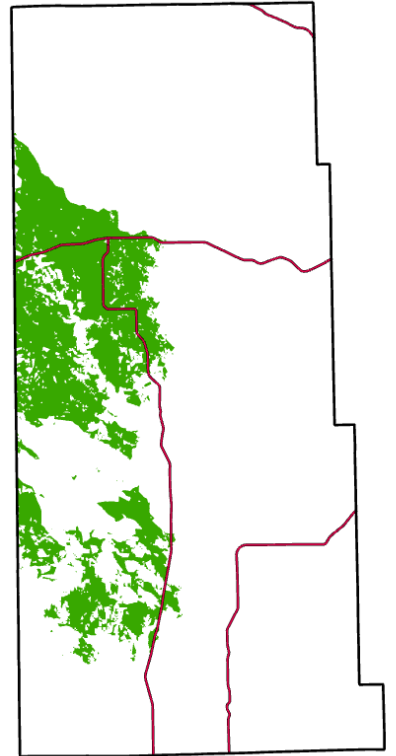


Elevation and soils explain Thick-billed Longspur's breeding distribution in northwestern Nebraska



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Identifying environmental variables associated with a species distribution is fundamental in ecology (Gaston 2003). Once relationships are identified and defined, the availability of modern spatial data provides the opportunity to display a species' distribution through statistical modeling. Species distribution models are useful tools that make linkages between an animal's distribution and the physical environment (Elith and Leathwick 2009). For rare, threatened, or endangered species, distribution models can aid conservation by identifying areas that should be prioritized for surveys, targeted conservation actions or both (Wang et al. 2015).

Grassland birds in the North American Great Plains occupy regions in which environmental gradients change gradually. Changes in habitats may not be as readily perceptible to humans as in other areas where environmental gradients are steep (e.g. mountains) or where there are abrupt changes in vegetation structure (e.g., trees transition to grassland in a savannah mosaic; Banko et al. 2002, Duclos et al. 2019). This fact can make delineating the extent or edges of ranges challenging. Grassland bird distributions are also known to be influenced by weather, climate (Thogmartin et al. 2006, Wilson et al. 2018) and disturbance (e.g., fire, grazing; Fuhlendorf et al. 2006), but these factors vary temporally and require real-time measurements to be used in analyses. Thus, identifying static environmental variables that influence species' distribution may be useful initial step before assessing additional variables whose condition may be transitory and require in-field measurement.

Elevation, slope, and soils are static variables known to be associated with species' distributions (Gaston 2003). Relationships between elevation and avian species' distribution have been established by various studies (e.g., Chamberlain et al. 2016, Lele et al. 2020) and such relationships may be associated with aspects such as species' physiology (Williamson and Witt 2021) or reduction in competition with other species (Terborgh 1985, Freeman et al. 2022). However, elevation is generally more influential or noticeable in cases where the gradient is steep (McCain 2009). Elevation has generally not been used or is not useful in identifying species' distributions of grassland birds in the Great Plains. Elevation gradients in the Great Plains are associated with changes in climate, which in turn influences vegetation (Cook and Irwin 1992, Allred et al. 2011). Thus, the role of elevation in shaping grassland communities and species' distribution may be underexplored relative to other ecosystems. Similarly, species distributions are also known to be associated with soil types (McConnell et al. 2009, Duchardt et al. 2018, Davis et al. 2020), and such relationships may be a consequence of edaphic changes to vegetation (Vander Wall and MacMahon 1984). As elevation and soil can greatly influence vegetative structure, these factors may be important variables associated with grassland bird distribution within the Great Plains.

Here, we use an existing avian monitoring dataset to determine whether the breeding distribution of one grassland species is associated with soil type and elevation at the edge of its range. The Thick-billed Longspur (*Rhynchophanes mccownii*; TBLO) is a grassland bird species endemic to the North American Great Plains that has declined by as much as 94% (PIF 2016). This species breeds in mixed- to shortgrass prairies extending from eastern Colorado north to southern Canada and winters from western Oklahoma to northern Mexico (With 2021). In 2020, The Nebraska Game and Parks Commission listed the species as threatened under auspices of the Nebraska Nongame and Endangered Species Conservation Act (§37-801-11). This change in status has placed a greater emphasis on refining the known breeding distribution of the species in the state. An improved understanding of this species distribution is needed to maximize the effectiveness of conservation investments directed toward the species by identifying areas of importance, as TBLO and other grassland species are also closely tied to

areas dominated by livestock. A refined distribution map coupled with key environmental drivers is needed to guide landowner outreach and potentially grazing management in the focal areas.

Methods

Study Area

In Nebraska, TBLOs breed primarily in two areas in the western panhandle, in the southwest corner, primarily Kimball County, and in central and southern Sioux Co in the northern panhandle (Silcock and Jorgensen 2022). Our study area is Sioux County which includes a large portion of the species' breeding range and is dominated by mixed- and short-grass rangeland (Fig. 1). Sioux County totals 536,158 ha, but portions of the county include rocky escarpments dominated by Ponderosa Pine forest (the western extent of the Pine Ridge region of Nebraska; Condra 1906), as well as irrigated areas of row-crop agriculture, primarily concentrated in the southern portion of the county. TBLOs were first known to breed in Sioux County since around the turn of the 20th Century (Bruner et al. 1904) and it has been considered a common migrant and a locally common breeder in the western Nebraska Panhandle since (Sharpe et al. 2001, Silcock and Jorgensen 2022).

TBLO Surveys

We used survey data from two sources. The first data set was from an ongoing grassland monitoring program coordinated by Playa Lakes Joint Venture (PLJV) in western Nebraska which uses the Integrated Monitoring in Bird Conservation Regions (IMBCR) implemented by Bird Conservancy of the Rockies. IMBCR uses an overall sampling frame divided into a 1 km × 1 km grid and 1-km² sampling units are selected within each stratum using generalized random tessellation stratified (GRTS) sampling (BCR 2021). Trained observers recorded all birds detected and estimate detection distances during 6 min point transect surveys. Only TBLO detections were used in this study. All surveys were conducted 7 May – 7 July, during the peak of Thick-billed Longspur breeding season.

The second dataset is from targeted TBLO surveys conducted during the breeding season of 2022. While the duration (6 mins), spatial limit (detections within 125m), and detection methods (aural and visual) were similar to the IMBCR framework, these counts were not placed within larger grids and were limited to road-based surveys. Counts were spaced by at least 250 meters and exclusively targeted short to mixed grassland habitats within Sioux county in areas not covered in the 2020 or 2021 PLJV surveys.

Data filtering

Data from the PLJV was available from 2020 and 2021, and data collection from the targeted TBLO monitoring took place in 2022. It has been suggested that TBLO moves eastward during dry years in the state (Rosche 1982), which could alter the distribution of the species in years with atypical precipitation. Rainfall totals at Agate, NE from April – June average 17 cm and was 11.4 cm in 2020, 8.4 cm in 2021 and 12.9 cm in 2022. Point counts located in habitats (wetlands or ponderosa pine forest) not used by the Thick-billed Longspur were excluded from analysis, as these would not be considered possible TBLO breeding locations. Counts conducted outside of the study area (Sioux county) were also eliminated regardless of habitat.

Multiple Modeling Approaches

We used two types of modeling frameworks to examine environmental impacts on longspur occurrence in Nebraska and predict TBLO distribution in Sioux county. The first was a presence-absence design using binomial logistic regression models (hereafter, PA). The second was a removal occupancy design (hereafter, occupancy). This approach accounts for imperfect detection and has been used with similar datasets successfully in multiple other studies (Pavlacky et al. 2017). We did not model within a multi-scale hierarchical framework as in previous studies with IMBCR data (Pavlacky et al. 2012, Pavlacky et al. 2017), as a larger or regional scale in our case was essentially the study area (Sioux county). Thus, there likely would not be enough meaningful variation between different scales in the context of our study. While landscapes can greatly impact species distribution and subsequent habitat selection and breeding success (Johnson 2007, Fahrig 2013, Brenner et al 2019), our study likely would not benefit from this analysis because: 1) TBLO's relatively limited 2nd order habitat requirements (i.e. short-grass prairie), 2) the targeted scope of our surveys (only grassland habitats in Sioux county) and 3) the limited existing information on species distribution within the state.

For the PA approach, we treated the entire 6-minute count as one survey and considered any TBLO detections within this period as an indication of longspur presence and included year as a random effect. For the occupancy approach, the larger 6 min survey was broken in three 2-minute count blocks, with the species considered present once detected during these subsequent blocks per standard removal sampling design (MacKenzie et al. 2006, Pavlacky et al. 2017). To accommodate sparse data and generally low (<70) detections per year, we pooled data from all years and modeled occupancy as a single-season framework across space and included year as a covariate for detection (Linden et al 2013, Fuller et al. 2016). We were primarily concerned with determining the main topographical and edaphic conditions that influence the overall range and distribution of this species in the county and not attempting to determine other dynamic factors related to productivity, annual climatic changes (e.g. precipitation or temperature), or settlement structure.

In both modeling approaches, we included multiple environmental covariates that we believed may be associated with TBLO presence (PA) or occupancy. The covariates tested were elevation, slope, soil type, longitude, topographic ruggedness (TRI) and landcover. We measured percent soil type and landcover within a 125m radius for each point using recent Nebraska land cover dataset (Bishop et al. 2009) and SSurgo soil dataset (NRCS 2022). Slope, elevation and longitude were measured at each point transect. Topographic ruggedness (TRI) has been shown to impact grassland songbird abundance in nearby northeastern Colorado (Davis et al. 2021) and we measured TRI within a 125m radius of each point using the Geomorphometry and Gradient Metrics toolbox (Evans et al. 2014) in ArcGIS (ESRI 2021). Longitude was included because western Nebraska represents the easternmost extent of the entire species' range, and thus we could expect a relationship between the TBLO distribution and this variable. TBLOs have not been recorded east of Sioux or Kimball counties (-103.378° W longitude) during the breeding season (Silcock and Jorgensen, 2022). We included year and longitude as detection covariates in the occupancy modeling approach. All landcover and soil data was analyzed in ArcGIS (ESRI 2021).

Percent landcover covariates were removed from final model consideration for two reasons. The first was that nearly all points had a high percentage (> 93%) of grassland cover within 125m of the point location. This was likely due to the sampling regime which only utilized points that could be considered potential TBLO habitat. Additionally, the next most frequent landcover class was sandsage prairie, which was both strongly correlated with valent soils and a more dynamic vegetation class that has a high potential to shift from year to year if encroachment continues unchecked or vegetation is deliberately

reduced by active management (mechanical removal or intensive grazing). Lastly, we would not expect TBLO to occur in areas of landcover that did not include at least a majority (> 50) percent grassland within the immediate home range of the bird, and thus modeling the impact of grassland cover on the occurrence of a grassland obligate species would likely not advance our understanding of longspur distribution in Sioux county.

We standardized all covariates for modeling and tested all relevant covariates for model selection using an AIC framework. We tested for possible quadratic effects (covariate²) for slope and longitude covariates. We used plausible combinations model selection (Bromaghin et al. 2013) to identify reduced covariate models for TBLO occupancy. Slope was not included in models that also included flat loam (< 9% slope) and valent soils (deep sand with 9-60% slope; NRCS 1998) as covariates, given that the classification of these soil types already included an element of slope. We examined all relevant models with a $\Delta AIC < 3$ and used modeling averaging techniques to determine the most likely coefficient estimates in the best performing models for both the PA and Occurrence modeling framework. We performed goodness-of-fit tests (GOF) on the top models (lowest AIC) using a Hoslem test for the PA framework and Pearson's χ^2 residuals test for the occupancy model. We found no evidence of poor fit or overdispersion for top models in either framework. All statistical testing was done in Program R (R Core Group 2022).

We used the model averaged coefficient values to create two separate TBLO distribution maps for Sioux county using each modeling framework to project the probability of occurrence and occupancy for TBLO in Sioux county. We removed as probable breeding locations all areas within an 800 m buffer of ponderosa pine forest landcover to account for woodland expansion into adjacent grasslands since our landcover dataset was created, as we expect TBLO to avoid mature pine forest edge. We then extracted from each map the highest confidence predictions of occurrence and occupancy (probabilities > 0.60) and measured the total area of these two ranges. We compared area totals to previous estimates of TBLO range generated from primarily landcover data and from previous expert opinion.

Estimate of TBLO numbers

We used distance sampling (Buckland et al. 2001) to estimate TBLO density. Distance sampling provides the ability to produce reliable density estimates when the assumptions of the technique are met (Buckland et al. 2001, Norvell et al. 2003), as is the case with IMBCR data (Bird Conservancy of the Rockies 2021). We included transect/route as a covariate and truncated all TBLO detections > 125 m using the six candidate models suggested by Buckland et al (2001) to determine the model with the best fit. We then calculated overall abundance using the density estimate along with area estimates from our highest confidence range maps.

Results

We used 283 point transect surveys: 133 from 2020, 113 from 2021, and 37 from 2022. We detected TBLOs at 56 point transects (20%). The average elevation we detected TBLO was at 1445m, which was well above the median survey elevation of 1403m (all survey range: 1093 – 1496) and we did not detect any TBLO below 1400m.

Table 1. Highest ranking model (lowest AIC) used in model averaging for TBLO occurrence and occupancy in Sioux county, Nebraska.

Presence-absence models

Model	logLik	AIC	Δ AIC	w_i
elevation+loam +valent+long+long ²	-91.41	197.30	0.00	0.53
Elevation+loam +valent+long+long ² +TRI	-90.76	197.52	0.22	0.47

Occupancy models

Model	logLik	AIC	Δ AIC	w_i
p long + Ψ elevation +loam +valent+long +long ²	-129.35	274.69	0.00	0.40
p long + year + Ψ elevation +loam +valent +long+long ²	-127.40	274.79	0.10	0.38
p long + Ψ elevation +loam +valent+ +long ²	-131.48	276.96	2.27	0.13
p long + year + Ψ elevation +loam +valent +long ²	-129.79	277.57	2.88	0.09

Table 2. Standardized model averaged parameter estimates from top performing models < 3 Δ AIC predicting TBLO occurrence/occupancy in Sioux county, NE. Parameters in bold are significant factors (adj. p value < 0.05) that did not include a value of 0 within confidence interval (90%) .

Presence Absence Framework

Parameter	Estimate	SE	LCL	UCL
Intercept	-2.595	0.960	-4.173	-1.017
Elevation	0.814	0.331	0.267	1.361
Flat loam soil	0.947	0.327	0.332	1.562
Valent soil	-2.408	1.873	-5.501	0.683
Longitude	-2.822	0.729	-4.021	-1.624
Longitude²	-2.068	0.509	-3.046	-1.090
TRI	-0.570	0.903	-2.059	0.918

Occupancy Framework

Parameter	Estimate	SE	LCL	UCL
p Intercept	-1.914	0.319	-2.436	-1.389
p Longitude	-2.053	0.406	-2.72	-1.375
p year 2021	0.263	0.427	-0.114	1.302
p year2022	0.593	0.765	0.043	2.309
Ψ Intercept	-5.112	4.980	-13.553	2.532
Ψ Elevation	9.202	4.350	3.368	15.009
Ψ Flat loam soil	5.388	2.062	1.996	8.782
Ψ Valent soil	-10.438	8.460	-24.885	2.721
Ψ Longitude	-6.235	4.615	-13.817	-1.566
Ψ Longitude²	-7.707	3.741	-13.760	-1.682

The highest-ranked PA model showed flat loam soils and elevation being positively associated with TBLO occurrence. The same model showed valent soils having a negative relationship on TBLO occurrence (Table 1). The highest ranked occupancy model showed flat loam soils and higher elevations as having a positive effect on TBLO occupancy (Table 2). There was also a non-linear effect of longitude in both models, suggesting that presence and occupancy probabilities generally decrease with increasing (eastward) longitude. TBLO occupancy is predicted to be higher in some locations in the center of the county, provided proper soil and elevation, but TBLO occupancy is also predicted to be very low in certain areas along the extreme western border of the state where elevation is low or valent soils dominate. This non-linear effect also suggests a likely longitudinal threshold in the eastern portion of the county where regardless of other environmental factors, the probability of longspur breeding is very low (Table 2, Fig 1-3).

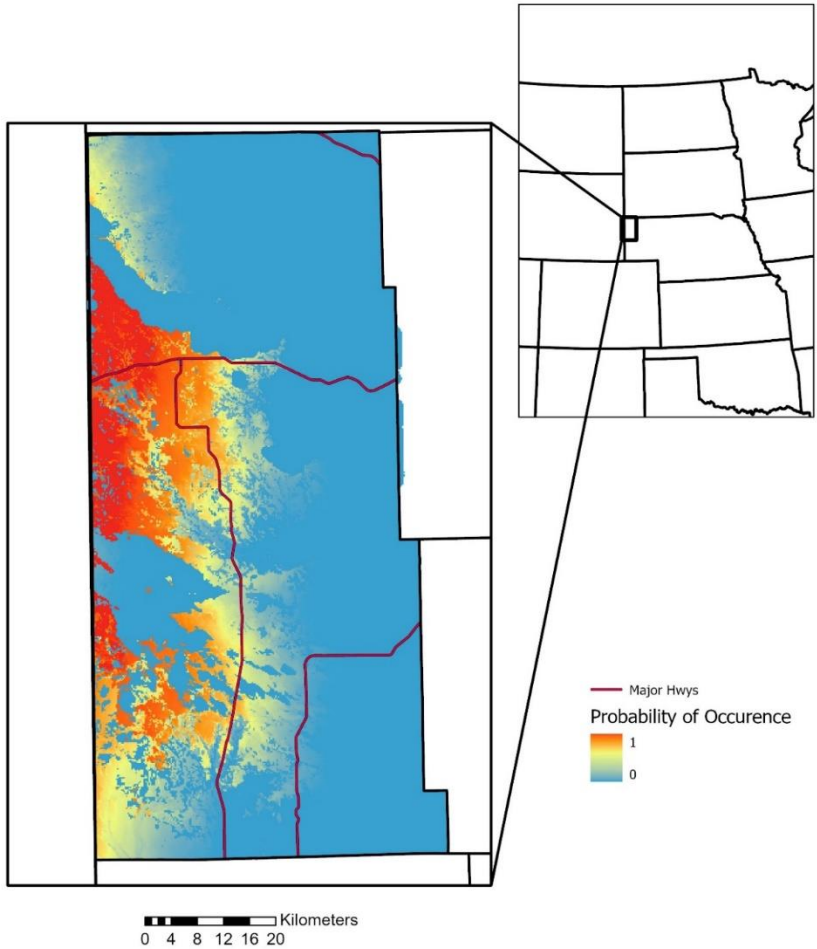


Figure 1. Full range of predicted distribution and probabilities of occurrence derived from presence absence modeling for TBLO in Sioux county, NE. Warmer colors (orange and reds) indicate higher probabilities and cooler colors (blues and yellows) indicate lower probabilities.

The total area of grassland habitat (mixed and short-grass prairie) in Sioux county is 435,676 Hectares. The TBLO breeding range in Sioux County outlined in Silcock and Jorgensen (2022), which is also used by the Nebraska Game and Parks Commission, totals 263,851 ha. Our high-confidence predicted distributions based on elevation, flat loam soil, valent soil complexes, and longitude in Sioux county developed from the occupancy model totals 126,060 Hectares (Fig 2). The predicted distribution from the PA model totals 91,802 ha (Fig 1) and totals 77,747 ha where both high-confidence distributions overlap (Fig 3).

Using the hazard-rate polynomial distance model and total areas from the high confidence distribution map, our estimate for TBLO density is 0.049 (± 0.009 , $cv = 0.18$) individuals/ha. When using this density estimate there is an estimated population size in Sioux county ranging from 4,476 using the PA model (95% LCL – UCL; 3,146 – 6,368) up to 6,144 (95% LCL-UCL; 4,319-8,740) based on the occupancy model. Using the overlapping areas from both model predicted distributions, the estimated population size for TBLO in Sioux county is 3,791 (95% LCL-UCL; 2,665-5393).

Discussion

Our study shows that soil type and elevation are variables associated with the TBLO's large-scale breeding distribution in Sioux Co, Nebraska. These findings are especially valuable as the TBLO is often associated only with native short-grass prairie with bare patches. This habitat can appear relatively uniform across large areas of rangeland in the west, including areas such as Sioux County. Another study (Davis et al. 2020) in nearby Colorado showed a strong relationship between soil type and TBLO abundance. Specifically, higher TBLO densities were found on grassland with loam soils than on grasslands with sandy soils and salt flats under the same grazing regimes (Davis et al. 2020). This finding comports with our result that TBLOs tend to avoid or occur at much lower densities on sandy soils. Large areas of sandy valent soils occur within the previously defined TBLO range in Sioux County (Silcock and Jorgensen 2022), but these areas should not be the focus of TBLO conservation efforts going forward.

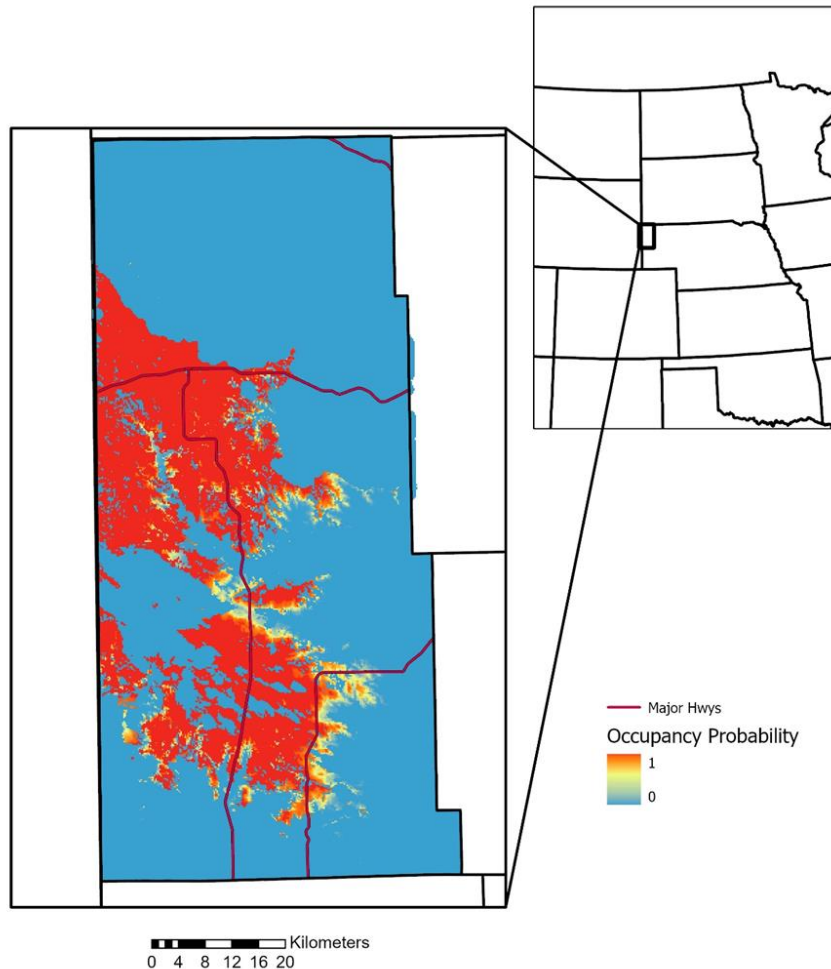


Figure 2. Full range of predicted distribution and probabilities of occupancy derived from occupancy modeling for TBLO in Sioux county, NE. Warmer colors (orange and reds) indicate higher probabilities and cooler colors (blues and yellows) indicate lower probabilities.

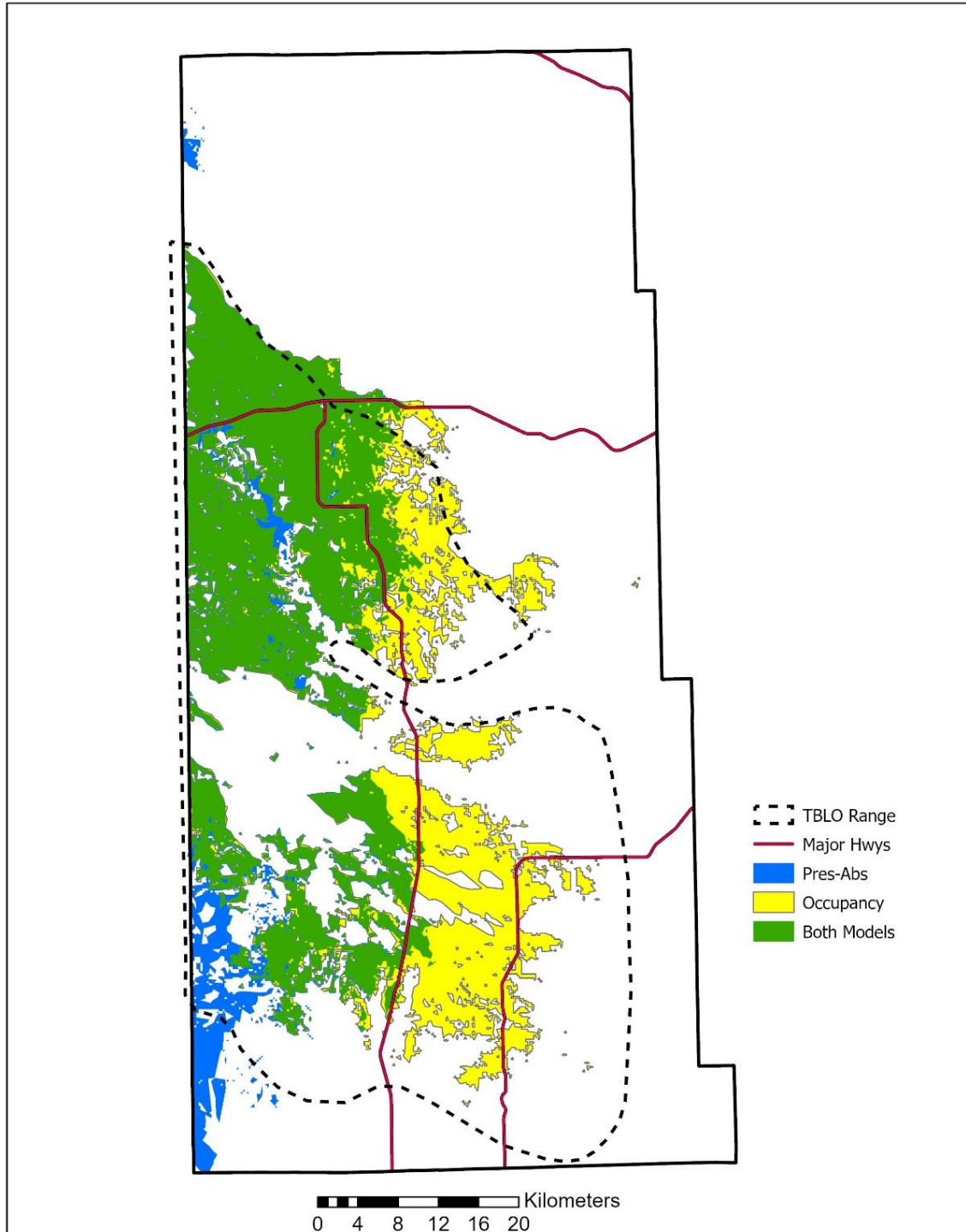


Figure 3. Predicted distribution for TBLO in Sioux county Nebraska based on multiple distribution modeling approaches. Each range (blue = presence-absence design, yellow=occupancy design) includes predicted occurrence/occupancy probabilities over 0.60, indicating highest-confidence from model outputs regardless of framework. Dashed line indicates the predicted range of TBLO in Sioux county based on expert opinion prior to this effort. The green area is where both predictions overlap.

We suspect the species' relationship with elevation is detectable primarily at the periphery of its range. Elevation is associated and interacts with other variables (e.g., climate) to produce environmental conditions which apparently serve as barriers (Gaston 2003) that preclude colonization by TBLOs at lower elevations. Sioux County represents the eastern limit of the TBLO's range and includes shifts and heterogeneity in grassland habitat structure. In this transition zone, edaphic conditions impacted by elevational gradients coupled with climate interactions that occur at higher elevations, likely encourage shorter grasses and bare ground, two essential conditions associated with TBLO breeding habitat (With 2021). It is also possible that grazing pressure increases or increased in the past within higher elevation areas in Sioux county. This would promote short-statured vegetation overall (Hartnett et al. 1996) and potentially encourage the dominance of two warm season grasses, Blue grama (*Bouteloua gracilis*) and Buffalo grass (*Bouteloua dactyloides*), associated with breeding TBLO; Somershoe 2018). Thus, while elevation may not directly influence TBLO habitat selection or territory establishment, high-elevation areas within Sioux county likely possess certain micro-habitat features at the territory scale that ultimately differentiate certain swaths of grassland from other similar and contiguous areas within our limited study area.

The breeding range of TBLO in southwestern Nebraska and the neighboring plains states also indicates some elevational effect on TBLO distribution at the periphery of its range. The only location outside Sioux county where TBLO reliably breed in the state is in the southwestern corner of Kimball County along the border of Colorado and Wyoming. The dominant soils in this area are primarily loam and elevations exceed 1500m across the entire southwestern quarter of the county. However, landcover is far more variable and fragmented, including high proportions of row-crop agriculture. TBLO in this area are known to nest in atypical habitat such as fallow winter wheat fields (Snyder and Bly 2009), but still occupy high elevation areas with loam soils and are generally not found at lower elevation sites to the north and east. In other plains states, elevations of grasslands in western North Dakota do not exceed 1000m, and outside of the forested Black Hills, western South Dakota grasslands range from 1000 – 1200m in elevation, and TBLO are extremely rare breeders in both of these states (Tallman et al. 2002, With 2021). This reinforces the notion that elevation serves as a proxy for some shift in environmental factors that attract and/or limit TBLO near the transitional zone of grasslands in the western US, but additional interactions of potential interspecific competition or community structure has yet to be explored for this species as it relates to elevation (Boyce et al 2019, Burner et al 2020).

This is also important given the limited range of the species and its threatened conservation status within the state of Nebraska, with the majority of the population confined to Sioux county grasslands. At smaller scales, vegetation structure within an individual bird's territory will provide valuable information related to species occurrence/occupancy as well as overall fitness within the region (Chalfoun and Martin 2007, Mahoney and Chalfoun 2016, Davis et al. 2021). However, considering these factors for TBLO in Sioux county would be considered a logical next-step after establishing the likely range limit, as predicting a broad range map-type distribution from these features is not available given the environmental variables at play (e.g. nest cover, distance to shrubs, percent bare ground within a territory) and are difficult to measure and map using larger scale ($\geq 50 \text{ m}^2$) digitized land cover datasets (Davis et al. 2021). Additionally, annual climatic and grazing factors during both current and previous years have been known to influence TBLO settlement and abundance in other parts of their range (Somershoe et al. 2018, Davis et al. 2020, Davis et al. 2021), and it has been suggested that this also influences the annual eastward extent of the species in Nebraska specifically (Rosche 1982, Silcock and

Jorgensen 2022). Thus, we consider the distribution maps generated from this work to be a solid foundation establishing the overall regular distribution of TBLO in Sioux county, with the ability to refine our understanding of what other factors at different scales might also impact TBLO distribution, abundance, and survival in Nebraska. Likewise, our abundance estimates represent a quantifiable starting point for further work, as our model structure was relatively simple and we did not account for temporal or spatial dynamics in immigration, emigration, or any demographic (i.e. sex bias) parameter. We expect this estimate to change as more information is acquired.

All predicted maps conform to a few general patterns: 1) TBLO are not likely to occur in the low elevation grasslands in the northern third of the county or any area with major valent soil complexes, regardless of landcover, longitude, or elevation. 2) predicted occupancy/occurrence is highest in the west-central area of the county south of the pine ridge. This region is characterized by relatively high elevation (> 1450m) and dominated by flat, loam soils. We expect a more 'optimistic' (i.e. larger distribution with higher probabilities) map generated from an occupancy framework because it assumes imperfect detection. Additionally, a few parameter estimates in this model, namely valent soil, had high variation and large values (> 10, -10) for an occupancy framework, likely do to the limited detections of TBLO in any area dominated by sandy soils and inclusion of a polynomial effect (longitude) in a model with limited detections. By contrast the PA design, while still informative, assume ostensibly that the target species will be detected if it is indeed present and would assume less variation overall. It is likely that the 'true' or 'most-reliable' range of TBLO in Sioux county is somewhere in-between these two predictions, with additional but likely limited and low-density occurrences within the ranges defined by previous expert-opinion and other sources. Our final range maps based on highest-confidence distributions estimates the overall breeding range for TBLO in Sioux county between 77,747 – 126,060 hectares (777 – 1,260 km²). This reduces the likely generalized TBLO breeding range based solely on suitable available grasslands by 71 - 82% and reduces the generalized TBLO breeding range map by Silcock and Jorgensen (2022) by 52 – 70%. Our results will aid in focusing future conservation actions where they have the most potential to be successful.

Our results provide a starting point where future research can now be more efficient by targeting areas more likely to be occupied by TBLOs. In addition, our results can also be used by agencies and developers interested in minimizing impacts of energy development in the region by avoiding those areas most likely to be occupied by breeding TBLOs. The same approach could be also used for potential management actions in the county. This could include recommending a particular grazing treatment intended to benefit TBLO on a pasture within the boundaries of the high-confidence map, whereas different regimes or land-management actions (i.e. burns, pasture rests, or other plantings) could be pursued in grasslands within the county that are in the low probability of the predicted distribution.

This study also reinforces the value of standardized and regional monitoring efforts when applied to a focal conservation species or suite of species. Data were collected and analyzed across multiple partner organizations, demonstrating the value of regional collaborations particularly in under-studied regions such as the western Nebraska grasslands. We were able to use these data to find large scale soil and topographic associations of TBLO in Sioux county, which allowed us to then establish a refined distribution map for an at-risk species. Accurately mapping species' distributions is typically one of the first steps in any long-term approach for avian conservation strategies and can be used to develop and explore TBLO dynamics at different scales in this region. Clarifying and defining range extents and large-scale habitat associations becomes particularly important when considering at-risk species in areas that

are in atypical or periphery regions. The dynamics of populations at the boundaries of a species' range can often identify potential threats to the species and add novel context to the behaviors of any species once outside of well-studied and high-density locations. This study along with additional TBLO research in Nebraska stemming from this work will add important information about TBLO distribution and conservation going forward.

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