weapon disassembly and assembly plant in the United States. Many of the fields surrounding the plant were purchased for security and allow both agricultural fields and grazing. These fields are occasionally allowed for research teams including ecologists to survey. |

Appendix B. The 23 response variables used for the distribution modeling along with a description, units, and source of the data.

| Name | Description | units | source |
|---|---|---|---|
| Bio1 = Annual Mean Temperature | Mean annual air temperature over 1 year | Celcius | CHELSA |
| Bio2 = Mean Diurnal Range | mean diurnal range of temperatures averaged over 1 year | Celcius | CHELSA |
| Bio3 = Isothermality | ratio of diurnal variation to annual variation in temperatures | Celcius | CHELSA |
| Bio4 = Temperature Seasonality | standard deviation of the monthly mean temperatures | Celcius | CHELSA |
| Bio5 = Max Temperature of Warmest Month | The highest temperature of any monthly daily mean maximum temperature | Celcius | CHELSA |
| Bio6 = Min Temperature of Coldest Month | The lowest temperature of any monthly daily mean maximum temperature | Celcius | CHELSA |
| Bio7 = Temperature Annual Range | The difference between the Maximum Temperature of Warmest month and the Minimum Temperature of Coldest month | Celcius | CHELSA |
| Bio8 = Mean Temperature of Wettest Quarter | The wettest quarter of the year is determined (to the nearest month) | Celcius | CHELSA |
| Bio9 = Mean Temperature of Driest Quarter | The driest quarter of the year is determined (to the nearest month) | Celcius | CHELSA |
| Bio10 = Mean Temperature of Warmest Quarter | The warmest quarter of the year is determined (to the nearest month) | Celcius | CHELSA |
| Bio11 = Mean Temperature of Coldest Quarter | The coldest quarter of the year is determined (to the nearest month) | Celcius | CHELSA |
| Bio12 = Annual Precipitation | Accumulated precipitation amount over 1 year | $kg/m^2$ | CHELSA |

| | | | |
|---|---|---|---|
| Bio13 = Precipitation of Wettest Month | The precipitation of the wettest month. | $kg/m^2$ | CHELSA |
| Bio14 = Precipitation of Driest Month | The precipitation of the driest month. | $kg/m^2$ | CHELSA |
| Bio15 = Precipitation Seasonality | The Coefficient of Variation is the standard deviation of the monthly precipitation estimates expressed as a percentage of the mean of those estimates (i.e. the annual mean) | $kg/m^2$ | CHELSA |
| Bio16 = Precipitation of Wettest Quarter | The wettest quarter of the year is determined (to the nearest month) | $kg/m^2$ | CHELSA |
| Bio17 = Precipitation of Driest Quarter | The driest quarter of the year is determined (to the nearest month) | $kg/m^2$ | CHELSA |
| Bio18 = Precipitation of Warmest Quarter | The warmest quarter of the year is determined (to the nearest month) | $kg/m^2$ | CHELSA |
| Bio19 = Precipitation of Coldest Quarter | The coldest quarter of the year is determined (to the nearest month) | $kg/m^2$ | CHELSA |
| Mean Canopy Cover | The mean percent canopy cover for the cell | percent | NLCD |
| Percent Open | The percent of the cell containing “open” terrestrial habitats (Developed Open Space, Barren Land, Herbaceous, Pasture, Cropland, Emergent Herbaceous Wetland) | percent | NLCD |
| Percent Grassland | The Percent of the Cell Containing Grassland/Herbaceous | percent | NLCD |
| Topographic Roughness | Difference between the highest point and lowest point | Meter | USGS DEM |

Appendix C. The 69 species and the number detected at each of the 14 sites (Tall (Tallgrass Prairie Preserve), Oka (Oka'Yahnali Preserve), WMWR (Wichita Mountains Wildlife Refuge), Hack (Hackberry Flats WMA), BK (Black Kettle National Grasslands), Pack (Packsaddle Wildlife Management Area), CHCB (Cimarron Hills and Cimarron Bluffs Wildlife Management Areas), Optima (Optima National Wildlife Refuge and Wildlife Management Area), Beav (Beaver River Wildlife Management Area), Kiowa (Kiowa National Grasslands), Rita (Rita Blanca National Grasslands), Mule (Muleshoe National Wildlife Refuge), Buff (Buffalo Lake National Wildlife Refuge), Pant (PANTEX Nuclear Site)), across all three years of effort. Species are listed using the 4-letter alpha code used by the U.S. Bird Banding Laboratory (https://www.pwrc.usgs.gov/bbl/manual/speclist.cfm). Species seen at the site by us but were not detected on a survey are denoted with an *.

| Species | Tall | Oka | WMWR | Hack | BK | Pack | CHCB | Optima | Beav | Kiowa | Rita | Mule | Buff | Pant |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| AMCR | 8 | * | 1 | * | 6 | 7 | | | | | | | | |
| AMGO | 7 | 8 | 64 | 80 | 2 | 21 | 4 | 3 | 22 | * | * | | | |
| AMKE | 6 | 5 | 11 | 7 | 3 | 1 | * | 4 | * | 1 | 4 | 4 | * | 1 |
| AMPI | * | | | * | | | | | 2 | | | | | |
| AMTS | 48 | | 10 | 1 | 8 | 57 | 42 | 9 | 14 | | | | | |
| BAEA | 3 | * | * | * | * | | | | | * | * | | | |
| BEWR | | 2 | 6 | * | 6 | 1 | | | | | | | | |
| BUOW | | | | | | | | | | | * | | | 1 |
| CCLO | 1 | * | 5851 | 8 | | | | | | 303 | 1440 | 32 | 10 | |
| CHRA | | | | | | | | * | | * | 66 | * | 3 | * |
| CHSP | | * | * | | 2 | 4 | | | | | | | | |
| COGR | | | | | | | | | 1 | | | | | |
| COHA | | | | | 1 | | | | | | | | | |
| CORA | | | | | 1 | | | | | | 2 | | | |
| DEJU | | 4 | 334 | | 185 | 101 | 26 | | | | | | | |
| EABL | 5 | 2 | 30 | | 13 | 13 | | | | | | | | |
| EAME | 78 | 170 | 886 | 1239 | 21 | 75 | 3 | | 23 | | | 1 | | |
| EAPH | | | 1 | | | 1 | | | | | | | | |
| EUCD | | | | | | | | | | 1 | 1 | | | |
| EUST | 2 | 3 | | | | | | | | | | | | |
| FEHA | 1 | | | 1 | | | | 1 | | 3 | 11 | | 1 | |
| FISP | 7 | 35 | 101 | | 48 | 81 | | 2 | 10 | | | | | |
| GHOW | | | | 4 | | 2 | | | 1 | | | | | |
| GOEA | 2 | | | | | | | | | | 2 | | 1 | |
| GRPC | 4 | | | | | | | | | | | | | |
| GRRO | | | 2 | | | | | | | | | | | |
| GRSP | 1 | 1 | | | | | | | | | | | | |
| HASP | | | 45 | 4 | 2 | 16 | | | 3 | | | | | |
| HOLA | 39 | 16 | 46 | 82 | 5 | 37 | | 440 | 13 | 652 | 3669 | | 21 | 272 |
| KILL | | 1 | 3 | 2 | | 1 | | | 1 | | 1 | | | |

| | | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| LALO | 19 | | | 381 | 6 | | | 38 | 16 | 26 | 1279 | | | 12 |
| LBWO | | | 1 | | | | 1 | | | | | | | |
| LCSP | 22 | 130 | 92 | 10 | 2 | 3 | | | 1 | | | | | |
| LEPC | | | | | | | * | | | | | | | |
| LISP | | | 3 | 1 | | | | | 1 | | | | | |
| LOSH | 2 | | 2 | 6 | 4 | | | | | 2 | | 6 | | |
| MAWR | | | | 3 | | | 1 | | | | | | | |
| MCLO | | | 1 | 7 | | 3 | | | | 2 | 136 | | | 79 |
| MERL | | | 1 | 2 | | | | | | | | | | |
| MOBL | | | 12 | | 23 | 29 | | | | | | | | |
| MODO | | 3 | 9 | 2 | 10 | 39 | | | | | | 2 | | |
| NOBO | 11 | | 2 | 3 | | | 1 | | 18 | | | 15 | | |
| NOFL | 22 | 2 | 8 | | 4 | 5 | 3 | 1 | | | | | 1 | |
| NOHA | 82 | 13 | 13 | 30 | | 7 | 10 | 3 | 3 | 6 | 8 | 2 | 3 | 4 |
| NOMO | | 9 | 1 | | | | | | | | | | | |
| NOSH | | | | | | | | | | | | | 1 | |
| PISI | | | 35 | | 35 | 99 | | | | | 7 | | | |
| PRFA | 1 | | 1 | | | | | 1 | | 1 | 2 | | 1 | |
| RCSP | | | 6 | | | | | | | | | | | |
| RINP | | | | | | | | | | | 1 | | | |
| RLHA | 13 | 1 | | 1 | | | | | | | 1 | | | |
| ROPI | | | | | | | | 2 | | | | | | |
| RTHA | 19 | 3 | 3 | | 1 | 4 | 3 | | 2 | 1 | 1 | | 3 | |
| RWBL | 86 | | 36 | 105 | 220 | | | | 795 | | | | | 500 |
| SAVS | 122 | 848 | 998 | 806 | 6 | 41 | 2 | 2 | 34 | 2 | 14 | 15 | 11 | 17 |
| SEOW | 9 | 1 | 1 | 1 | | 1 | | | | | 3 | | | |
| SEWR | 4 | 4 | 1 | | | | | | | | | | | |
| SMLO | 252 | * | 107 | | | | | | | | | | | |
| SOSP | 26 | 81 | 212 | 75 | 26 | 41 | 10 | | 52 | | | | | |
| SPPI | 2 | | | | | * | | | | | | | | |
| SPTO | | 1 | 17 | | 7 | | | | | | | | | |
| SSHA | | | 1 | 1 | | | | | | | | | | |
| SWSP | | 4 | | 5 | | | | | | | | | | |
| TOSO | | | | | 1 | | | | | | | | | |
| VESP | | 1 | 22 | 5 | 1 | 1 | | | | | 1 | | | |
| WCSP | | | 1 | 87 | 4 | 74 | 1 | 4 | 37 | | 1 | 8 | | 1 |
| WEME | 1 | 1 | 146 | 201 | 7 | 21 | 8 | 126 | 180 | 29 | 187 | 57 | 74 | 169 |
| WISN | 5 | 1 | 1 | | | | | | | | | | | |
| WWDO | | | 1 | | 1 | | | | | | | | | |

Appendix D.1. Table showing the densities for Western Meadowlark (WEME), Eastern Meadowlark (EAME), Horned Lark (HOLA), and Northern Harrier (NOHA), at the 14 field sites for the three years of surveys. Densities and confidence intervals as well as the Standard Error are reported. Birds seen at the study site but not on transects or not found in high enough numbers for density analysis are denoted with an *.

| Location | Year | | WEME | EAME | HOLA | NOHA |
|---|---|---|---|---|---|---|
| | | | Birds/km$^2$ | Birds/km$^2$ | Birds/km$^2$ | Birds/km$^2$ |
| Tallgrass Prairie Preserve | 1 | Density | 0.15 (0.027-0.9) | 8.3 (3.4-20.1) | 0.61 (0.1-3.5) | 1.64 (0.8-3.3) |
| | | SE | 0.15 | 3.7. | 0.61 | 0.56 |
| | 2 | Density | 0.00 | 7.8 (4.1-15.1) | * | 2.5 (1.5-4.3) |
| | | SE | 0.00 | 2.50 | * | 0.65 |
| | 3 | Density | 0.00 | 11.2 (3.9-32.4) | 5.6 (.96-33.1) | 2.9 (1.4-5.8) |
| | | SE | 0.00 | 6.00 | 5.70 | 1.00 |
| Hackberry Flats Wildlife Management Area | 1 | Density | 96.3 (33.3-278.2) | 271.9 (147.5-501.4) | 9.03 (1.8-45.4) | 1.86 (0.7-5.2) |
| | | SE | 46.20 | 76.15 | 6.98 | 0.86 |
| | 2 | Density | 8.2 (1.6-41) | 329.8 (120.3-904.3) | 18.3 (4.8-70.3) | 3.2 (1.5-6.5) |
| | | SE | 6.30 | 149.90 | 11.30 | 1.03 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Wichita Mountains Wildlife Refuge | 1 | Density | 6.1 (2.7-13.2) | 61.1 (31.1-120.4) | * | 0.40 (0.13-1.2) |
| | | SE | 2.70 | 20.58 | * | 0.23 |
| | 2 | Density | 6.5 (1.4-31.5) | 30.37 (13.4-68.6) | 4 (0.7-22.7) | 0.4 (0.19-0.9) |
| | | SE | 5.30 | 12.46 | 4.00 | 0.16 |
| | 3 | Density | 1.2 (0.5-2.8) | 5.1 (2.6-9.8) | 0.00 | 0.00 |
| | | SE | 0.05 | 1.70 | 0.00 | 0.00 |
| Oka'Yanahli Preserve | 1 | Density | 0.5 (0.08-3.5) | 60.6 (22.4-163.5) | * | 0.47 (0.12-1.8) |
| | | SE | 0.50 | 28.35 | * | 0.31 |
| | 2 | Density | 0.00 | 36.8 (19.9-68.2) | * | 1.5 (0.8-2.7) |
| | | SE | 0.00 | 10.71 | * | 0.42 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Packsaddle Wildlife Management Area | 1 | Density | 2.4 (.67-8.5) | 18.6 (2.9-119.7) | * | 1.0 (0.19-5.2) |
| | | SE | 1.40 | 17.40 | * | 0.80 |
| | 2 | Density | 8.7 (2.4-31.2) | 0.7 (0.098-5.03) | 29.7 (3.6-243.4) | 1.5 (0.28-8.0) |
| | | SE | 5.10 | 0.71 | 31.10 | 1.20 |
| | 3 | Density | 0.00 | 13.8 (2.6-9.8) | 0.00 | 0.00 |
| | | SE | 0.00 | 1.70 | 0.00 | 0.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Black Kettle National Grasslands | 1 | Density | 1.3 (.53-3.3) | 5.08 (1.5-17.4) | * | * |
| | | SE | 0.58 | 3.17 | * | * |
| | 2 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Beaver River Wildlife Management Area | 1 | Density | 74.8 (18.6-300.9) | 8.9 (1.3-61.6) | 0.92 (0.1-7.8) | 0.26 (0.03-2.2) |
| | | SE | 44.10 | 7.85 | 0.92 | 0.26 |
| | 2 | Density | 10.6 (2.1-55) | 2.5 (0.5-12.7) | * | 0.39 (0.046-3.3) |
| | | SE | 7.60 | 1.78 | * | 0.39 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Optima National Wildlife Refuge | 1 | Density | 84.9 (12.9-554.6) | 0.00 | 124.8 (16.9-921.3) | 0.78 (0.18-3.4) |
| | | SE | 71.30 | 0.00 | 113.90 | 0.49 |
| | 2 | Density | 25.4 (5.7-113.9) | 0.00 | 291.7 (0.35-2433.9) | 0.39 (0.04-3.3) |
| | | SE | 16.30 | 0.00 | 288.70 | 0.39 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Rita Blanca National Grasslands | 1 | Density | 9.7 (6.1-15.2) | 0.00 | 178.3 (112.6-282.5) | 0.176 (0.06-0.5) |
| | | SE | 2.10 | 0.00 | 39.40 | 0.09 |
| | 2 | Density | 5 (2.5-9.9) | 0.00 | 87 (49.7-152.3) | 0.178 (0.05-0.7) |
| | | SE | 1.70 | 0.00 | 23.50 | 0.12 |
| | 3 | Density | 5.8 (3.3-10.1) | * | 124.6 (70.6-219.7) | 0.00 |
| | | SE | 1.50 | * | 34.10 | 0.00 |
| Muleshoe National Wildlife Refuge | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 20.4 (6.1-68.6) | 0.00 | 0.00 | 0.19 (0.02-1.77) |
| | | SE | 9.40 | 0.00 | 0.00 | 0.19 |
| | 3 | Density | 4.9 (1.6-14.6) | * | 0.00 | 0.00 |
| | | SE | 2.10 | * | 0.00 | 0.00 |
| Buffalo Lake National Wildlife Refuge | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 32.2 (7.8-133.2) | 0.00 | 19.2 (1.06-90.8) | 0.58 (0.09-3.6) |
| | | SE | 15.20 | 0.00 | 10.30 | 0.38 |
| | 3 | Density | 10.3 (1.4-75.1)- | 0.00 | 8.31 (1.1-62.5) | 0.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | SE | 7.20 | 0.00 | 5.90 | 0.00 |
| Pantex | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 172.9 (.017-17596.9) | 0.00 | 381.6 (322.4-451.7) | 2.3 (1.8-3) |
| | | SE | 146.30 | 0.00 | 24.40 | 0.31 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Kiowa National Grasslands | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 4.5 (1.4-14.7) | 0.00 | 15.6 (8.7-28.2) | 0.34 (0.15-0.78) |
| | | SE | 2.20 | 0.00 | 3.90 | 0.12 |
| | 3 | Density | 5.7 (1.4-23.3) | 0.00 | 84.1 (24.9-282.6) | 0.27 (.058 - 1.3) |
| | | SE | 3.40 | 0.00 | 42.10 | 0.17 |
| Cimarron Hills Wildlife Management Area | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 13.4 (.017-106663.8) | 2.26 (0.0002-61254.5) | 0.00 | 1.17 (0.00006-22000) |
| | | SE | 8.20 | 2.27 | 0.00 | 1.18 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Cimarron Bluffs WMA | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 0.00 | 0.75 (.022-25.8) | 0.00 | 7 (3.7-13.1) |
| | | SE | 0.00 | 0.76 | 0.00 | 1.64 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |

Appendix D.2. Table showing the densities for Chestnut-collared Longspur (CCLO), Thick-billed Longspur (TBLO), Smiths Longspur (SMLO) and Lapland Longspur (LALO) at the 14 field sites for the three years of surveys. Densities and confidence intervals as well as the Standard Error are reported. Birds seen at the study site but not on transects or not found in high enough numbers for density analysis are denoted with an *.

| Location | Year | | CCLO | TBLO | SMLO | LALO |
|---|---|---|---|---|---|---|
| | | | Birds/km$^2$ | Birds/km$^2$ | Birds/km$^2$ | Birds/km$^2$ |
| Tallgrass Prairie Preserve | 1 | Density | 0.00 | 0.00 | 70.3 (18.8-261.9) | * |
| | | SE | 0.00 | 0.00 | 49.10 | * |
| | 2 | Density | 0.22 (.03-1.2) | 0.00 | 39.7 (11.8-132.6) | 0.00 |
| | | SE | 0.22 | 0.00 | 25.10 | 0.00 |
| | 3 | Density | 0.00 | 0.00 | 18.7 (.02-1560.6) | 0.00 |
| | | SE | 0.00 | 0.00 | 217.50 | 0.00 |
| Hackberry Flats Wildlife Management Area | 1 | Density | 1.49 (.21-10.5) | * | 0.00 | 29.1 (7.2-117.9) |
| | | SE | 1.48 | * | 0.00 | 19.60 |
| | 2 | Density | 2.61 (.36-18.6) | * | 0.00 | 20 (3-134.2) |
| | | SE | 2.61 | * | 0.00 | 20.10 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Wichita Mountains Wildlife Refuge | 1 | Density | 152.9 (79.4-294.4) | * | 5.6 (2.4-12.7) | 0.00 |
| | | SE | 45.50 | * | 2.30 | 0.00 |
| | 2 | Density | 406.2(222.3-742.2) | 0.00 | 2.4 (0.86-6.6) | 0.00 |
| | | SE | 121.10 | 0.00 | 1.20 | 0.00 |
| | 3 | Density | 1109.3 (626.8-1963.5) | * | 0.7 (0.1-4.4) | 0.00 |
| | | SE | 311.10 | * | 0.70 | 0.00 |
| Oka'Yanahli Preserve | 1 | Density | 0.00 | 0.00 | * | 0.00 |
| | | SE | 0.00 | 0.00 | * | 0.00 |
| | 2 | Density | * | 0.00 | * | 0.00 |
| | | SE | * | 0.00 | * | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Packsaddle Wildlife Management Area | 1 | Density | 0.00 | 0.00 | 0.00 | 0.00 |
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| | 2 | Density | 0.00 | * | 0.00 | 0.00 |
| | | SE | 0.00 | * | 0.00 | 0.00 |
| | 3 | Density | 0.00 | 0.00 | 0.00 | 0.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| Black Kettle National Grasslands | 1 | Density | * | 0.00 | 0.00 | * |
| | | SE | * | 0.00 | 0.00 | * |
| | 2 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Beaver River Wildlife Management Area | 1 | Density | 0.00 | 0.00 | 0.00 | 0.00 |
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| | 2 | Density | 0.00 | 0.00 | 0.00 | 11.9 (1.42-99.3) |
| | | SE | 0.00 | 0.00 | 0.00 | 12.20 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Optima National Wildlife Refuge | 1 | Density | 0.00 | 0.00 | 0.00 | 13.2 (3.7-46.8) |
| | | SE | 0.00 | 0.00 | 0.00 | 7.20 |
| | 2 | Density | 0.00 | 0.00 | 0.00 | 2.9 (0.34-24.6) |
| | | SE | 0.00 | 0.00 | 0.00 | 2.90 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Rita Blanca National Grasslands | 1 | Density | 94.3 (35.8-248.1) | * | 0.00 | 51.7 (25.3-105.3) |
| | | SE | 45.50 | * | 0.00 | 18.20 |
| | 2 | Density | 21.8 (7.4-64.9) | * | 0.00 | 31.3 (14.8-66.1) |
| | | SE | 12.10 | * | 0.00 | 11.60 |
| | 3 | Density | 193.2 (118.6-314.5) | * | 0.00 | 30.2 (14.5-62.9) |
| | | SE | 45.50 | * | 0.00 | 11.00 |
| Muleshoe National Wildlife Refuge | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 22.9 (3.3-158.1) | 0.00 | 0.00 | 0.00 |
| | | SE | 18.20 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | 0.00 | 0.00 | 0.00 | 0.00 |
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| Buffalo Lake National Wildlife Refuge | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 0.9 (.07-12.9) | 0.00 | 0.00 | 0.00 |
| | | SE | 0.90 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | 28.4 (2.1-389.6) | 0.00 | 0.00 | 0.00 |
| | | SE | 28.60 | 0.00 | 0.00 | 0.00 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Pantex | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 0.00 | * | 0.00 | 21.2 (.001-5141) |
| | | SE | 0.00 | * | 0.00 | 15.60 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Kiowa National Grasslands | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 4.2 (.4-39.1) | 0.00 | 0.00 | 3.4 (0.5-21) |
| | | SE | 4.46 | 0.00 | 0.00 | 2.80 |
| | 3 | Density | 237.3 (95.1 - 592.1) | 0.00 | 0.00 | 5.2 (1.8-14.8) |
| | | SE | 89.20 | 0.00 | 0.00 | 2.70 |
| Cimarron Hills Wildlife Management Area | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 0.00 | 0.00 | 0.00 | 0.00 |
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Cimarron Bluffs WMA | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | * | 0.00 | 0.00 | 0.00 |
| | | SE | * | 0.00 | 0.00 | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |

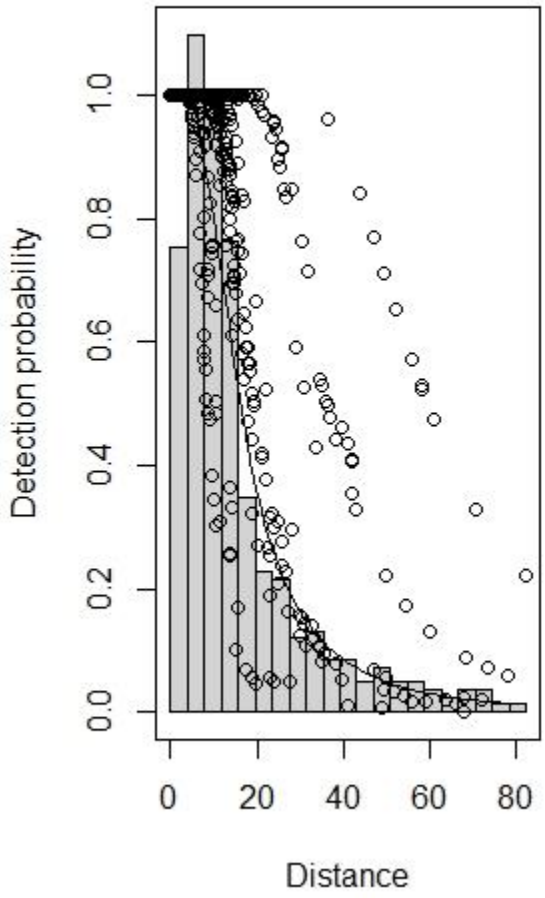
Appendix D.3. Table showing the densities for Savannah Sparrow (SAVS), LeConte's Sparrow (LCSP), Song Sparrow (SOSP), and Field Sparrow (FISP) at the 14 field sites for the three years of surveys. Densities and confidence intervals as well as the Standard Error are reported. Birds seen at the study site but not on transects or not found in high enough numbers for density analysis are denoted with an *.

| Location | Year | | SAVS | LCSP | SOSP | FISP |
|---|---|---|---|---|---|---|
| | | | Birds/$km^2$ | Birds/$km^2$ | Birds/$km^2$ | Birds/$km^2$ |
| Tallgrass Prairie Preserve | 1 | Density | 15.3 (6.5-36.1) | 25.8 (10.4-64) | 4.6 (1.7-12.1) | 2.94 (.88-7.9) |
| | | SE | 6.50 | 11.60 | 2.20 | 1.80 |
| | 2 | Density | 53.1 (34.6-81.3) | 20.3 (6.7-61.7) | 7.3 (3.1-17.2) | 0.00 |
| | | SE | 10.90 | 11.50 | 3.10 | 0.00 |
| | 3 | Density | 10.4 (5.2-21.04) | 20.4 (9.2-45.2) | 1.7 (0.4-6.7) | 0.00 |
| | | SE | 3.60 | 7.99 | 1.20 | 0.00 |
| Hackberry Flats Wildlife Management Area | 1 | Density | 818.5 (418.6-1600.5) | 56.7 (19.1-167.5) | 19.1(7.7-47.3) | 0.00 |
| | | SE | 238.70 | 27.50 | 7.70 | 0.00 |
| | 2 | Density | 369.8 (216.7-631.0) | 8.9 (2.2-36.4) | 34.7 (17.2-69.7) | 0.00 |
| | | SE | 85.50 | 5.80 | 10.60 | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Wichita Mountains Wildlife Refuge | 1 | Density | 263.4 (182.4-380.2) | 68.6 (42.7-110.3) | 31 (16.7-57.7) | 11.17 (4.2-29.1) |
| | | SE | 46.80 | 15.80 | 9.40 | 5.42 |
| | 2 | Density | 168.4 (116.8-242.8) | 15.5 (7.3-32.7) | 10.3 (4.8-21.9) | 10.1 (4.8-25.5) |
| | | SE | 30.00 | 5.80 | 3.90 | 3.62 |
| | 3 | Density | 68.5 (45.6-102.7) | 62.9 (39.8-99.6) | 18 (12.3-26.3) | 12.1 (4.2-34.7) |
| | | SE | 13.50 | 14.10 | 3.40 | 6.60 |
| Oka'Yanahli Preserve | 1 | Density | 359.9 (254.4-508.8) | 382.6 (280.8-521.3) | 66.9 (30-149) | 7.13 (1.6-31.8) |
| | | SE | 56.40 | 54.70 | 24.70 | 5.31 |
| | 2 | Density | 660.7 (499.6-873.9) | 208.7 (126.7-343.9) | 7.9 (38.5-164.6) | 17.5 (6.2-49.6) |
| | | SE | 84.00 | 47.40 | 26.50 | 8.60 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Packsaddle Wildlife Management Area | 1 | Density | 30.01 (10.5-85.8) | 13.2 (1.9-95.1) | 33.3 (14.9 -74.1) | 82.4 (32.4-208.8) |
| | | SE | 14.00 | 13.30 | 11.80 | 35.90 |
| | 2 | Density | 12.3 (3.9-38.9) | 0.00 | 22.9 (5.3-98.2) | 41.5 (6.2-275.9) |
| | | SE | 6.40 | 0.00 | 15.70 | 40.20 |
| | 3 | Density | 25.2 (4.8-133.4) | 0.00 | 7.8 (1.1-55.9) | 11.4 (2.1-63.2) |

| | | | | | | |
|---|---|---|---|---|---|---|
| | | SE | 20.20 | 0.00 | 7.80 | 9.70 |
| Black Kettle National Grasslands | 1 | Density | 3.3 (1.4-7.9) | 5.1 (1.3--19.6) | 8 (2.7-23.4) | 22.3 (7.7-64.1) |
| | | SE | 1.37 | 3.50 | 4.20 | 11.55 |
| | 2 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Beaver River Wildlife Management Area | 1 | Density | 41.9 (10.1-173.4) | 5.9 (.69-50.1) | 48.9 (13.9-171.8) | 11.3 (2.7-46.2) |
| | | SE | 25.10 | 5.90 | 25.70 | 6.80 |
| | 2 | Density | 15.5 (3.42-70.5) | 0.00 | 12.7 (2.8-57.1) | 0.00 |
| | | SE | 10.00 | 0.00 | 8.10 | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Optima National Wildlife Refuge | 1 | Density | * | 0.00 | 0.00 | 3.4 (0.4-28.7) |
| | | SE | * | 0.00 | 0.00 | 3.41 |
| | 2 | Density | 0.00 | 0.00 | 0.00 | 0.00 |
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Rita Blanca National Grasslands | 1 | Density | 2.61 (0.67-10.1) | 0.00 | 0.00 | 0.00 |
| | | SE | 1.85 | 0.00 | 0.00 | 0.00 |
| | 2 | Density | 0.22 (0.004-1.19) | 0.00 | 0.00 | 0.00 |
| | | SE | 0.20 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | 3.86 (1.4-10.5) | 0.00 | * | 0.00 |
| | | SE | 1.90 | 0.00 | * | 0.00 |
| Muleshoe National Wildlife Refuge | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 17.4 (5.68-53.3) | 0.00 | 0.00 | 0.00 |
| | | SE | 7.40 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | 0.00 | 0.00 | 0.00 | 0.00 |
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| Buffalo Lake National Wildlife Refuge | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 9.65 (2.2-43.4) | 0.00 | 0.00 | 0.00 |
| | | SE | 4.90 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | 3.64 (0.27-21.8) | 0.00 | 0.00 | 0.00 |
| | | SE | 3.65 | 0.00 | 0.00 | 0.00 |

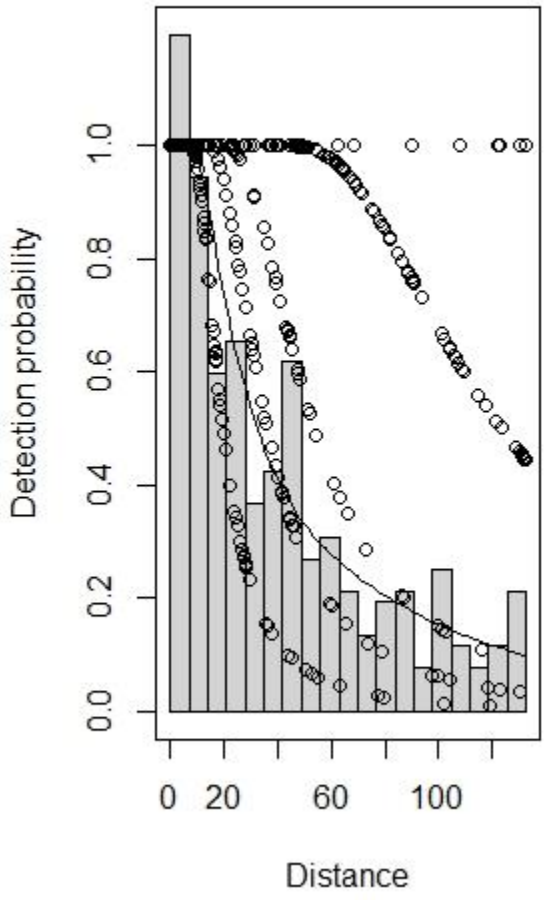
| | | | | | | |
|---|---|---|---|---|---|---|
| Pantex | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 68.7 (39.9-118.4) | 0.00 | 0.00 | 0.00 |
| | | SE | 6.50 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Kiowa National Grasslands | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 0.00 | 0.00 | 0.00 | 0.00 |
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | 0.00 | 0.00 | 0.00 | 0.00 |
| | | SE | 0.00 | 0.00 | 0.00 | 0.00 |
| Cimarron Hills Wildlife Management Area | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | 2.37 (.06- 8.3) | 0.00 | 0.00 | 0.00 |
| | | SE | 2.37 | 0.00 | 0.00 | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| Cimarron Bluffs WMA | 1 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |
| | 2 | Density | * | 0.00 | 32.8 (2.1-514.1) | 0.00 |
| | | SE | * | 0.00 | 24.10 | 0.00 |
| | 3 | Density | NA | NA | NA | NA |
| | | SE | NA | NA | NA | NA |

Appendix E.1. Detection curve for Chestnut-collared Longspur (*Calcarius ornatus*).



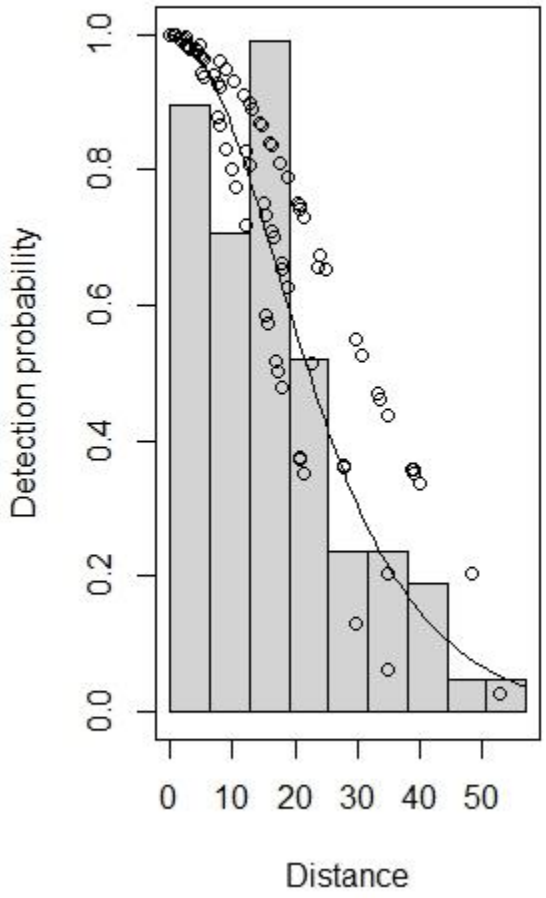

Number of Observations: 433
Effective detection range 0-82.3m
Detection probability: 0.25
Model: Hazard-rate key function with scale variable of Detection Type and Observer

Appendix E.2. Detection Curve for Eastern Meadowlark (*Sturnella magna*).



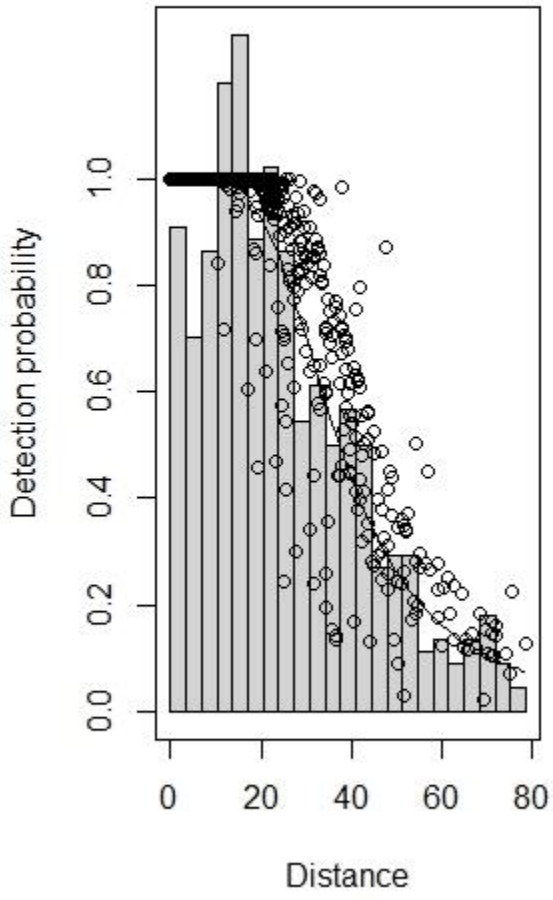

Number of Observations: 362
Effective detection range 0-132.5m
Detection probability: 0.37
Model: Hazard-rate key function with scale variable of Detection Type

Appendix E.3. Detection Curve for Field Sparrow (*Spizella pusilla*).



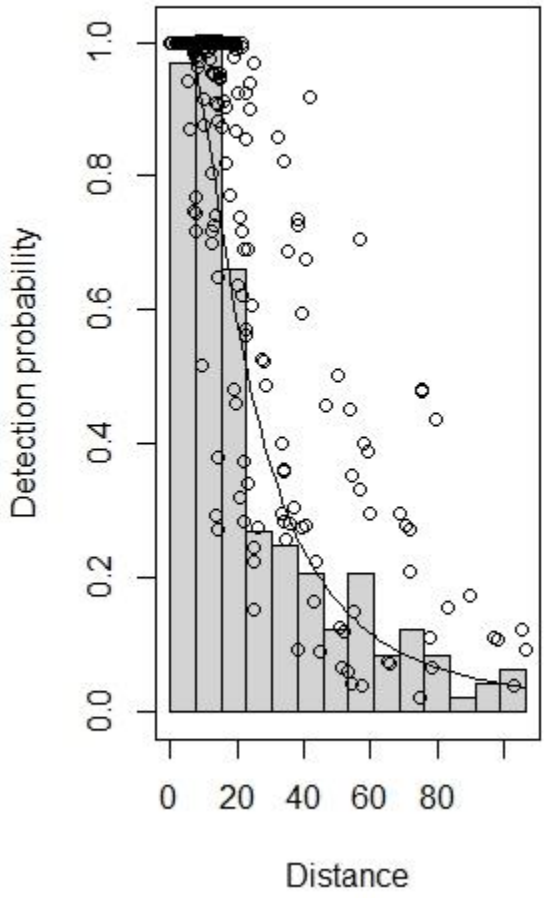

Number of Observations: 82
Effective detection range 0-57.1m
Detection probability: 0.43
Model: Half-normal key function

Appendix E.4. Detection Curve for Horned Lark (*Eremophila alpestris*).



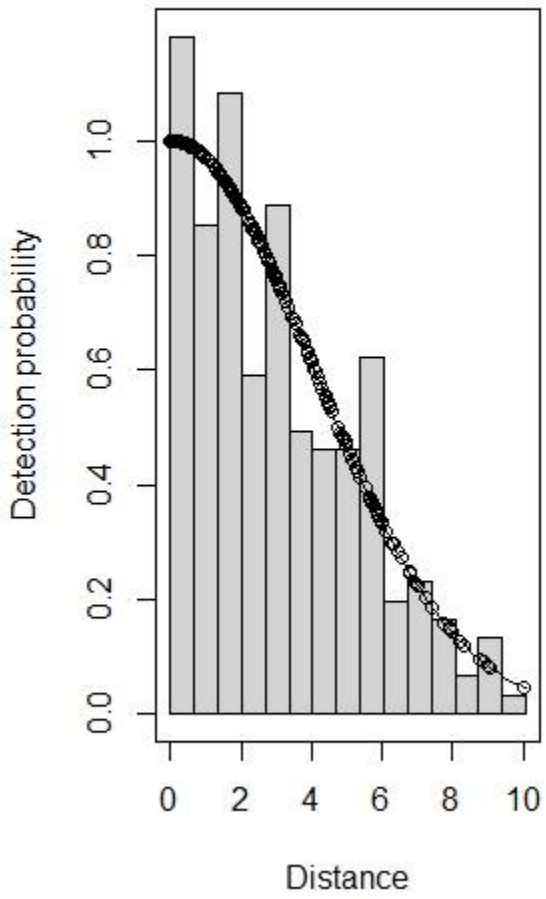

Number of Observations: 532
Effective detection range 0-78.8m
Detection probability: 0.52
Model: Hazard-rate key function with scale variable of Detection Type

Appendix E.5. Detection Curve for Lapland Longspur (*Calcarius lapponicus*).



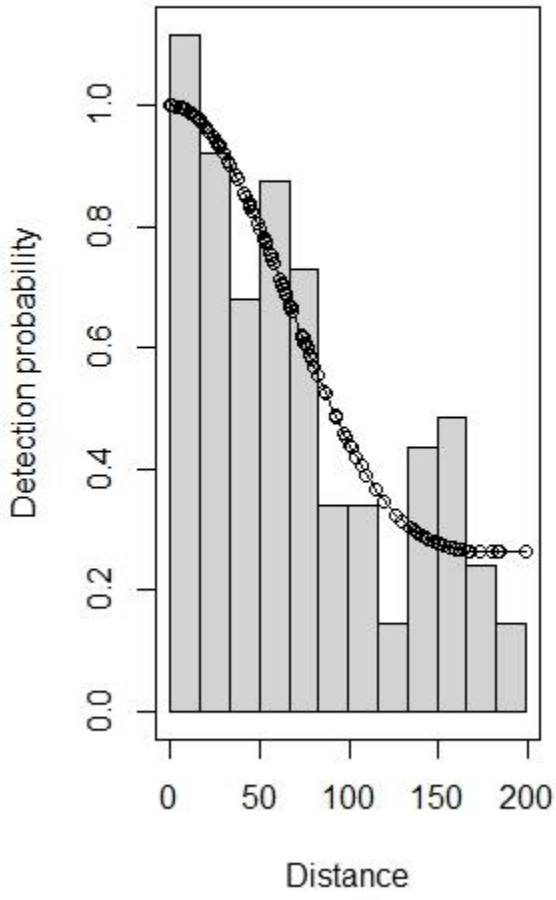

Number of Observations: 199
Effective detection range 0-106.7m
Detection probability: 0.29
Model: Hazard-rate key function with scale variable of Detection Type and Observer

Appendix E.6. Detection Curve for LeConte's Sparrow (*Ammodramus leconteii*).



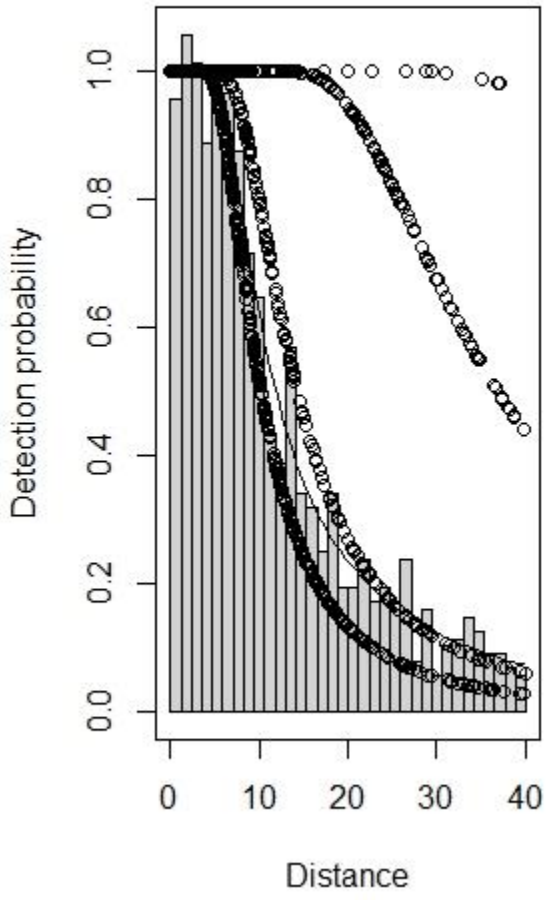

Number of Observations: 227
Effective detection range 0-10.1m
Detection probability: 0.49
Model: Half-normal key function

Appendix E.7. Detection Curve for Northern Harrier (*Circus hudsonius*).



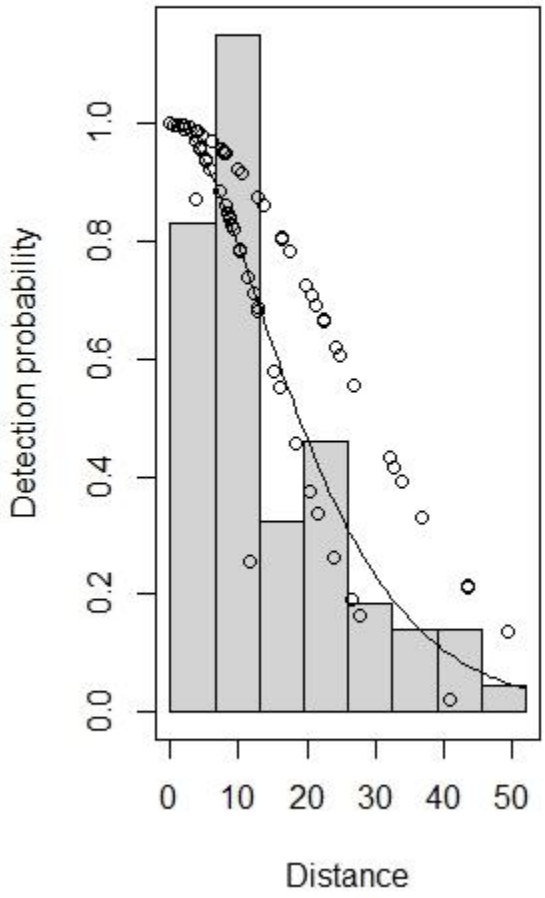

Number of Observations: 133
Effective detection range 0-199.1m
Detection probability: 0.54
Model: Uniform key function with Cosine adjustment terms of order 1,2

Appendix E.8. Detection Curve for Savannah Sparrow (*Passerculus sandwichensis*).



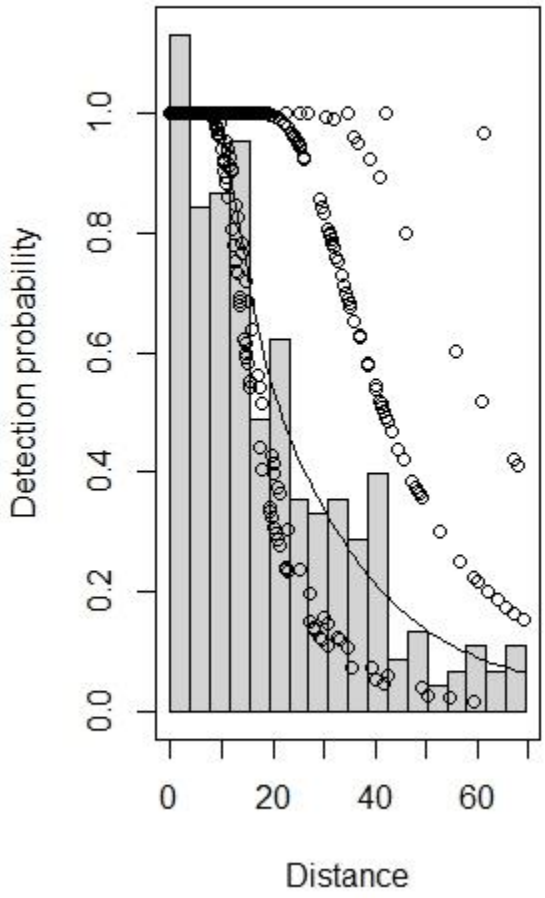

Number of Observations: 1162
Effective detection range 0-40.1m
Detection probability: 0.39
Model: Hazard-rate key function with scale variable of Detection Type

Appendix E.9. Detection Curve for Smith's Longspur (*Calcarius pictus*).



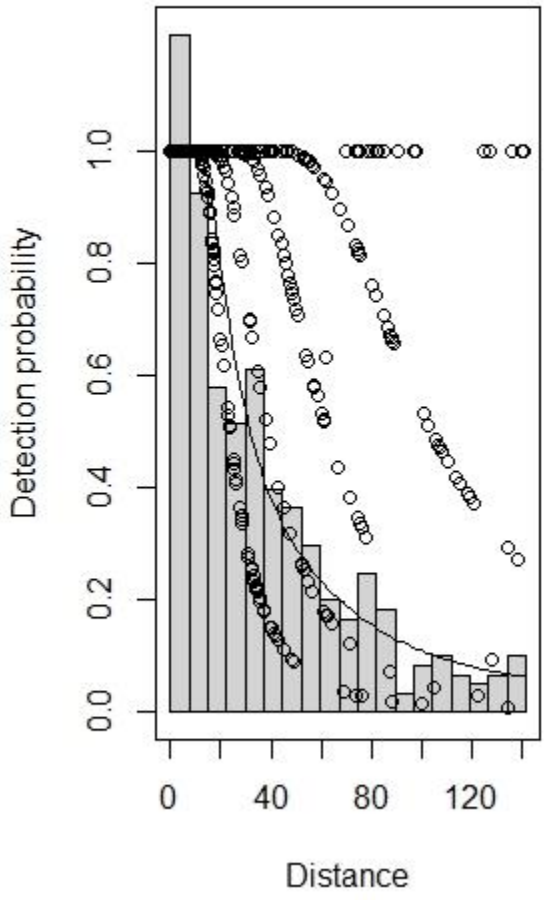

Number of Observations: 71
Effective detection range 0-52.1m
Detection probability: 0.41
Model: Half-normal key function with scale variable of Detection Type

Appendix E.10. Detection curve for Song Sparrow (*Melospiza melodia*).



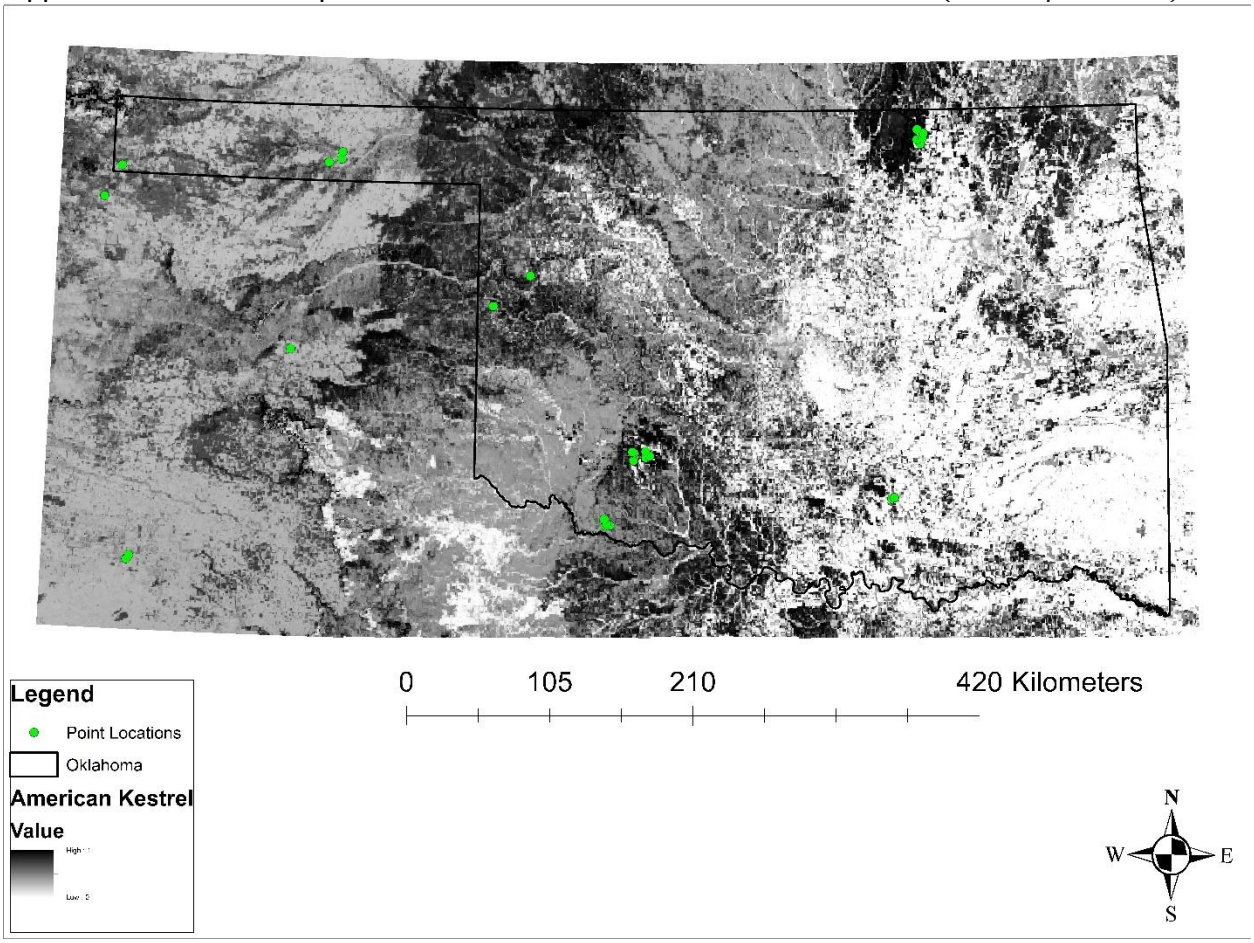

Number of Observations: 327
Effective detection range 0-69.4m
Detection probability: 0.4
Model: Hazard-rate key function with scale variable of Detection Type

Appendix E.11. Detection Curve for Western Meadowlark (*Sturnella neglecta*).

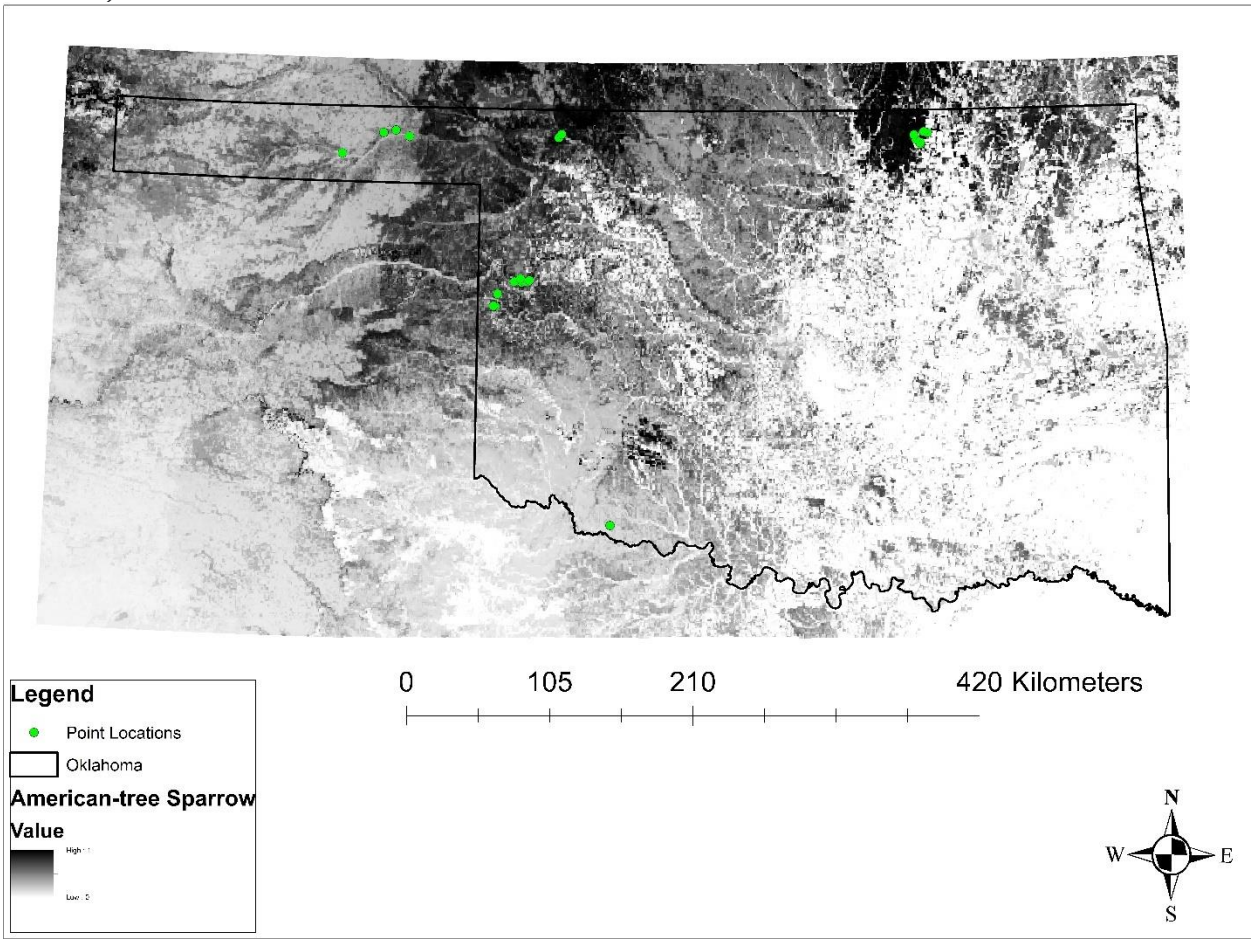



Number of Observations: 374
Effective detection range 0-141.3m
Detection probability: 0.32
Model: Hazard-rate key function with scale variable of Detection Type

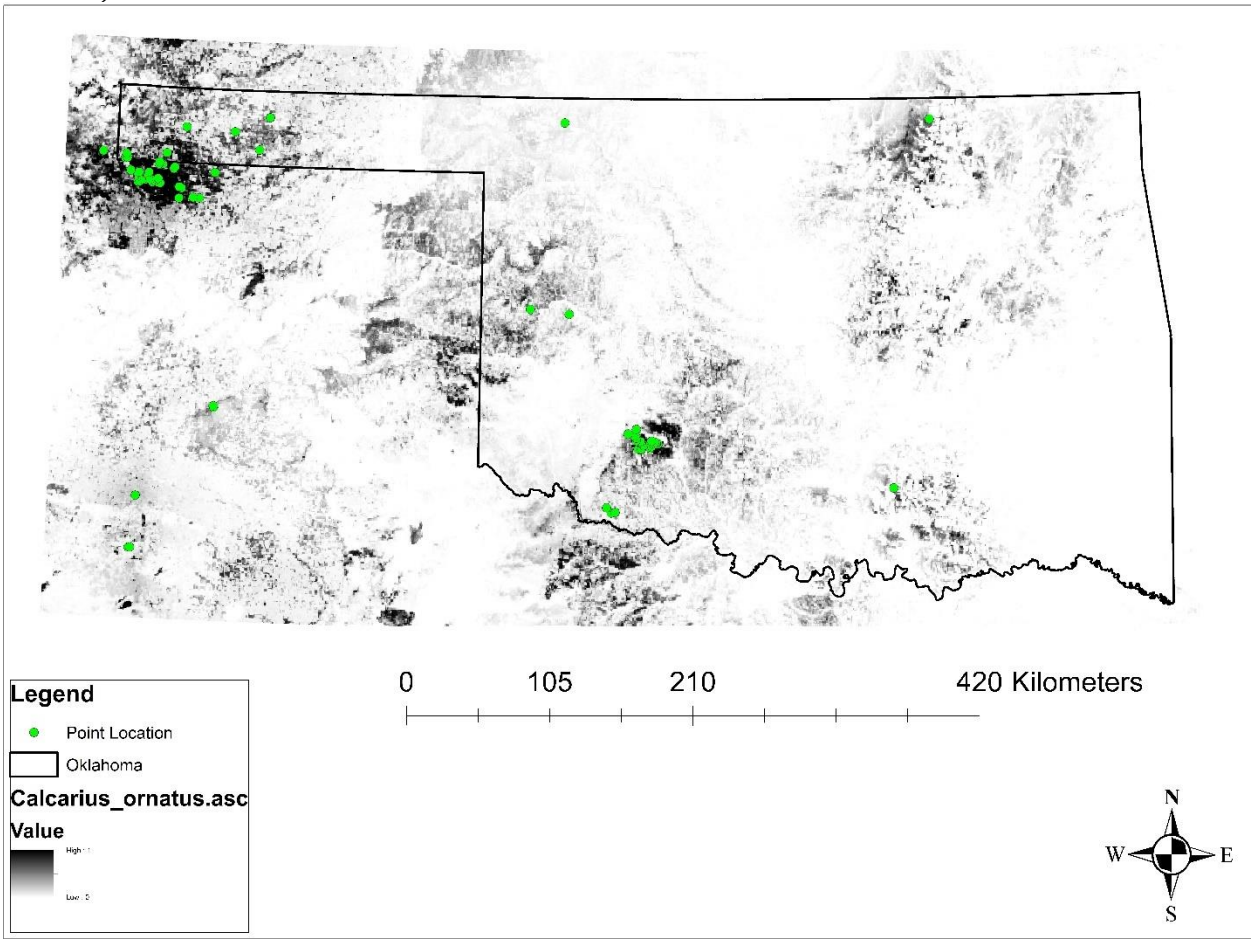
Appendix F.1. Maxent Species Distribution Model for American Kestrel (*Falco sparverius*).



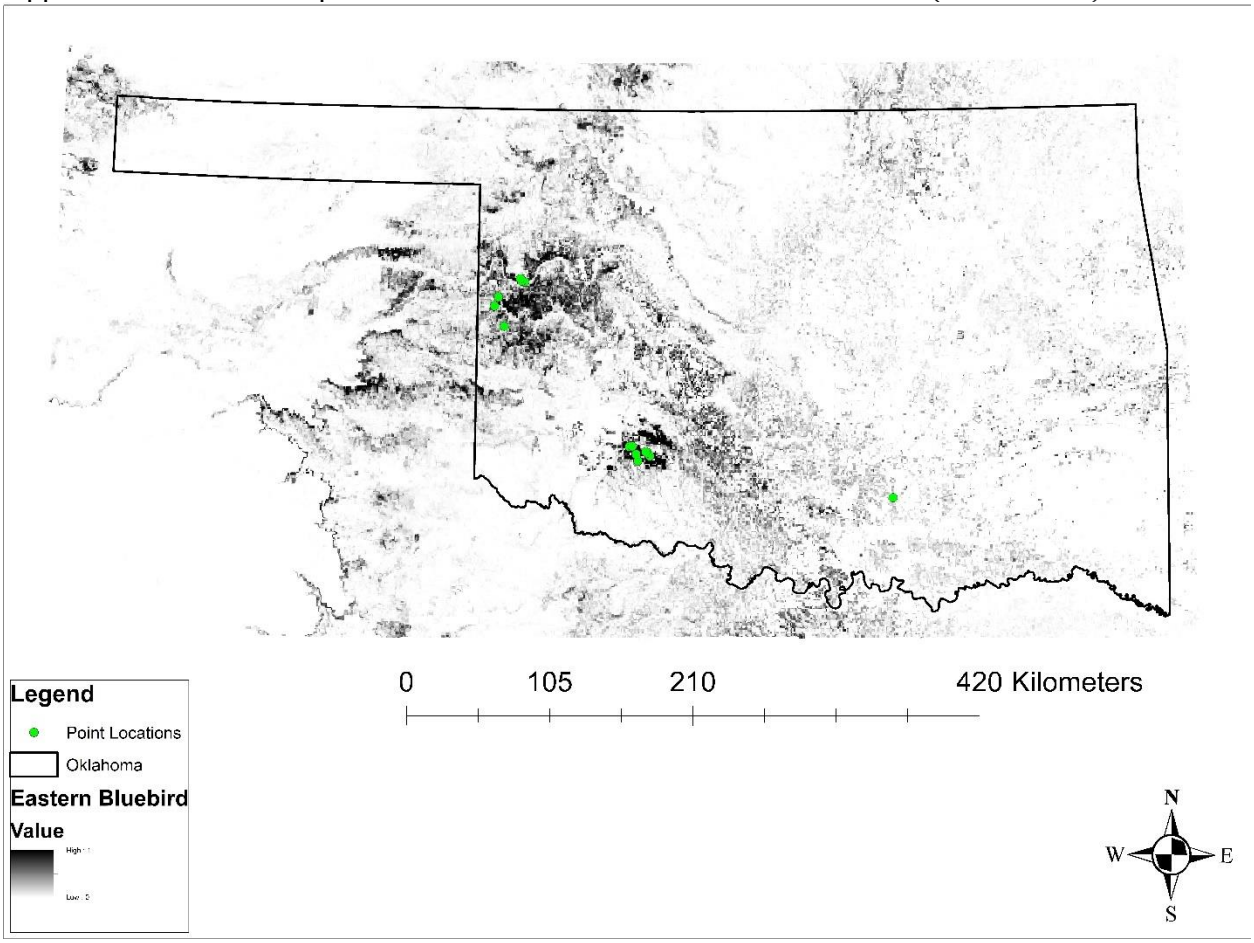
Appendix F.2. Maxent Species Distribution Model for America Tree Sparrow (*Spizelloides arborea*).



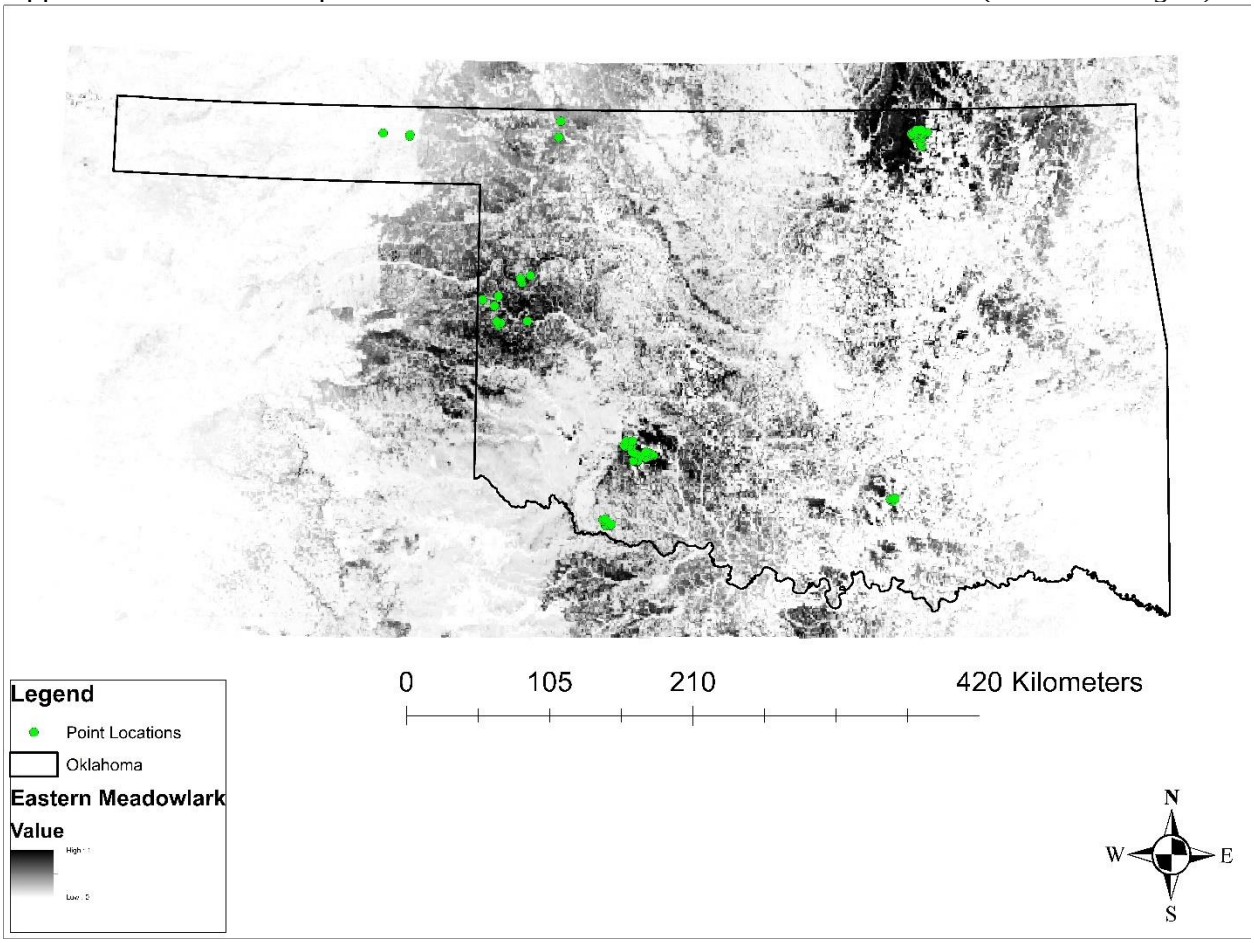
Appendix F.3. Maxent Species Distribution Model for Chestnut-collared Longspur (*Calcarius ornatus*).



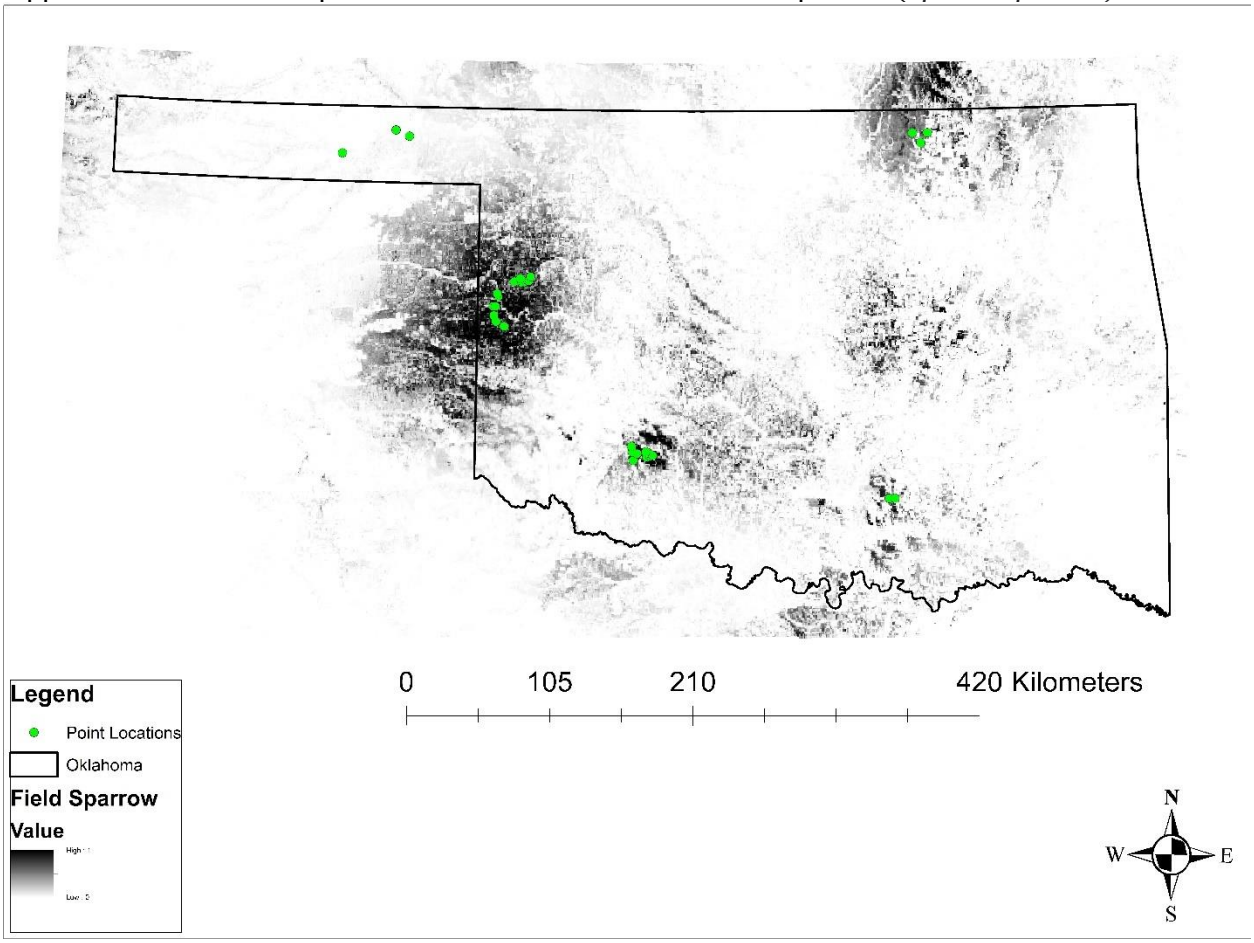
Appendix F.4. Maxent Species Distribution Model for Eastern Bluebird (*Sialia sialis*).



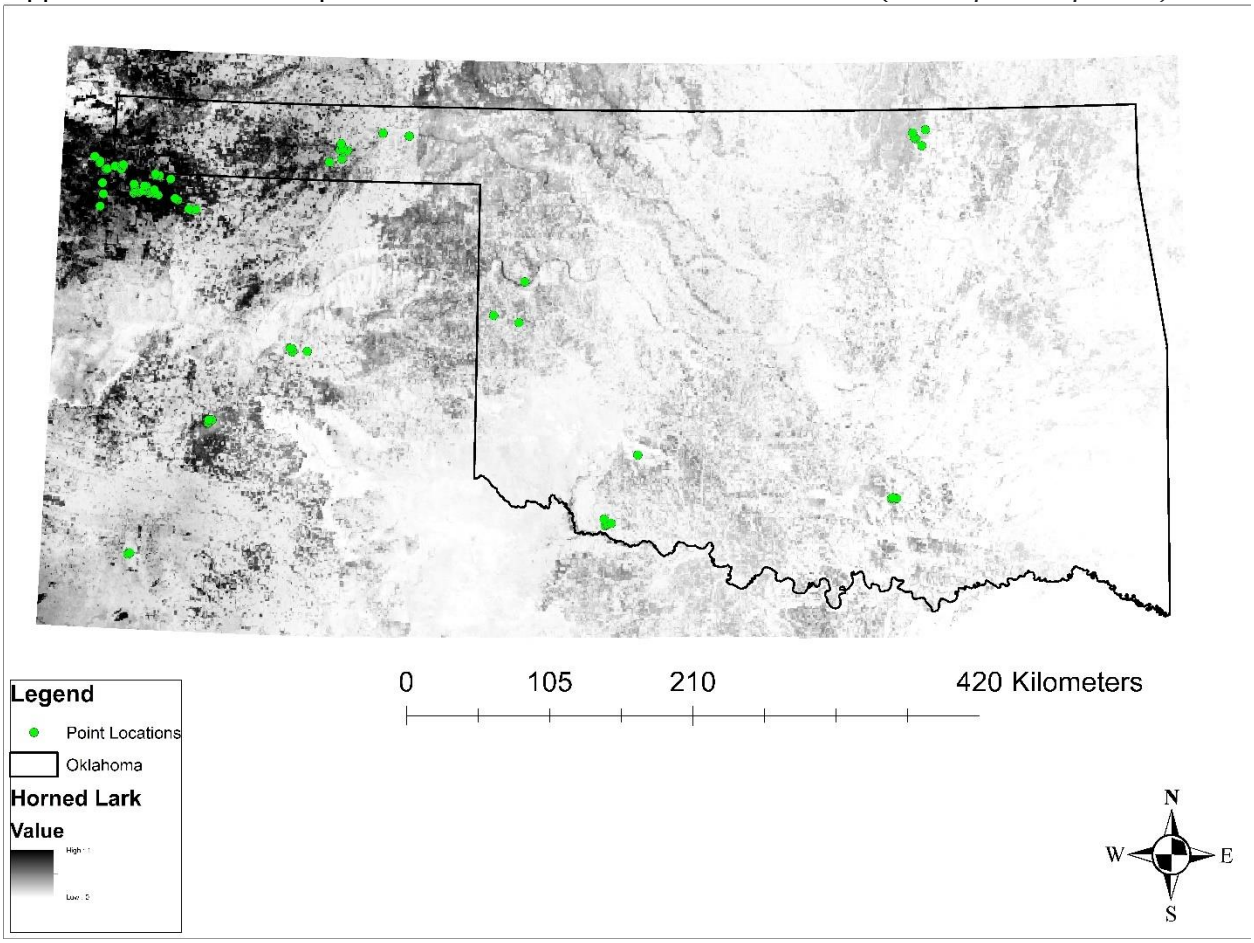
Appendix F.5. Maxent Species Distribution Model for Eastern Meadowlark (*Sturnella magna*).



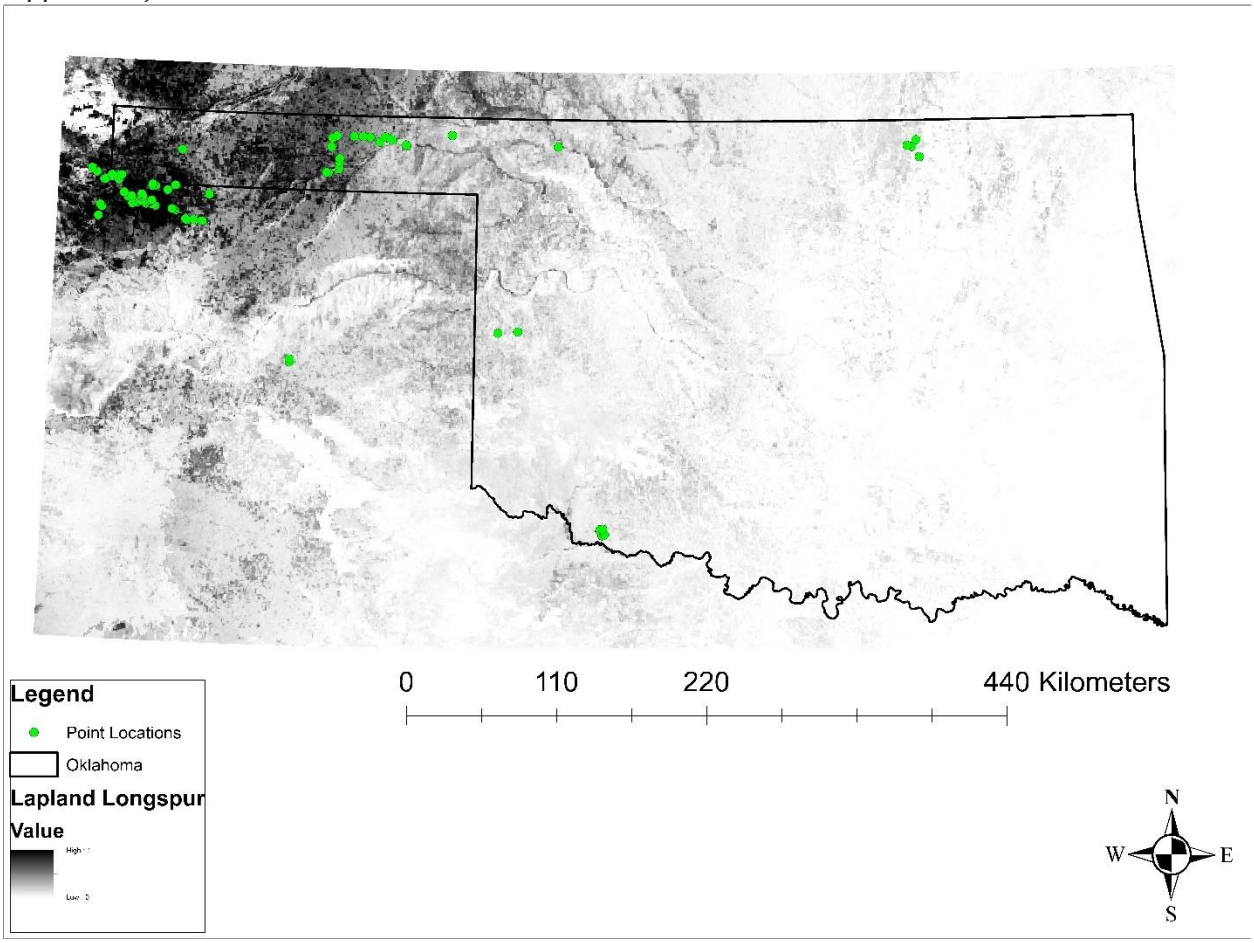
Appendix F.6. Maxent Species Distribution Model for Field Sparrow (*Spizella pusilla*).



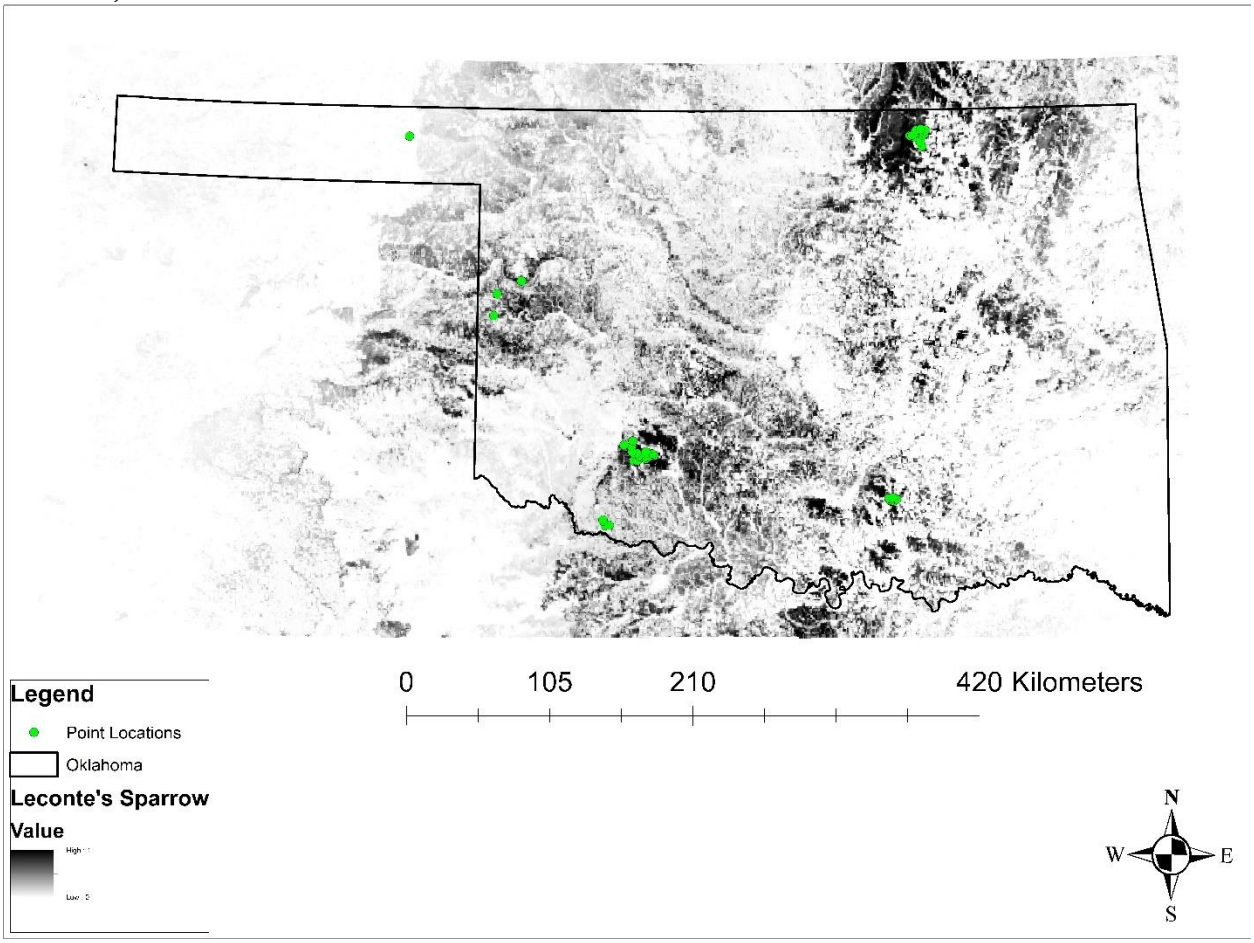
Appendix F.7. Maxent Species Distribution Model for Horned Lark (*Eremophila alpestris*).



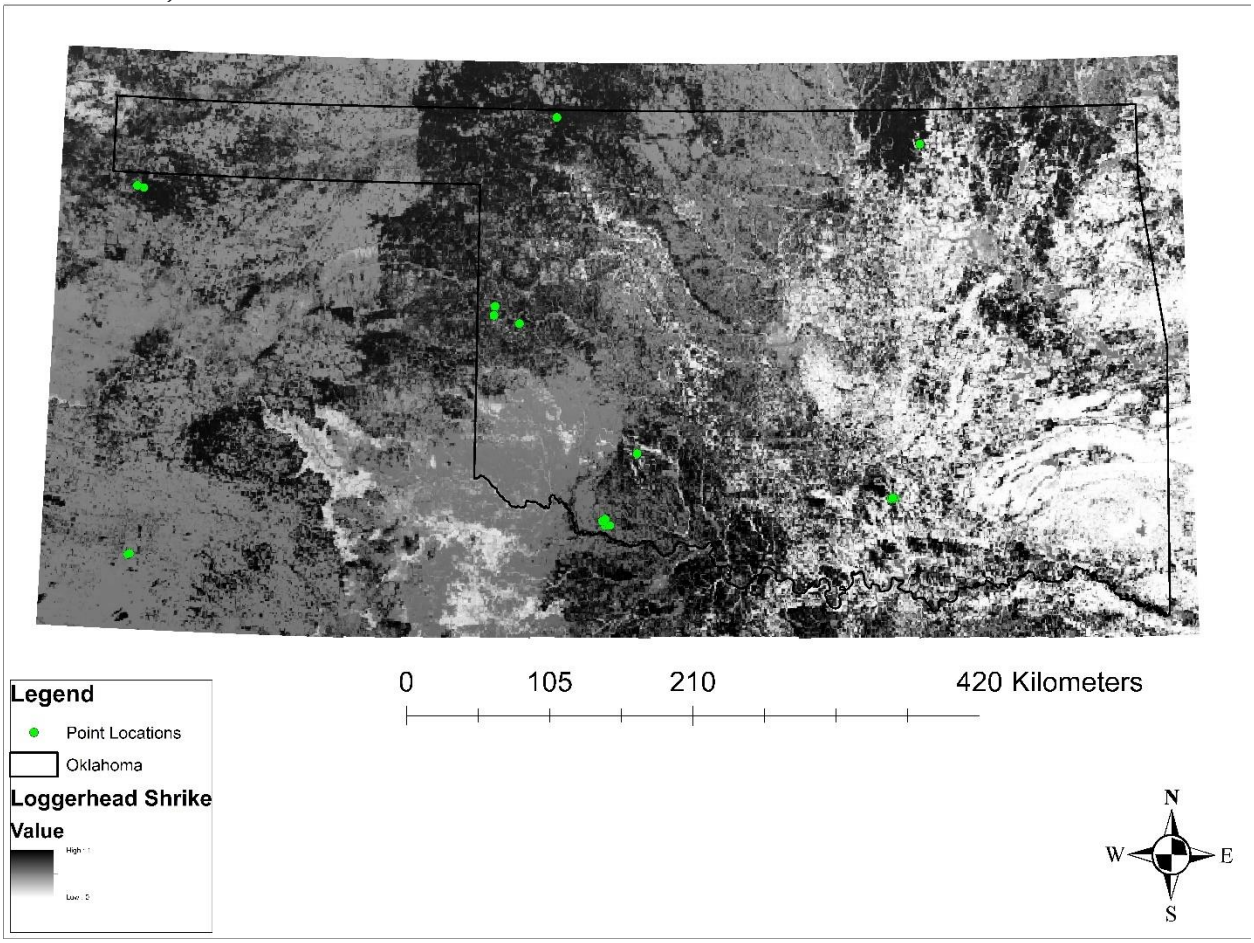
Appendix F.8. Maxent Species Distribution Model for Lapland Longspur (*Calcarius lapponicus*).



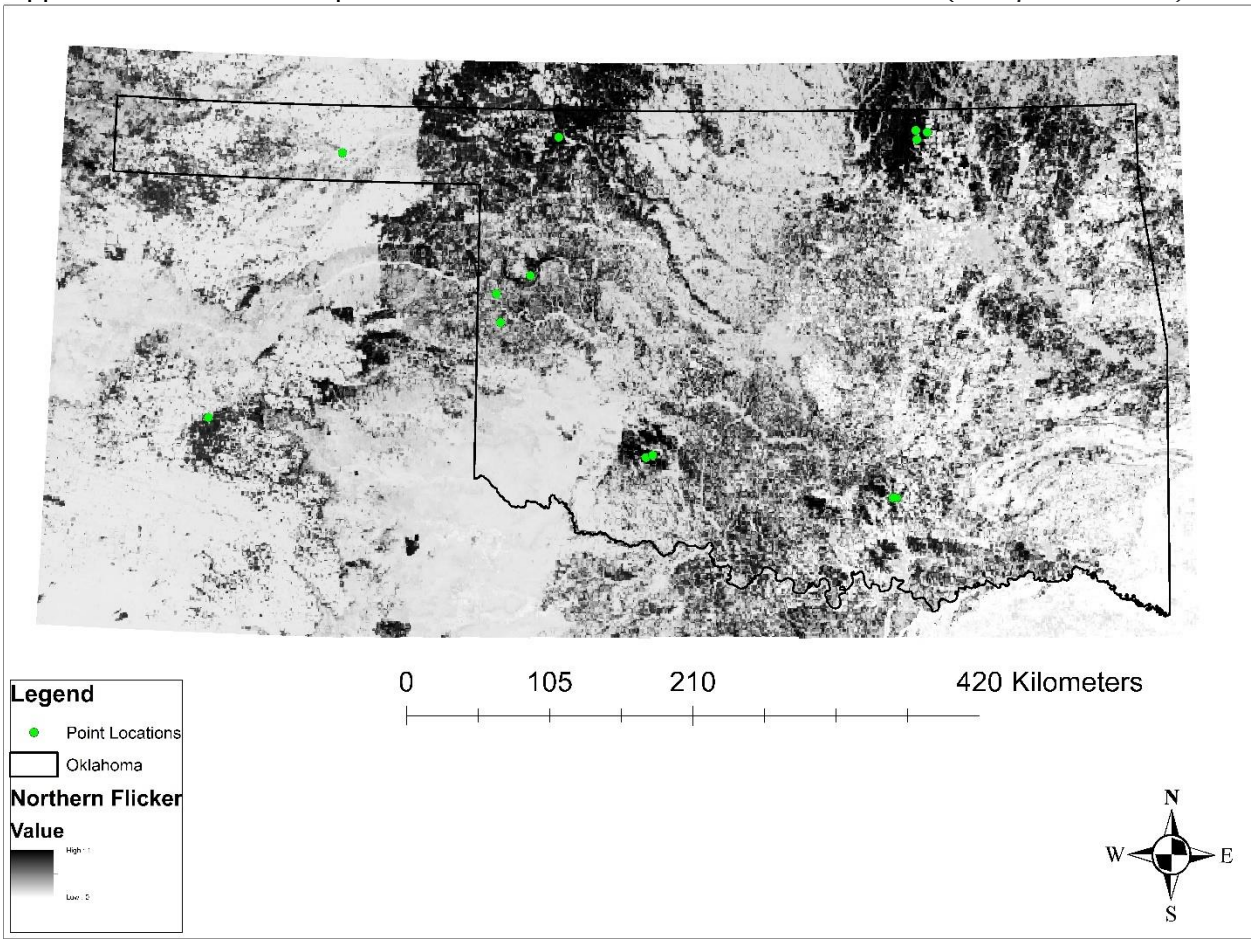
Appendix F.9. Maxent Species Distribution Model for LeConte's Sparrow (*Ammodramus leconteii*).



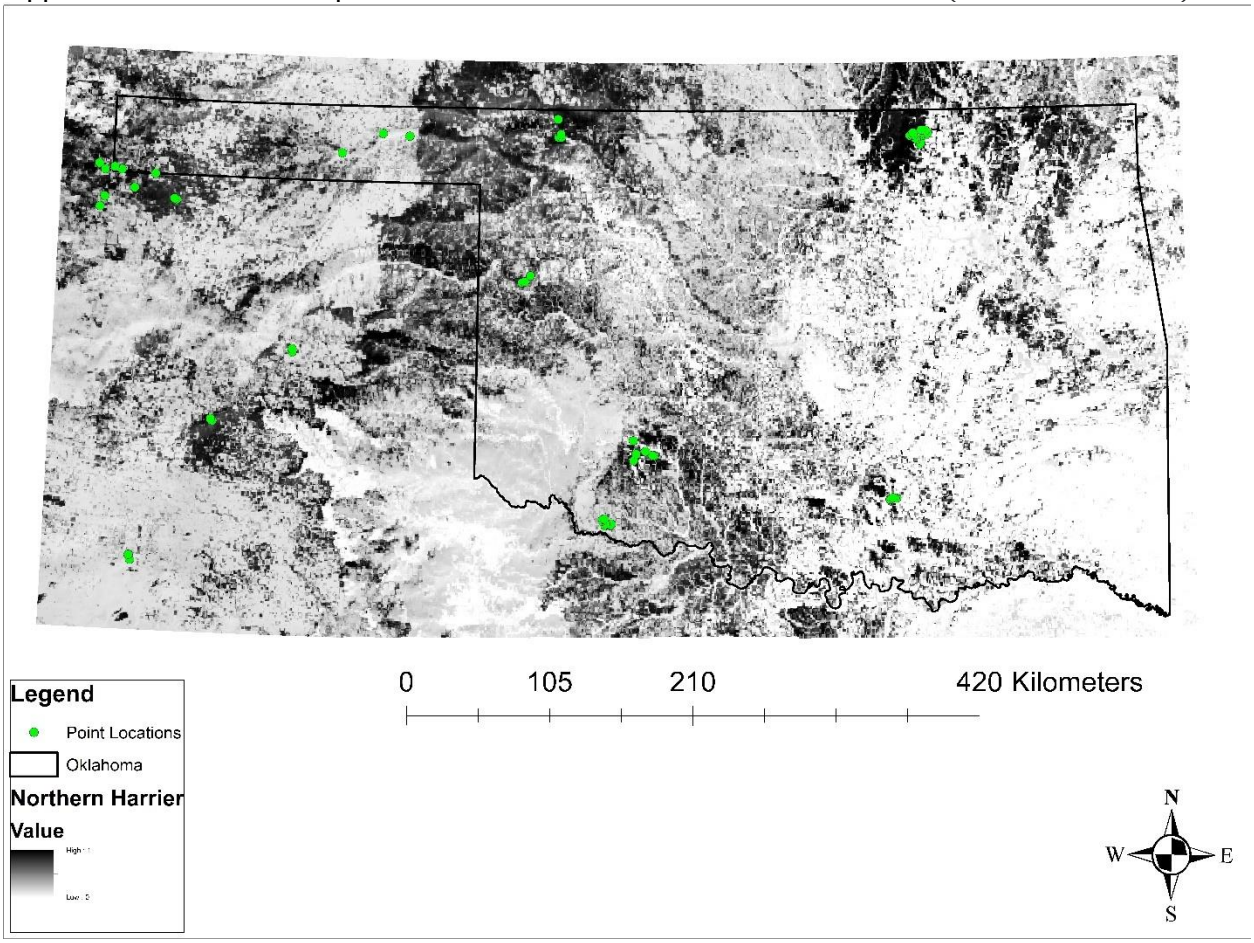
Appendix F.10. Maxent Species Distribution Model for Loggerhead Shrike (*Lanius ludovicianus*).



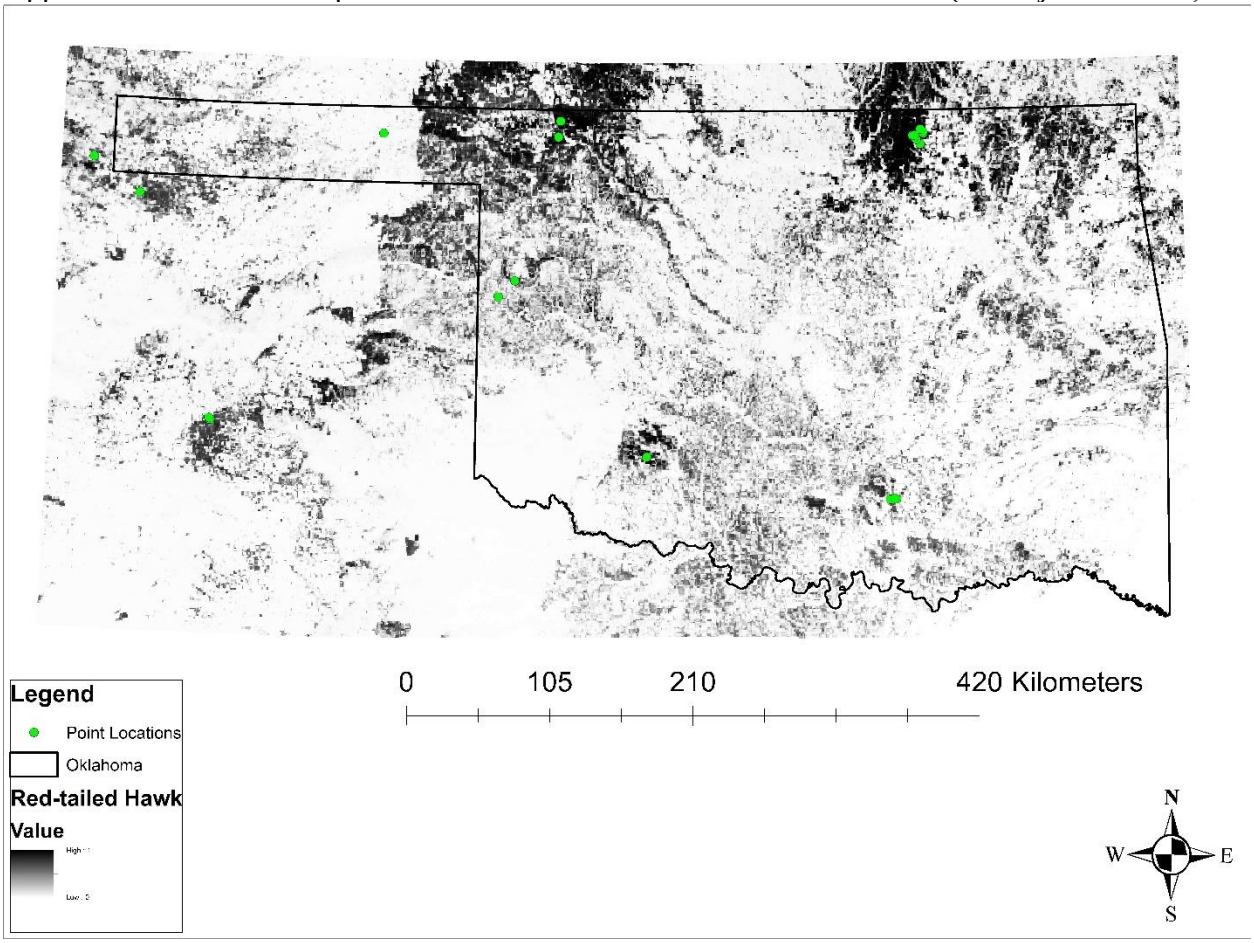
Appendix F.11. Maxent Species Distribution Model for Northern Flicker (*Colaptes auratus*).



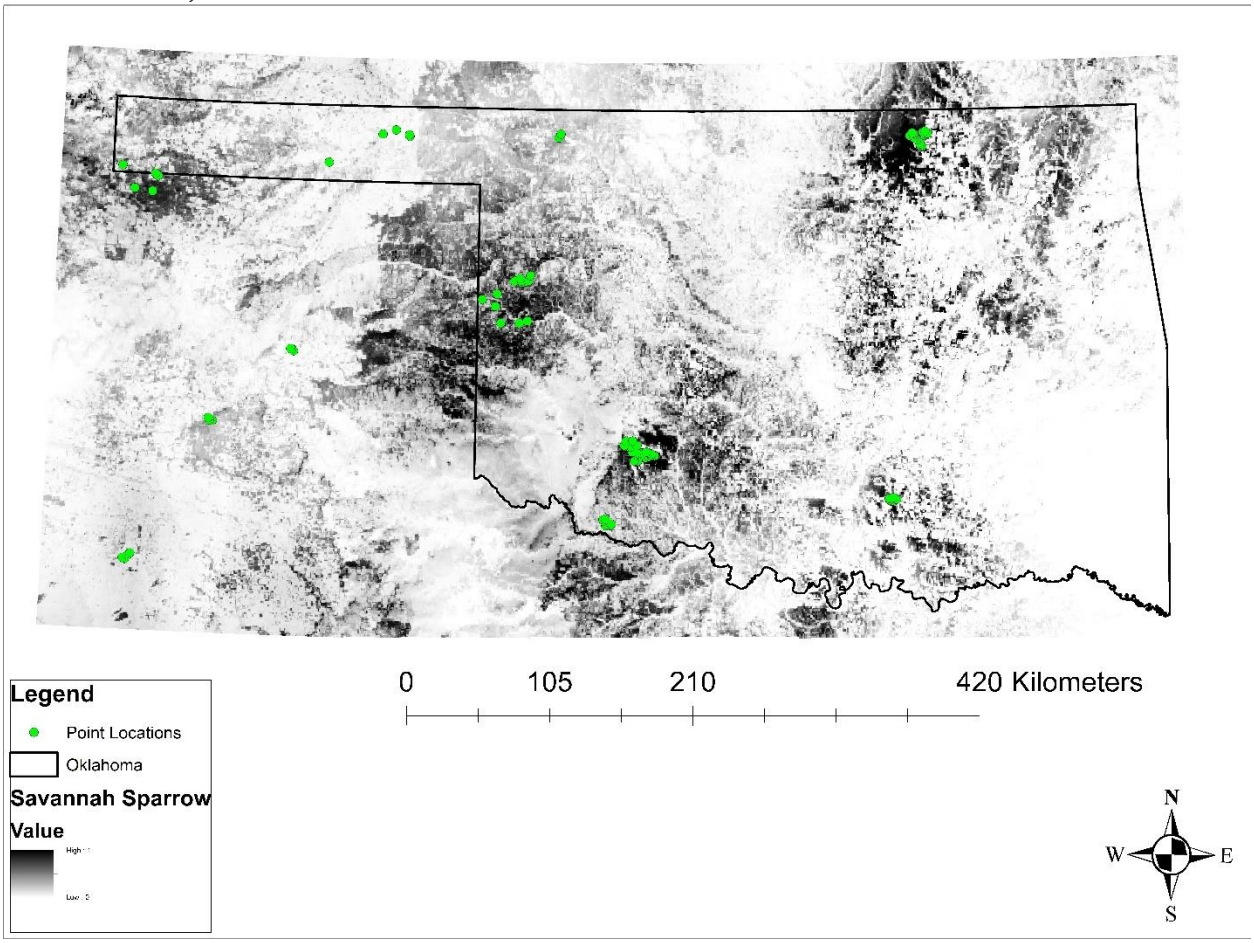
Appendix F.12. Maxent Species Distribution Model for Northern Harrier (*Circus hudsonius*).



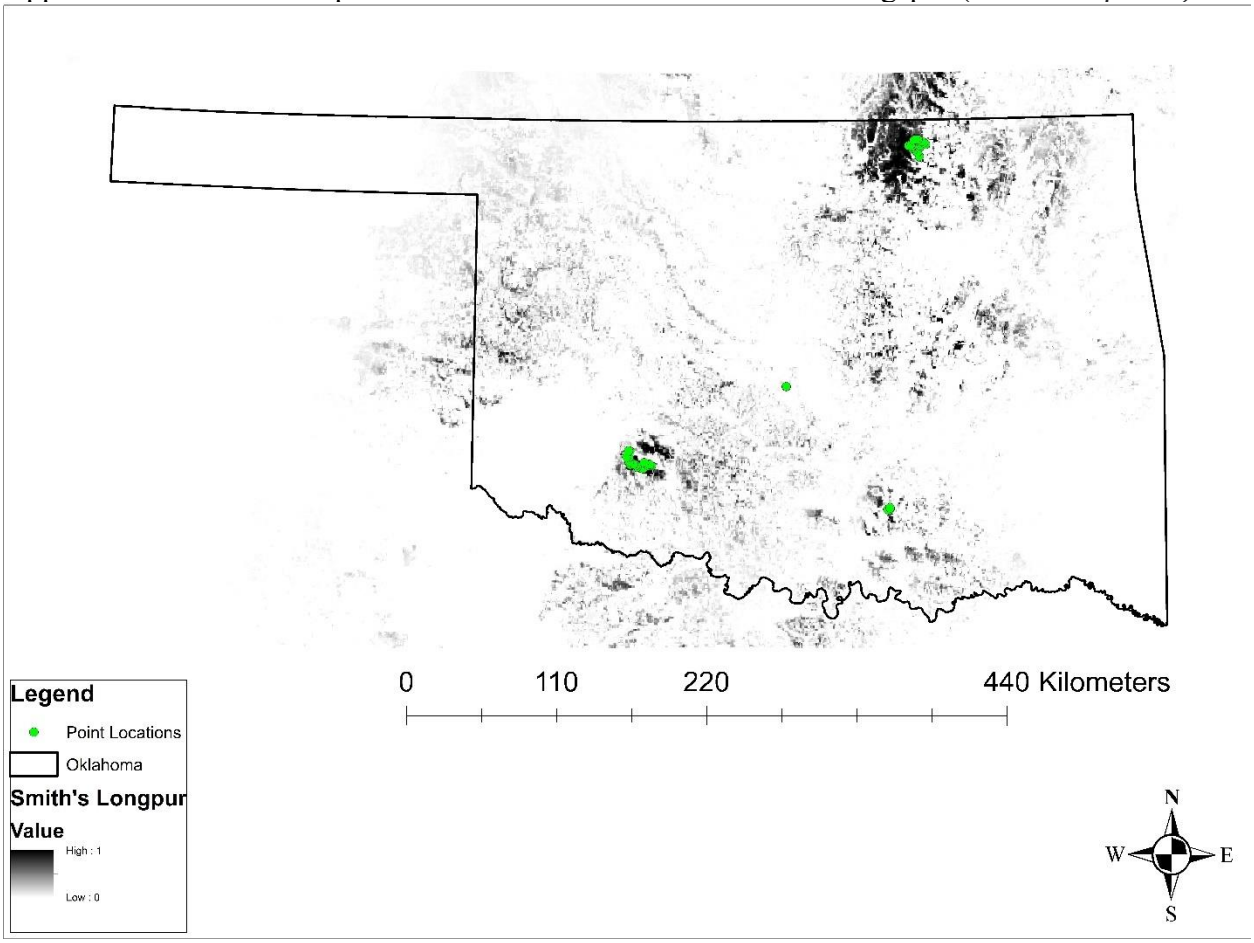
Appendix F.13. Maxent Species Distribution Model for Red-tailed Hawk (*Buteo jamaicensis*).



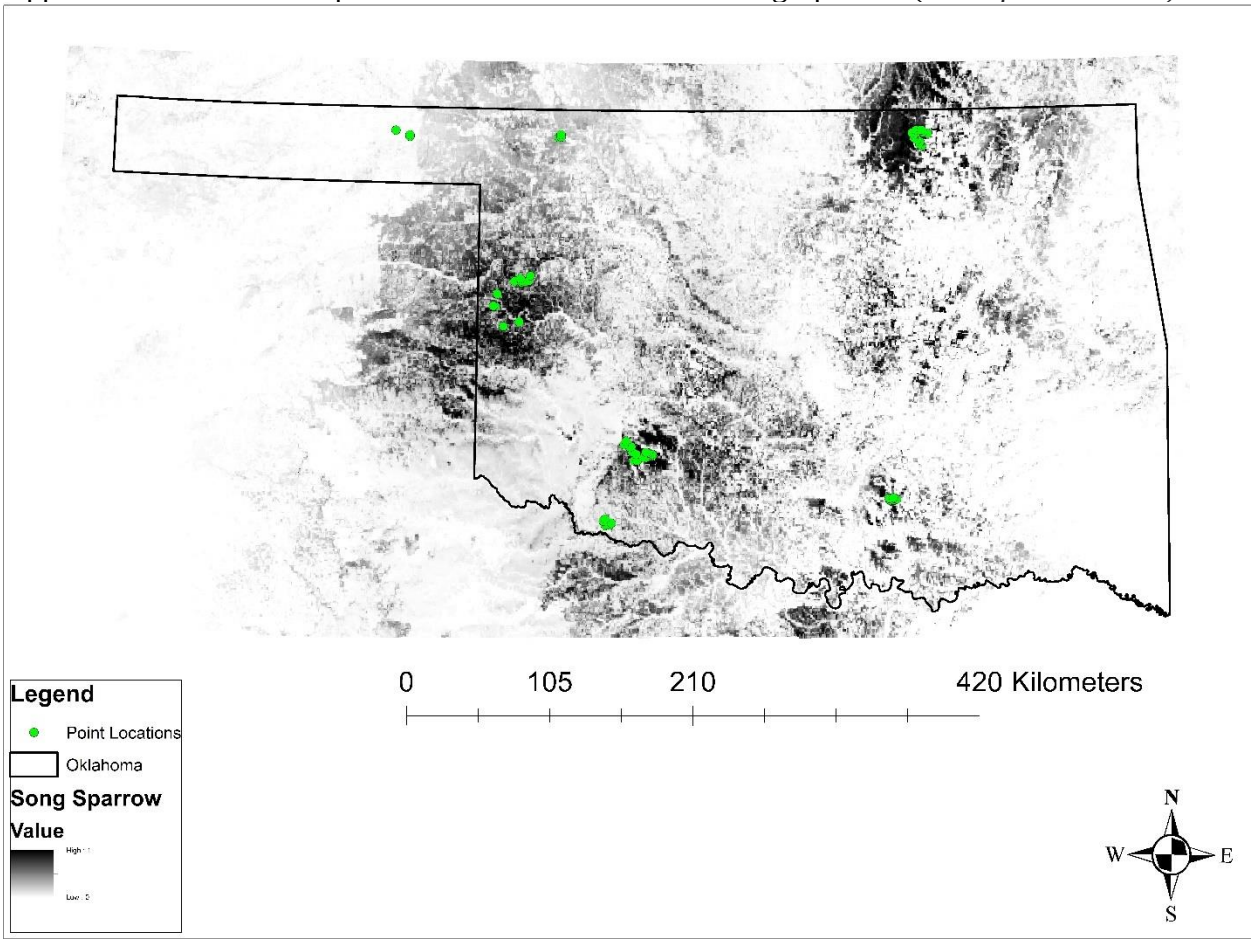
Appendix F.14. Maxent Species Distribution Model for Savannah Sparrow (*Passerculus sandwichensis*).



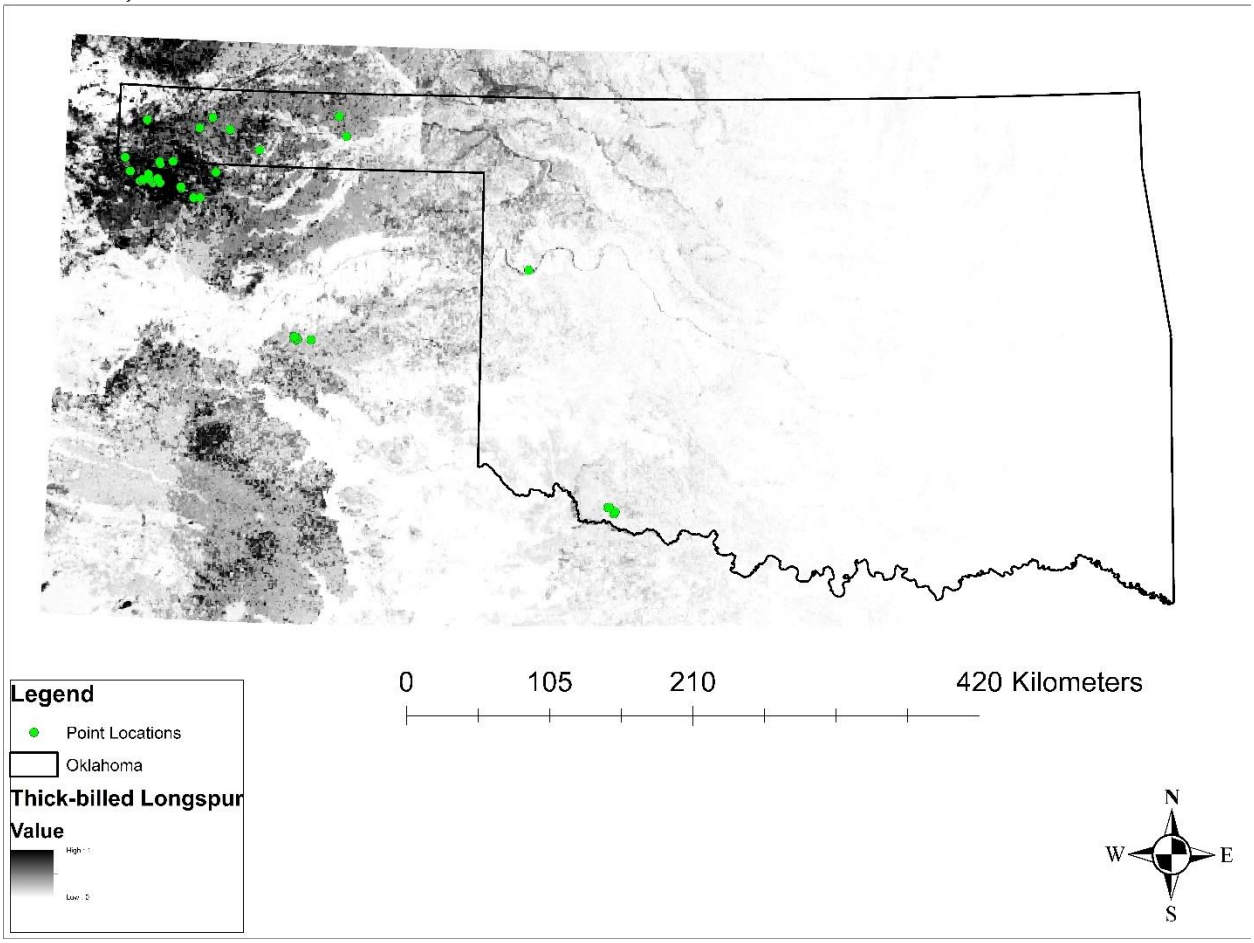
Appendix F.15. Maxent Species Distribution Model for Smith's Longspur (*Calcarius pictus*).



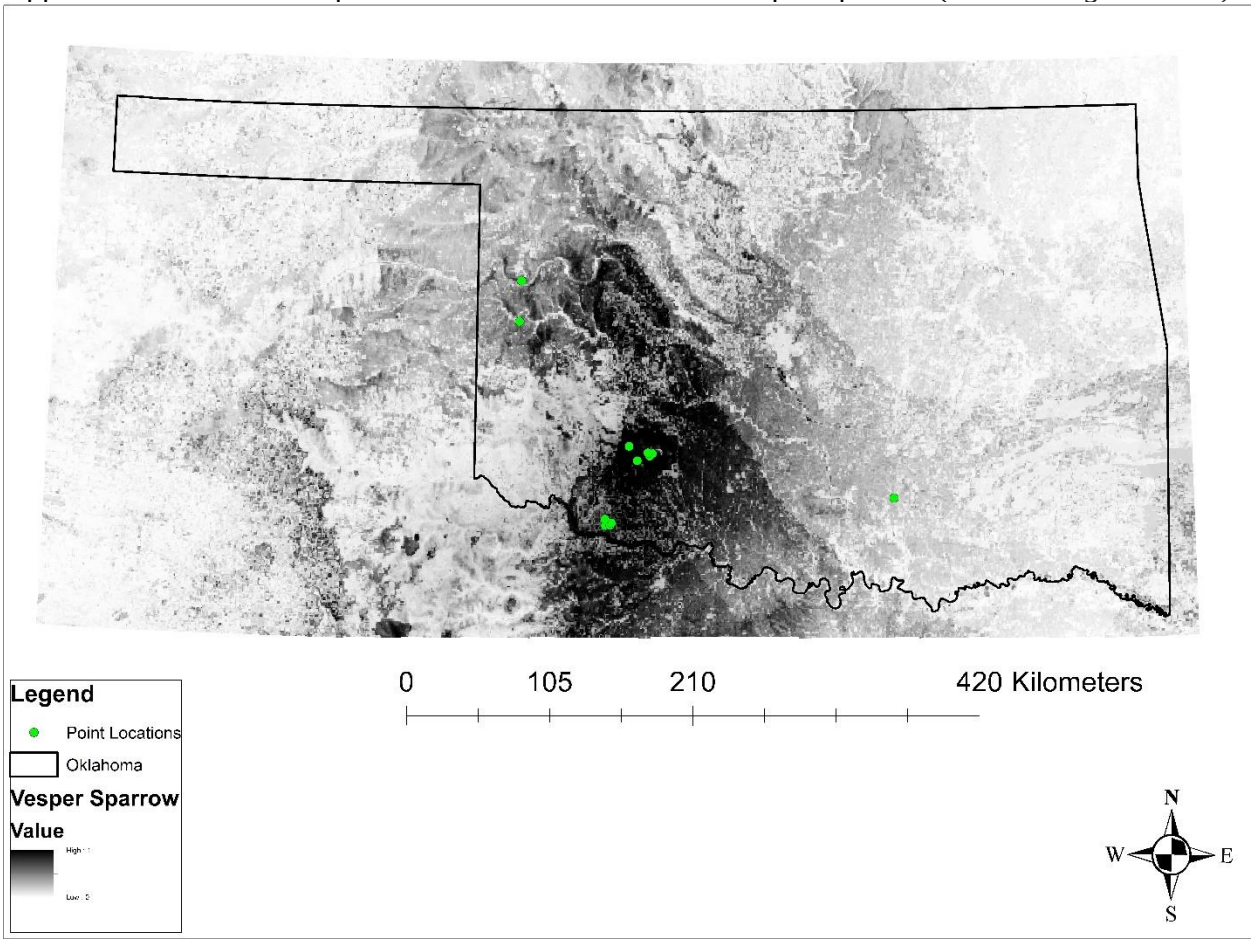
Appendix F.16. Maxent Species Distribution Model for Song Sparrow (*Melospiza melodia*).



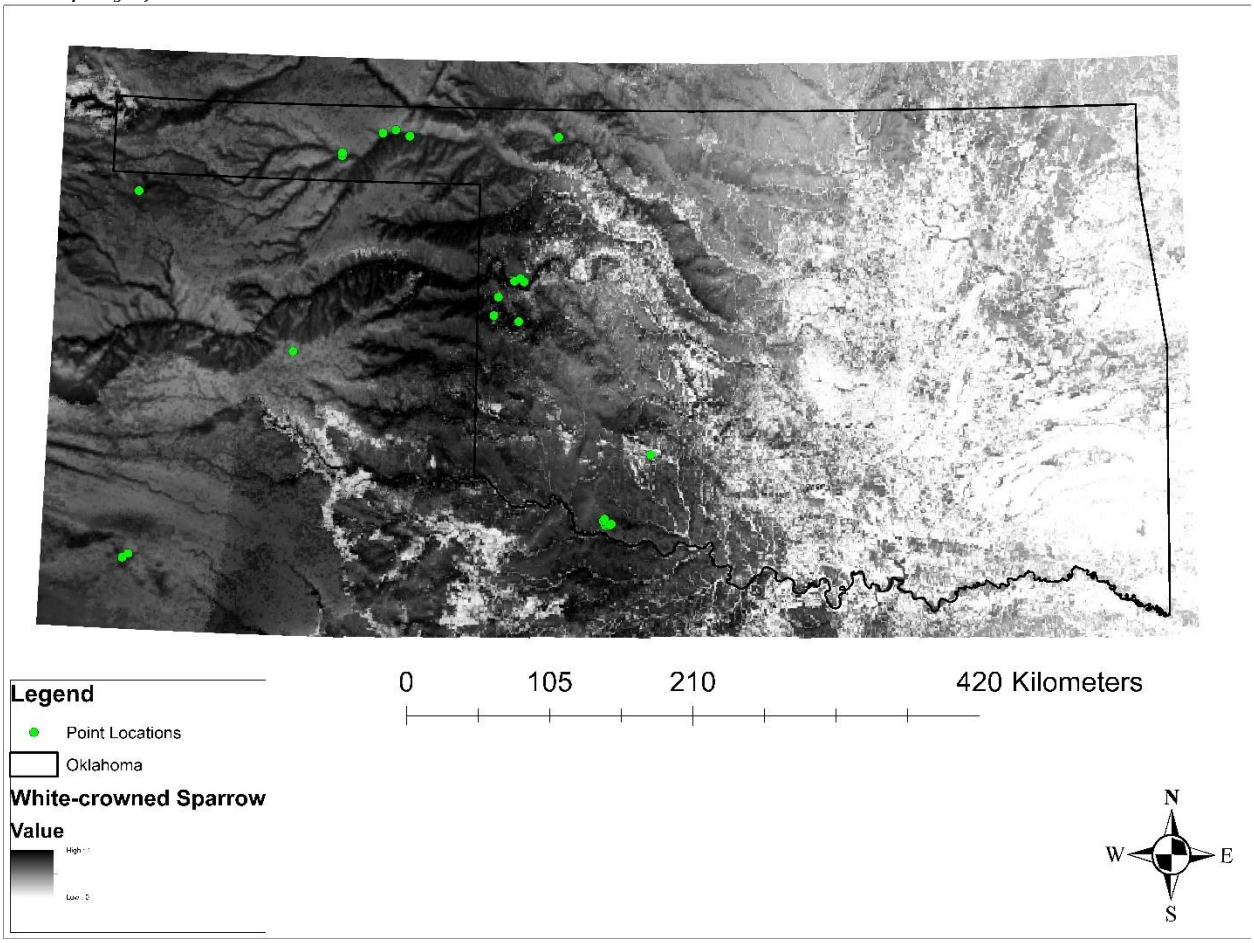
Appendix F.17. Maxent Species Distribution Model for Thick-billed Longspur (*Rhynchophanes mccownii*).



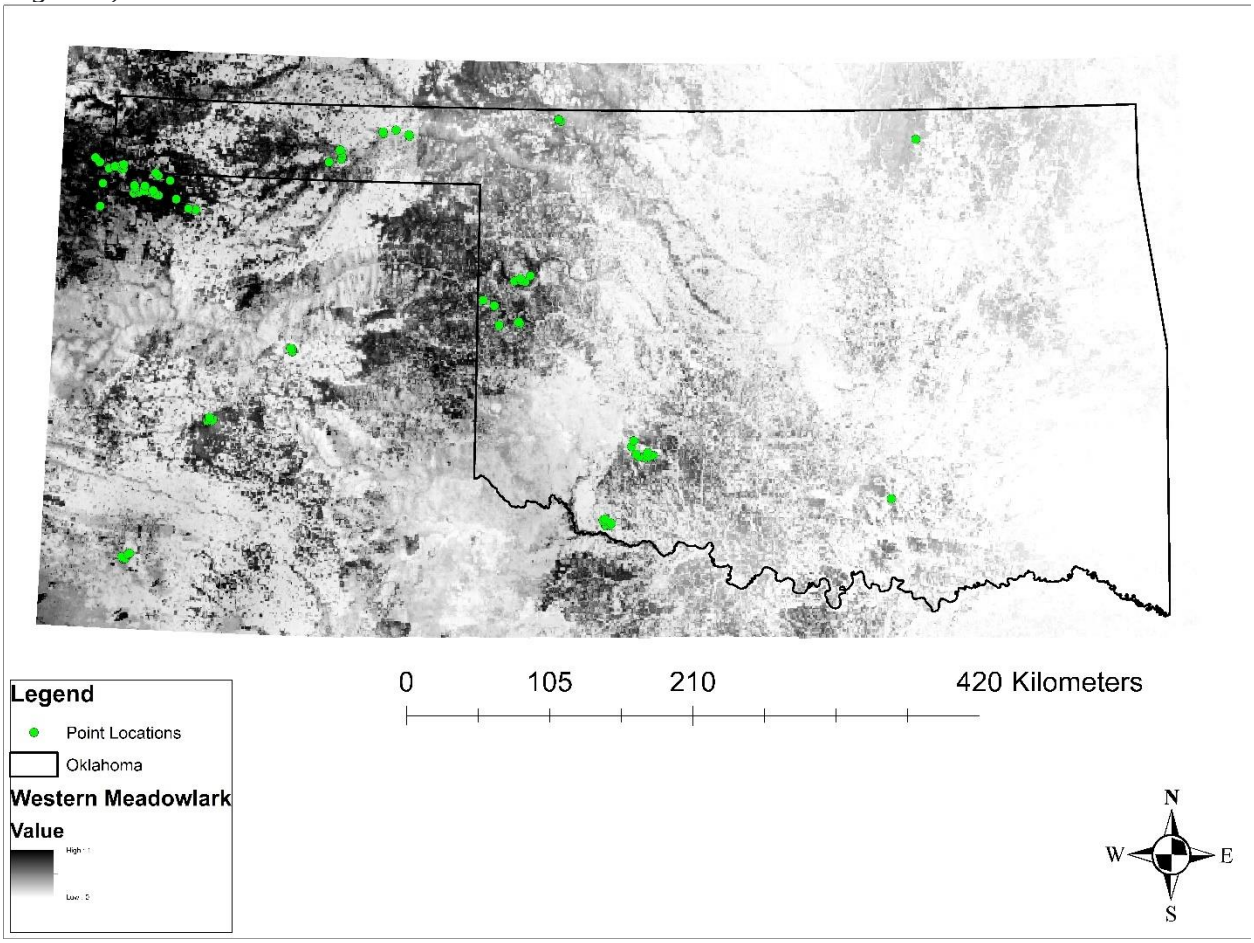
Appendix F.18. Maxent Species Distribution Model for Vesper Sparrow (*Pooecetes gramineus*).



Appendix F.19. Maxent Species Distribution Model for White-crowned Sparrow (*Zonotrichia leucophrys*).



Appendix F.20. Maxent Species Distribution Model for Western Meadowlark (*Sturnella neglecta*).



## Chapter 3: Fine-scale Habitat Associations of Oklahoma's Longspurs

John A. Muller and Jeremy D. Ross

*Submitted to the Journal of Wildlife Management*

**ABSTRACT** Overwintering is a key demographic stage for migratory birds but remains poorly understood, especially among multiple steeply declining grassland bird species. Non-breeding ranges of all 4 species of Longspur, including Chestnut-collared (*Calcarius ornatus*), Smith's (*C. pictus*), Lapland (*C. lapponicus*) and Thick-billed (*Rhynchophanes mccownii*), overlap in Oklahoma and the Texas panhandle making this region an ideal location for studying their wintering ecology. We evaluated the relationship between wintering longspur occupancy and fine-scale habitat characteristics using a combination of standardized bird surveys and paired occupied-random vegetation plot sampling. Our study encompassed large, representative tracts of the 3 major types of prairie ecosystems (i.e., shortgrass, mixed-grass, and tallgrass prairies) that intersect within the Southern Great Plains. Using both randomization tests and classification trees we both characterized longspur habitats and compared these associations across the 3 prairie ecosystems. We found that habitat use varied among all 4 species, departed at very fine scales, and species' associations shifted across grassland types. Our findings can be applied to the management of grasslands and help develop full-life cycle conservation for Chestnut-collared and Thick-billed Longspurs which have experienced severe population declines.

**KEY WORDS** classification tree, grassland, longspur, Oklahoma, winter ecology, winter habitat

### INTRODUCTION

Overwintering is a key demographic stage for migratory birds but remains poorly understood, especially in temperate prairie ecosystems. The Southern Great Plains (SGP) encompasses a

region where the 3 major grassland ecosystems of North America abut — Tallgrass, Mixed-grass, and Shortgrass Prairie. As each habitat type has been reduced from historical sizes by 98%, 76%, and 46%, respectively (Comer et al. 2018), the resulting negative impacts upon the health of wintering grassland bird populations is serious and widespread. Drastic habitat loss in this biome is likely why grassland birds compared to other bird groups are estimated to have suffered the worst population declines over the past fifty years (Vickery et al. 1999, Sauer et al. 2017, Rosenberg 2019), and described as a conservation crisis (Brennan and Kuvlesky 2005). Although much focus on stemming these losses has been placed on breeding populations, evidence is increasing that survival during the nonbreeding season can have a strong influence on migratory bird population trends (Calvert et al. 2009, Morrison et al. 2013, Macias-Duarte 2017).

The theory of Ideal Free Distribution (Fretwell 1972) posits that individuals distribute themselves in proportion to the availability of resources and is well-suited to wintering birds where high mobility and a relaxation of fixed-territory constraints affords individuals greater freedom to choose where they occupy. Indeed, wintering grassland birds have shown an ability to alter their fine scale winter distributions based on resource availability (Pool et al. 2012, Kristensen et al. 2013, Macías-Duarte et al. 2018). If we assume that the relative density at which a species occurs reflects its perception of habitat quality (Jones 2001, MacKenzie 2005), then characterizing those habitats should provide a good description of favorable environments for the species. Our ability to understand habitat use decisions is constrained, in part, by our ability to accurately define habitat quality (Johnson 2007). *Partners In Flight*, an avian conservation organization, recommends the identification and conservation of high quality habitats among the highest research needs for conserving migratory birds (Donovan et al. 2002). Identification and management of fine-scale habitats has proven to benefit at-risk species conservation (Klaus and

Buehler 2001, Banks and Skilleter 2007, Gilioli et al. 2018) and can be a critical part in developing full life-cycle management of declining migratory grassland birds flagged as research priorities, such as the longspurs of the SGP (Bleho 2020, Briskie 2020, With 2020).

Few winter habitat studies have been published for grassland birds of the SGP (Grzybowski 1982, Ormston 2000). This applies to the 4 species of longspur that primarily winter in this region, including 2 that have shown recent population declines [Chestnut-collared (*Calcarius ornatus*; hereafter CCLO) and Thick-billed (*Rhynchophanes mccownii*; hereafter TBLO)], one that is apparently stable [Smith's (*C. pictus*; hereafter SMLO)], and one that is seemingly proliferating [Lapland (*C. lapponicus*; hereafter LALO)]. Studies focused on longspurs, either used generalized habitat measurements (Grzybowski 1982) or were conducted in desert grasslands (Desmond et al. 2005, Macías-Duarte et al. 2009, 2017), leaving major research gaps in terms of spatial resolution or geographic representation. For example, across the SGP there remain fundamental unknowns concerning the habitat needs, mortality risks, flocking behavior, and seasonal movements of at-risk longspur species (Somershoe 2018, Bleho et al. 2020, Briskie 2020, With 2020). This is particularly important because both the declining and apparently secure longspur species regularly occur in relatively high numbers in the SGP, and for all but LALO, the region represents a large portion of their global wintering distributions.

General habitat types occupied by longspurs in the SGP vary by species. CCLO primarily winter in shortgrass prairie dominated by grasses and forbs <0.5 m (Grzybowski 1982), although others have suggested the species uses a wider range of habitats, such as taller grasses (Desmond et al. 2005). In Chihuahuan Desert grasslands CCLO are positively associated with grass cover and grass height, but negatively associated with shrub cover (Desmond et al. 2005, Macías-Duarte et al. 2009). TBLO winter in open shortgrass prairie habitats with sparse vegetation such

as plowed fields and overgrazed pastures (With 2020), and in West Texas they were most abundant in lightly grazed pastures with vegetation height <0.5 m (Grzybowski 1982). Smith et al. (2004) found that playa wetlands managed for waterfowl attracted feeding flocks of TBLO during winter. SMLO are said to winter in sections of large, open prairies dominated by *Aristida* grasses with lesser, but perhaps still important, associations with grasses of the genera *Andropogon*, *Panicum*, and *Sporobolus*, alongside various mosses (Grzybowski 1982, 1983; Dunn and Dunn 1999; Ormston 2000; Holimon et al. 2012). Finally, LALO appear to winter in any open habitats with no or light snow cover that allow ground foraging access to seeds (Hussell and Montgomerie 2020), including shortgrass fields, grain stubble, and bare ground (Grzybowski 1982, Godfrey 1986, Byers et al. 1995).

All 4 species of longspur ranges overlap in winter at various places in the SGP, but their breeding ranges are more distinct. SMLO and LALO, for instance, breed on the Arctic tundra (Briskie 2020, Hussell and Montgomerie 2020). In contrast, CCLO and TBLO remain obligated to grassland habitats throughout the annual cycle, never leaving the Great Plains as they migrate to its Northern reaches to breed (Ellison et al. 2017, Bleho et al. 2020, With 2020). This year-round association with rapidly-declining ecosystems, may explain why CCLO and TBLO have experienced among the steepest population declines (-87.3% and -94.2%, respectively) of any North American bird species since the 1960's (Sauer et al. 2017). Although there is no comparable Breeding Bird Survey data for LALO and SMLO due to the remoteness of their breeding grounds, data from Christmas Bird Counts indicate an increase of 503% and 204%, respectively, since 1970 (Meehan et al. 2018). Although confidence intervals for both species show high levels of uncertainty, leading us to question whether or not the species are actually increasing. Wintering habitat quality can dictate the condition that migratory species arrive at

breeding grounds and, therefore, have carry-over effects on subsequent reproduction (Norris et al. 2004, Studds and Marra 2005, Harrison et al. 2011, Akresh et al. 2019). Thus, we have sought to fill knowledge gaps and link this information to grassland management recommendations that could increase the availability of critical wintering habitat for those longspur species of greatest conservation concern.

In this study we have evaluated the relationship between wintering longspur occupancy and fine-scale habitat characteristics using a combination of standardized bird surveys and paired occupied-random vegetation plot sampling. Our coverage included large grasslands representative of the 3 major types of prairie ecosystems that intersect in the mid-northern reaches of the SGP (Texas panhandle and Oklahoma), with the goals of: (1) characterizing fine-scale habitat structure and composition at points occupied by each longspur species detected; (2) contrasting these associations across sites to determine which habitat characteristics, if any, were suitably consistent in predicting occupancy by each respective longspur species across grassland types; and (3) separately outlining which management scenarios would likely increase the availability of suitably configured grassland tracts for each of the 4 longspur species. We specifically tested the hypotheses: (1) that each species of longspur is selecting habitats that are different than the other species of co-occurring longspur; and (2) that each longspur species will use the same habitat structure across their winter range regardless of grassland type.

## STUDY AREA

Large parts of Oklahoma encompass 3 major ecoregions of the great plains, Tallgrass Prairie, Mixed-grass Prairie and Shortgrass Prairie (Fig. 1). We sampled from 1 large field site at each of these 3 grassland systems.

### Tallgrass Prairie (TALL)

The Joseph H. Williams Tallgrass Prairie Preserve in northeastern Oklahoma is owned and managed by the Nature Conservancy-Oklahoma. Its 16,046 ha is the largest protected remnant of tallgrass prairie left on earth and managers employ a "patch-burn" model using 2,500 free-ranging American Bison (*Bison bison*) to mimic the ecosystem's natural disturbance regime. The preserve is located in the Flint Hills region of Kansas and Oklahoma, where rocky rolling hills protected the preserve from the plow and development. The prairie has an annual precipitation mean of 989.6 mm and a mean daily temperature of -3.4° C during the winter (Karger et al. 2017). The prairie is dominated by the perennial warm season grasses *Andropogon gerardii, Schizachyrium scoparium, Sorghastrum nutans,* and *Panicum virgatum*.

**Mixed-grass Prairie (WMWR)**

The Wichita Mountains Wildlife Refuge in southwestern Oklahoma is just north of the city of Lawton and Fort Sill Military Base. The refuge is 23,884 ha and contains a variety of habitats including approximately 8,093 ha of mixed-grass prairie as well as substantial scrubland areas dominated by blackjack (*Quercus marilandica*) and post oak (*Q. stellata*). The refuge has an annual precipitation mean of 833.6 mm and a mean daily temperature of -2.3° C during the winter (Karger et al. 2017). The Wichita Mountains are one of the oldest mountain ranges in the world. Hence, most of the mountains have worn down to expose their granite core, with eroded soil collecting below to form "bowls" which have become grasslands that often are separated from one another by granite hills and scrubland. The rocky soil of these grasslands helped spare the Wichita Mountains from agricultural development. The dominant grasses include *Aristida sp*., *Panicum virgatum, Schizachyrium scoparium, Bouteloua gracilis,* and *B. hirsuta.* The area was designated a national game reserve in 1905 and was added to the national refuge system in 1936, making it one of the oldest wildlife refuges in the US. In 1907 the refuge introduced 15

bison from the New York Zoological Society, and in 1927 a herd of longhorn cattle (*Bos taurus*) was introduced to reflect the cultural history of the region. These “free ranging” bison and cattle provide a grazing regime that is actively managed at the refuge through livestock roundups and auctions.

**Shortgrass Prairie (RBK)**

We treated as 1 site the adjacent tracts of shortgrass prairie comprising the Rita Blanca National Grassland, a patchwork of 37,632 ha straddling the Texas (Dallam County) and Oklahoma (Cimarron County) border, and the eastern unit of Kiowa National Grassland, an additional 20,235 ha in Union County, New Mexico. RBK has an annual precipitation mean of 393.8 mm and a mean daily temperature of -5.03° C during winter (Karger et al. 2017). Both grasslands are administered by the U.S. Forest Service and are interspersed among private ranchland and irrigated fields. Dominated by various species of *Aristida* and *Bouteloua*, as well as *Sporobolus cryptandrus*, these areas were protected to halt further grassland degradation and are products of the U.S. Government's attempt to prevent another “Dust Bowl” by buying failed cropland and transferring authority to the Soil Conservation Service and eventually U.S. Forest Service.

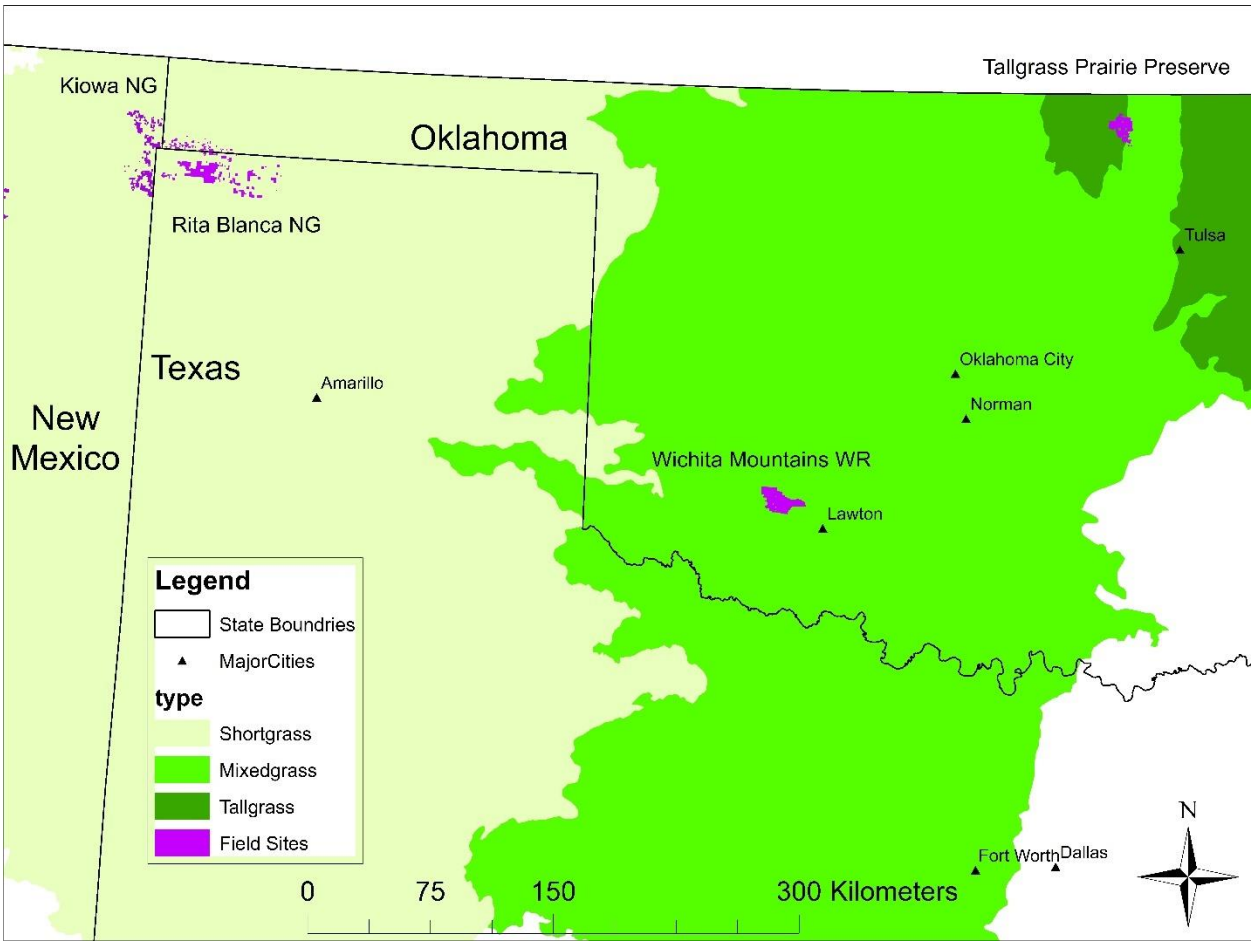



Figure 2~~1~~. Distribution of the three field sites (Wichita Mountains Wildlife Refuge Northwest of Lawton, Rita Blanca and Kiowa National Grasslands at the intersection of Texas, Oklahoma, and New Mexico, and Joseph H. Williams Tallgrass Prairie Preserve Northwest of Tulsa).

## METHODS

### Bird Sampling

We searched for longspurs using walking line transects. We constructed these transects by randomly plotting in ArcGIS a collection of starting points and vector bearings constrained to grassland habitats designated within the National Land Cover Database (NLCD) (Homer et al. 2020). Transects that fell substantially outside a study site boundary or outside of grassland habitat were eliminated. For each study site, this resulted in us covering 17 to 22 transects

varying in length from 1-5 km, depending on the size of the property and availability of grassland habitat.

Each transect was surveyed at least 3 times/ winter at approximately 4-week intervals, typically once in December, January, and February. We did not search for or plot longspur-occupied habitats during high winds (>8 m/sec), when precipitation exceeded light rain/snow, or when birds were detected farther than 250 m away. We recorded GPS locations of all birds that flushed from grass as well as opportunistic sightings of focal species (e.g., longspurs that flushed while driving roads or walking to or from survey transects).

At WMWR we collected night roost locations from a subset of CCLO, which had been radio-marked for home range analysis (Muller et al. in review). By tracking individuals, we were able to determine locations that CCLO used at night to roost.

**Vegetation Sampling**

We measured vegetation structure and composition in circular plots at 3 different levels. First at locations where longspurs were flushed either during surveys or opportunistically sighted (flush). Second at randomly generated points located throughout the field site (site-random) and third at points 25 m in a random direction away from the flush points (adjacent-random). We did this so we could compare the habitats each species actively used (flush) with habitats that were immediately available to the bird (adjacent-random) and habitats that were available more broadly at the site (site-random). We only measured vegetation for species of which there were sufficient number of sightings (>15 /site/yr).

All herbaceous species within a 5-m radius with >10% cover were counted as present or absent. We also counted the number of woody plants within a 10-m radius of each point. If there were no woody stems within a 10-m radius, we used a laser range finder to estimate distance of

the nearest woody plant or "perchable" object such as fence post. If the closest woody vegetation occurred beyond our range finder's capacity (~250 m) we used 251 m as this measure in subsequent analyses. Such adaptive sampling has been found to be efficient for finding relatively rare or clustered plants, such as woody species in grasslands (Yang et al. 2011). We also recorded several bivariate variables including evidence of grazing, presence of Black-tailed Prairie Dogs (*Cynomys ludovicianus*), and evidence of recent (<1 yr) burns. Since WMWR and TALL use an "open" grazing system in which cattle and bison are free to roam across plots, we would call a point "grazed" if we saw recent signs of grazing (e.g. fresh manure, clipped or trampled vegetation). This was necessary because although large herbivores were often present in an area, they did not necessarily graze the entire landscape uniformly.

We used digital photo-based techniques to measure vegetation plot composition since such analyses can result in significantly lower variance (e.g., reduced inter-observer variability) and provide greater repeatability for studies spanning multiple seasons or years relative to in-field measurements (Limb et al. 2007). We examined 4 plots associated with each flush, adjacent-random or site-random point, each 2 m away toward the respective cardinal directions. At each plot we captured nadir (ground-facing) and orthogonal images using a Casio EX-H2OG IS camera. We positioned our nadir images to fully capture from directly overhead a 1 m x 1 m "L" frame of ½" diameter PVC pipe placed on the ground so that the edges of the frame aligned with the edges of the photograph (Cagney et al. 2011) (Fig. 2). We then used SamplePoint v1.56 software (Booth et al. 2006) to distribute a grid of 49 (7 x 7) points over each digital image and assign to each point a ground cover category of bare ground, grass, forb, rock, litter, woody, bovid scat, cactus, or unknown. We then derived a percentage of total cover for each type and compiled these data across all 4 cardinal directions to calculate means of relative predominance

for each ground cover type for the respective random or flush point.

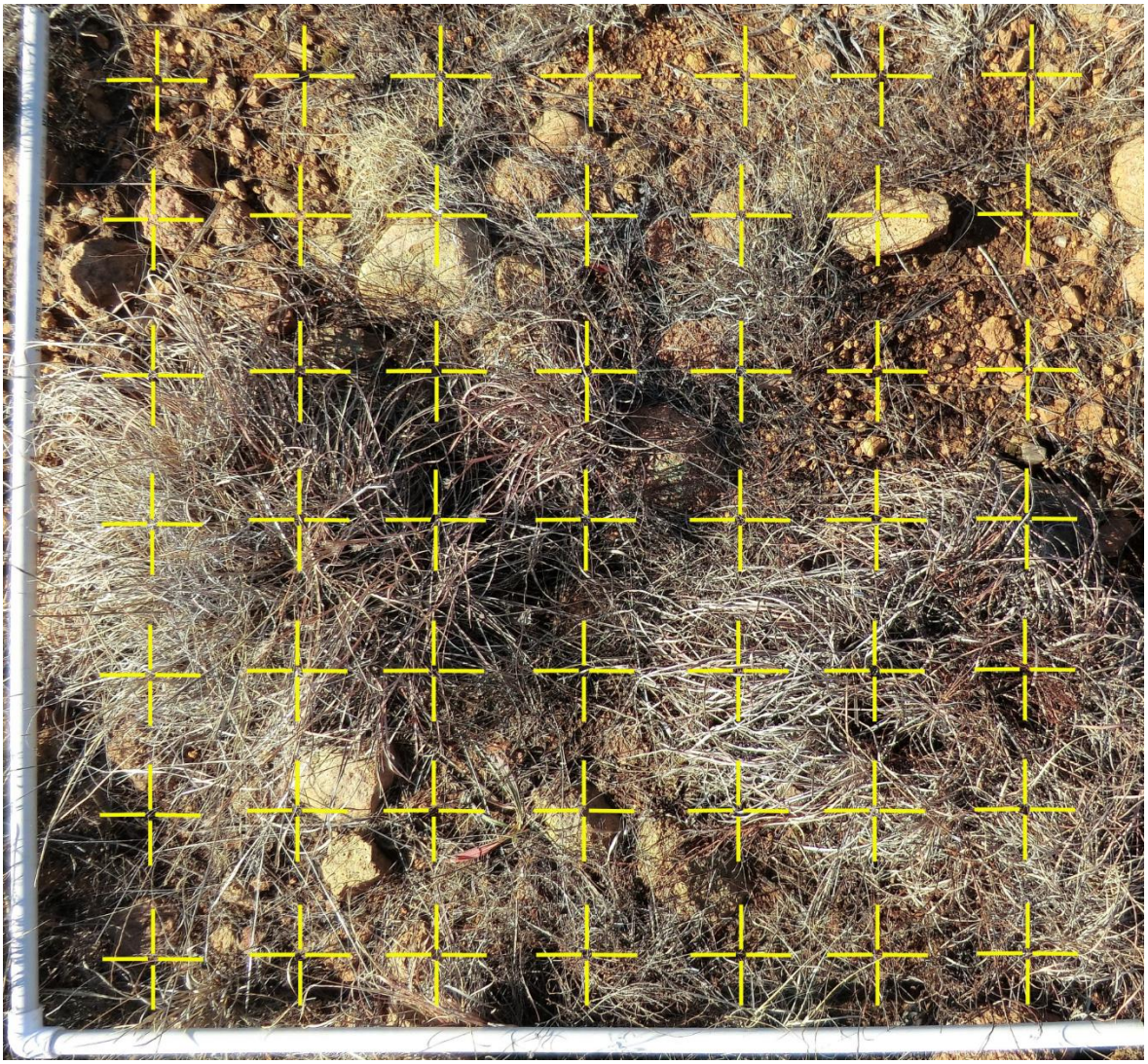


Figure 3~~2~~. Nadir image with the 49 crosshairs used to estimate vegetation cover.

We similarly estimated the vertical structure of vegetative cover 2 m away from the flush or random point in the 4 cardinal directions. Using a 2 m Robel pole measured at 2 cm intervals (Robel et al. 1970) crouching from the point we measured the height of 50% visual obstruction, maximum vegetation height, and minimum vegetation height. Obstruction values were selected

according to the highest segment that appeared more than 50% covered by vegetation, and both maximum and minimum vegetation height represented absolute measures at any point along the 2 m line from the central point to each cardinal direction. We counted minimum vegetation height as zero if this line passed over any roughly 8 cm x 8 cm (i.e., longspur sized) patch of bare ground. Values from each cardinal direction were again averaged together to provide a mean for each measure at each respective point.

**Analyses**

We tested for differences (randomization test) and relative importance (classification tree) of vegetation variables that may influence habitat use. We used a classification tree base (binary recursive partitioning) to test habitat use as a binary response of 2 groups, either occupied (flush points) and available but not occupied (adjacent or site-random locations). We also used classification trees to test for habitat use differences between 2 field sites (same species but 2 different locations). Classification trees are nonparametric tests that allow for powerful comparisons of categorical and continuous data simultaneously (De'ath and Fabricius 2000). Classification trees have the advantage of avoiding overfitting data and producing easily interpretable graphs. We used the 'ctree' function in package "party" (Hothorn et al. 2006) and "partykit" (Hothorn and Zeileis 2015) in program R (R Core Team 2018), both of which determine splits via a chi-square-based algorithm. The classification tree used a Bonferroni adjustment to account for multiple comparisons when making splitting decisions. We included all variables to test for significant factors, including continuous variables (i.e., percent grass, forb, bare ground, rock, litter, woody, scat, or cactus; number of shrubs within 10 m; 50% obstruction height; and maximum and minimum vegetation height) and binary variables (i.e., recently grazed, within prairie dog colony, evidence of recent burning, year of study, and presence of individual plant species). This results in a tree in which the "nodes" are the habitat

variables which best split the 2 groups (longspur use/response variable and available habitat/independent variable) and the "leaf" which are the final ratio of the 2 groups (percent of response variable is presented).

We also used a randomization test to determine which continuous response variables were significantly different among 2 groups (flush or random point), the randomization test compared the difference in means of 2 observed (actual) groups of points (CCLO, TBLO, LALO, SMLO, adjacent-random or site-random) to differences in means of 2 groups of randomized data. The randomization test pooled the 2 groups of points and then randomly distributed the individual values into 2 new groups with sizes equal to the original 2 groups. Each mean of the 2 new groups was calculated and the difference between these 2 new means was determined. This randomization process was repeated 1,000 times to form a null distribution that was then used to derive a *p* value to compare to the observed means (Veech 2012). The randomization test assessed how likely it is to obtain a difference in the observed means as great or greater than the difference obtained if the data (point locations) were randomly distributed among the 2 groups being compared. We also used the randomization test to determine if there were differences in the response variables between locations. For the binary response variables, we used a two-proportion *z*-test to determine if the 2 groups differed from one another.

**RESULTS**

We collected 1,308 vegetation points across the 3 sites field sites in Oklahoma and Texas. Vegetation data were collected on flush locations of the 4 species of longspur (454 points Table 1) as well as 59 points of CCLO roosting locations at WMWR. We also collected data at both adjacent (451 points) and site-random points (344 points).

Table 1. Number of observations for vegetation analysis for each of the 4 longspur species (Chestnut-collared (CCLO), Smith's (SMLO), Lapland (LALO), and Thick-billed (TBLO)) and site-random (RANDOM) at the 3 study sites, species that were present but at <15 observations are denoted with an x, species that were not detected are denoted with n/a.

| | Wichita Mountains | Tallgrass Prairie Preserve | Rita Blanca/ Kiowa |
|---|---|---|---|
| CCLO | 128 | x | 94 |
| SMLO | 45 | 72 | n/a |
| LALO | x | x | 79 |
| TBLO | x | n/a | 36 |
| RANDOM | 109 | 122 | 113 |

**Randomization Tests**

There were many differences between the 4 longspur species, both types of random points, and different field sites. Below we summarize the main findings for each species (Table 2), while the full results can be found in Appendix 1.

At WMWR and compared to site-random points, CCLO occurred in areas with higher amounts of grass (73.76%) and less amounts of rock (2.25%) and litter (9.34%) ($P$<0.05, Appendix A). They were more associated with grazing (70.3%) and prairie dogs (10.3%) and occurred in areas further away from (109.9 m) and with fewer trees and shrubs (0.01 shrubs) ($P$<0.05, Appendix B). They also occurred in shorter vegetation (11.04 cm) ($P$<0.05, Appendix B) and associated more with *Aristida sp*. (71.1%), and *Bouteloua gracilis* (16.4%), and less with *Schizachyrium scoparium* (28.1%), *Sorghastrum nutans* (2.3%), *Panicum virgatum* (10.1%) and *Sporobolus compositus* (0%) ($P$<0.05, Appendix C). At RBK, CCLO occurred in areas with higher amounts of grass (73.42%) and less bare ground (8.1%) and litter (12.8%) ($P$<0.05, Appendix A). There were no associations with grazing, prairie dogs, or shrubs. With vertical

vegetation CCLO occurred in areas of taller Maximum (39.32 cm) and shorter Minimum (0.76 cm) ($P$<0.05, Appendix B). CCLO also occurred more often in areas with *Aristida sp.* (39.4 %), *Sporobolus compositus* (14.9%), and *S. cryptandrus* (27.6%) ($P$<0.05, Appendix C). CCLO differed among sites in that at WMWR they were positively associated with grazing and negatively associated with shrubs but had no association with either at RBK (Appendix B).

At the WMWR CCLO differed from CCLO roosting locations (CCLON) in that roosting locations had higher percentages of Grass (93.56%) and taller vegetation (20.2 cm) ($P$<0.05, Appendix A). CCLON also occurred in areas less associated with grazing (13.6%), and further from trees (192.2 m) ($P$<0.05, Appendix B). Roosting locations occurred less often in areas with *Aristida sp.* (32.2%), *Bouteloua gracilis* (0%) and *B. hirsuta* (0%) while occurring more often in areas with *Panicum virgatum* (30.5%), *Sporobolus compositus* (10.2%), and *Schizachyrium scoparium* (52.5%) ($P$<0.05, Appendix C).

SMLO at WMWR occurred in areas with higher amounts of grass (80.02%) but lower amounts of bare ground (3.77%) and litter (7.59%) ($P$<0.05, Appendix A). They occurred in areas with shorter overall vegetation (10.32 cm) and were associated positively with grazing (82.2%) and negatively with shrubs (0.02 shrubs) ($P$<0.05, Appendix B). SMLO also associated more with *Aristida sp.* (75.5%), and *Bouteloua gracilis* (26.7%) ($P$<0.05, Appendix C). At TALL, SMLO occurred in areas with less grass (80.64%) and higher amounts of bare ground (4.94%), litter (7.56%), and scat (0.51%) ($P$<0.05, Appendix A). SMLO associated more often with grazing (95.8%) and in areas further away from shrubs (178.8 m) and with shorter vegetation (12.88 cm) ($P$<0.05, Appendix B). SMLO also were positively associated with *Aristida sp.* (68.05%), and *Bouteloua hirsuta, B.gracilis.* (8.3%, 12.5%) and less associated with *Andropogon gerardii* (0%) and *Sorghastrum nutans* (13.89%) ($P$<0.05, Appendix C).

TBLO occurred in areas with less grass (39.99%) and more bare ground (34.28%) and litter (19.87%) ($P$<0.05, Appendix A). TBLO were associated positively with grazing (88.9%) and negatively with shrubs (217.3 m) ($P$<0.05, Appendix B). TBLO occurred in areas of shorter vegetation (2.6%) and were negatively associated with *Bouteloua curtipendula* (11.1%) ($P$<0.05, Appendix B and C). Even at the constrained random level TBLO occurred in areas with less grass and more bare ground and litter, as well as shorter overall vegetation ($P$ <0.05, Appendix A and B).

LALO occurred in areas with less forb (3.7%) and litter (12.1%), but more bare ground (22.1%) ($P$<0.05, Appendix A). LALO were positively associated with grazing (73.4%) and Black-tailed Prairie Dogs (16.4%) but negatively with shrubs (191.6 m) and vegetation height (7.72cm) ($P$<0.05, Appendix B). LALO were negatively associated with *Bouteloua curtipendula* (13.9%) and *Yucca sp.* (0%) but positively associated with *Aristida sp.* (44.3%), *Sporobolus compositus* (8.87%), and *S. cryptandrus* (21.5%) ($P$<0.05, Appendix C).

Table 2. Showing the general Positive (+) or Negative (-) associations for each of the 4 species of longspur, Chestnut-collared Longspur (CCLO), Lapland Longspur (LALO), Thick-billed Longspur (TBLO), Smith's Longspur (SMLO) at each of the 3 sites for which there was enough data Rita Blanca/Kiowa National Grasslands, Wichita Mountain Wildlife Refuge, and Tallgrass Prairie Preserve. Associations are only shown for 4 variables Horizontal Grass Cover (%grass), Vertical Vegetation Height, Distance to the nearest shrub, and presence of grazing. Note CCLO at Rita Blanca/ Kiowa National Grasslands was positively associated with maximum vegetation height but negatively associated with minimum vegetation height.

| Location | Species | %grass | Vertical Vegetation | Shrub distance | Grazing |
|---|---|---|---|---|---|
| Rita Blanca/Kiowa | CCLO | + | +- | | |
| | LALO | | - | - | + |
| | TBLO | - | - | - | + |
| Wichita Mountains | CCLO | + | - | - | + |
| | SMLO | + | - | - | + |
| Tallgrass Prairie Preserve | SMLO | - | - | - | + |

**Classification Trees**

At TALL, we compared SMLO to both site-random points (Fig. 3, Panel A) and to adjacent-random points (Fig. 3, Panel B). Presence of *Aristida* was the greatest predictor for both trees, in that 98% of the points in the combined pool of SMLO and site-random, that contained Aristida were SMLO points. Grazing was the second predictor for site-random and grass height was the secondary predictor for adjacent-random comparisons.

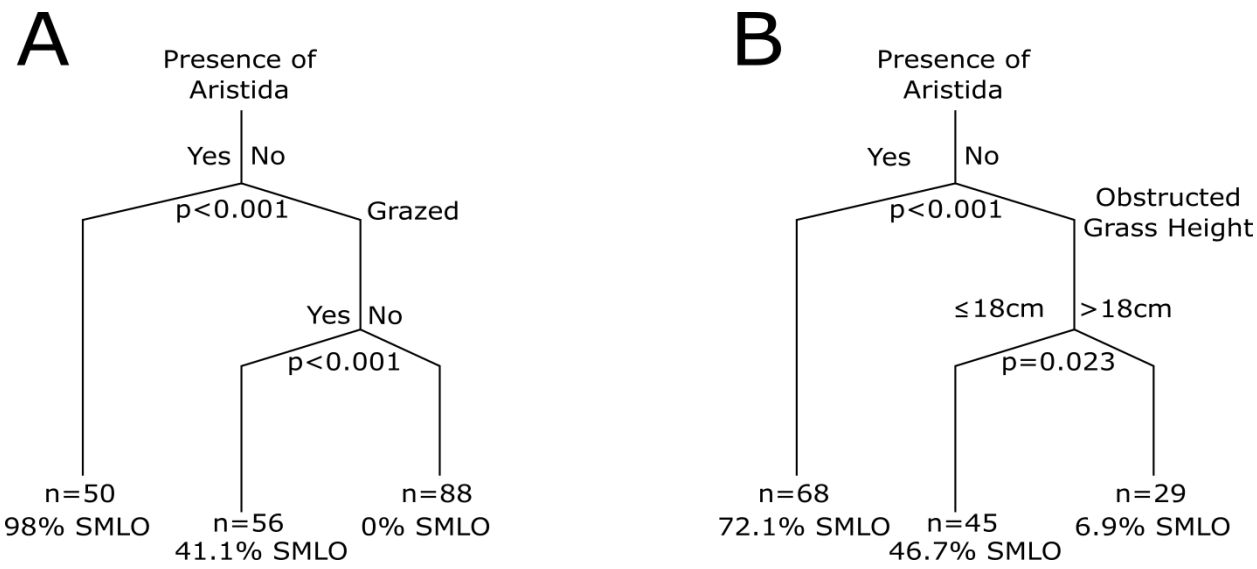



Figure 3. Classification Trees for Smiths Longspur (SMLO) at Tallgrass Prairie Preserve. Panel A is for the comparison of SMLO and site-random, while Panel B is for SMLO and adjacent-random.

At WMWR we compared SMLO to site-random (Fig. 4, Panel C) and adjacent-random (Fig. 4, Panel E). We also compared CCLO to site-random (Fig. 4, Panel D), adjacent-random (Fig. 4, Panel A), and CCLO roosting locations (Fig. 4, Panel B). For SMLO the greatest predictor differing from site-random was distance to shrub followed by grass height. SMLO showed no differences compared to adjacent-random. For CCLO, distance to shrub was the greatest predictor followed by various vegetation heights when compared to site-random. When compared to adjacent-random points CCLO were in shorter grass. Grass height was the biggest predictor for CCLO when comparing to CCLO roosting locations, in that CCLO are using shorter less dense grass during the day than at night.

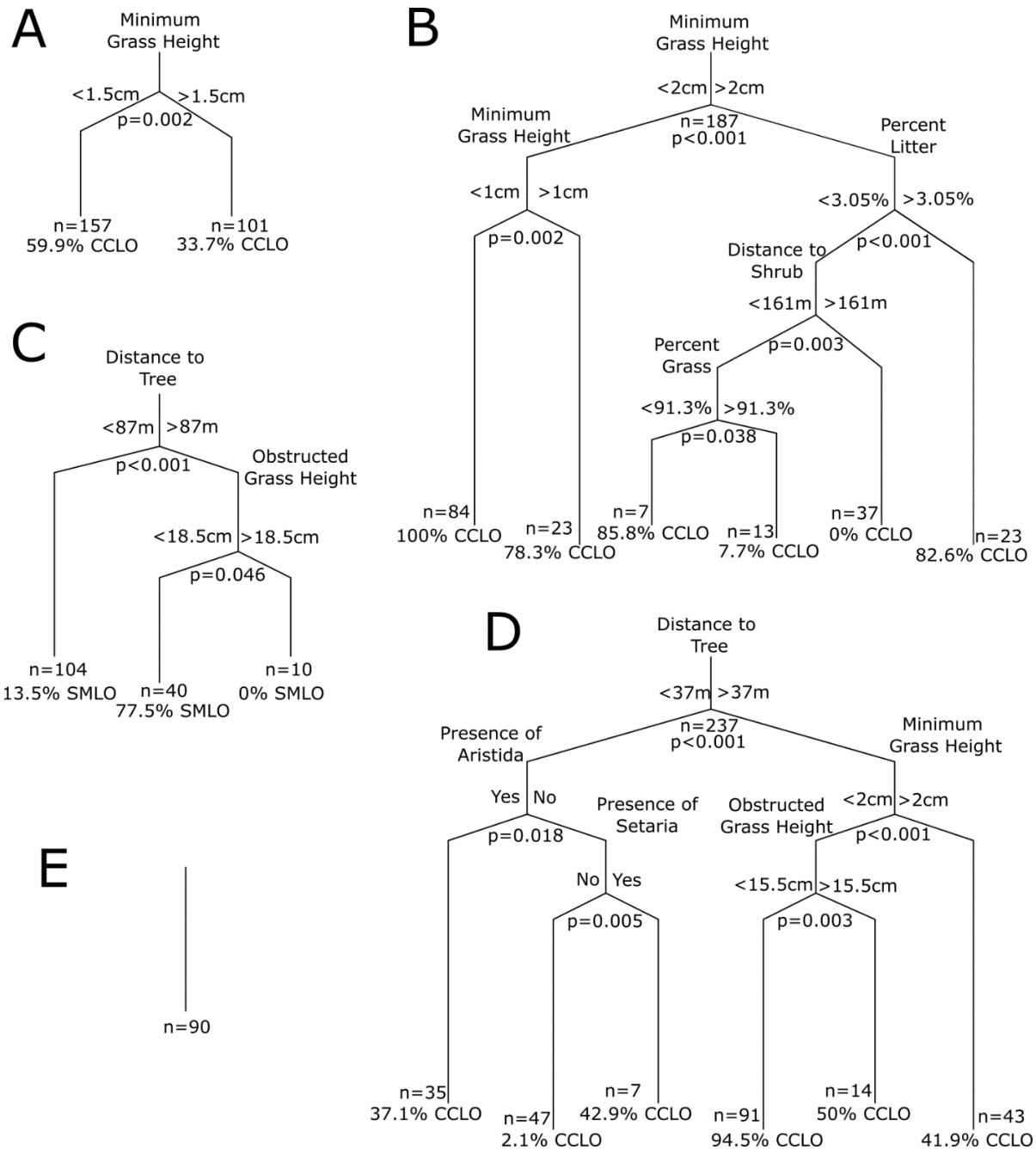



Figure 4. Classification Trees for Smiths Longspur (SMLO) and Chestnut-collared Longspur (CCLO) at Wichita Mountains Wildlife Refuge. Panel A is between CCLO and adjacent-random, Panel B is between CCLO and CCLO roosting locations, panel C is between SMLO and site-random, panel D is between CCLO and site-random, and panel E is between SMLO and adjacent-random.

At RBK we compared CCLO, LALO and TBLO to both site-random and adjacent-random. CCLO when compared to site-random points (Fig. 5, Panel B), minimum grass height was the greatest predictor followed by amount of grass. When compared to adjacent-random CCLO occurred more often in areas with higher percentages of grass (Fig. 5, Panel A). LALO compared to site-random locations occurred in areas of shorter grass (Fig. 5, Panel C). When compared to adjacent-random, LALO occurred in areas with higher bare ground and litter (Fig. 5, Panel D). TBLO compared to site-random occurred in areas of shorter vegetation and less grass (Fig. 5, Panel E). When compared to adjacent-random, TBLO occurred in areas with shorter vegetation (Fig. 5, Panel F).

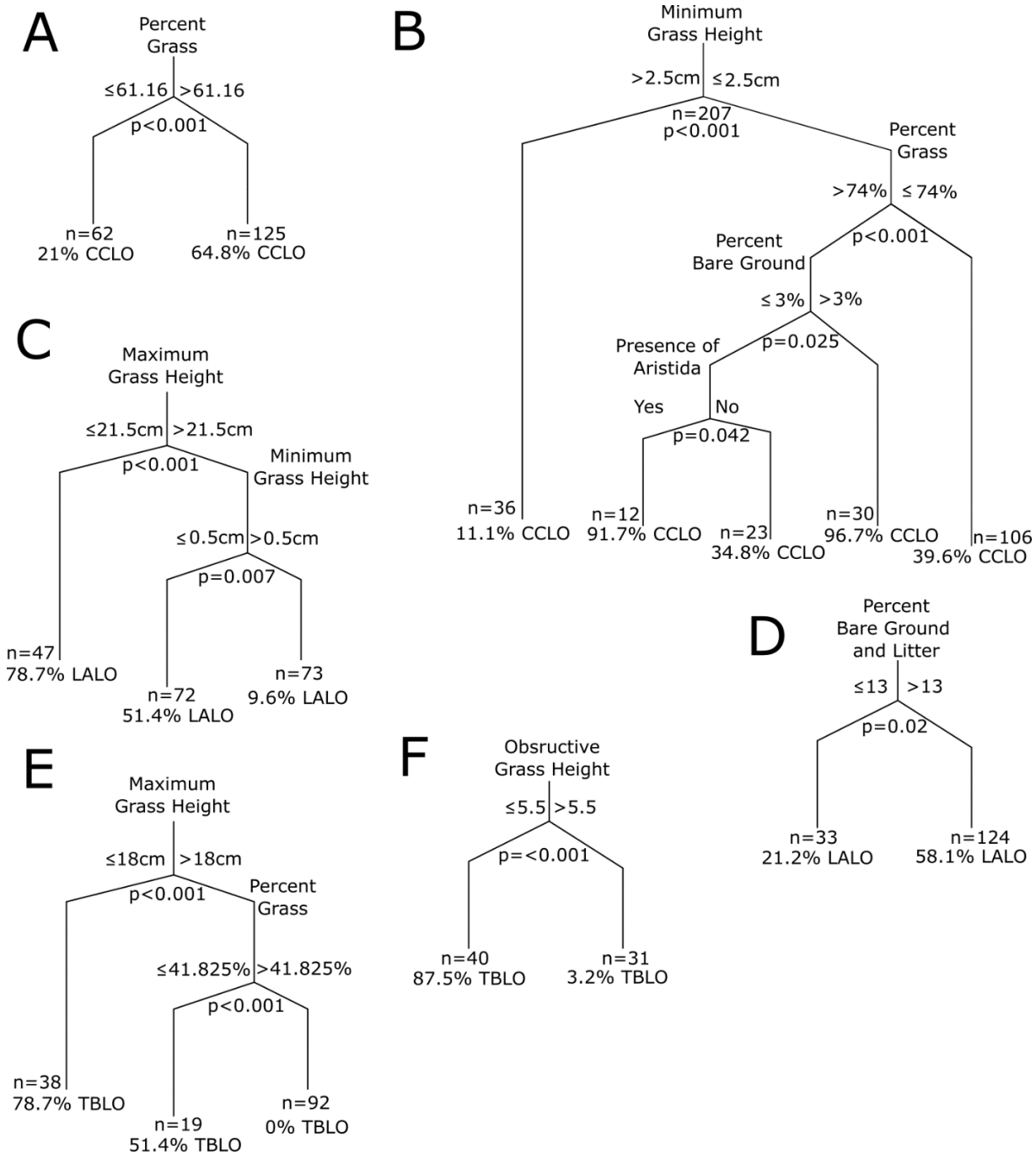



Figure 5. Classification Trees for Lapland Longspur (LALO), Chestnut-collared Longspur (CCLO), and Thick-billed Longspur (TBLO) at Rita Blanca and Kiowa National Grasslands. Panel A is between CCLO and adjacent-random, panel B is between CCLO and site-random, panel C is between LALO and site-random, panel D is between LALO and adjacent-random, panel E is between TBLO and site-random, and panel F is between TBLO and adjacent-random.

**DISCUSSION**

Our goal was to identify fine-scale habitat associations and key habitat features that predict occupancy for each of the 4 overwintering species of longspur in Oklahoma. As well as to determine if those associations changed based on ecoregion. Our first hypothesis that each species will use different habitat types was supported. We found that the major predictors for each species varied across vegetation height, horizontal composition, grass species presence, and proximity to shrubs. We also found that the strength and direction of those associations changed based on scale and location, but the overall structure of habitat species used was consistent across sites. This implies that different factors affect longspur occupancy and that management for each species should not focus on any one area (i.e., vertical, horizontal, shrub density), but on managing the land in a way that directs the habitats toward a the desired structure for the species of interest (i.e., vertical, horizontal, species composition, and shrub density).

We found positive associations with grazing for all 4 species of longspur with the exception of CCLO at RBK. Previous studies found mixed results with wintering CCLO and livestock grazing. For example, Bock and Bock (1988) found a positive relationship between grazing and CCLO in Arizona. In contrast, Desmond (2004) found that whereas CCLO may be positively associated with grazing in the Chihuahuan Desert, overgrazing may reduce abundance and (Kelly et al. 2006) found that grazing played an important factor in some years but not others. This means that the effect of grazing on CCLO has more to do with the resulting grass structure and not the inherent occurrence of grazing. If land managers choose to manage grasslands for CCLO through grazing regimes. Those regimes will need to be assessed depending on current grassland structure (i.e., vertical, horizontal) and locally tailored so that grass can be kept at a suitable height and density.

We showed a positive association between prairie dog towns and CCLO at WMWR, and LALO at RBK. Prairie dogs can act much in the same way that cattle grazing can, in that they reduce grass cover and height (Winter et al. 2002, Connell et al. 2018). Prairie dogs have also been shown to reduce shrub density in western grasslands (Connell et al. 2018, Hale et al. 2020). Due to recent plague (*Yersinia pestis)* outbreaks there are just a few small remaining Prairie Dog towns at RBK. Therefore, there were not many opportunities to test whether longspur species associated with prairie. Because TBLO had such a negative association with grass cover and height as well as shrubs, we believe that the positive relationship between TBLO and prairie dogs was insignificant due to small sample size and that TBLO occurrence is likely positively associated with prairie dog towns.

CCLO and SMLO were positively associated with *Aristida* sp. at both sites where they occurred. The association of SMLO to *Aristida* has been broadly purported (Landholt 1970, Grzybowski 1982, Ormston 2000, Holimon 2012)**,** and our results further support this. Many *Aristida* species are associated with early successional grasslands and disturbed soils (Diggs et al. 1999, Loflin et al. 2006). It is short compared to other dominant grasses in the shortgrass and mixed-grass prairies but produces less litter and allows more open ground, thus allowing the ground foraging longspurs adequate horizontal conditions (Landholt 1970, Holimon et al. 2012). Landholt (1970), collected 2 SMLO in a field composed almost entirely of *Aristida*, but their stomachs contained no *Aristida* seeds. This suggests that SMLO are associated with *Aristida* because of its structure or perhaps association with disturbance (grazing, trampling), and not because it is a food source. Many species of *Aristida* are not considered a favorable grass for cattle grazing as they can be unpalatable and the long awns can irritate or injure grazers, hence many private ranches attempt to eliminate *Aristida* (Humphrey 1958, Owensby and

Launchbaugh 1977, Loflin et al. 2006). Reduction of *Aristida* from private ranches may be a contributing factor to the population reduction of CCLO. Most random points at TALL and WMWR had no *Aristida* (99.18% and 67%), therefore, increasing presence of *Aristida* at both sites would likely grow the habitat available to wintering longspurs.

Many wintering grassland birds have shown a negative association to shrubs and woody vegetation (Pool et al. 2012, Ferrato et al. 2021). All 4 species of longspur were negatively associated with shrubs, except for CCLO at RBK. This is likely because RBK has so few shrubs compared to WMWR, the average distance to shrub at WMWR for random points was 45.65 m compared to 154.9 m at RBK. Shrub distance was the most important factor at WMWR in the classification tree for CCLO occupancy. This parallels what Macias-Duarte et al. (2009) found in the Chihuahuan Desert where CCLO were negatively associated with shrubs. Removal of shrubs should be a conservation priority for many declining grassland species including longspurs both at fine spatial scales and across the broader landscape, because many grassland birds are known to avoid shrub encroachment at multiple hierarchical scales (Thompson et al. 2014, Muller et al. 2018). That said, some native bird species do show a positive association with shrubs (Pulliam and Mills 1977), so optimal regional conservation of biodiversity would likely encompass heterogeneous management toward a mosaic of grassland types that range from zero to relatively-high shrub densities.

CCLO had seemingly contradictory associations with grass structure. CCLO was negatively associated with overall grass height at WMWR but positively associated with maximum grass height at RBK. The most important variable from the classification trees at RBK was shorter minimum grass height, and the randomization tests showed that they positively associate with horizontal grass coverage. This means that even though CCLO were associating

with denser taller grasses, CCLO needs areas of short grass and bare ground at very fine scales. This makes sense as CCLO are ground foragers and will need short grass to maneuver and forage but may be using taller grasses as cover from predation or cold. CCLO also use very different habitats during the day when compared to the night. During the night CCLO are roosting in taller and thicker vegetation compared to daytime habitats. We speculate this divergence in habitat use is due to the benefits of denser cover. During winter in Oklahoma, nighttime temperatures drop considerably lower than during the day, so potentially birds are using thicker vegetation for cover from weather and insulation (Ginter and Desmond 2005). Also, birds may be using this additional cover as protection from predators (Pulliam and Mills 1977, Grzybowski 1983). CCLO at fine scales as well as across sites need a mosaic of grass heights to satisfy the needs of both foraging, roosting, concealment, and protection.

There were many differences between longspur occurrence points and those of adjacent-random points, proving that longspurs are selecting habitat at multiple scales including scales smaller than 25 m. For example, relative to adjacent-random points CCLO were flushed from shorter vegetation at WMWR and higher percentages of grass at RBK. While at RBK TBLO and LALO associated with microhabitats of shorter vegetation, with TBLO further associating with less horizontal grass coverage. At TALL although we saw very few large patches of *Aristida* (just 0.82% of random points), SMLO were strongly associated with these patches (68.05% of points), including when compared to adjacent-random points (27.1%) (Appendix C). Our findings collectively suggest that variation in habitat use by all 4 species of wintering longspurs is occurring at scales smaller than 25 m.

Grasslands are critically important landscapes given their large spatial and temporal extent (O'Mara 2012), varied ecological services (e.g., water catchments, carbon sinks, and

wildlife habitat), and economic importance for agricultural and energy development (Samson and Knopf 1994, Wilsey et al. 2019). Economic exploitation has historically reduced ecologically functional grasslands across North America and, although losses have slowed, have continued to decline (Gage et al. 2016, Olimb and Robinson 2019, Homer et al. 2020). Grassland dynamics are heavily influenced by variation in the timing, frequency, duration, and intensity of precipitation, fire, grazing, and other management or disturbance, with these factors potentially contributing compounding or offsetting effects (Collins et al. 1998, Knapp et al. 1999, 2002, Griffen-Nolan et al. 2018). Particularly because of interacting factors grasslands can experience some of the most amplified rates of annual change in ecological processes, which has contributed to their rapid decline to being one of the most continuously threatened ecosystems in North America (Blancher 2003).

Along with general patterns of each species' habitat associations we also tested whether these associations shifted across grassland types. Our hypothesis that vegetation structure will be the same across the range of species regardless of grassland type was not supported. Variation in vegetative structure and composition occurred across ecoregions and field sites. Optimal management in one part of the range may not be optimal or even translatable to other areas. Much like in the Chihuahuan Desert grasslands (Macías-Duarte et al. 2009) we found CCLO at RBK have significantly positive associations between occurrence and vegetation height, yet this relationship completely flipped at WMWR. SMLO also showed a similar contrast in their association with horizontal grass coverage at separate sites, with a negative association emerging in the wetter, tallgrass prairie ecotype (TALL), versus a positive association in the drier, mixed-grass prairie (WMWR). What emerges is that as you move to more arid grassland environments, general management for CCLO and SMLO needs to increasingly shift away from reducing grass

height and density and toward promoting grass height and density. We found the tallest vegetation at SMLO flush sites had a mean height of 46-48 cm, while the obstructed vegetation had only a mean of 10-13 cm, which was similar to that previously reported in Oklahoma (Grzybowski 1980, Ormston 2000) but much taller than the 32 cm mean maximum heights reported in Arkansas (Holimon et al. 2012), although this study was in heavily modified human habitat (airport runways).

Individuals as well as populations of grassland birds have shown to have high levels of transience both throughout and between winter seasons (Gordon 2000, Pool et al. 2012, Muller et al. in review). Because of this transience, grassland birds are adaptable and are likely able to move into previously un-occupied areas if adequate fine-scale management occurs. We showed that longspurs on the wintering grounds are closely tied to specific vegetation heights, densities, and compositions. Longspurs are also generally associated with grazing, as well as negatively associated with woody vegetation. Our findings also show it is imperative to not only study species throughout their range, but that management for a particular species will be different and perhaps opposite depending on the current vegetative structure of the site.

**MANAGEMENT IMPLICATIONS**

Projections of expanding aridity are expected to push the shortgrass ecozone further north and east in the coming decades due to climate change (Wilsey et al. 2019). Peripheral locations on the edge of the wintering ranges of CCLO and TBLO, such as the WMWR or RBK, could become core winter range sites for the species and highlight the importance of maintaining and expanding the mosaic nature of their grassland habitats. Outreach and engagement to private landowners to help educate and convince them to participate in coordinated, landscape-scale management strategies such as a mosaic of grazing and prescribed fire regimes to emulate the

natural management pressures that maintained grassland ecosystems for millennia (Collins 2000, Samson et al. 2004). Positive management actions for wintering longspurs include the adaptive use of grazing to result in appropriate vegetation structure. For example, in terms of a continuum of vegetation height such as that presented in Knopf (1996), at shortgrass prairie sites if the default condition is sparse vegetation, reducing grazing would allow greater availability of taller bunch grasses, thus, increasing habitat for CCLO. But, in mixed-grass prairie where the default grass configuration would be too thick, an increase in grazing would be needed to induce more structural variation, thus providing more habitat for CCLO. These two different starting points on the grassland height and density continuum each use various grazing strategies to move the respective habitat toward the CCLO species optimum. Both SMLO and TBLO typically inhabit the shortest sparsest vegetation in their typically occurring respective ecotypes (tallgrass and shortgrass prairie), therefore, increased grazing or disturbance would likely be beneficial for both species. Other positive actions can include reducing shrub density and the reintroduction of Prairie Dogs. To reduce or turn around the negative population trends of CCLO and TBLO, management on the wintering grounds will likely need to be increased. Luckily, there are many different potential management actions that will benefit longspurs, that are easy to implement and will also be beneficial economically (e.g., grazing and mowing), or for other wildlife species (i.e., prairie dogs).

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## Appendix

Appendix A. Mean Percentages for the 8 land cover types for each species and each random point. An R on the end of the species denotes "adjacent" random point, and N on the end of the species denotes a "Night" or roosting point. Significant differences are denoted by a= difference from site-random, b=difference from adjacent-random, c=difference from other location, d=difference from CCLO.

| Location | Species | n | Grass | Litter | Forb | Bare | Woody | Scat | Cactus | Rock |
|---|---|---|---|---|---|---|---|---|---|---|
| WMWR | CCLO | 128 | 73.76$^{ab}$ | 9.34$^{ac}$ | 7.51$^{bc}$ | 6.8 | 0$^{ac}$ | 0.21$^{a}$ | 0.1 | 2.25$^{ac}$ |
| | CCLOR | 130 | 77.6 | 8.09 | 5.59 | 5.7 | 0 | 0.19 | 0.07 | 2.75 |
| | CCLON | 59 | 93.56$^{ad}$ | 1.57$^{ad}$ | 4.4$^{ad}$ | 0.2$^{ad}$ | 0$^{a}$ | 0.07$^{d}$ | 0$^{d}$ | 0.16$^{ad}$ |
| | SMLO | 45 | 80.02$^{ab}$ | 7.59$^{ab}$ | 5.68$^{ac}$ | 3.77$^{a}$ | 0.01$^{ac}$ | 0.2$^{ac}$ | 0.07$^{c}$ | 2.63$^{c}$ |
| | SMLOR | 45 | 72.4 | 12.2 | 7.67 | 5.98 | 0 | 0.21 | 0.05 | 1.48 |
| | Random | 109 | 66.7 | 12.7 | 7.68 | 6.2 | 1.94 | 0.13 | 0.07 | 4.7 |
| TALL | SMLO | 72 | 80.64$^{a}$ | 7.56$^{a}$ | 3.47$^{abc}$ | 4.94$^{ab}$ | 0.07$^{ac}$ | 0.51$^{ac}$ | 0$^{c}$ | 0.96$^{c}$ |
| | SMLOR | 70 | 81.2 | 6 | 6.08 | 1.23 | 0.06 | 0.39 | 0 | 0.68 |
| | Random | 122 | 88.7 | 5.23 | 2.02 | 2.71 | 0.21 | 0.07 | 0 | 0.5 |
| RBK | CCLO | 94 | 73.42$^{ab}$ | 12.8$^{abc}$ | 4.2$^{abc}$ | 8.1$^{ab}$ | 0.18$^{ac}$ | 0.13$^{a}$ | 0.21$^{a}$ | 0.08$^{ac}$ |
| | CCLOR | 93 | 61 | 17 | 6.6 | 12 | 0.1 | 0.2 | 0.9 | 0.1 |
| | TBLO | 36 | 39.99$^{ab}$ | 19.87$^{ab}$ | 2.63$^{ab}$ | 34.28$^{ab}$ | 0.05$^{a}$ | 0.88$^{ab}$ | 0.04$^{a}$ | 0.35$^{a}$ |
| | TBLOR | 35 | 62.4 | 14.2 | 9.35 | 14.2 | 0.27 | 0.53 | 0 | 0.14 |
| | LALO | 79 | 60.4$^{b}$ | 12.1$^{a}$ | 3.7$^{a}$ | 22.1$^{ab}$ | 0.11$^{ab}$ | 0.5 | 0$^{a}$ | 0.31$^{a}$ |
| | LALOR | 78 | 70.6 | 9.2 | 3.44 | 14.8 | 0 | 0.3 | 0.3 | 0.1 |
| | Random | 113 | 64 | 14.8 | 7.77 | 15.6 | 0.02 | 0.37 | 1.1 | 0.02 |

Appendix B. Percentages for grazing, burned, prairie dogs, number of trees with 10m, and distance to nearest tree, and the vertical vegetation structure for each species and each random point. An R on the end of the species denotes “adjacent” random point, and N on the end of the species denotes a “Night” point. Significant differences are denoted by a= difference from site-random, b=difference from adjacent-random, c=difference from other location, d=difference from CCLO.

| Location | Species | n | Grazing | Prairie Dogs | Burned | Trees | Tree Distance | Observed | Maximum | Minimum |
|---|---|---|---|---|---|---|---|---|---|---|
| TALL | SMLO | 72 | 95.8[ac] | 0[c] | 1.4[a] | 0.014[a] | 178.8[ac] | 12.88[abc] | 46.18[ab] | 1.26[ab] |
| | SMLOR | 70 | 84.2 | 0 | 1.4 | 0.014 | 170.3 | 19.14 | 58.96 | 3.8 |
| | Random | 122 | 27.87 | 0 | 11.4 | 0.28 | 124.7 | 26.86 | 71.14 | 11.78 |
| | CCLO | 94 | 41.5[c] | 2.1 | 0 | 0.43[c] | 168.2[c] | 14.06[c] | 39.32[a] | 0.766[abc] |
| | CCLOR | 93 | 31.2 | 6.4 | 0 | 0.48 | 167 | 14.6 | 37.8 | 1.18 |
| RBK | TBLO | 36 | 88.9[a] | 11.1 | 0 | 0[a] | 217.3[a] | 2.6[ab] | 11.2[ab] | 0.054[ab] |
| | TBLOR | 35 | 88.6 | 8.6 | 0 | 0 | 211 | 10.4 | 24.82 | 1.64 |
| | LALO | 79 | 73.4[a] | 16.4[a] | 0 | 0.09[a] | 191.6[a] | 7.72[ab] | 25[a] | 0.44[ab] |
| | LALOR | 78 | 75.6 | 7.7 | 0 | 0.06 | 190.2 | 9.86 | 28.2 | 1.088 |
| | Random | 113 | 50.4 | 3.5 | 1.77 | 1.2 | 154.9 | 12.84 | 36.32 | 2.38 |
| WMWR | CCLO | 128 | 70.3[ac] | 10.3[a] | 2.3 | 0.01[ac] | 109.98[ac] | 11.04[abc] | 41.58[ab] | 1.4[abc] |
| | CCLOR | 130 | 68.46 | 9.2 | 2.3 | 0.04 | 105.5 | 14.16 | 49.5 | 2.8 |
| | CCLON | 59 | 13.6[ad] | 3.4 | 0 | 0[a] | 192.2[ad] | 20.2[d] | 52.2[d] | 3.12[ad] |
| | SMLO | 45 | 82.2[ac] | 8.89[c] | 0 | 0.02[a] | 121.4[ac] | 10.32[ac] | 48.44[a] | 1.732[a] |
| | SMLOR | 45 | 75.5 | 8.89 | 0 | 0.02 | 120.6 | 11.12 | 50.48 | 2.6 |
| | Random | 109 | 37.6 | 1.8 | 0.9 | 3.5 | 45.65 | 17.98 | 57.8 | 4.84 |

Appendix C. Table showing the percentage of points that contained specific species of vegetation. An R on the end of the species denotes “adjacent” random point, and N on the end of the species denotes a “Night” point. Significant differences are denoted by a= difference from site-random, b=difference from adjacent-random, c=difference from other location, d=difference from CCLO.

| Location | Species | n | Ambrosia sp. | Andropogon gerardii | Aristida sp. | Bouteloua curtipendula | Bouteloua dactyloides | Bouteloua gracilis | Bouteloua hirsuta | Gutierrezia sp. | Panicum virgatum | Schizachyrium scoparium | Setaria sp. | Sorghastrum nutans | Sporobolus compositus | Sporobolus cryptandrus | Yucca sp. |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| WMWR | CCLO | 128 | 17.2$^{c}$ | 3.1 | 71.1$^{abc}$ | 5.5$^{c}$ | 0 | 16.4$^{ac}$ | 17.9$^{c}$ | 0$^{c}$ | 10.1$^{abc}$ | 28.1$^{ac}$ | 5.5 | 2.3$^{a}$ | 0$^{ac}$ | 3.1$^{c}$ | 0$^{c}$ |
| | CCLOR | 130 | 19.2 | 3.07 | 58.5 | 3.8 | 0 | 13.1 | 15.4 | 0.77 | 23.1 | 36.9 | 9.23 | 8.46 | 2.3 | 3.8 | 0 |
| | CCLON | 59 | 25 | 0 | 32.2$^{d}$ | 1.7 | 0 | 0$^{d}$ | 0$^{ad}$ | 0 | 30.5$^{d}$ | 52.5$^{d}$ | 0 | 13.5$^{d}$ | 10.2$^{d}$ | 1.7 | 0 |
| | SMLO | 45 | 11 | 0 | 75.5$^{a}$ | 6.7 | 0 | 26.7$^{a}$ | 11 | 0 | 8.9$^{a}$ | 36 | 4.4$^{c}$ | 20$^{d}$ | 0$^{c}$ | 4.4 | 0 |
| | SMLOR | 45 | 11 | 2.2 | 71 | 2.2 | 0 | 20 | 6.7 | 0 | 13 | 24 | 8.9 | 24 | 4.4 | 2.2 | 0 |
| | Random | 109 | 20 | 4.6 | 33 | 1.8 | 0 | 6.4 | 17 | 0 | 20 | 41 | 4.6 | 21 | 5.7 | 5.5 | 0 |
| TALL | SMLO | 72 | 15.3 | 0$^{a}$ | 68.05$^{ab}$ | 4.2 | 0 | 12.5$^{ab}$ | 8.3$^{a}$ | 1.39 | 19.4 | 38.9 | 26.4$^{c}$ | 13.89$^{a}$ | 13.89$^{c}$ | 0 | 0 |
| | SMLOR | 70 | 11 | 1.4 | 27 | 1.4 | 0 | 0 | 4.2 | 8.5 | 27 | 53 | 27 | 26 | 26 | 0 | 0 |
| | Random | 122 | 9.01 | 13.1 | 0.82 | 0.82 | 0 | 0 | 0.82 | 7.37 | 18.9 | 48.4 | 23.8 | 45.9 | 13.1 | 0 | 0 |
| RBK | CCLO | 94 | 0$^{c}$ | 1.1 | 39.4$^{ac}$ | 32.97$^{c}$ | 0 | 40.4$^{c}$ | 1.1$^{c}$ | 7.4$^{c}$ | 0$^{c}$ | 2.1c | 0 | 0 | 14.9$^{ac}$ | 27.6$^{ac}$ | 5.3$^{c}$ |
| | CCLOR | 93 | 0 | 0 | 31 | 26 | 1.1 | 40 | 1.1 | 12 | 0 | 2.1 | 0 | 0 | 13 | 29 | 6.5 |
| | TBLO | 36 | 0 | 0 | 31 | 11.1$^{a}$ | 8.3 | 39 | 0 | 5.6 | 0 | 0 | 0 | 0 | 2.8 | 17 | 0 |
| | TBLOR | 35 | 0 | 0 | 37 | 29 | 0 | 29 | 0 | 5.7 | 0 | 0 | 0 | 0 | 5.7 | 14 | 0 |
| | LALO | 79 | 1.3 | 0 | 44.3$^{a}$ | 13.9$^{a}$ | 1.3 | 51 | 0 | 6.3 | 0 | 0 | 0 | 0 | 8.87$^{a}$ | 21.5$^{a}$ | 0$^{a}$ |
| | LALOR | 78 | 0 | 0 | 47 | 15 | 1.3 | 51 | 0 | 6.4 | 0 | 0 | 0 | 0 | 7.7 | 13 | 2.6 |
| | Random | 113 | 3.5 | 0 | 23 | 31.9 | 0.88 | 54.9 | 1.76 | 15.9 | 0 | 2.65 | 0 | 0 | 0.88 | 8.8 | 11.5 |

## Chapter 4: Winter Space Use and Sex-ratio's of Chestnut-collared Longspur (*Calcarius ornatus*) in Oklahoma

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**Abstract-** As grasslands have become the most threatened ecosystem in North America, so too have many migratory obligate grassland birds endemic to the continent. Chestnut-collared Longspurs (*Calcarius ornatus*), are a great example, as they have experienced an 89% population decline during the last 5 decades. We captured and tracked individuals during the winters of 2018-19 and 2019-20 and calculated their home ranges as both Minimum Convex Polygons (MCP) and Fixed Kernel Density Estimates (KD). Across the two years we captured and banded 116 longspurs (roughly 75% male), fitting 90 of these with VHF radio transmitters. The winter (December 5 through March 8) home ranges defined by MCP averaged 128.8 ha, while the 95% KD indicated a mean of 29.87 ha. Wintering Chestnut-collared Longspurs used larger areas and displayed higher nomadism than reported for other grassland bird species. Therefore, management for the species scales beyond the relatively small areas that longspurs aggregate into flocks within and will require landscape-level coordination to maintain habitat adequate for effective winter population.

**Key Words**

Winter ecology, Grassland birds, Great Plains, Wichita Mountains, Winter habitat

Grasslands are the ecosystem most reduced from historical levels and now most threatened in North America (Blancher 2003). Tallgrass, Mixed-grass, and Shortgrass Prairie — the three major grassland ecosystems in North America—have been reduced from their historic

sizes by 98%, 76%, and 46%, respectively (Comer et al. 2018). Grasslands are critically important ecosystems, providing ecological value as water catchments, carbon sinks, and habitat for wildlife, while also serving as an economic resource via cattle grazing and energy development (Samson and Knopf 1994, Wilsey et al. 2019). Conversion of grasslands to agriculture has been a leading cause for the reduction of ecologically functional grasslands here in North America, and these grasslands continue at a high rate of decline (Gage et al. 2016, Olimb and Robinson 2019, Homer et al. 2020). Parallel to this drastic loss of grassland habitat is a decline in grassland birds, which have suffered worse population declines over the past fifty years than any other bird assemblage (Vickery et al. 1999, Sauer et al. 2017, Rosenberg et al. 2019). Overall, 31 species of grassland birds have undergone a cumulative population reduction of 53% since 1970, with 74% of species still in decline (Rosenberg et al. 2019). This dramatic reduction of both individuals and, in some cases, entire populations has been described as a conservation crisis (Brennan and Kuvlesky 2005).

Chestnut-collared Longspurs (*Calcarius ornatus*) hereafter (longspur), are migratory obligate grassland birds endemic to North America. Longspurs breed in short and mixed-grass prairie in the Northern Great Plains including Saskatchewan, Manitoba, Montana, and North Dakota. During Fall and Spring migration they travel east of the Rockies where they winter in the short- and mixed-grass prairies of the Southern Plains and desert grasslands of North-Central Mexico and Southwest US (Ellison et al. 2017, Bleho et al. 2020). On the breeding grounds longspurs appear to be native grassland specialists (Lloyd and Martin 2005), whereas on the wintering grounds they may use anthropogenic habitats such as crop waste and leftover wheat grains (Bleho et al. 2020). Longspur winter habitats include shortgrass prairies with cover less than 0.5m in height (Grzybowski 1982) and where shrub cover is minimal (Macías-Duarte et al.

2009). Thought to be one of the most abundant birds in northern prairies before European settlements (Coues 1878), longspurs are a clear example of a recent population decline, with an 89% population reduction from 1966-2017 (Sauer et al. 2017). We routinely observed flocks as large as 150 birds during our study, although most flocks were 15-30 birds.

To conserve and manage these rapidly declining species there is a need for full life-cycle conservation (Hostetler et al. 2015, Marra et al. 2015). Although breeding habitat for grassland birds has steadily declined in recent decades, changes associated with these species' wintering grounds have been suggested as a potential cause for the population declines of many migratory species (Rappole and McDonald 1994, Morrison et al. 2013, Macías-Duarte et al. 2017, Correll et al. 2019). Nevertheless, most research has been conducted on the breeding grounds with few studies focusing on wintering ecology (Faaborg et al. 2010, Marra et al. 2015). Longspurs exemplify this problem with few wintering studies on the species and most of those occurring in one part of their wintering range, the Chihuahuan desert grasslands of northwestern Mexico and the southwestern US (Desmond 2004, Kelly et al. 2006, Macías-Duarte et al. 2009, Pool et al. 2012). As a species that depends on grassland habitat for both breeding and wintering, it is in need of conservation and research efforts that account for the full life-cycle of the species.

Wintering habitats must provide the basic resources needed for individuals to survive, including food, fresh water, and shelter from predators or weather (Burt 1943), as well as sufficient resources to fuel spring migration (Briedis et al. 2018, Akresh et al. 2019). Longspurs start arriving in Southwestern Oklahoma in the middle of October, but don't arrive in large numbers until the middle of November and birds appear to start leaving at the end of February and are mostly gone by early April (Sullivan et al. 2009, personal observations). In the case of longspurs, wintering habitats must also be conducive to flocking behavior. Most grassland birds

do not form persistent wintering flocks, but longspurs are an exception, typically occurring in flocks throughout the winter. Flocking increases sociality and perhaps transience, in that individuals are not defending territories *per se*, and require individuals to use larger areas because of increased density. Because of this increased sociality, we hypothesized that longspurs would use larger areas relative to other overwintering grassland passerines. The primary goal of this study was to quantify movement and space use of wintering longspurs in southwestern Oklahoma and to assess whether individual longspurs use larger areas compared to similar species of migratory grassland birds. This is an important question to address as the scale at which these wintering longspurs use could affect the scale at which affective management needs to happen for these rapidly declining species (Fauvelle et al. 2017). To answer these questions, we captured longspurs over two winters (2018-19 and 2019-20) and attached Very High Frequency (VHF) transmitters that allowed us to quantify movements and space use throughout much of the non-breeding season.

Our tracking efforts afforded an opportunity to test for bias in the sex ratio of a wintering population longspurs. Sex ratios are of interest here because many migratory bird species show variation in the distribution of the sexes during the non-breeding period, wherein males tend to winter farther north than females (Phillips et al. 2004, Komar et al. 2005, Townsend et al. 2011). This sex-biased distribution is particularly strong in species that show a discrepancy in size (Myers 1981, Bai and Schmidt 2012). There are several competing hypotheses for why there is a skewed sex ratio. First is the Body Size Hypothesis which posits that the larger sex (usually males) are more cold-tolerant due to the lower Surface Area to Volume Ratio (Ketterson and Nolan 1976, Cristol et al. 1999). An alternative is the Arrival Time Hypothesis, which reasons that males winter further North to shorten their spring migration and advance their arrival on the

breeding grounds (Ketterson and Nolan 1976, Cristol et al. 1999). In many migratory bird species, early arrival at the breeding grounds is positively correlated with reproductive success (Møller 1994, Lozano et al. 1996); hence, there may be selective pressure to winter farther north. Both of these hypotheses could be true for longspurs; males are larger than females, and Oklahoma is in the northern part of the wintering range. We sought to test if there was a deviation from 1:1 in the ratio of wintering males to females on the wintering grounds.

By testing for increased home range requirements and biased sex ratios, we hope to fill in existing research gaps that are known priorities for the conservation of longspurs. Our work also provides new insight into key demographic and life history parameters including seasonal movement, home range, age and sex distributions (Somershoe 2018, Bleho et al. 2020). With this information we move a step closer to having the capacity for full-life-cycle demographic modeling for longspurs, which we argue is the necessary foundation for effective conservation and management of any migratory bird species.

## Methods

### Study system

The Wichita Mountains Wildlife Refuge (WMWR) (Fig. 1) is located in Comanche County in Southwestern Oklahoma and abuts along the entirety of its southern border the US Army's Fort Sill military base. The refuge itself is 23,884 ha and contains a variety of habitats, including approximately 8,093 ha of mixed-grass prairie as well as substantial scrubland areas dominated by blackjack and post oak (*Quercus marilandica and Q. stellata*), and riparian forests. The Wichita Mountains are one of the oldest mountain ranges in the world. Hence, most of the mountains have worn down to expose their granite core with eroded soil collecting between

remnant peaks to form grasslands. Within WMWR, grassland areas are often naturally isolated from one another, separated by granite hills and scrubland, as well as managed as a mosaic of grazing units for American bison (*Bison bison*) and heritage herds of longhorn cattle in recognition of the area's importance as part of the post-Civil War cattle drive route known as the Chisholm Trail. The rocky soil of these grasslands meant that this area was never subject to crop development and the area was designated a national game reserve in 1905 and later added to the national refuge system in 1936, making it one of the oldest wildlife refuges in the US.

We captured and tracked longspurs at the WMWR during consecutive winters 2018-19 and 2019-20. Birds were captured within 3 major tracts of grassland in the refuge that were separated by more than 5 km. We named these tracts Meers Turnoff (MT), Visitor Center (VC) and Headquarters (HQ) (Fig. 1). Wintering grassland birds, including longspurs are notoriously hard to capture (Martin 1969, Ralph et al. 2004), which compelled us to develop two novel capture techniques that exploit the longspurs roosting and flushing behaviors (Muller et al., in review). For the first technique we attempted a typical "flush-netting" approach wherein we established a long (60-84 m) line of mist nets near a known roosting area and had a team of field assistants slowly herd an alighted flock of birds toward the nets. We found that this capture method could be employed only around dusk, when longspurs typically fly low and horizontally if flushed. The second method involved a completely novel approach, wherein at least two people carried a mistnet spread taut between them and held parallel to the ground, with one or more researchers walking close behind the net to flush the flock. This technique required us to operate in the post-twilight evening and maneuver the net toward and over the area where a flock of longspurs had been seen to alight in the pre-twilight period. As the longspurs flushed largely upwards the net directly entangled the birds or the team would gently lower the nets to the

ground to restrain the birds' ability to escape laterally. We found this method to be highly successful, but only if we advanced without the assistance of headlamps or the light of a full moon. Although both techniques were new and untested, we observed no injuries, no behaviors indicative of stress (e.g., panting, excessive blinking, body stiffness or limpness) all birds were released in seemingly good health and there were no observed indications of early mortality.

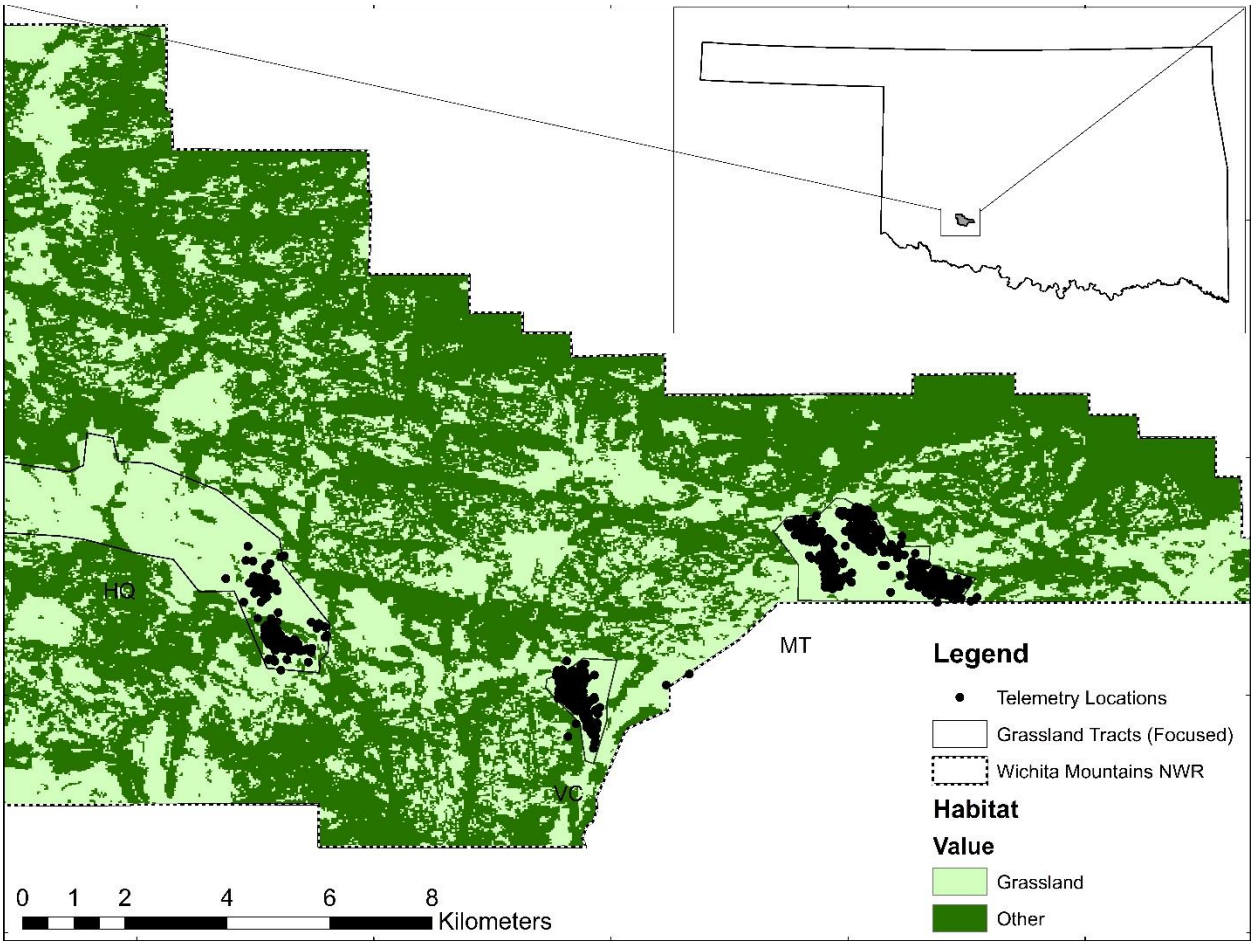


Figure 41. Grassland tracts at the Wichita Mountains Wildlife Refuge. Chestnut-collared Longspurs were banded at three focused locations Meers Turnoff (MT), Visitor Center (VC) and Headquarters (HQ).

Once captured, longspurs were banded with a numbered United States Geological Survey aluminum band, and we took morphometric measurements, including lengths of wing, tail, tarsus, and spur (hallux), along with beak dimensions at the nares and body weight. Radios were attached to the birds with a fitted figure-8 leg-loop harness (Rappole and Tipton 1991), made from degradable elastic thread. We used Radio Transmitters from Jim Cochran (JDJC Corp., Dewey, IL, USA) and Philip Blackburn (Blackburn Telemetry, Nacogdoches, TX, USA). Transmitters had an expected battery life of 45-60 days and weighed approximately 0.6 grams, which would amount to 2-3% of a typical body weight of a longspur. We focused our capture efforts during the middle of the wintering period from approximately December 5 through January 20. Ellison et al. 2017 found that longspurs reach their wintering locations by the first week of December, therefore, capturing during this period ensured that the birds were winter residents and not early or late migrants, but still provided enough time to collect sufficient telemetry data for home range analysis. We did not attach radios to birds after January 31, as it was too late in the season and we were uncertain when migration would begin, and we may not get enough data for analysis. Because, the population at WMWR is male dominated and older bird dominated we did not attach radios to every older male longspur and instead tried to attach radios to younger and female birds for sufficient sample size.

Using a handheld receiver, we attempted to triangulate the position (±10 m) of radio-tagged longspurs 1-3 times per day. During year 1 this tracking occurred during mornings and afternoons, while during the second year we also attempted to locate a subset of birds in the post-twilight (i.e., roosting) period. Tracking efforts ceased at the end of the field season (approx. March 8), after the batteries expected life had been exceeded and the bird had not been detected for at least a week, the transmitter became detached and was recovered, or the bird had been

predated. We used R2000 and R410 receivers and 3 element Yagi antennas (Advanced Telemetry Systems, Inc., Isanti, MN). We located individuals by scanning at their last location, as well as at spots with good line of sight as the WMWR is extremely hilly. At every location we would scan for all potential radio-tagged birds and once we detected a signal, the observer would scan for any other of the radio-tagged birds in the same direction, then walk toward the bird(s) until they flushed and there gathered GPS coordinates and weather data. If a flock of longspurs were flushed and we were uncertain which individual from the flock was the tagged individual, we collected the GPS location from the center of where the flock flushed. Collected weather data included wind, temperature, precipitation, and any noteworthy observations (e.g., proximity of large herbivores). We also attempted at least once a week to search grasslands that contained longspurs outside of the three main areas (Fig. 1).

**Analyses**

We evaluated home ranges by calculating minimum convex polygons (MCP) that contained all of the geographic locations we mapped for each tracked individual animal (Mohr 1947). We restrained our analysis of MCP to individuals for which we recorded at least 15 locations. There are several advantages to using MCPs, including its simplicity and the fact that it can be used when there are too few points for more intensive analysis such as kernel density, which is often the case when working with radios that have a relatively short life and birds that are hard to find. Yet, MCP typically overestimates home range size because of sample bias; that is, home range increases with the number of locations plotted (Turner et al. 1969) and through the outsized impact of outliers (Seaman et al. 1999). A simple application of MCP also assumes that all areas within the polygon are used equally as part of the home range which is unlikely considering habitats are typically heterogeneous. Because MCP overestimates home range, it is often best

used as a total range estimator. The total range metric is useful for managers and conservationists, addressing management scale, or sensitivity to a rare external threat encountered when an individual forays outside of their home range.

For individuals with sufficient tracking data (≥30 locations) (Seaman et al. 1999) we also estimated home range (Fig. 2) by calculating a Fixed Kernel Density (FKD) estimator (Worton 1989), using the Geospatial Modeling Environment Version 0.7.4 (Beyer 2015) and the *ks* package Version 1.11.7 (Duong 2020) in Program R Version 3.5.1 (r core team 2018), and ArcMap Version 10.3. We estimated the 95% and 50% isopleths at a grid size of 30m. We used a least squares cross validation (LSCV) bandwidth estimator because other estimators are known to over-estimate home range size (Seaman and Powell 1996).

We also measured home range overlap, to get an estimate of how much an individual longspurs home range overlapped with other individuals in the same area. We used the R package "adehabitatHR" to calculate the utilization distribution and overlap of each individual longspur with all other individual longspurs (Fieberg and Kochanny 2005). We then calculated the mean percent overlap of each individual with all other individuals at each of the 3 focused grassland tracts. Once we had each individuals mean overlap we took the mean of all individuals at each tract for a mean percent overlap of each individual with every other individual. We included all individuals that had at least 15 points and did not move between tracts.

We sexed and aged longspurs by plumage, looking at feather wear in the inner primary coverts and outer rectrices (Pyle 1997). Because our field season overlapped with January 1st, we aged birds not into hatch-year/second-year (HY/SY) or after hatch-year/after second-year (AHY/ASY) but as first winter (FW) or after first winter (AFW) (i.e., at least its second winter).

We conducted a Fisher's Exact Test in program r to test whether the sex ratios were different than 1:1.

## Results

We captured and banded 55 and 61 longspurs in our first and second field seasons, of which we radio-tagged and attempted to track 44 and 46 individuals, respectively (Table 1). We recorded a total of 1,976 telemetry locations across the two years (825 in 2018-19 and 1,151 in 2019-20). Nine of the radios (11% of those deployed) fell off before we were able to relocate them enough times for analysis. We found 2 blood-stained, damaged harnesses with feathers attached, that were under small shrubs suggesting small aerial predator (although we cannot be certain) while another two radio transmitters directly tracked the movements of a Northern Harrier (*Circus hudsonius*) in a way that indicated these birds as longspur predators. Hence, a minimum of 4.9% of the tagged longspurs were depredated across the two years. Forty-six of the 90 transmitters deployed (51%) ceased transmission within 30 days either because of predation, emigration from the study areas, or radio malfunction. Thirty birds that were tracked had at least 30 points collected, and we were able us to conduct a KDE analysis. We were also able to track 12 birds (14.8%) that moved over 5 km, including one bird that moved three times over 5 km and visited and stayed at all three focused grassland tracts we monitored. Twenty birds (22%) stayed at their banding location either until the radio's battery died, the harness failed and fell off, or the field season ended. All of the movements that exceeded 5 km involved a bird emigrating from the VC tract to either the HQ or MT, except for one individual which dispersed from the VC to spend 2 days in the MT and then moved again to spend 10 days in the HQ, but eventually resettled back in the VC.

Table 1. Sex and age ratio of Chestnut-collared Longspurs captured at the Wichita Mountains Wildlife Refuge during the two winters of the study period. * denotes significant difference p>0.001. We did not test for significance difference in age as we do not know what the expected ratio should be.

| | 2018-19 | 2019-20 |
|---|---|---|
| M/F | 42/13* | 48/13* |
| AFW/FW | 37/18 | 43/18 |
| n Captured/tracked | 55/44 | 61/46 |
| Early Radio fall | 4 | 4 |
| Late Radio fall | 0 | 2 |
| >15 Locations | 27 | 24 |
| >30 Locations | 14 | 16 |
| Depredated | 2 | 2 |
| Moved >5km | 10 | 2 |
| Stationary | 13 | 7 |
| Unknown Fate | 15 | 31 |

**Home Range Estimates and Age/ Sex Ratios**

We captured 116 individual longspurs across both years with significantly more males than females ($P$<0.001) both years, we also captured more AFW than FW longspurs (Table 1). We did not recapture any birds between years. We collected at least fifteen-point locations for a total

of 51 longspurs (24 in year 1 and 27 in year 2). Their MCP home ranges varied widely from 5.7 to 1,783.5 ha, with a mean of 128.8 ha (SD = 291.9). A linear regression of the number of points collected versus the MCP area did not indicate a significant relationship ($R^2 = 0.018$; $p = 0.76$). Among the 30 longspurs relocated at least thirty times the sex-ratio was male-biased (9F:21M) and the age-ratio skewed toward older birds (6 FW:24 AFW). The 95% KDE across all longspurs indicated a mean area of 29.87 ha (range = 1.15 to 101.58; SD = 22.49) while the mean area of the "core" 50% KDE was 5.3 ha (range = 0.02 - 20.73; SD = 4.31) (Table 2). We found no significant differences in either MCP, 50% KD, or 95% KD between sexes or ages in either year or between years.

Table 3. Mean percent overlap for individual longspurs at the three focus grassland tracts across both years of the study. The locations are Visitor center (VC), Meers Turnoff (MT) and Headquarters (HQ) and n is the number of individuals with enough points for analysis.

| YEAR | LOCATION | AVERAGE OVERLAP | SD | n |
|---|---|---|---|---|
| 1 | VC | 51.70% | 15.30 | 8 |
| 2 | | 61.90% | 13.90 | 8 |
| 1 | Meers | 43.00% | 18.20 | 10 |
| 2 | | 33.40% | 14.30 | 14 |
| 1 | HQ | 78.80% | 20.70 | 5 |
| **2** | | 48.00% | 12.20 | 5 |

**Home Range Overlap**

There were high levels of overlap between individuals at all three major grassland tracts. The HQ tract had the highest degree of overlap with 78.8% and 48%, and MT had the lowest with 43% and 33.4% in year 1 and 2 respectively (Table 3).

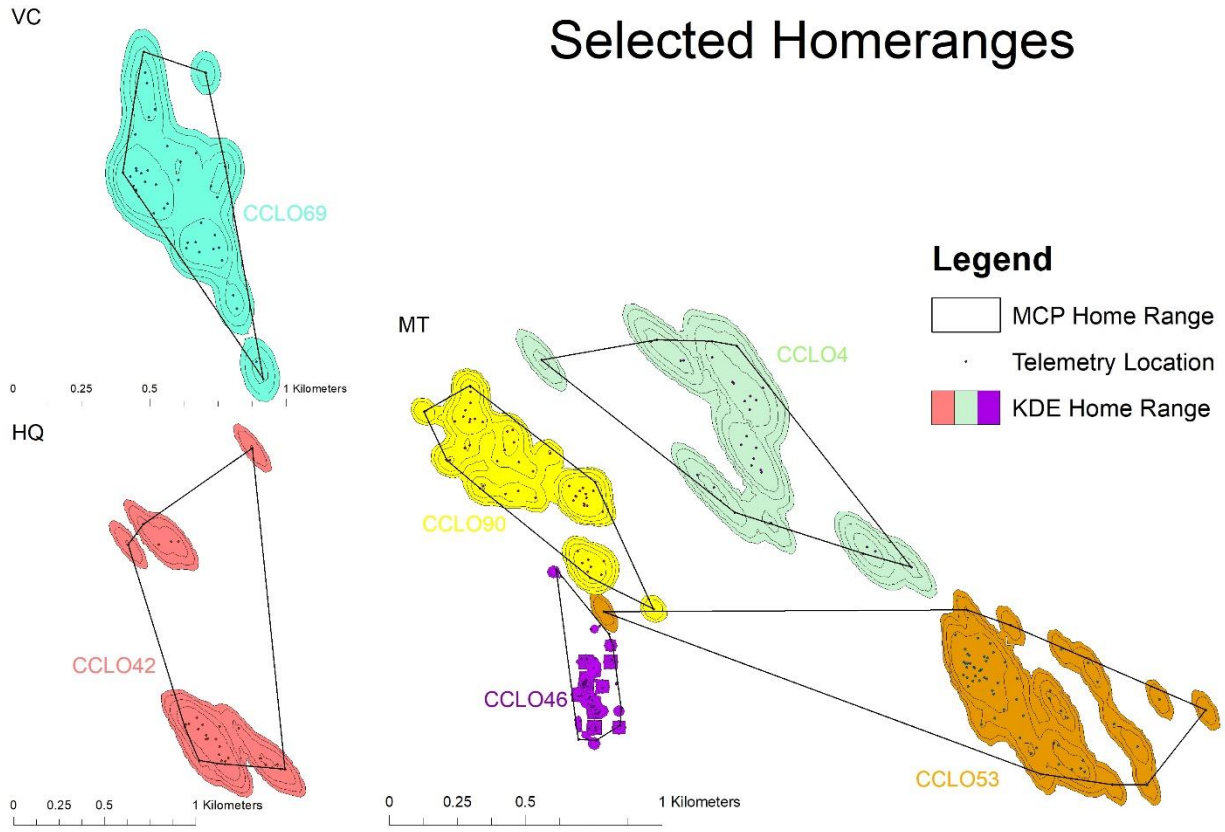


Figure 5~~2~~. Six of the 30 home ranges with >30 points including four individuals at Meers Turnoff (MT), one at each of Visitor Center (VC) and Headquarters (HQ). Isopleths are 50%, 75%, 90% and 95% although only 50% and 95% are reported.

## Discussion

Longspurs use more space than other members of their grassland assemblage during winter (Table 2). We found that longspur winter home ranges were almost three times the size of Sprague's Pipit (*Anthus spragueii*), over three times the size of Savannah Sparrow (*Passerculus sandwichensis*) and roughly 5-6 times larger than Baird's and Grasshopper Sparrow (*Ammodramus bairdii, A. savannarum*) (Table 2). Along with relatively large home ranges, 51% of the birds we tracked moved out of the study area before we were able to get a sufficient number of points for analysis, and roughly 15% of the birds were confirmed to move > 5km. Because of these confirmed long distance movements, we believe many of the longspurs that we

were unable to track for a sufficient amount of time moved out of our study area, leading us to believe that our mean home range estimates are smaller than the true home range size. This increased space use is likely due to differences in sociality. Sprague's Pipit and most grassland sparrows typically do not flock during winter and, even if they do, they occur in only loosely formed and temporary groups. All species of longspur on the other hand flock during winter, and we routinely observed longspur flocks of >100 individuals. Consumable resources, such as seeds, are depleted faster when a flock is present because of the increased density, and because resources are being depleted faster, the flock will have to range widely for its members to meet their needs.

As expected, due to their social behavior longspur home ranges overlapped to a high degree with some areas up to 78.8% average overlap between individuals (Table 3). In territorial species home range is inversely proportional to population density (Efford et al. 2016). But in flocking species where there is minimal to no territoriality this increased overlap should lead to an increase in home range size due to faster depletion of resources from increased density of individuals. WMWR has a relatively high density of longspurs averaging 371 birds/km$^2$ over the two winters of the study according to our distance sampling effort (unpublished data). In New Mexico at Sevilleta National Wildlife Refuge, Kelly et al. 2006, had less than 100 birds/km$^2$. Across the Chihuahuan Desert Grasslands there was an average density of 143.2 birds/km$^2$ with some sites containing as high as 807.5 birds/km$^2$, and others with 0 birds/km$^2$ (Pool et al. 2012, Macías-Duarte et al. 2018). But without home range analyses across the species winter range we cannot determine if the relatively high density of longspurs at WMWR has an effect on average longspur home range size. Research on relative population density and home range sizes of non-

territorial flocking species would be an interesting and important topic for future studies to explore.

Table 2. Comparison of Chestnut-collared Longspur home ranges to that of other migratory passerine winter grassland birds, in the southern Great Plains or Chihuahuan grasslands using (Least Squares Cross Validation).

| Species | 95% KDE in ha (Range) | Location | Source |
|---|---|---|---|
| Chestnut-collared Longspur | 29.87 (1.15-101.58) | Southern Oklahoma | |
| Sprague's Pipit (*Anthus spragueii*) | 11.4 (6.6-22.9) | Northern Mexico | Strasser and Ruvalcaba-Ortega 2019 |
| Savannah Sparrow (*Passerculus sandwichensis*) | 9.1 (0.2-31.7) | South Texas | Ginter and Desmond 2005 |
| Baird's Sparrow (*Ammodramus bairdii*) | 6.58 (0.9-54.91) | West Texas | Perez-Ordonez 2019 |
| Grasshopper Sparrow *(Ammodramus savannarum*) | 4.74 (0.8-26.84) | West Texas | Perez-Ordonez 2019 |

Along with home range size, grassland birds in arid environments tend to show some level of nomadism, with some species showing higher levels of wandering than others (Gordon 2000). Nomadism can exist as both inter and intraseasonal movements (Davies 1984), driven by

the tendency of grasslands and arid environments to be boom/bust ecosystems depending on the vagaries of seasonal rainfall patterns (Macías-Duarte et al. 2018). We did not recapture any marked longspurs returning between years, suggesting a low level of site fidelity. Even so, our density sampling estimates for the WMWR population shows roughly 20,000 longspurs during the winter of 2019-20 (unpublished data). The 55 birds marked in the first year would have represented less than a 3% chance of randomly recapturing any individuals in the second year, even if we assume very unlikely annual survival and return rates of 100%. Either a much higher level of effort or a much more efficient capture method (e.g., solar-powered >1 year transmitters, <2.0 g GPS units, wide scale comprehensive motus network) is needed to fully discern the site fidelity on the wintering grounds.

Understanding space use and movement patterns provides important information for determining the scale at which management of habitat should happen (Fauvelle et al. 2017). The apparent transience or intraseasonal nomadism of longspurs presents several challenges for management of the species. MCPs averaged 128.8 ha (with one individual using 1,783.5 ha), while the estimate for home range core size (50% KDE) was 5.3 ha. Therefore, even though birds were typically found within a few hectares, individuals moved throughout many times larger areas throughout the season. By confirming that certain individuals move throughout the area we found that management, even for the individual, requires a landscape-level approach. The WMWR appears to be high-quality habitat given that the species was common in the large grassland tracts and many tracked individuals moved relatively long distances but still remained within the refuge. Many individuals with undetermined fates may have moved similar distances onto suitable grassland tracts on adjacent private properties or the Fort Sill military base. This underscores the importance of management of wintering longspurs at scales larger than a few

acres, and the need for landscape scale management approaches that incorporate multiple stakeholders including public lands, private landowners, governments and NGO's such as those described in Drum et al. 2015. Effective management of the species, even at the site level, is going to require adjacent landowners and properties to work together. Habitat fragmentation is believed to be a major driver in the downward population trends of many grassland birds (Koper and Schmiegelow 2006, Winter et al. 2006, Haddad et al. 2015, Wimberly et al. 2018). This fragmentation complicates the management of species such as longspurs, as unfragmented landscapes are rare.

Out of the 90 tracked longspurs, 4 were confirmed to be depredated either by finding a bloody harness/transmitter or by observing signals of the radio coming from predators. We observed 4 species of aerial predator attempting to capture longspurs including American Kestrel (*Falco sparverius*), Merlin (*F. columbarius*), Cooper's Hawk (*Accipiter cooperii*), and Northern Harrier. We also have anecdotal evidence that longspurs move more during extreme weather events. During the study, we had several snowfall events (>5 cm), and the day after each of these events we "lost" several individuals that we had been following the day before the snow event.

The limitations of traditional radio-telemetry (e.g. short battery lifespan, required line-of-sight for detection, and that the researcher has to be within a detectable distance to the object being tracked) restrict our ability to track potential long distance movements, or movements between seasons. A targeted Motus style network throughout the southern plains would allow researchers to answer many remaining and newly discovered questions about wintering grassland bird ecology, including whether or not the individuals that are tagged and immediately leave the study area were still migrating, settled somewhere else, perished, or continued to move throughout the winter. It would also allow researchers to see if weather affected bird movements,

(e.g. did longspurs move further south when weather got bad), and to test winter site fidelity during and between years.

We observed a sex ratio favoring males over females of roughly 3:1 across both years. We do not believe that our capture methodology was biased towards males, which leads us to assume that our sample reflected the sex ratio of the study population. The observed sex-ratio may be due to the fact that our study area lies within the northern portion of the wintering range. In similar species of migratory birds males tend to winter in more northerly locations than females (Ketterson and Nolan 1976, 1979, Macdonald et al. 2016), and this geographical sex deviation may result from increased selective pressure on males to migrate to breeding sites early in the spring to compete for breeding territories, a sort of protandry (Ketterson and Nolan 1976, Møller 1994, Lozano et al. 1996, Cristol et al. 1999). There is evidence for this explanation in Sutton (1967), wherein males were observed leaving the wintering grounds earlier than females in Oklahoma. A corollary explanation is that males are larger than females (Pyle 1997), which may render them more cold-tolerant and therefore better suited to the northern portion of the wintering range. Of course, future studies from a larger portion of the longspur wintering range will need to be sampled before we can establish with certainty that there is a geographical bias on the wintering grounds.

Grassland birds are declining fastest of any bird assemblage in North America (Rosenberg et al. 2019). Wintering grounds for Grassland specialists have been strongly associated with downward population trends (Correll et al. 2019). Therefore, identifying factors affecting longspurs on the wintering grounds can be crucial for management and conservation of these species. But, grassland conservation is challenging because 85% of remaining grasslands are on private lands (NABCI U.S. Committee 2013, Drum et al. 2015, Olimb and Robinson

2019). Public lands such as those at the Wichita Mountains are crucial wintering sites for the species and other public sites that host large populations should be identified and protected. Due to climate change predictions, western grasslands will move further north within the coming decades (Wilsey et al. 2019), this means that sites such as the Wichita Mountains, which are currently along the Northern edge of the species winter distribution, may become a more valuable wintering area for the conservation of the species, if not crucial already.

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Appendix 1. Table showing data for the 90 individual CCLO including the sex (Male (M) and Female (F)), age (First Winter (FW) and After First Winter (AFW)), number of GPS locations, home range estimates as Minimum Convex Polygons (MCP), and Kernel Density Estimates (KDE), date banded, location (Visitor center (VC), Meers Turnoff (MT) and Headquarters (HQ)) and number of confirmed days on the bird.

| Id | Sex | Age | Locations | Area MCP | 50% KD | 95% KD | Date Banded | Location | Time On (days) |
|---|---|---|---|---|---|---|---|---|---|
| 1 | M | AFW | 4 | | | | 12/2/2018 | VC | 3 |
| 2 | F | FW | 1 | | | | 12/2/2018 | VC | 1 |
| 3 | M | FW | 2 | | | | 12/3/2018 | VC | 1 |
| 4 | M | AFW | 30 | 43.49 | 7.8 | 35.36 | 12/5/2018 | MT | 66 |
| 5 | M | AFW | 41 | 74.66 | 1.14 | 9.96 | 12/5/2018 | MT | 71 |
| 6 | F | AFW | 54 | 35.7 | 3.94 | 25 | 12/6/2018 | VC | 56 |
| 10 | M | AFW | 33 | 179.5 | 1.07 | 8.69 | 12/15/2018 | VC | 37 |
| 7 | M | FW | 8 | | | | 12/15/2018 | VC | 26 |
| 8 | M | AFW | 11 | | | | 12/15/2018 | VC | 9 |
| 9 | M | AFW | 16 | 15.26 | | | 12/15/2018 | VC | 17 |
| 11 | M | FW | 11 | | | | 12/17/2018 | VC | 10 |
| 12 | F | FW | 25 | 16.83 | | | 12/17/2018 | VC | 18 |
| 13 | M | AFW | 3 | | | | 12/17/2018 | VC | 15 |
| 14 | M | AFW | 51 | 890.5 | 9.97 | 62.68 | 12/17/2018 | VC | 71 |
| 15 | F | AFW | 4 | | | | 12/17/2018 | VC | 4 |
| 16 | M | AFW | 20 | 5.7 | | | 12/17/2018 | VC | 19 |
| 17 | M | AFW | 14 | 14.32 | | | 12/17/2018 | VC | 18 |
| 18 | M | FW | 2 | | | | 12/17/2018 | VC | 1 |
| 19 | M | AFW | 40 | 571.7 | 11.42 | 54.16 | 1/4/2019 | VC | 56 |
| 20 | M | AFW | 30 | 1783 | 20.73 | 101.6 | 1/4/2019 | VC | 48 |
| 21 | M | AFW | 32 | 87.21 | 7.66 | 43.51 | 1/5/2019 | MT | 63 |
| 22 | M | AFW | 13 | | | | 1/5/2019 | MT | 48 |
| 23 | M | AFW | 1 | | | | 1/5/2019 | MT | 1 |
| 24 | F | AFW | 9 | | | | 1/5/2019 | MT | 10 |
| 25 | M | AFW | 3 | | | | 1/5/2019 | MT | 16 |
| 26 | F | AFW | 2 | | | | 1/5/2019 | MT | 5 |
| 27 | F | AFW | 1 | | | | 1/5/2019 | MT | 1 |
| 28 | F | AFW | 25 | 86.34 | | | 1/6/2019 | MT | 53 |
| 29 | M | AFW | 27 | 79.12 | | | 1/13/2019 | MT | 46 |
| 30 | M | FW | 18 | 28.36 | | | 1/13/2019 | MT | 46 |
| 31 | M | AFW | 37 | 37.36 | 5.46 | 28.51 | 1/13/2019 | MT | 54 |
| 32 | F | FW | 35 | 52.03 | 7.61 | 37.02 | 1/13/2019 | MT | 54 |
| 33 | M | AFW | 4 | | | | 1/20/2019 | MT | 7 |
| 34 | M | FW | 11 | | | | 1/20/2019 | MT | 21 |
| 35 | M | AFW | 3 | | | | 1/20/2019 | MT | 3 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 36 | M | AFW | 31 | 17.82 | 5.89 | 27.44 | 1/20/2019 | MT | 39 |
| 37 | M | AFW | 32 | 34.19 | 1.35 | 9.89 | 1/23/2019 | HQ | 44 |
| 38 | M | FW | 32 | 39.44 | 2.56 | 17.71 | 1/23/2019 | HQ | 44 |
| 39 | M | AFW | 26 | 49.05 | | | 1/23/2019 | HQ | 37 |
| 40 | M | FW | 17 | 670 | | | 1/23/2019 | HQ | 21 |
| 41 | M | AFW | 10 | | | | 1/23/2019 | HQ | 16 |
| 42 | M | AFW | 31 | 78.13 | 5.23 | 30.7 | 1/23/2019 | HQ | 37 |
| 43 | F | AFW | 23 | 33.83 | | | 1/31/2019 | MT | 36 |
| 44 | F | AFW | 2 | | | | 1/31/2019 | MT | 2 |
| 45 | F | AFW | 30 | 74.64 | 8.97 | 41.82 | 12/8/2019 | MT | 24 |
| 46 | M | AFW | 53 | 8.24 | 0.2 | 3.69 | 12/8/2019 | MT | 48 |
| 47 | F | FW | 2 | | | | 12/10/2019 | MT | 2 |
| 48 | F | AFW | 14 | | | | 12/10/2019 | MT | 8 |
| 49 | M | AFW | 4 | | | | 12/10/2019 | MT | 4 |
| 50 | M | FW | 24 | 32.84 | | | 12/10/2019 | MT | 29 |
| 51 | F | AFW | 50 | 31.14 | 3.39 | 25.86 | 12/10/2019 | MT | 36 |
| 52 | F | FW | 64 | 72.86 | 0.68 | 7.59 | 12/10/2019 | MT | 47 |
| 53 | F | AFW | 65 | 67.88 | 5.44 | 31.74 | 12/10/2019 | MT | 51 |
| 54 | M | AFW | 18 | 20.83 | | | 12/11/2019 | VC | 12 |
| 55 | M | AFW | 6 | | | | 12/11/2019 | VC | 5 |
| 56 | M | AFW | 5 | | | | 12/14/2019 | MT | 4 |
| 57 | M | FW | 11 | | | | 12/14/2019 | MT | 8 |
| 58 | M | AFW | 16 | 16.35 | | | 12/14/2019 | MT | 16 |
| 59 | M | AFW | 25 | 16.05 | | | 12/14/2019 | MT | 14 |
| 60 | M | FW | 28 | 33.66 | | | 12/18/2019 | VC | 16 |
| 62 | M | FW | 25 | 20.9 | | | 12/18/2019 | VC | 25 |
| 63 | M | AFW | 19 | 36.97 | | | 12/18/2019 | VC | 11 |
| 64 | M | AFW | 38 | 537.8 | 10.6 | 88.67 | 12/18/2019 | VC | 48 |
| 65 | M | FW | 10 | | | | 12/18/2019 | VC | 13 |
| 66 | M | FW | 10 | | | | 12/18/2019 | VC | 12 |
| 67 | M | AFW | 8 | | | | 12/18/2019 | VC | 13 |
| 68 | M | AFW | 17 | 28.26 | | | 12/18/2019 | VC | 14 |
| 69 | M | AFW | 44 | 26.69 | 8.22 | 33.44 | 12/18/2019 | VC | 51 |
| 70 | M | AFW | 11 | | | | 12/22/2019 | VC | 7 |
| 71 | M | AFW | 13 | | | | 12/22/2019 | VC | 12 |
| 72 | M | AFW | 28 | 27.15 | | | 12/22/2019 | VC | 20 |
| 73 | M | FW | 31 | 46.77 | 5.99 | 32.25 | 12/24/2019 | HQ | 36 |
| 74 | F | AFW | 43 | 84.09 | 3.7 | 22.13 | 12/24/2019 | HQ | 36 |
| 75 | F | AFW | 8 | | | | 12/24/2019 | HQ | 7 |
| 76 | M | AFW | 11 | | | | 12/24/2019 | HQ | 13 |
| 77 | M | FW | 35 | 131.5 | 1.1 | 15.58 | 12/24/2019 | HQ | 31 |
| 78 | M | FW | 39 | 122.5 | 3.86 | 22.94 | 12/24/2019 | HQ | 45 |
| 79 | F | AFW | 5 | | | | 1/11/2020 | MT | 14 |

| | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| 80 | F | AFW | 65 | 20.31 | 0.09 | 1.55 | 1/11/2020 | MT | 45 |
| 81 | M | AFW | 1 | | | | 1/11/2020 | MT | 1 |
| 82 | M | AFW | 14 | | | | 1/11/2020 | MT | 11 |
| 83 | M | AFW | 44 | 72.42 | 6.8 | 30.57 | 1/12/2020 | HQ | 43 |
| 84 | M | AFW | 12 | | | | 1/12/2020 | HQ | 7 |
| 85 | M | FW | 10 | | | | 1/12/2020 | HQ | 20 |
| 86 | M | AFW | 7 | | | | 1/12/2020 | HQ | 20 |
| 87 | M | FW | 27 | 12.42 | | | 1/14/2020 | MT | 22 |
| 88 | F | AFW | 37 | 33.27 | 1.47 | 11.08 | 1/14/2020 | MT | 22 |
| 89 | M | AFW | 17 | 20.48 | | | 1/19/2020 | MT | 41 |
| 90 | M | AFW | 52 | 23.45 | 5.27 | 23.87 | 1/26/2020 | MT | 34 |
| 91 | M | AFW | 52 | 24.5 | 1.52 | 10.97 | 1/30/2020 | MT | 30 |