

Detecting Ecological Traps in Human-Altered Landscapes: A Case Study of the Thick-billed Longspur Nesting in Croplands

Amber Swicegood¹, Kevin Ellison², Marisa Sather³, Scott Somershoe⁴, and Lance McNew¹

¹Montana State University

²American Bird Conservancy

³US Fish and Wildlife Service

⁴US Fish and Wildlife Service Mountain-Prairie Region

November 21, 2022

Abstract

Conversion of the North American prairies to cropland remains a prominent threat to grassland bird populations. Yet, a few species nest in these vastly modified systems. The thick-billed longspur (*Rhynchophanes mccownii*) is an obligate grassland bird whose populations have declined 4% annually during the past 50 years. Thick-billed longspurs historically nested in recently disturbed or sparsely vegetated patches within native mixed-grass prairie, but observations of longspurs in crop fields during the breeding season suggest such fields also provide cues for habitat selection. Maladaptive selection for poor quality habitat may contribute to ongoing declines in longspur populations, but information on thick-billed longspur breeding ecology in crop fields is lacking. We hypothesized that crop fields may function as ecological traps; specifically, we expected that crop fields may provide cues for territory selection but frequent human disturbance and increased exposure to weather and predators would have negative consequences for reproduction. To address this hypothesis, we compared measures of habitat selection (settlement patterns and trends in abundance) and productivity (nest density, nest survival, and number of young fledged) between crop fields and native sites in northeastern Montana, USA. Settlement patterns were similar across site types and occupancy ranged from $0.52 \pm 0.17SE$ to 0.99 ± 0.01 on April 7 and 30, respectively. Early season abundance differed by year and changes in abundance during the breeding season were associated with precipitation-driven vegetation conditions, rather than habitat type. Standardized nest density ($0.19 \pm 0.27SD$ nests/plot/hour), the number of young fledged per successful nest ($2.9 \pm 0.18SE$), and nest survival ($0.24 \pm 0.03 SE$; $n=222$ nests) were similar for crop and native sites. Collectively, the data did not support our hypothesis that crop fields are ecological traps: longspurs did not exhibit a clear preference for cropland and reproductive output was not significantly reduced. Our results indicate that crop fields provide alternative breeding habitat within a human-dominated landscape.

14 November 2022

RH: Swicegood et al. * Longspurs Nesting in Cropland: An Ecological Trap?

Detecting Ecological Traps in Human-Altered Landscapes: A Case Study of the Thick-billed Longspur Nesting in Croplands

Amber E. Swicegood, Department of Animal and Range Sciences, Montana State University, Bozeman, MT, USA

Kevin S. Ellison, Program Manager, Northern Great Plains, American Bird Conservancy, Bozeman, MT, USA

Marisa Sather, Partners for Fish and Wildlife Program, U.S. Fish and Wildlife Service, Glasgow, MT, USA

Scott G. Somershoe, Division of Habitat Conservation, Land Bird Coordinator U.S. Fish and Wildlife Service Migratory Birds Program, Denver, CO, USA

Lance B. McNew, Department of Animal and Range Sciences, Montana State University, Bozeman, MT, USA

Correspondence : Lance McNew, Montana State University, 103 Animal Bioscience Building, Bozeman, MT 59717, USA. Email: lance.mcnew@montana.edu

ABSTRACT Conversion of the North American prairies to cropland remains a prominent threat to grassland bird populations. Yet, a few species nest in these vastly modified systems. The thick-billed longspur (*Rhynchophanes mccownii*) is an obligate grassland bird whose populations have declined 4% annually during the past 50 years. Thick-billed longspurs historically nested in recently disturbed or sparsely vegetated patches within native mixed-grass prairie, but observations of longspurs in crop fields during the breeding season suggest such fields also provide cues for habitat selection. Maladaptive selection for poor quality habitat may contribute to ongoing declines in longspur populations, but information on thick-billed longspur breeding ecology in crop fields is lacking. We hypothesized that crop fields may function as ecological traps; specifically, we expected that crop fields may provide cues for territory selection but frequent human disturbance and increased exposure to weather and predators would have negative consequences for reproduction. To address this hypothesis, we compared measures of habitat selection (settlement patterns and trends in abundance) and productivity (nest density, nest survival, and number of young fledged) between crop fields and native sites in northeastern Montana, USA. Settlement patterns were similar across site types and occupancy ranged from $0.52 \pm 0.17SE$ to 0.99 ± 0.01 on April 7 and 30, respectively. Early season abundance differed by year and changes in abundance during the breeding season were associated with precipitation-driven vegetation conditions, rather than habitat type. Standardized nest density ($0.19 \pm 0.27SD$ nests/plot/hour), the number of young fledged per successful nest ($2.9 \pm 0.18SE$), and nest survival ($0.24 \pm 0.03 SE$; $n=222$ nests) were similar for crop and native sites. Collectively, the data did not support our hypothesis that crop fields are ecological traps: longspurs did not exhibit a clear preference for cropland and reproductive output was not significantly reduced. Our results indicate that crop fields provide alternative breeding habitat within a human-dominated landscape.

KEYWORDS Agricultural landscapes, ecological trap, grassland birds, maladaptive selection, *Rhynchophanes mccownii*, thick-billed longspur

1 | INTRODUCTION

In North America, grassland birds have experienced steeper long-term declines than any other avian guild during the past 50 years (Rosenberg et al., 2019; Sauer, 2020) and more than 79% of grasslands have been lost since the early 1800s (Samson and Knopf, 1994; White, 2000). While factors such as fire suppression, overgrazing, desertification, and the introduction of non-native plant species have contributed to degradation of native prairies, conversion to large-scale, row-crop agriculture remains one of the greatest threats to grassland ecosystems (Knapp et al., 1999; Blann, 2006; Ellis et al., 2010; Wright and Wimberly, 2013). Indeed, intensification of agricultural practices is considered a leading driver of grassland bird population declines worldwide (Wilson et al., 2005; Quinn et al., 2017; Davis et al., 2020). While row-crop monocultures support lower avian diversity than native grasslands (Best et al., 1997; Davis et al., 2020), the few species that nest in crop fields face a myriad of hazards. Farming operations (e.g., tilling, discing, harvest) may result in nest destruction (Devries et al., 2008; Santangeli et al., 2018). Soil instability in crop fields may lead to nest failures during floods and heavy rains (Van Pelt et al., 2017). Herbicide and pesticide applications may directly harm adults and nestlings or may indirectly affect bird populations by reducing invertebrate food resources (Pimentel et al., 1995; Loss et al., 2015). In addition, most crops grow rapidly into dense monocultures, with vegetation conditions changing from short-stature (5–15 cm tall) with large amounts of bare ground to tall (60–70 cm), closed-canopy conditions within 2–3 months of seeding (Wilson et al., 2005).

Ecological traps occur when there is a mismatch between habitat selection cues and habitat quality (Battin,

2004) and are most commonly identified where human activities produce novel environmental cues or alter habitat quality associated with a particular cue (Robertson et al., 2013; Hale and Swearer, 2016; Simon and Fortin, 2019). An ecological trap differs from a demographic sink in that animals often exhibit strong preference for trap habitat (Pulliam, 1988; Gilroy et al., 2011). Such maladaptive selection leads to negative fitness consequences and reduced population viability (Schlaepfer et al., 2002; Battin, 2004; Gilroy et al., 2011). The ideal free distribution theory that underpins source-sink population models assumes animals exhibit optimal habitat selection when distributing themselves among habitat patches and that the fittest individuals obtain the highest-quality territories. In reality, individuals likely select habitat according to evolutionarily predisposed cues and ecological traps are attractive because they provide such cues (Delibes et al., 2001; Abrams et al., 2012; Fletcher Jr et al., 2012; Hale et al., 2015; Hale and Swearer, 2016).

The thick-billed longspur (*Rhynchophanes mccownii* ; hereafter “longspur”) is a grassland songbird endemic to the short- and mixed-grass prairies of North America (Knopf, 1996). Like most obligate grassland birds, populations of thick-billed longspurs have declined precipitously (4% per year on average; Figure 1) since the advent of the North American Breeding Bird Survey (Rosenberg et al., 2019; Sauer, 2020), but mechanisms driving the decline are poorly understood. Habitat for longspurs is patchy within native mixed-grass prairie, limiting distributions at regional scales and making this a focal species for federal conservation efforts (Somershoe, 2018). Unlike many other grassland birds, longspurs have a unique preference for recently disturbed or sparsely vegetated habitats, and historically relied on large-scale disturbance regimes to maintain suitable habitat patches through spatial-temporal interactions of soil, precipitation, fire, and intensive periodic defoliation by native herbivores (e.g., bison [*Bison bison*], locusts [chiefly *Melanoplus spretus*]) (Mickey, 1943; Felske, 1971; Samson et al., 2004; McLachlan, 2007; Shaffer et al., 2019; With, 2021). However, these dynamic processes that once shaped prairie ecosystems are largely absent in today’s Northern Great Plains (Samson and Knopf, 1996; Fuhlendorf and Engle, 2004; Samson et al., 2004; Hovick et al., 2015). Modern rangeland management is focused on preventing overgrazing, maintaining desirable plant communities, and homogenizing defoliation at consistent and moderate levels to create sustainable and profitable livestock production (Briske et al., 2005; Toombs et al., 2010; Holechek, 2011; Fuhlendorf et al., 2012). The resulting landscapes often support habitat for a narrower suite of wildlife species (Samson and Knopf, 1996; Samson et al., 2004; Fuhlendorf et al., 2012) and those that require habitat found at the extremes of the disturbance-succession gradient, including longspurs, likely do not benefit from modern rangeland management.

Row-crop agriculture is the dominant disturbance factor producing extensive bare ground at large scales in the Northern Great Plains. Sporadic reports of longspurs occurring in crop fields during the breeding season (Felske, 1971; Shaffer et al., 2019) suggest that crop fields may resemble suitable nesting habitat as longspurs arrive on the breeding grounds in April. However, the selection of crop fields during territory establishment could contribute to population declines if reproductive success is depressed through 1) destruction of nests by discing, seeding, and herbicide/pesticide application, and 2) abandonment of nests or territories in response to rapid changes in vegetation conditions or disturbance by farming activity. If crop fields provide attractive nesting habitat where longspurs experience low reproductive success, modern agricultural landscapes may be operating as ecological traps for this short-grass prairie specialist.

Identifying an ecological trap involves demonstrating habitat preference (i.e., disproportionate selection) that results in reduced vital rates (e.g., nest survival). Importantly, high population densities do not necessarily equate to preference for that habitat type (Van Horne, 1983; Vickery et al., 1992) and comparisons of relative selection metrics between habitat types are needed to discern preferences. A demonstrated preference for crop fields coupled with reduced reproductive success relative to native prairie would indicate an ecological trap with significant implications for longspur conservation (Lloyd and Martin, 2005; Robertson and Hutto, 2006). Delayed settlement in crop fields after native sites are occupied, coupled with lower reproductive success, would suggest crop fields simply provide spill-over habitat, which is characteristic of source-sink population dynamics (Gilroy and Sutherland, 2007).

We conducted a 2-year field study to evaluate whether crop fields operate as ecological traps for nesting longspurs within the core of their breeding distribution in northeastern Montana, USA (Figure 2). We

compared settlement patterns, temporal trends in abundance, and nest density between crop and native sites, assuming that earlier settlement and higher use of crop fields indicated that either longspurs preferred crop sites for nesting or that native sites were limited (Robertson and Hutto, 2006). We measured reproductive success in both habitat types to quantify the relative quality of crop fields as breeding habitat for longspurs. Our objectives were to compare the following in crop and native sites: 1) settlement patterns of territorial male longspurs, 2) longspur abundance and nest densities, as well as changes in abundance over the breeding season, 3) nest survival and fledging success, and 4) structural changes in vegetation during the breeding season.

2 | MATERIALS AND METHODS

2.1 | Study Area

The study area was located within the core of the remaining breeding distribution of longspurs in northern Valley County, Montana, USA (Figure 2). The climate in this region is semi-arid with long, cold winters and short, hot summers producing frequent thunderstorms, hail, and flash floods (Cooper et al., 2001). Average daily temperatures range seasonally from below 0° C to 20–25° C. Annual precipitation averages 25–35 centimeters and typically comes as rain in late May and early June (Lenard et al., 2006; PRISM 2022). The region is at about 915 meters in elevation. Clay shale is the most abundant substrate and the landscape is dominated by glacial till (Cooper et al., 2001). The study area incorporated cultivated crop fields in the eastern portion and native mixed-grass prairie in the western portion. Federal lands and private ranches occurred west of Opheim and Baylor, and the Bitter Creek Wilderness Study Area, characterized by its undeveloped badlands, was located at the center of the study area.

Native grassland in this region is classified as northern mixed-grass prairie (Coupland, 1961; Charboneau et al., 2013). Cool season grasses dominated and common species included western wheatgrass (*Pascopyrum smithii*), needle-and-thread (*Hesperostipa comata*), prairie junegrass (*Koeleria macrantha*), green needlegrass (*Nassella viridula*), Sandberg bluegrass (*Poa secunda*) and threadleaf sedge (*Carex filifolia*). One warm season grass, blue grama (*Bouteloua gracilis*), was present at some sites. Spikemoss (*Selaginella densa*) was locally abundant as well. Shrub cover was low-moderate across most of this region (Charboneau et al., 2013).

Northern Valley County is characterized by large expanses of poor soils unsuitable for cultivation and more productive areas used for row-crop production. Arid patches within large tracts of native mixed-grass prairie provide habitat for longspurs, known to be locally abundant in such areas. These native sites consist of aridic, well-drained glacial soils of the Elloam series and have relatively low (<1000 kg ha⁻¹) vegetation production potential (Lenard et al., 2006; Lipsey, 2015). Primary crops in the region included spring wheat, barley, lentil, pea, flax, and canola. In some areas wheat farming was conducted on a 50:50 rotation with 50% of the acreage fallowed each year to conserve soil moisture and nutrients (M. Sather, USFWS, pers. comm.). Pulse crops such as peas and lentils are often planted between wheat rotations to add nitrogen, conserve soil moisture, and disrupt weeds, pests, and diseases (Miller et al., 2002; Long et al., 2014). Pulse crop rotations have replaced summer fallow over most of the region (M. Sather, USFWS, pers. comm.).

2.2 | Field Methods

2.2.1 | Longspur Settlement

We deployed 24 autonomous acoustic recorders (Wildlife Acoustics model SM4, Maynard, MA; hereafter “song meters”) to assess settlement patterns of territorial male longspurs on the breeding grounds. We consulted local biologists and used observations from the USFWS Breeding Bird Survey (BBS) and eBird (Sauer et al., 2020; Sullivan et al., 2020) to identify locations previously used by longspurs. We deployed 8 and 16 song meters in 2020 and 2021, respectively, with half (4 in 2020, 8 in 2021) in crop fields and half in native grassland sites. We selected sites that were no more than 25 km apart to minimize regional variation in weather patterns between site types. We deployed song meters on 7 April and retrieved them on 30 April

after territory establishment (With, 2021). We affixed song meters to 1.8-m t-posts at a height of 1.2 m and covered each microphone with an extra layer of foam to reduce recorded wind noise.

We programmed song meters to collect a 3-minute recording every half hour starting 15 minutes before sunrise and ending by 09:00 hours to coincide with morning breeding choruses of longspurs (With, 2021), resulting in six 3-minute recordings collected each morning. Upon removal from the field, a trained technician manually reviewed each 3-minute recording and documented longspur presence. We excluded any recordings [?] 25% obscured by wind or other noise.

2.2.2 | Longspur Abundance

Initial Occurrence Surveys. – To identify areas used by thick-billed longspurs, we randomly generated 100, 64-ha sampling plots in both crop and native sites. We only included survey plots that had rangeland productivity [?]1,100 kg ha⁻¹ (Lipsey and Naugle, 2017) and that were located within land parcels where we secured permission to conduct fieldwork. Plots were separated by [?]200 meters to ensure independence. Random plots in crop fields that contained >1 crop type were discarded because different crop types grow at different rates, potentially confounding results. In native sites, we discarded plots if they contained badlands or water bodies covering [?]1/4 of the plot because longspurs do not nest in such areas (DuBois, 1937; Felske, 1971; With and Webb, 1993).

We conducted initial surveys within the 64-ha plots during 30 Apr–11 May, 2020–21. We surveyed [?]25 plots in each site type each year. Observers walked a U-shaped line transect within each plot, starting 200 meters inward from a randomly selected plot corner (Figure 3). We identified species and recorded perpendicular distance and direction from the transect line for each bird or group of birds seen or heard to maintain consistency with distance sampling methods. Estimated distances were recorded in bins: 0–25, 26–50, 51–75, 76–100, and 101–200 meters. We walked at a pace of 2–3 km hr⁻¹ and completed each transect within 40 minutes. Observers were trained to avoid double-counting birds. Surveys began one half hour before sunrise and were completed by 10:00 hours. We did not conduct surveys if wind speed was >25 km hr⁻¹ or it was raining. We recorded survey covariates including observer, cloud cover, temperature, wind speed, date, GPS starting point, and transect start/end times.

Abundance surveys. – Within initial plots occupied by longspurs, we generated smaller, 16-ha survey plots within which we monitored longspur populations for the remainder of the nesting season. We identified occupied crop fields, randomly selected [?]20 of these fields, and generated a single 16-ha plot within the center of each selected field. This ensured crop plots were [?]200 m from field edges, roads, and other plots. In native sites, we delineated large patches of occupied habitat by tracing the extent of occupied areas on foot with a GPS unit and later transferred this information to ArcMap 10.7.1 (ESRI, 2019). Patches were discovered after determination of longspur occupancy during initial surveys, and patch edges were defined by presence/absence of singing longspurs and were typically coupled with apparent changes in vegetation composition. We then overlaid a grid of 16-ha cells over occupied patches and used ArcMap to randomly select [?]20 cells from these patches. Only non-adjacent cells were used to ensure plots were [?]200 m apart. Each site selection process allowed us to select only occupied sites and guaranteed independence.

We conducted six rounds of line transect surveys within each 16-ha survey plot during 10 May–15 July 2020–21. Survey rounds were separated by [?]5 d. Observers walked a U-shaped line transect within each plot, starting 100 meters inward from a randomly selected plot corner (Figure 4). We collected data as described above but limited observations to thick-billed longspurs and distance bins included 0–25, 26–50, 51–75, and 76–100 m. We completed each transect within 30 minutes and surveys began 15 minutes before sunrise and ended at 9:00 hours.

2.2.3 | Nest Phenology, Survival, and Reproductive Output

Nest Searching. – We searched for nests during 9 May–22 July, 2020 and 5 May–8 July, 2021 to assess reproductive effort throughout the entire nesting season (With, 2021). Nest searching began at sunrise and ended at 11:00 hours on days without precipitation and observers were randomly assigned a group of plots to

search each morning. Observers alternated between crop and native sites during subsequent days and used behavioral observations to find nests (Martin and Geupel, 1993; Winter et al., 2003). We observed longspurs from a distance of [?]30 m and moved to a new plot after 60 minutes if no female longspurs were detected. In addition, we supplemented behavioral nest searching with standard rope dragging methods (Klett et al., 1986; Koford, 1999).

Nest Monitoring. – Upon finding a nest, we recorded the geographical coordinates and marked the nest location with 15-cm bamboo stakes placed 2 m north and east of the nest to aid in relocation. Nests were checked every 2–4 days until fledging or failure (Martin and Geupel, 1993; Ralph, 1993). We recorded adult behavior, number of eggs and young, number of brown-headed cowbird (*Molothrus ater*) eggs or nestlings, date, time, observer, time spent at nest, and any relevant notes. We aged nestlings according to developmental cues described in Jongsomjit et al. (2007) so the nest could be checked on predicted date of fledging. We considered a nest failed if eggs were gone before expected hatch date, if nestlings disappeared before nearing expected fledge date, or if dead nestlings or depredated eggs were found in or near the nest. A nest was considered successful if [?]1 chick fledged. We deemed nests successful if nearby adults were observed feeding fledglings, [?]1 fledgling was observed, territorial adults were present with food or directed aggressive behaviors toward observers, or fecal material was present and nestlings had reached the appropriate age to fledge (Ralph, 1993; Jones et al., 2010).

2.2.4 | Habitat Conditions

We collected vegetation measurements at two spatial scales, the nest site and the survey plot (16-ha). Measures were collected at each nest within 3 days of fledge or expected fledge for failed nests. In addition, we randomly selected 3 and 10 habitat sampling points within the 16 ha survey plots in crop fields and native prairie sites, respectively. Vegetation conditions in crop fields were fairly homogenous and required fewer sampling points (Swicegood, 2022). We measured vegetation conditions three times throughout the longspur breeding season, once in May, June, and July. At each sampling point, we recorded visual obstruction readings (VOR) in each cardinal direction from a distance of 4 m and a height of 1 m (Robel et al., 1970). We measured overlapping percent cover of grass, forb, shrub, litter, and bare ground within a 20 x 50 cm sampling frame at the sampling point and at 4 locations 0.5 m from the point in each cardinal direction (Daubenmire, 1959). Cover was recorded within six percentage classes (0%, 1–5%, 6–25%, 26–50%, 51–75%, 76–95%, and 96–100%). We listed all plant species, lichen, and spikemoss in order of decreasing abundance, found within a 2-m radius of the point center. We measured litter depth (mm) in the northwest corner of the Daubenmire frame and recorded the species, distance (m), and height (cm) of the nearest shrub within 25 m as shrubs influence nest density or detection of nests for many grassland passerines (Davis, 2005; Pulliam et al., 2021).

2.3 | Analyses

2.3.1 | Longspur Settlement

We used multi-season occupancy models to evaluate whether longspur settlement patterns differed between crop and native sites (MacKenzie et al., 2003). Multi-season occupancy models use detection/non-detection data collected with a robust design (Pollock, 1982) to estimate initial occupancy and subsequent rates of local colonization (e.g., settlement) and extinction (e.g., site abandonment) while accounting for spatially variable detection probability (MacKenzie et al., 2003; Mackenzie, 2006). The design used k secondary survey periods within T primary periods; each day represented a primary period and each 3-minute recording a closed secondary period (i.e., 6 secondary periods occurred over 24 days in each year).

We fitted multi-season occupancy models using the ‘colect’ function in R package ‘unmarked’ (Fiske and Chandler, 2011; Kery and Chandler, 2016) and used information theory to evaluate support for competing models representing hypotheses about detection probability, initial occupancy, and settlement patterns (MacKenzie et al., 2003). We evaluated support for our *a priori* models in a phased approach. First, we evaluated how well a fully parameterized model fit the data and estimated a variance inflation factor (\hat{c}

) using the *mb.gof.test* in the R package ‘AICcmodavg’. Bootstrapping was based on 500 simulations to generate a chi-squared statistic and to calculate average \hat{c} , where a \hat{c} value >1 indicates overdispersion in the data, but much higher values (>4) may indicate lack-of-fit (Mazerolle, 2020). We found evidence of moderate overdispersion ($\hat{c} = 1.9$) and inflated estimated standard errors by $\sqrt{\hat{c}}$ and based subsequent model evaluation and inference on the quasi-Akaike’s Information Criterion adjusted for finite samples (QAIC_c; Burnham and Anderson, 2002).

We developed models that evaluated the effects of survey conditions on detection probability. Variables hypothesized to influence detection included daily precipitation, minimum daily temperature, minutes past sunrise, and Julian day (Table 1). We evaluated a quadratic effect of minutes past sunrise because bird detections were previously found to be highest mid-morning (With, 2021). Because all detection covariates we measured are known to affect the detectability of songbirds, we used a backward selection approach based on QAIC_c to eliminate uninformative parameters (Pagano and Arnold, 2009; Arnold, 2010; Montgomery et al., 2021). Models with large relative weights (w_i) and QAIC_c values ≤ 2 from the best-fit model were considered equally parsimonious (Devries et al., 2008; Arnold, 2010; Burnham et al., 2011). After we identified a parsimonious sub-model for detection, it was retained in subsequent evaluations of occupancy and settlement.

Because some birds had already arrived at the study area prior to song meter deployment, we evaluated whether initial occupancy differed by habitat type (crop vs. native) before evaluating the effects of habitat type and Julian day on settlement probability (Table 1). In addition to these main effects, our candidate set for settlement probability included a model with an interaction between habitat type and Julian day because we hypothesized that settlement rates would change over the season differentially by habitat type. We hypothesized that abandonment rates would be extremely low; once territorial longspurs arrive at a breeding site post-migration, they are unlikely to abandon the site (With, 2021). Therefore, we did not include any models with covariates on abandonment rates. Model selection was again based on QAIC_c (Burnham and Anderson, 2002). We used empirical Bayes methods to derive estimates of latent occupancy from the most parsimonious model for each primary period from predicted posterior distributions using the ‘ranef’ function in R package ‘unmarked’ (Fiske and Chandler, 2011). All analyses were performed using R Statistical Software (v 4.1.2; R Core Team 2021).

2.3.2 | Longspur Abundance

We used open-population distance sampling models to estimate longspur abundance in crop and native sites and assess whether abundance changed differentially throughout the breeding season (Royle et al., 2004; Sollmann et al., 2015). Distance sampling is a common method for estimating abundance or density of wildlife populations and allows simultaneous estimation of detection probability without requiring repeat site visits (Buckland et al., 2001). Open-population distance sampling models allow explicit modeling of population dynamics over space and time, where data from repeat distance sampling surveys are used and populations are assumed open between survey periods (Sollmann et al., 2015).

We fitted open-population distance sampling models using the ‘distsampOpen’ function in R package ‘unmarked’ (Fiske and Chandler, 2011) and used information theory to evaluate support for competing models representing hypotheses about detection, initial abundance, and trends in abundance over the breeding season (Sollmann et al., 2015). We evaluated support for our *a priori* models in a phased approach. First, we used null models with the ‘trend’ dynamics parameterization to estimate the best-fitting detection function and mixture type based on our data. We then evaluated how well a fully parameterized model fit the data and estimated a variance inflation factor (\hat{c}) using the *Nmix.gof.test* in the R package ‘AICcmodavg’ from 500 bootstrapped simulations. Because the negative binomial model can overestimate population abundance (Ver Hoef and Boveng, 2007; Kery and Royle, 2015), we used the Poisson distribution for all subsequent models, inflating estimated standard errors by $\sqrt{\hat{c}}$ and basing model evaluation and inference on the quasi-Akaike’s Information Criterion adjusted for finite samples (QAIC_c; Burnham and Anderson, 2002). We found evidence of moderate overdispersion using the Poisson distribution ($\hat{c} = 1.9$ for 2020 data, $\hat{c} = 1.7$ for 2021 data).

We developed models to evaluate the effects of survey conditions on detection probability. Variables hypothesized to influence detection probability included observer, wind speed, temperature, and start time (minutes past sunrise; Table 2). We evaluated a quadratic effect of start time because bird detections are usually highest 1–2 hours after sunrise (With, 2021). Initial screening indicated that detection was variable across observers, so we separated observers into 2 groups for each year (‘high’ and ‘low’ detection rates) based on relative coefficient estimates from a full model to reduce the number of parameters in candidate models while retaining large observer effects on detection. We used the backward selection approach described previously to eliminate uninformative parameters and identify a parsimonious sub-model for detection probability, which was retained in subsequent evaluations of abundance and seasonal trend.

We evaluated if initial abundance and seasonal trends differed by habitat type (crop vs. native; Table 2). We developed models that included the effect of habitat type on both initial abundance and trend, as well as all submodels. Model selection was again based on QAIC_c (Burnham and Anderson, 2002). We used Bayesian methods to derive true abundance estimates from the most parsimonious model for each survey round from predicted posterior distributions using the ‘ranef’ function in R package ‘unmarked’ (Fiske and Chandler, 2011). We analyzed data separately for the two years because differences in weather and drought conditions were likely to produce different population responses.

2.3.3 | Nest Phenology, Survival, and Reproductive Output

Nest Phenology. – For each nest, we calculated initiation date as the day the last egg was laid, although actual initiation of incubation is variable for passerines (Hébert, 2002; Badyaev et al., 2003). Initiation date was estimated based on clutch size, hatch date, or chick age and assuming an incubation period of 12 d (With, 2021). For nests found after clutch completion but destroyed before hatch, we assumed initiation to be 6 d prior to the midpoint of the active period. We plotted nest initiation dates to visualize patterns of nest initiation between crop and native sites and to assess differences between years.

Nest Survival. – We used the nest survival model in program MARK to model daily nest survival rate (DSR) and we fitted models in the R package ‘RMark’ (White and Burnham, 1999; Rotella et al., 2004; Laake, 2013). We built and evaluated a set of competing models representing *a priori* hypothesized relationships between DSR and habitat type (crop or native), nest initiation date, and year (2020, 21). We evaluated 15 models with all combinations of habitat type, initiation date, and year (Table 3). We also included a model with a quadratic effect of initiation date because other studies have shown DSR to be higher or lower mid-season (Weintraub et al., 2016; Skagen et al., 2018). We predicted DSR may exhibit a pseudo-threshold response in crop sites only, being low for nests initiated early and leveling off after fields were planted. Therefore, we included a model with a pseudo-threshold effect of initiation date and one including an interaction term with habitat type. We evaluated the relative support of models using Akaike’s Information Criterion corrected for finite sample size (AIC_c). Supported models with large model weights (AIC_c w_i) and AIC_c values [?]2 from the best fit model were considered parsimonious; when supported models differed by one parameter, we considered this parameter uninformative (Arnold, 2010; Burnham et al., 2011). To estimate nest survival probability, we used a 26-day nesting cycle beginning with the start of the laying period and multiplied DSR for each daily interval over a 25-day period from nest initiation to fledging (e.g., DSR²⁵ for constant model). We calculated standard error for nest survival estimates using the Delta method (Powell, 2007).

Reproductive Output. – We calculated an index of nest density for each plot by dividing the number of nests located in each plot by the total search effort (hours) for that plot. We report the mean and standard deviation of relative nest density for each habitat type (crop vs. native). Incidental nests located outside of survey plots and nests found via rope dragging methods were excluded from this calculation. Importantly, we were unable to account for detectability of nests with behavioral search methods and it is possible detectability differed in crop and native sites. Detectability almost certainly differed by observer (Diefenbach et al., 2003; Giovanni et al., 2011); therefore, observers were rotated through different plots each day.

We tabulated maximum clutch size for all nests with known fates and the number of young fledged per successful nest. The number of young fledged was recorded as the number of chicks present 8–10 d after

hatching, the typical fledging time for longspurs (With, 2021), unless some dead and some live fledglings were found during the final visit. We developed a set of generalized linear models to analyze the effects of habitat type and initiation date on the number of young fledged per successful nest using a Poisson distribution with a log link. We included an interaction term to test if the number of young fledged differed by both habitat type and initiation date (Table 4). Nests were removed from analysis if the number of young fledged was unknown. We evaluated relative model support AIC_c and used the best-fitting model to estimate the number of young fledged per successful nest.

2.3.4 | Habitat Conditions

We used generalized linear models to test hypotheses that specific vegetation attributes differed significantly between crop and native sites, longspur habitat changed structurally over the summer as plants grew, and such changes were more extreme in crop sites than in native sites. Variables included VOR, bare ground cover, grass and forb cover, litter cover and litter depth. For proportional response data (e.g., percent coverages), we used the binomial distribution and logit link function to fit GLMs (Chen et al., 2017). For all other vegetation measures, including VOR and litter depth, we used the identity link and log transformed the response variables to meet the assumptions of linear regression (Dunn and Smyth, 2018). For each habitat variable, we built and evaluated the same set of competing models representing *a priori* hypothesized relationships between habitat type and survey round (Appendix I).

We evaluated relative model support using AIC_c . Supported models with large model weights ($AIC_c w_i$) and AIC_c values ≤ 2 from the best fit model were considered equally parsimonious (Burnham et al., 2011). When a supported model differed from a top model by a single parameter, the additional parameter was considered uninformative (Arnold, 2010). We based inferences on effect sizes from a single top model and calculated model averaged estimates when models shared support ($\Delta AIC_c \leq 2$; Burnham et al., 2011).

3 | RESULTS

3.1 | Longspur Settlement

We deployed song meters at 8 and 16 sites in 2020 and 2021, respectively, half in crop fields and half in native sites. Due to equipment malfunction and failure of longspurs to establish territories at some sites, we were able to obtain data from 2 song meters in native sites and 4 song meters in crop sites in 2020, and 7 song meters in native sites and 7 song meters in crop sites in 2021. Overall, we collected >37 hr of useable recordings in 2020 and >100 hr in 2021.

Detection probability. – The top model for detection probability contained an effect of Julian day, minimum temperature, and a quadratic effect of minutes past sunrise ($QAIC_c w_i = 0.97$; Table 1). Detection probability increased with Julian day ($\beta = 0.99 \pm 0.13$ SE) and increased in response to minimum temperature ($\beta = 0.08 \pm 0.02$). Detection probability was highest at $\sim 90 - 100$ minutes past sunrise, or 1.5 hours after sunrise (Figure 5).

Initial occupancy and settlement probability. – We found no evidence for an effect of habitat type on initial occupancy with the null model carrying virtually all support ($QAIC_c w_i = 0.98$; Table 1). We found no evidence that settlement probability differed by habitat type with the model containing an effect of Julian day carrying virtually all support ($QAIC_c w_i = 0.98$). Settlement probability increased for both habitat types with Julian day ($\beta = 2.24 \pm 0.68$). Derived estimates of true occupancy for both crop and native sites increased from $0.52 (\pm 0.17$ SE) on 7 April to $0.99 (\pm 0.01)$ on 30 April (Figure 6).

3.2 | Longspur Abundance

In 2020, we conducted initial occurrence surveys in 80 plots (36 crop and 44 native); 67% of crop and 20% of native plots were occupied. In 2021, we conducted initial surveys in 62 plots (35 crop and 27 native); 91% of crop and 33% of native plots were occupied. In 2020, we conducted 287 longspur abundance surveys at 24 crop sites and 22 native sites during 14 May – 19 July. We observed 5.4 ± 4.4 (mean \pm SD) male longspurs

in crop sites and 4.2 ± 3.3 in native sites. In 2021, we conducted 325 surveys at 25 crop sites and 25 native sites during 10 May – 14 July. We observed an average of 3.8 ± 3.2 and 3.2 ± 2.3 males per plot in crop and native sites, respectively. Most crop plots contained spring wheat (28 plots); we surveyed 4 summer fallow plots in 2020 and 8 in 2021 (Table 5).

Detection probability. – For both years, the top model contained an effect of observer group (Table 2). Detection probability was lower for observer group 2 and effect sizes were -1.67 ± 0.54 SE in 2020 and -0.95 ± 0.39 in 2021 (Figure 7). Confidence intervals for the effect sizes for other covariates on detection overlapped 0; therefore, only observer group was retained in subsequent abundance modeling (Arnold, 2010).

Initial abundance and seasonal trends. – We found support for an effect of habitat type on both initial abundance and seasonal trend for data collected in 2020 (QAIC_c $w_i = 0.91$; Table 2). Expected initial abundance in crop sites was 17.4 ± 4.1 SE birds per plot and the estimated seasonal trend was $\lambda = 0.84 \pm 0.04$, indicating that abundance decreased by 16% over the season. Empirical estimates of true abundance for crop sites decreased from 16.8 (95% CI = 15.7–18.0) during the first survey round to 6.5 (5.6–7.8) during the sixth round. Expected initial abundance in native sites was 8.6 ± 2.0 birds per plot and increased slightly during the season ($\lambda = 1.02 \pm 0.05$). Derived empirical abundance for native was 8.7 (95% CI = 7.8–9.7) during the first survey round and 9.4 (8.4–10.7) during the sixth round (Figure 8).

In 2021, we found no support for an effect of habitat type on either initial abundance or seasonal trend, with the null model carrying the most support (QAIC_c $w_i = 0.54$; Table 2). Because of model uncertainty, we averaged results across all four supported candidate models. Expected initial abundance was similar in crop and native sites (12.5 ± 3.3 SE) and seasonal population sizes did not change much during the season ($\lambda = 1.03 \pm 0.04$ SE in crop sites; 1.01 ± 0.04 in native sites). Derived estimates of true abundance for crop sites increased slightly from 12.3 (95% CI = 11.1–13.3) during the first survey round to 15.1 (13.2–17.0) during the sixth round. Derived estimates of true abundance for native sites were fairly stable across the season (12.7 (95% CI = 11.5–14.1) during the first survey round; 12.1 (10.8–13.4) during the sixth round; Figure 8).

3.3 | Nest Phenology, Survival, and Reproductive Output

We located 240 longspur nests, 111 in crop sites and 129 in native sites. Of these, 174 were located using behavioral cues of adults, 14 using rope-dragging methods, and 52 were incidental finds while observers were conducting other fieldwork. We spent 515 hours behavioral searching in crop fields and 421 hours behavioral searching on native sites, for a total of 936 hours nest searching using behavioral cues. Using 2–3 observers, we spent 76.5 person-hours rope dragging in crop fields and 22.5 person-hours rope dragging in native sites, for a total of 99 rope dragging person-hours.

Of the 240 nests, 222 had known fates (96 crop, 126 native). For the 18 remaining nests, we were unable to determine nest fate due to either conflicting clues at the nest site or weather events/farming operations preventing timely nest checks near expected fledge date. We were able to estimate the number of young fledged for 87 successful nests, 41 crop and 46 native. Apparent nest success was 44% in crop sites and 37% in native sites. Predation was the main cause of nest failure in both crop fields and native plots (Table 6). Other causes included weather, farming operations (crop only), and abandonment. Brown-headed cowbird (*Molothrus ater*) parasitism rates were 1.8% and 7.8% in crop and native sites, respectively.

Nest Phenology. – Patterns of nest initiation were similar within crop and native sites each year, but median initiation dates in native sites were 6–11 d later than median dates in crop sites (Figure 9). In addition, the first and third quartiles were 6–10 d later in native sites. In 2020, median initiation date was 29 May (IQR = 25 d, n = 68) and 9 June (IQR = 26 d, n = 71) in crop fields and native sites, respectively. Longspurs nested through mid-July and there were two prominent peaks in nest initiation. In 2021, median date of initiation was 28 May (IQR = 17 d, n = 28) in crop sites and 3 June (IQR = 13 d, n = 55) in native sites. Nesting slowed significantly in late-June – early-July and there was only one main peak in nest initiation. Notably, the interquartile distance for initiation dates was 32% shorter in crop sites and 50% shorter in native sites during the 2021 drought year than during 2020.

Nest Survival. – The null model of constant daily nest survival was the best supported in the candidate set ($AIC_c w_i = 0.18$; Table 3). Models including effects of habitat type, year, and initiation date, including models with different functional forms of initiation date, had approximately equal support as the null model, indicating that these parameters were uninformative. Average daily nest survival estimated from the null model was $0.944 \pm 0.005SE$ and estimated nest survival over the 26-day exposure period (DSR^{25}) was 0.236 ± 0.028 .

Reproductive Output. – Relative nest density ($\pm SD$) was 0.153 ± 0.215 nests/hour/plot in crop sites and 0.233 ± 0.317 nests/hour/plot in native sites. Mean clutch sizes $\pm SD$ were 3.5 ± 0.8 and 3.3 ± 0.8 for nests occurring in crop fields and native sites, respectively. The mean number of young fledged per successful nest was 3.0 ± 1.1 SD in crop sites and 2.8 ± 0.9 in native sites. The null model was the best supported model in our candidate set of generalized linear models for number of young fledged per successful nest ($AIC_c w_i = 0.49$; Table 4), indicating that neither nest initiation date nor habitat type was related to the number of young fledged. Models including the effects of habitat type and initiation date had approximately equal support as the null model, indicating that these parameters were uninformative. Estimated from the null model, the average number of young fledged per successful nest in both crop and native sites was 2.90 ± 0.18 SE.

3.4 | Habitat Conditions

We observed significant differences in vegetation conditions between crop and native sites that varied across survey rounds (Figure 10). Visual obstruction reading (VOR) estimates ($cm \pm SE$) in 2020 changed from 0.81 ± 1.42 in May to 17.81 ± 1.43 in July in crop sites and from 1.95 ± 1.51 to 2.61 ± 1.46 in native sites. In 2021, VOR estimates ($cm \pm SE$) changed from 0.72 ± 1.35 to 1.48 ± 1.35 in crop sites and from 0.68 ± 1.34 to 0.28 ± 1.34 in native sites. Bare ground coverage was significantly lower on native sites than crop sites during both years. Estimated bare ground ($\% \pm SE$) in 2020 was 45 ± 6 in crop fields and 10 ± 4 in native sites. In 2021, estimated bare ground was 42 ± 6 in crop fields and 14 ± 4 in native sites.

Estimated litter coverage in 2020 ($\% \pm SE$) was 25 ± 5 in crop fields and 8 ± 3 in native sites. In 2021, estimated litter coverage was 26 ± 5 in crop fields and 11 ± 3 in native sites. Estimated litter depth in 2020 ($mm \pm SE$) changed from 4.66 ± 1.30 in May to 0.58 ± 1.31 in July in crop sites and from 1.57 ± 1.34 to 1.05 ± 1.32 in native sites. In 2021, estimates changed from 2.75 ± 1.12 in May to 1.35 ± 1.12 in July in crop sites and from 1.01 ± 1.12 to 0.91 ± 1.12 in native sites. Models of residual, forb, and grass cover indicated that these vegetation conditions were similar across habitat types and survey rounds. The same results were true for grass cover when we only compared native sites to wheat crop types (e.g., all crop plots classified as forb were removed).

4 | DISCUSSION

Collectively, our results did not support the hypothesis that crop fields are ecological traps for breeding thick-billed longspurs because, compared with longspur use of native grassland sites, there was no evidence of preference for crop habitat or of suppressed reproduction in crop fields. Specifically, settlement patterns of singing males were similar between crop and native sites and relative nest density was slightly lower in crop sites, providing no evidence for preferential selection of crop habitat. Nest survival, average clutch size, and the number of young fledged were similar between crop and native sites, providing no evidence for suppressed reproduction in crop fields. Additionally, precipitation and associated vegetation growth appeared to mediate longspur abundance and use of crop fields. Longspur abundance decreased throughout the breeding season in crop fields during a normal year (2020) as plant biomass increased whereas abundance did not decrease during a drought year (2021). Annual variation in timing of seeding coupled with drought effects on vegetation may increase the unpredictability of crop habitat among years.

We found that median nest initiation dates occurred 6–11 days earlier in crop sites despite similar settlement patterns for the two habitat types. Longspurs appeared to shift timing of nesting in crop sites, and perhaps this phenological shift is beneficial in habitat that changes structurally to become unsuitable late in the

breeding season. Based on our results, crop sites may provide thick-billed longspur populations with viable alternative nesting opportunities in an area where native habitat has been reduced.

4.1 | Crop Fields as Potential Traps

We observed similar settlement patterns within breeding territories in crop fields and native prairie, indicating that selection cues and preference of longspurs were similar between habitat types. Although 50% of our study plots were occupied prior to song meter deployment in early April, increases in daily longspur occupancy were similar across habitat types and all sites were occupied by 27 April. Also, our nest density index was 29% lower in crop sites, though estimated precision was low and confidence intervals overlapped. Together, these findings suggest a similar preference of longspurs for crop fields and native rangeland habitats.

All measures of reproductive output (nest survival, clutch size, number of young fledged per successful nest) were similar between habitat types. Although we observed higher early nest failures in crop sites as a result of farming activities (e.g., seeding, discing, and plowing), thick-billed longspurs are quick to renest (<10 d) (Mickey, 1943; Felske, 1971; With, 2021), and we often found new nests close to failed nest locations. While the most common cause of nest failure in both habitat types was predation, higher predation rates on native sites resulted in overall similar nest survival rates (~24%) in crop fields and native prairie habitat.

In contrast to expectations, some farming activities, including rolling (field leveling) and spraying, did not result in nest damage or abandonment, and harvest of crops occurred too late in the season to affect nesting longspurs. Longspur nest bowls were constructed below the soil surface; farming activities such as rolling that did not disturb the soil did not negatively affect nests (n=9) regardless of nest stage. Most (>95%) of our crop fields were sprayed with herbicides (glyphosate, 2-4 dichlorophenoxyacetic acid [2-4D]) twice per season and [?]5 fields were also sprayed once with organic fertilizers. Herbicide application typically consisted of a pre-spray to eliminate weeds around the time of seeding and a second application in June when plants were 12–15 cm tall (M. Sather, USFWS, pers. comm.). Although nests were active when fields were sprayed, spraying did not directly result in losses of eggs or nestlings. However, we did not assess potential indirect effects of herbicide and fertilizer spraying on nestling growth rates or subsequent fledging survival.

Flooding and hail destroyed nests in both crop (n=8) and native sites (n=4). Nest abandonment was often due to partial predation, weather, brown-headed cowbird parasitism, and possibly frequent disturbance by predators or perceived predators. On a few occasions in native sites (n=3 nests), we found all nestlings apparently uninjured but laying outside the nest. These nestlings never survived and were never returned to the nest by adult longspurs. We suspect this to be the activity of brown-headed cowbirds or other passerine nest predators (Pietz and Granfors, 2000; Pietz et al., 2012).

4.2 | Longspur Abundance and Use of Crop Fields

Precipitation and vegetation structure appeared to mediate longspur abundance in crop fields but not native sites. Longspur abundance was relatively stable throughout the season within native sites in both years and averaged 8–12 birds per plot (0.63 birds per ha). In a season of normal precipitation (2020), longspur abundance was higher in crop sites than native sites early in the season (April–May) when crop biomass was low but declined with the growth of crops. In contrast, longspur abundance increased slightly throughout the breeding season in crop fields during a drought year (2021) when crop growth was minimal. Because rates of nest abandonment were ubiquitously low, declining abundances of longspurs across time imply reduced nesting attempts in crop sites during a year of normal precipitation, though we could not confirm this with unmarked birds.

Longspurs used all types of crop fields in our study area, including lentil, pea, flax, wheat, canola, mixed cover crop, and summer fallow. Although we didn't have sufficient sample plots in summer fallow treatments (n = 12) to include this as a separate category in our analyses, we consistently observed fewer longspurs in summer fallow fields compared to other crop types. We found very few nests in summer fallow fields over both years (n = 10). Summer fallow fields were planted in strips, with fallow sections intermixed with planted sections. Fields planted in the narrowest strips, and hence having more abrupt edges, were rarely used by longspurs

(on 4–5 out of 6 surveys we detected 0 birds). Lower abundance of longspurs in these areas is consistent with avoidance of habitat edges in grassland birds (Johnson and Igl, 2001; Renfrew et al., 2005; Sliwinski and Koper, 2012; Thompson et al., 2015). In addition, fallow portions are tilled multiple times during the breeding season to control weeds. Therefore, nests in unplanted portions of summer fallow fields have a higher risk of being destroyed later in the season, unlike nests in annual crop sites. It is also possible that frequent tilling of fallow fields results in different soil conditions, generating different invertebrate resource availability than that found in minimum-tilled fields (Stinner and House, 1990; Kladvko, 2001).

4.3 | Timing of Nesting

In native prairie habitats, longspurs select territories on south-facing slopes during the early breeding season where snow melts and the ground warms faster (Felske, 1971; Greer, 1988; Shaffer et al., 2019). Bare ground cover was higher in crop fields than native sites throughout the breeding season, and exposed soils warm faster than vegetated soils (Song et al., 2013). Although territory settlement phenology was similar between habitat types, median nest initiation dates during both years occurred 6–11 days earlier in crop fields than in native sites. Thus, earlier warming of crop fields may allow earlier nest initiation and egg laying resulting from favorable microclimatic conditions or an earlier invertebrate food supply (Felske, 1971; Greer and Anderson, 1989). However, we did not assess thermal or other microclimatic conditions at nests. In addition, the range of nest initiation dates and therefore length of nesting period was significantly shorter during the drought year in 2021. Longspurs are known to forego nesting or experience lower reproductive success during periods of extreme drought (Felske, 1971; Shaffer et al., 2019). Our results indicate that longspurs may initiate nests earlier in crop than native sites but experience a shorter breeding period in both site types during drought.

4.4 | Data Limitations

A broader demographic analysis including seasonal adult, annual adult, juvenile, and post-fledging survival rates would increase our ability to identify population sources and sinks and more fully test the ecological trap hypothesis. Our estimates for nest survival and the number of young fledged per successful nest are similar to estimates reported in other studies of thick-billed longspur and similar species in native prairie habitats, including horned lark (*Eremophila alpestris*) and chestnut-collared longspur (*Calcarius ornatus*) (Sedgwick, 2004; Lloyd and Martin, 2005; Mahoney and Chalfoun, 2016; Gaudet et al., 2020; Pulliam et al., 2021; Reintsma et al., 2022). Because double-brooding in longspurs can be affected by seasonal habitat conditions that vary differentially in crop fields and native prairie, future research should evaluate the relative contribution of each habitat type to overall fecundity (i.e., fledglings per female per season). To better understand mechanisms driving longspur population declines, additional information is needed on vital rates across life stages (e.g., renesting rates, juvenile survival, adult survival). Grassland birds are highly sensitive to variation in annual adult survival (Sedgwick, 2004; Perlut et al., 2008), however, low site fidelity in breeding areas for longspurs may make estimation of these vital rates difficult (Sedgwick, 2004; With, 2021). Recent advancements in VHF technology (e.g., Motus Wildlife Tracking System) may allow for expanded assessments of seasonal fecundity and annual survival of both adults and juveniles, in addition to movement rates between habitat types.

Evaluating stress hormone levels *sensu* Des Brisay (2018) of fledglings, juveniles, and adult longspurs in crop sites could provide additional insight on habitat quality. Body condition at the start of migration often influences survival of adults and juveniles during migration and winter (Merila and Svensson, 1997; Angelier et al., 2011; Labocha and Hayes, 2012). Lower post-fledging survival in crop sites, reduced condition of adults or young, or lower seasonal fecundity in crop sites would provide evidence for reduced habitat quality of crop sites.

4.5 | Conclusion

The loss of native grasslands through conversion to cropland is a primary driver of grassland bird population declines, including thick-billed longspurs (Samson et al., 2004; Blann, 2006; Ellis et al., 2010; Wright and Wimberly, 2013). Nevertheless, we show that longspurs breeding in a region of relatively intact grasslands

in northeastern Montana can successfully nest in nearby crop fields. While hazards for nests (e.g., farming activities, predation) differed between crop and native sites, overall seasonal reproductive effort and nesting success were similar. Because suitable native prairie habitat may be reduced under modern rangeland management, crop fields may effectively expand nesting habitat for this grassland obligate bird, supporting higher overall carrying capacity than existing native sites in this region alone. However, our study area contained large tracts of both crop and native habitats and we have not assessed the use of crop landscapes by longspurs in areas with less-extensive native prairie. Potential population-level benefits of expanding nesting sites to crop fields may be limited to areas close to historical native prairie habitats, depending on habitat selection behavior at higher spatial scales (e.g., 1st order habitat selection; Johnson, 1980).

Though overall nest survival rates were similar in crop fields and native prairie, reproductive output might be improved with modified farming practices that minimize the destruction of nests. Early seeding (< 10 May) and reducing summer fallowing should result in greater use and higher nest survival by longspurs in crop fields. Pesticides, including fungicides, can harm adults and nestlings (McEwen and Ells, 1975; Martin et al., 1998; Mineau and Whiteside, 2013). We recommend reducing or eliminating widespread application of herbicides, pesticides, and fungicides when possible, until their potential impacts on the survival of nesting longspurs can be evaluated. Given the great weight of evidence that conversion to cropland is detrimental to grassland bird populations, we strongly recommend against any conversion of native prairie to benefit longspurs. Future research should explore management practices that promote dynamic patterns of disturbance, bare ground, and short grass in native prairies, especially in early spring when longspurs select territories. Further investigation into population demographics, body condition, and resource availability may provide additional insight into the relationship between longspurs and agricultural landscapes.

REFERENCES CITED

- Abrams, P. A., L. Ruokolainen, B. J. Shuter, and K. S. McCann. 2012. Harvesting creates ecological traps: consequences of invisible mortality risks in predator–prey metacommunities. *Ecology* 93:281-293.
- Angelier, F., C. M. Tonra, R. L. Holberton, and P. P. Marra. 2011. Short-term changes in body condition in relation to habitat and rainfall abundance in American Redstarts *Setophaga ruticilla* during the non-breeding season. *Journal of Avian Biology* 42:335-341.
- Arnold, T. W. 2010. Uninformative parameters and model selection using Akaike’s Information Criterion. *The Journal of Wildlife Management* 74:1175-1178.
- Badyaev, A. V., G. E. Hill, and M. L. Beck. 2003. Interaction between maternal effects: onset of incubation and offspring sex in two populations of a passerine bird. *Oecologia* 135:386-390.
- Battin, J. 2004. When good animals love bad habitats: ecological traps and the conservation of animal populations. *Conservation Biology* 18:1482-1491.
- Best, L. B., H. Campa III, K. E. Kemp, R. J. Robel, M. R. Ryan, J. A. Savidge, H. P. Weeks Jr, and S. R. Winterstein. 1997. Bird abundance and nesting in CRP fields and cropland in the Midwest: a regional approach. *Wildlife Society Bulletin*: 864-877.
- Blann, K. 2006. Habitat in agricultural landscapes: how much is enough. A state-of-the-science literature review. West Linn, OR: Defenders of Wildlife.
- Briske, D. D., S. D. Fuhlendorf, and F. Smeins. 2005. State-and-transition models, thresholds, and rangeland health: a synthesis of ecological concepts and perspectives. *Rangeland Ecology & Management* 58:1-10.
- Buckland, S. T., D. R. Anderson, K. P. Burnham, J. L. Laake, D. L. Borchers, and L. Thomas. 2001. *Introduction to distance sampling: estimating abundance of biological populations*. Oxford University Press, New York, NY, USA.

- Burnham, K. P., and D. R. Anderson. 2002. *Model selection and multimodel inference*. New York: Springer.
- Burnham, K. P., D. R. Anderson, and K. P. Huyvaert. 2011. AIC model selection and multimodel inference in behavioral ecology: some background, observations, and comparisons. *Behavioral ecology and sociobiology* 65:23-35.
- Charboneau, J. L., B. Nelson, and R. L. Hartman. 2013. A floristic inventory of Phillips and Valley Counties, Montana (USA). *Journal of the Botanical Research Institute of Texas*: 847-878.
- Chen, K., Y. Cheng, O. Berkout, and O. Lindhiem. 2017. Analyzing proportion scores as outcomes for prevention trials: a statistical primer. *Prevention Science* 18:312-321.
- Cooper, S. V., P. Hendricks, and C. Jean. 2001. *Biological survey of a prairie landscape in Montana's glaciated plains*. Bureau of Land Management.
- Coupland, R. T. 1961. A reconsideration of grassland classification in the Northern Great Plains of North America. *The Journal of Ecology*: 135-167.
- Daubenmire, R. F. 1959. Canopy coverage method of vegetation analysis. *Northwest Sci* 33:39-64.
- Davis, S. K. 2005. Nest-site selection patterns and the influence of vegetation on nest survival of mixed-grass prairie passerines. *The Condor* 107:605-616.
- Davis, S. K., D. A. Kirk, L. M. Armstrong, J. H. Devries, and R. J. Fisher. 2020. Shifting from spring wheat to winter wheat: a potential conservation strategy for grassland songbirds in cultivated landscapes? *Biological Conservation* 245:108530.
- Delibes, M., P. Ferreras, and P. Gaona. 2001. Attractive sinks, or how individual behavioural decisions determine source-sink dynamics. *Ecology Letters* 4:401-403.
- Des Brisay, P. G. 2018. Effects of oil development on habitat quality and its perception by mixed-grass prairie songbirds.
- Devries, J. H., R. W. Brook, D. W. Howerter, and M. G. Anderson. 2008. Effects of spring body condition and age on reproduction in mallards (*Anas platyrhynchos*). *The Auk* 125:618-628.
- Diefenbach, D. R., D. W. Brauning, and J. A. Mattice. 2003. Variability in grassland bird counts related to observer differences and species detection rates. *The Auk* 120:1168-1179.
- DuBois, A. D. 1937. The McCown Longspurs of a Montana Prairie. *The Condor* 39:233-238.
- Dunn, P. K., and G. K. Smyth. 2018. *Generalized linear models with examples in R*. Volume 53. Springer.
- Ellis, E. C., K. Klein Goldewijk, S. Siebert, D. Lightman, and N. Ramankutty. 2010. Anthropogenic transformation of the biomes, 1700 to 2000. *Global ecology and biogeography* 19:589-606.
- ESRI. 2019. Version 10.4.1. Environmental Systems Research Institute, 245 Redlands, CA, USA.
- Felske, B. E. 1971. *Population dynamics and Productivity of McCown's Longspur at Matador, Saskatchewan*. Thesis. University of Saskatchewan, Saskatoon, Canada. 144 pages.
- Fiske, I., and R. Chandler. 2011. Unmarked: an R package for fitting hierarchical models of wildlife occurrence and abundance. *Journal of Statistical Software* 43:1-23.
- Fletcher Jr, R. J., J. L. Orrock, and B. A. Robertson. 2012. How the type of anthropogenic change alters the consequences of ecological traps. *Proceedings of the Royal Society B: Biological Sciences* 279:2546-2552.
- Fuhlendorf, S., and D. Engle. 2004. Application of the fire-grazing interaction to restore a shifting mosaic on tallgrass prairie. *Journal of Applied ecology* 41:604-614.

- Fuhlendorf, S. D., D. M. Engle, R. D. Elmore, R. F. Limb, and T. G. Bidwell. 2012. Conservation of pattern and process: developing an alternative paradigm of rangeland management. *Rangeland Ecology & Management* 65:579-589.
- Gaudet, C. A., E. N. Green, R. M. Brigham, and S. K. Davis. 2020. Nesting ecology and reproductive success of mixed-grass prairie songbirds. *The Wilson Journal of Ornithology* 132:952-966.
- Gilroy, J., G. Anderson, J. Vickery, P. Grice, and W. Sutherland. 2011. Identifying mismatches between habitat selection and habitat quality in a ground-nesting farmland bird. *Animal Conservation* 14:620-629.
- Gilroy, J. J., and W. J. Sutherland. 2007. Beyond ecological traps: perceptual errors and undervalued resources. *Trends in ecology & evolution* 22:351-356.
- Giovanni, M. D., M. P. Van Der Burg, L. C. Anderson, L. A. Powell, W. H. Schacht, and A. J. Tyre. 2011. Estimating nest density when detectability is incomplete: variation in nest attendance and response to disturbance by western meadowlarks. *The Condor* 113:223-232.
- Greer, R. D. 1988. Effects of habitat structure and productivity on grassland birds. Ph.D. dissertation. University of Wyoming, Laramie, Wyoming. 128 pages.
- Greer, R. D., and S. H. Anderson. 1989. Relationships between population demography of McCown's Longspurs and habitat resources. *The Condor* 91:609-619.
- Hale, R., and S. E. Swearer. 2016. Ecological traps: current evidence and future directions. *Proceedings of the Royal Society B: Biological Sciences* 283:20152647.
- Hale, R., E. A. Trembl, and S. E. Swearer. 2015. Evaluating the metapopulation consequences of ecological traps. *Proceedings of the Royal Society B: Biological Sciences* 282:20142930.
- Hebert, P. 2002. Ecological factors affecting initiation of incubation behaviour. *Avian incubation: behaviour, environment, and evolution & Deeming DC. 2002* pp. 271–279. Eds. *in* New York, NY: Oxford University Press.
- Holechek, J. 2011. *Range management: principles and practices*. 6th edition. Prentice Hall, Boston, MA, USA.
- Hovick, T. J., R. D. Elmore, S. D. Fuhlendorf, D. M. Engle, and R. G. Hamilton. 2015. Spatial heterogeneity increases diversity and stability in grassland bird communities. *Ecological Applications* 25:662-672.
- Johnson, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65-71.
- Johnson, D. H., and L. D. Igl. 2001. Area requirements of grassland birds: a regional perspective. *The Auk* 118:24-34.
- Jones, S. L., J. S. Dieni, and P. J. Gouse. 2010. Reproductive biology of a grassland songbird community in northcentral Montana. *The Wilson Journal of Ornithology* 122:455-464.
- Jongsomjit, D., S. L. Jones, T. Gardali, G. R. Geupel, and P. J. Gouse. 2007. A guide to nestling development and aging in altricial passerines.
- Kery, M., and R. Chandler. 2016. *Dynamic Occupancy Models in Unmarked*. <https://mran.microsoft.com/snapshot/2017-06-27/web/packages/unmarked/vignettes/coltext.pdf> (Accessed 3 January 2022).
- Kery, M., and J. A. Royle. 2015. *Applied hierarchical modeling in ecology: Analysis of distribution, abundance and species richness in R and BUGS. Volume 1: Prelude and Static Models*. Academic Press. Elsevier Science.
- Kladivko, E. J. 2001. Tillage systems and soil ecology. *Soil and Tillage Research* 61:61-76.

- Klett, A. T., H. F. Duebber, C. A. Faanes, and K. F. Higgins. 1986. Techniques for studying nest success of ducks in upland habitats in the prairie pothole region. U.S. Fish & Wildlife Service, Jamestown ND.
- Knapp, A. K., J. M. Blair, J. M. Briggs, S. L. Collins, D. C. Hartnett, L. C. Johnson, and E. G. Towne. 1999. The keystone role of bison in North American tallgrass prairie: Bison increase habitat heterogeneity and alter a broad array of plant, community, and ecosystem processes. *BioScience* 49:39-50.
- Knopf, F. L. 1996. Prairie legacies-birds. In *Prairie conservation: preserving North America's most endangered ecosystem*, eds. F. B. Samson and F. L. Knopf, 135-48. Island Press. Covela, CA, USA.
- Koford, R. R. 1999. Density and fledging success of grassland birds in Conservation Reserve Program fields in North Dakota and west-central Minnesota. *Studies in Avian Biology* 19:187-195.
- Laake, J. L. 2013. RMark: An R Interface for Analysis of Capture-Recapture Data with MARK. AFSC Processed Rep 2013-01, 25p. Alaska Fish. Sci. Cent., NOAA, Natl. Mar. Fish. Serv., 7600 Sand Point Way NE, Seattle WA 98115.
- Labocha, M. K., and J. P. Hayes. 2012. Morphometric indices of body condition in birds: a review. *Journal of Ornithology* 153:1-22.
- Lenard, S., J. Carlson, P. Hendricks, and C. Currier. 2006. Grassland bird surveys in north Valley County, Montana: progress report. Report to the Bureau of Land Management. Montana Natural Heritage Program, Helena, MT.
- Lipsey, M. K., and D. E. Naugle. 2017. Precipitation and soil productivity explain effects of grazing on grassland songbirds. *Rangeland Ecology & Management* 70:331-340.
- Lipsey, M. K. S. 2015. Cows and plows: science-based conservation for grassland songbirds in agricultural landscapes. University of Montana.
- Lloyd, J. D., and T. E. Martin. 2005. Reproductive success of Chestnut-collared Longspurs in native and exotic grassland. *The Condor* 107:363-374.
- Long, J. A., R. L. Lawrence, P. R. Miller, L. A. Marshall, and M. C. Greenwood. 2014. Adoption of cropping sequences in northeast Montana: A spatio-temporal analysis. *Agriculture, ecosystems & environment* 197:77-87.
- Loss, S. R., T. Will, and P. P. Marra. 2015. Direct mortality of birds from anthropogenic causes. *Annual Review of Ecology, Evolution, and Systematics* 46:99-120.
- Mackenzie, D. I. 2006. Modeling the probability of resource use: the effect of, and dealing with, detecting a species imperfectly. *The Journal of Wildlife Management* 70:367-374.
- MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson, and A. B. Franklin. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. *Ecology* 84:2200-2207.
- Mahoney, A., and A. D. Chalfoun. 2016. Reproductive success of Horned Lark and McCown's Longspur in relation to wind energy infrastructure. *The Condor: Ornithological Applications* 118:360-375.
- Martin, P. A., D. L. Johnson, D. J. Forsyth, and B. D. Hill. 1998. Indirect effects of the pyrethroid insecticide deltamethrin on reproductive success of chestnut-collared longspurs. *Ecotoxicology* 7:89-97.
- Martin, T. E., and G. R. Geupel. 1993. Nest-Monitoring Plots: Methods for Locating Nests and Monitoring Success (Metodos para localizar nidos y monitorear el exito de estos). *Journal of field Ornithology*:507-519.
- Mazerolle, M. J. 2020. AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). R Package version 2.3-1, <https://cran.r-project.org/package=AICcmodavg>.
- McEwen, L. C., and J. O. Eells. 1975. Field ecology investigations of the effects of selected pesticides on wildlife populations. Colorado State University.

- McLachlan, M. M. 2007. Habitat use by birds in the northern shortgrass prairie of North America: a local and landscape approach. Thesis. Oklahoma State University, Stillwater, Oklahoma. 87 pages.
- Merila, J., and E. Svensson. 1997. Are fat reserves in migratory birds affected by condition in early life? *Journal of Avian Biology*:279-286.
- Mickey, F. W. 1943. Breeding habits of McCown's Longspur. *The Auk*:181-209.
- Miller, P. R., B. G. McConkey, G. W. Clayton, S. A. Brandt, J. A. Staricka, A. M. Johnston, G. P. Lafond, B. G. Schatz, D. D. Baltensperger, and K. E. Neill. 2002. Pulse crop adaptation in the northern Great Plains. *Agronomy journal* 94:261-272.
- Mineau, P., and M. Whiteside. 2013. Pesticide acute toxicity is a better correlate of US grassland bird declines than agricultural intensification. *PloS one* 8:e57457.
- Montgomery, D. C., E. A. Peck, and G. G. Vining. 2021. Introduction to linear regression analysis. 6th edition. John Wiley & Sons, Hoboken, NJ, USA.
- Pagano, A. M., and T. W. Arnold. 2009. Detection probabilities for ground-based breeding waterfowl surveys. *The Journal of Wildlife Management* 73:392-398.
- Perlut, N. G., A. M. Strong, T. M. Donovan, and N. J. Buckley. 2008. Regional population viability of grassland songbirds: Effects of agricultural management. *Biological Conservation* 141:3139-3151.
- Pietz, P. J., and D. A. Granfors. 2000. Identifying predators and fates of grassland passerine nests using miniature video cameras. *The Journal of Wildlife Management*:71-87.
- Pietz, P. J., D. A. Granfors, C. A. Ribic, and F. Thompson. 2012. Knowledge gained from video-monitoring grassland passerine nests. *Video surveillance of nesting birds* 43:3-22.
- Pimentel, D., C. Harvey, P. Resosudarmo, K. Sinclair, D. Kurz, M. McNair, S. Crist, L. Shpritz, L. Fitton, and R. Saffouri. 1995. Environmental and economic costs of soil erosion and conservation benefits. *Science* 267:1117-1123.
- Pollock, K. H. 1982. A capture-recapture design robust to unequal probability of capture. *The Journal of Wildlife Management* 46:752-757.
- Powell, L. A. 2007. Approximating variance of demographic parameters using the delta method: a reference for avian biologists. *The Condor* 109:949-954.
- PRISM Climate Group, O. S. U. <http://prism.oregonstate.edu>, Accessed April 2022.
- Pulliam, H. R. 1988. Sources, sinks, and population regulation. *The American Naturalist* 132:652-661.
- Pulliam, J. P., S. Somershoe, M. Sather, and L. B. McNew. 2021. Nest density drives productivity in chestnut-collared longspurs: Implications for grassland bird conservation. *PloS one* 16:e0256346.
- Quinn, J. E., T. Awada, F. Trindade, L. Fulginiti, and R. Perrin. 2017. Combining habitat loss and agricultural intensification improves our understanding of drivers of change in avian abundance in a North American cropland anthrome. *Ecology and Evolution* 7:803-814.
- R Core Team. 2021. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.
- Ralph, C. J. 1993. Handbook of field methods for monitoring landbirds. Volume 144. Pacific Southwest Research Station.
- Reintsma, K. M., M. M. Delamont, L. I. Berkeley, and V. J. Dreitz. 2022. Thick-billed Longspur (*Rhynchophanes mccownii*) reproduction shows minimal short-term response to conservation-based program. *The Wilson Journal of Ornithology* 134(2):365-372.

- Renfrew, R. B., C. A. Ribic, and J. L. Nack. 2005. Edge avoidance by nesting grassland birds: a futile strategy in a fragmented landscape. *The Auk* 122:618-636.
- Robel, R., J. Briggs, A. Dayton, and L. Hulbert. 1970. Relationships between visual obstruction measurements and weight of grassland vegetation. *Rangeland Ecology & Management/Journal of Range Management Archives* 23:295-297.
- Robertson, B. A., and R. L. Hutto. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87:1075-1085.
- Robertson, B. A., J. S. Rehage, and A. Sih. 2013. Ecological novelty and the emergence of evolutionary traps. *Trends in ecology & evolution* 28:552-560.
- Rosenberg, K. V., A. M. Dokter, P. J. Blancher, J. R. Sauer, A. C. Smith, P. A. Smith, J. C. Stanton, A. Panjabi, L. Helft, and M. Parr. 2019. Decline of the North American avifauna. *Science* 366:120-124.
- Rotella, J. J., S. J. Dinsmore, and T. L. Shaffer. 2004. Modeling nest-survival data: a comparison of recently developed methods that can be implemented in MARK and SAS. *Animal Biodiversity and Conservation* 27:187-205.
- Royle, J. A., D. K. Dawson, and S. Bates. 2004. Modeling abundance effects in distance sampling. *Ecology* 85:1591-1597.
- Samson, F., and F. Knopf. 1994. Prairie conservation in north america. *BioScience* 44:418-421.
- Samson, F. B., and F. L. Knopf. 1996. *Prairie conservation: preserving North America's most endangered ecosystem*. Island Press, Covela, CA, USA.
- Samson, F. B., F. L. Knopf, and W. R. Ostlie. 2004. Great Plains ecosystems: past, present, and future. *Wildlife Society Bulletin* 32:6-15.
- Santangeli, A., A. Lehikoinen, A. Bock, P. Peltonen-Sainio, L. Jauhiainen, M. Girardello, and J. Valkama. 2018. Stronger response of farmland birds than farmers to climate change leads to the emergence of an ecological trap. *Biological Conservation* 217:166-172.
- Sauer, J. R., W. A. Link, and J. E. Hines. 2020. *The North American Breeding Bird Survey, Results and Analysis 1966-2019: U.S. Geological Survey Data Release*, <https://doi.org/10.5066/P96A7675>.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in ecology & evolution* 17:474-480.
- Sedgwick, J. 2004. *McCown's longspur (Rhynchophanes mccownii): a technical conservation assessment*. USDA Forest Service, Rocky Mountain Region.
- Shaffer, J. A., L. D. Igl, D. H. Johnson, M. L. Sondreal, C. M. Goldade, P. A. Rabie, T. L. Wooten, and B. R. Euliss. 2019. *The effects of management practices on grassland birds—McCown's Longspur (Rhynchophanes mccownii)*. US Geological Survey. Report 2330-7102.
- Simon, R. N., and D. Fortin. 2019. Linking habitat use to mortality and population viability to disarm an ecological trap. *Biological Conservation* 236:366-374.
- Skagen, S. K., D. J. Augustine, and J. D. Derner. 2018. Semi-arid grassland bird responses to patch-burn grazing and drought. *The Journal of Wildlife Management* 82:445-456.
- Sliwinski, M., and N. Koper. 2012. Grassland bird responses to three edge types in a fragmented mixed-grass prairie. *Avian Conservation and Ecology* 7(2):6.
- Sollmann, R., B. Gardner, R. B. Chandler, J. A. Royle, and T. S. Sillett. 2015. An open-population hierarchical distance sampling model. *Ecology* 96:325-331.

- Somershoe, S. 2018. A full annual-cycle conservation strategy for Sprague's pipit, chestnut-collared and McCown's longspurs, and Baird's sparrow. U.S. Department of the Interior, Fish and Wildlife Service, Washington D.C.
- Song, Y., D. Zhou, H. Zhang, G. Li, Y. Jin, and Q. Li. 2013. Effects of vegetation height and density on soil temperature variations. *Chinese Science Bulletin* 58:907-912.
- Stinner, B. R., and G. House. 1990. Arthropods and other invertebrates in conservation-tillage agriculture. *Annual review of entomology* 35:299-318.
- Sullivan, B. L., C.L. Wood, M.J. Iliff, R.E. Bonney, D. Fink, and S. Kelling. 2020. eBird: a citizen-based bird observation network in the biological sciences. *Biological Conservation* 142: 2282-2292.
- Swicegood, A. E. 2022. Fatal attraction for an imperiled songbird: Is cropland in the northern Great Plains an ecological trap for breeding thick-billed longspur? M.Sc. Thesis. Montana State University. 86 pp.
- Thompson, S. J., D. H. Johnson, N. D. Niemuth, and C. A. Ribic. 2015. Avoidance of unconventional oil wells and roads exacerbates habitat loss for grassland birds in the North American Great Plains. *Biological Conservation* 192:82-90.
- Toombs, T. P., J. D. Derner, D. J. Augustine, B. Krueger, and S. Gallagher. 2010. Managing for biodiversity and livestock. *Rangelands* 32:10-15.
- Van Horne, B. 1983. Density as a misleading indicator of habitat quality. *The Journal of Wildlife Management*: 893-901.
- Van Pelt, R. S., S. X. Hushmurodov, R. L. Baumhardt, A. Chappell, M. A. Nearing, V. O. Polyakov, and J. E. Strack. 2017. The reduction of partitioned wind and water erosion by conservation agriculture. *Catena* 148:160-167.
- Ver Hoef, J. M., and P. L. Boveng. 2007. Quasi-Poisson vs. negative binomial regression: how should we model overdispersed count data? *Ecology* 88:2766-2772.
- Vickery, P. D., M. L. Hunter Jr, and J. V. Wells. 1992. Is density an indicator of breeding success? *The Auk* 109:706-710.
- Weintraub, K., T. L. George, and S. J. Dinsmore. 2016. Nest survival of tricolored blackbirds in California's Central Valley. *The Condor: Ornithological Applications* 118:850-861.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird study* 46:S120-S139.
- White, R. P., S. Murray, M. Rohweder, S. Prince, and K. Thompson. 2000. *Grassland ecosystems*. World Resources Institute Washington, D. C.
- Wilson, J. D., M. J. Whittingham, and R. B. Bradbury. 2005. The management of crop structure: a general approach to reversing the impacts of agricultural intensification on birds? *Ibis* 147:453-463.
- Winter, M., S. E. Hawks, J. A. Shaffer, and D. H. Johnson. 2003. Guidelines for finding nests of passerine birds in tallgrass prairie. USGS Northern Prairie Wildlife Research Center:160.
- With, K. A. 2021. Thick-billed Longspur (*Rhynchophanes mccownii*).in *Birds of the World* (A. F. Poole, Editor), Cornell Lab of Ornithology, Ithaca, NY, USA. <https://doi.org/10.2173/bow.mcclon.01.1>.
- With, K. A., and D. Webb. 1993. Microclimate of ground nests: the relative importance of radiative cover and wind breaks for three grassland species. *The Condor* 95:401-413.
- Wright, C. K., and M. C. Wimberly. 2013. Recent land use change in the Western Corn Belt threatens grasslands and wetlands. *Proceedings of the National Academy of Sciences* 110:4134-4139.

TABLES

Table 1. Model selection results for detection probability, initial occupancy, and settlement probability from acoustic data collected in Valley County, Montana during the month of April in 2020 and 2021. The number of parameters (K), QAIC_c values, ΔQAIC_c values, and model weights (QAIC_cWt) are reported.

Model	K	QAIC _c	ΔQAIC _c	QAIC _c Wt
<i>Detection</i>				
Time ² + Mintemp + Day	9	834.02	0.00	0.97
Time ² + Mintemp + Day + Precip	10	841.04	7.02	0.03
Null	5	990.06	156.04	0.00
<i>Initial Occupancy</i>				
Null	9	834.02	0.00	0.98
Habitat	10	842.15	8.13	0.02
<i>Settlement</i>				
Day	10	824.74	0.00	0.98
Null	9	834.02	9.29	0.01
Day + Habitat	11	834.36	9.63	0.01
Habitat	10	842.40	17.67	0.00
Day × Habitat	12	846.58	21.84	0.00

Table 2. Support for candidate models predicting effects on detection, initial abundance and seasonal trends of thick-billed longspur populations. Data comes from line transect surveys conducted in Valley County, Montana from May-July, 2020–21. The number of parameters (K), QAIC_c values, ΔQAIC_c values, and model weights (QAIC_cWt) are reported.

Model	K	QAIC _c	ΔQAIC _c	QAIC _c Wt
<i>Detection 2020</i>				
p(Obs)	6	1010.17	0.00	0.62
p(Obs + Temp)	7	1011.32	1.15	0.35
p(Obs + Temp + Start ²)	9	1016.30	6.13	0.03
p(Obs + Wind + Temp + Start ²)	10	1019.05	8.87	0.01
p(.)	5	1026.12	15.95	0.00
<i>Initial Abundance, Trend 2020</i>				
N(Habitat)?(Habitat)	8	994.99	0.00	0.91
N(Habitat)?(.)	7	999.56	4.56	0.09
N(.)?(Habitat)	7	1010.00	15.01	0.00
N(.)?(.)	6	1010.17	15.18	0.00
<i>Detection 2021</i>				
p(Obs)	6	1294.38	0.00	0.53
p(Obs + Start)	7	1295.48	1.10	0.31
p(Obs + Temp + Start)	8	1297.93	3.55	0.09
p(.)	5	1299.28	4.90	0.05
p(Obs + Temp + Start ²)	9	1300.67	6.29	0.02

Model	K	QAIC _c	ΔXAI _c	QAIC _c Wt
p(Obs + Wind + Temp + Start ²)	10	1303.81	9.43	0.00
<i>Initial Abundance, Trend</i>				
<i>2021</i>				
N(.)?()	6	1294.38	0.00	0.54
N(.)?(Habitat)	7	1295.94	1.56	0.25
N(Habitat)?()	7	1297.08	2.70	0.14
N(Habitat)?(Habitat)	8	1298.68	4.30	0.06

Table 3. Support for candidate models predicting daily nest survival rate (DSR) of 222 thick-billed longspur nests in Valley County, Montana 2020–21. Included are the effects of nest initiation date, nest initiation date², year, and habitat type (crop, native). The number of parameters (K), AIC_c values, ΔAIC_c values, and model weights (AIC_cWt) are reported.

Model	K	AIC _c	ΔAI _c	AIC _c Wt
S(.)	1	746.38	0.00	0.18
S(Initiation)	2	747.13	0.75	0.12
S(Initiation ²)	2	747.43	1.06	0.11
S(Year)	2	747.46	1.09	0.10
S(ln(Initiation))	2	747.99	1.62	0.08
S(Habitat)	2	748.35	1.97	0.07
S(Year + Initiation)	3	748.38	2.00	0.07
S(Year × Initiation)	4	748.86	2.48	0.05
S(Habitat + Initiation)	3	748.98	2.60	0.05
S(Habitat × Initiation)	4	749.04	2.67	0.05
S(Habitat × ln(Initiation))	4	749.39	3.01	0.04
S(Habitat + Year)	3	749.39	3.01	0.04
S(Habitat + Year + Initiation)	4	750.16	3.79	0.03
S(Habitat × Year)	4	750.90	4.52	0.02
S(Habitat × Year × Initiation)	8	752.98	6.60	0.01

Table 4. Support for candidate models predicting number of chicks fledged from 220 thick-billed longspur nests in Valley County, Montana 2020–21. Included are the effects of nest initiation date and habitat type (crop, native). The number of parameters (K), AIC_c values, ΔAIC_c values, and model weights (AIC_cWt) are reported.

Model	K	AIC _c	ΔAI _c	AIC _c Wt
Null	1	286.32	0.00	0.49
Habitat	2	287.98	1.66	0.21
Initiation Date	2	288.18	1.86	0.19
Habitat + Initiation Date	3	289.84	3.52	0.08
Habitat × Initiation Date	4	292.01	5.68	0.03

Table 5. Breakdown of crop types for both years of the study (2020–2021). This table shows the number of survey plots in each crop type and percentage of the total for each type.

2020			2021		
Wheat	13	54%	Wheat	15	60%
Summer Fallow	4	17%	Summer Fallow	8	32%
Lentil/Flax	3	13%	Lentil/Flax	2	8%
Cover Crop	2	8%			
Pea	1	4%			
Canola	1	4%			
Totals	24	100%		25	100%

Table 6. Apparent causes of nest failure for thick-billed longspur nests in Valley County, Montana, 2020–21. Percentages are based on 40 failed crop nests and 46 failed native nests in 2020 and 14 failed crop nests and 34 failed native nests in 2021. Determination was based on sign around the nest near time of failure; failed nests with uncertainty regarding the cause of failure were removed from these calculations.

Cause of Nest Failure	2020		2021			
	Crop	Native	Native	Crop	Native	Native
Predation	54%	70%	70%	69%	79%	79%
Abandonment ^a	11%	21%	21%	12.5%	21%	21%
Weather ^b	18%	9%	9%	6%	0%	0%
Farming Operations	18%	N/A	N/A	12.5%	N/A	N/A

^aAbandonment often occurred after weather or partial predation events in both site types.

^bWeather events included flooding, hail, or storm damage which resulted in nest destruction or destruction of nest contents.

FIGURE CAPTIONS

Figure 1. Estimated decline of thick-billed longspur populations based on Breeding Bird Survey data from 1966 – 2019 (Sauer et al. 2020). Estimated population size is shown on the y-axis and years are shown on the x-axis. Outer lines indicate estimated 95% confidence intervals.

Figure 2. Map of study area and study plots on crop and native habitat sites in Valley County, Montana, 2020–21. Clustering of native plots is due to patchy distribution of thick-billed longspurs in native habitats.

Figure 3. Conceptualization of layout of initial breeding bird survey transects in Valley County, Montana, 2020–21. The dashed lines indicate the transect walked and the outer edge represents the 64-ha survey plot.

Figure 4. Conceptualization of layout of line transect surveys in Valley County, Montana, 2020–21. The dashed lines represent the transect walked and the outer edge represents the 16-ha survey plot.

Figure 5. Estimated probability of detecting a thick-billed longspur on a song meter recording relative to Julian day (top left), daily minimum temperature (top right), and minutes past sunrise (bottom) in Valley County, Montana, during the month of April 2020–21. Shaded regions depict 95% confidence intervals.

Figure 6: Estimates of latent occupancy (proportion of sites occupied by thick-billed longspurs) in both crop and native sites in Valley County, Montana, from 7 April – 30 April in 2020 and 2021. Whiskers indicate 95% confidence intervals.

Figure 7. Effect of observer group (1 = high detection, 2 = low detection) on the distance detection function for thick-billed longspur surveys conducted in 2020 (top) and 2021 (bottom).

Figure 8. Bayesian estimates of mean site-level abundance of thick-billed longspurs in both crop and native sites in Valley County, Montana, 2020 (top) and 2021 (bottom). Whiskers depict 95% confidence intervals. Survey rounds were evenly spaced between 10 May – 15 July each year.

Figure 9. Estimated nest initiation dates in both crop and native sites for 222 thick-billed longspur nests found in Valley County, Montana, 2020–21. Results are based on 139 nests in 2020 (68 crop, 71 native) and 83 nests in 2021 (28 crop, 55 native). Overall nest initiation patterns were similar between crop and native sites given the year; 2020 was relatively cool and wet and 2021 was a drought year.

Figure 10. Differences in habitat conditions between crop and native sites and changes in conditions over the growing season (May, June, and July, survey rounds 1–3) for four habitat measures collected in northern Valley County, Montana, 2020–21. Measured variables include visual obstruction reading (VOR; top), percent bare ground cover (second), percent litter cover (third), and litter depth (bottom). VOR and litter depth were log-transformed to meet the assumptions of linear regression.

Data Accessibility Statement

Sampling locations, data, and scripts used for analysis are all available at the Dryad Digital Repository doi:

Conflict of Interest

None declared.

Author Contributions

LBM, SS, KE, and MS conceived the study. AES collected and analyzed data. AES and LBM wrote the manuscript. All authors participated in study design and contributed to revisions.

Acknowledgements

This research was funded by the National Fish and Wildlife Foundation (grant #1201.19.066604), the U.S. Fish and Wildlife Service Cooperative Agreement Award (F16AC01242), the Prairie Pothole Joint Venture, and the World Wildlife Fund. We are grateful to all those who aided in data collection and reviewing of the manuscript. We are also appreciative of the private landowners who allowed access to their land for data collection.















